

# Climate change and coral reef connectivity

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Received: 1 August 2008 / Accepted: 9 December 2008 / Published online: 14 January 2009  
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**Abstract** This review assesses and predicts the impacts that rapid climate change will have on population connectivity in coral reef ecosystems, using fishes as a model group. Increased ocean temperatures are expected to accelerate larval development, potentially leading to reduced pelagic durations and earlier reef-seeking behaviour. Depending on the spatial arrangement of reefs, the expectation would be a reduction in dispersal distances and the spatial scale of connectivity. Small increase in

temperature might enhance the number of larvae surviving the pelagic phase, but larger increases are likely to reduce reproductive output and increase larval mortality. Changes to ocean currents could alter the dynamics of larval supply and changes to planktonic productivity could affect how many larvae survive the pelagic stage and their condition at settlement; however, these patterns are likely to vary greatly from place-to-place and projections of how oceanographic features will change in the future lack sufficient certainty and resolution to make robust predictions. Connectivity could also be compromised by the increased fragmentation of reef habitat due to the effects of coral bleaching and ocean acidification. Changes to the spatial and temporal scales of connectivity have implications for the management of coral reef ecosystems, especially the design and placement of marine-protected areas. The size and spacing of protected areas may need to be strategically adjusted if reserve networks are to retain their efficacy in the future.

Communicated by Ecology Editor Prof. Peter Mumby

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**Keywords** Climate change · Population connectivity ·  
Global warming · Larval dispersal · Habitat fragmentation ·  
Marine-protected areas

## Introduction

Most coral reef animals have a complex life cycle with a demersal adult stage that is relatively site attached and a pelagic larval stage that is subject to dispersal. For such species, connectivity between populations inhabiting different patches of reef is expected to be maintained primarily by the dispersive larvae (Sale 1991). The scale of larval dispersal can vary greatly both within and among taxa (Sale and Kritzer 2003; Kinlan and Gaines 2003; Shanks et al. 2003); some larvae may disperse just a few

metres from where they were spawned, others may disperse 10s–100s km to populations on distant reefs (Gaines et al. 2007). Several factors are known or expected to influence the scale of dispersal and the magnitude of settlement resulting from dispersal. These factors include the pelagic larval duration (PLD), water currents that the eggs and larvae experience, behaviour of the larvae, the number of reproductive propagules produced and the proportion that survive to settlement, and the availability of suitable habitat for the settling larvae (Cowen 2002; James et al. 2002; Cowen et al. 2007; Gerlach et al. 2007; Leis 2007). Climate change has the potential to affect all these factors and, thus, significantly alter patterns of biological connectivity in coral reef ecosystems (Munday et al. 2008a).

Population connectivity is a whole-of-life process that depends on adults producing eggs and larvae that disperse between patchily distributed populations and the survival of those offspring in the new population until they breed and reproduce (Pineda et al. 2007). The length of the larval phase and the current regime experienced by larvae could obviously influence the dispersal pattern of a small, pelagic animal. Behavioural attributes of the larvae, such as vertical migration, swimming ability and orientation towards reefs or other important cues, could also influence dispersal patterns. These behaviours, and the timing of their development during the pelagic stage, appear to be critically important in determining dispersal outcomes and the spatial scales over which dispersal takes place (Armsworth 2000; Paris and Cowen 2004; Cowen et al. 2006; Leis 2007).

In most marine organisms, cumulative mortality during the pelagic stage is extremely high, and therefore, small changes in mortality rates have a large effect on the numbers of individuals surviving to settlement (Caley et al. 1996). Furthermore, any spatial variation in mortality patterns would have a substantial influence on the spatial pattern of dispersal. Due to the high mortality expected in marine larval stages, dispersal of demographic significance can only be expected over a limited distance (Cowen et al. 2000), although long distance dispersal by small numbers of larvae can still be important in maintaining genetic connectivity between populations (Planes 2002). Finally, to make the transition to a reef-based existence, those larvae that survive the pelagic stage must find appropriate settlement habitat, and often their settlement requirements are very specific (Öhman et al. 1998; Holbrook et al. 2000; Leis and Carson-Ewart 2002).

Human activities since the late 18th century have changed the composition of the atmosphere, causing the global temperature to warm rapidly (Trenberth et al. 2007). Coral reef ecosystems, although located in the world's naturally warmest marine waters, are considered to be particularly vulnerable to rapid climate change (Hughes

et al. 2003; Hoegh-Guldberg et al. 2007). Key environmental variables for coral reef ecosystems include water temperature, circulation patterns, water chemistry (e.g. pH, salinity and nutrient supply), sea level, occurrence of tropical cyclones and sources of climatic anomalies such as El Niño-Southern Oscillation (ENSO) events. All of these variables are likely to be affected by climate change, which in turn will affect the distribution of coral reef organisms, the structure of reef communities, and the function of key ecological processes, such as population connectivity.

Predicting how climate change will affect connectivity in coral reef ecosystems is important because dispersal of larvae between reefs is a key component of population dynamics for most coral reef organisms (Caley et al. 1996; Armsworth 2002). The number of reproductive propagules produced by adults, the spatial scale of dispersal during the pelagic phase, the number of larvae surviving to settlement and their success in recruiting to the benthic populations could all be affected by climate change, with potentially far-reaching implications for the dynamics and sustainability of adult populations. Understanding the scale of connectivity is also an important consideration for designing effective networks of marine-protected areas (MPAs) (Jones et al. 2007; Almany et al. 2009) and managing coral reef fisheries. The scale of population connectivity helps determine the optimal size and spacing of reserves for the conservation of biodiversity and the potential for larval dispersal and recruitment to non-reserve areas (Botsford et al. 2001; Shanks et al. 2003). Finally, the degree of connectivity between populations will influence the ability of populations of coral reef organisms to adapt to rapid climate change through the exchange of favourable genotypes between populations (Munday et al. 2008a).

This review assesses the likely effects that rapid climate change will have on connectivity of reef fish populations. Fishes are used as model organisms because connectivity of fish populations has been an area of intense research over the past decade (Cowen et al. 2007) and much more is known about the ecological patterns of connectivity in fishes than most other coral reef organisms. First, the environmental changes that rapid climate change will bring to coral reef ecosystems are outlined, particularly those changes that are likely to have significant impacts on population connectivity. The effects that these environmental changes will have on adult reproduction, larval dispersal and recruitment patterns are then considered in detail, as well as the effects that climate-induced habitat fragmentation could have on population connectivity. The benefits and utility of biophysical models for predicting the effects of climate change on coral reef connectivity are discussed and, finally, the implications of changes in connectivity patterns for the design and placement of MPAs are considered.

Many of the predictions made in this review are highly speculative because of uncertainty about how environmental conditions will change in tropical waters over the next 50–100 years and even greater uncertainty about how coral reef organisms will respond to these changes. Nevertheless, climate change could have important effects on coral reef connectivity, and this review highlights areas of concern and identifies key areas for further research.

## Projected climate changes for coral reef ecosystems

### Sea surface temperatures

Over the instrumental record period, 1871–2007, global average land and sea temperatures have warmed  $\sim 0.70^\circ\text{C}$ , at a rate of  $0.05^\circ\text{C}/\text{decade}$  (Fig. 1a) (Brohan et al. 2006). Over the same time period, average tropical sea surface temperatures (SSTs) ( $30^\circ\text{N}$ – $30^\circ\text{S}$ ) have warmed  $\sim 0.51^\circ\text{C}$  (Rayner et al. 2003), at a rate of  $0.04^\circ\text{C}/\text{decade}$  (Fig. 1b). The global and tropical SST instrumental records are significantly correlated ( $r = 0.92$ ,  $n = 137$ ), with the observed warming of the tropical ocean surface being

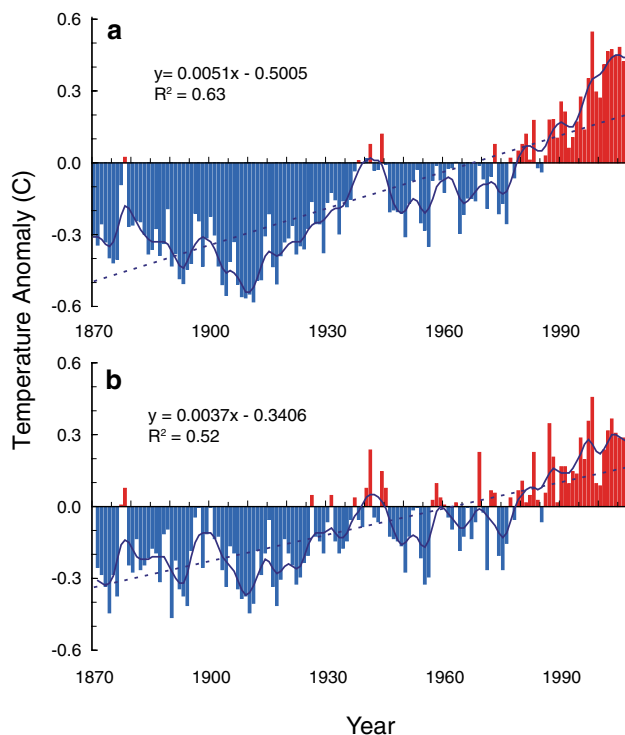
$\sim 70\%$  of the global average. This correlation is useful for considering what future global temperature projections might mean for tropical oceans. Current projections of average global warming by the end of the 21st century (2090–2099 relative to 1980–1999) range from  $1.8^\circ\text{C}$  (range  $1.1$ – $2.9^\circ\text{C}$ ) for the most optimistic (SRES B1) scenario to  $4.0^\circ\text{C}$  (range  $2.4$ – $6.4^\circ\text{C}$ ) for the most pessimistic (SRES A1F1) scenario (Meehl et al. 2007). If the observed relationship between global average and tropical SST is maintained, this would translate to average warming of tropical ocean temperatures of between  $1.3^\circ\text{C}$  (range  $0.8$ – $2.0^\circ\text{C}$ ) and  $2.8^\circ\text{C}$  (range  $1.7$ – $4.5^\circ\text{C}$ ).

The rate of global warming appears to have increased in recent decades (Trenberth et al. 2007). For the period 1950–2007, global average land and sea temperatures (Fig. 1a) have increased at  $0.12^\circ\text{C}/\text{decade}$  and tropical SSTs by  $0.08^\circ\text{C}/\text{decade}$  (Fig. 1b). These averages disguise considerable spatial variation in the magnitude and significance of observed warming (Fig. 2) (Lough 2008). The entire Indian Ocean, western and southern Pacific and south Atlantic are all significantly warmer than they were in the period 1950–1969, but there is no significant increase in temperature in the central, eastern and northern Pacific and central Caribbean. Indeed, some parts of the north Pacific have significantly cooled over this time period. Nevertheless, the general trend is one of warming, with 90% of the tropical ocean area warming, 68% warming significantly and only 2% showing significant cooling. If continued into the future, these spatial patterns of SST changes imply that there will be regional differences in the amount of warming to coral reef waters. Recent studies highlight, for example, the relatively lower rate of warming in the Western Pacific Warm Pool as a consequence of the ocean thermostat (Kleypas et al. 2008).

Although surface waters are warming in most tropical regions, there is considerable variation in patterns of warming at spatial scales relevant to the dispersal of coral reef organisms. For example, the magnitude of thermal anomalies near coral reefs can vary at scales of 100s m–100s km (e.g. Skirving and Guinotte 2001) and reefs that experience more warming in one year may experience less warming in other years (Berkelmans et al. 2004). Such differences mean that there will be considerable spatial and temporal variation in how warmer SSTs affect coral reef organisms.

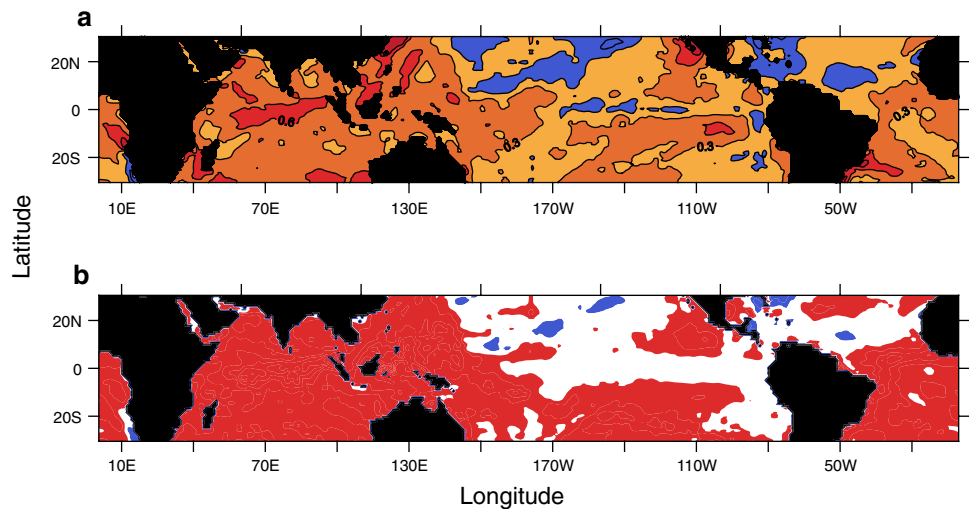
### Ocean circulation

Little is yet known about how ocean currents will change as global warming continues. Nevertheless, there is some evidence that poleward-flowing currents are strengthening and extending further into high latitudes, as observed for the East Australian Current (Cai et al. 2005; Hobday et al.



**Fig. 1** Annual average **a** global land and sea temperatures (data from Climate Research Unit <http://www.cru.uea.ac.uk/cru/info/warming/>), **b** tropical sea surface temperatures,  $30^\circ\text{N}$ – $30^\circ\text{S}$ , 1871–2007 (data from British Atmospheric Data Centre <http://badc.nerc.ac.uk/home/index.html>). Both series expressed as anomalies from 1961 to 1990 average. Thick line is 10-year Gaussian filter to emphasize decadal variability and dashed line is the linear trend

**Fig. 2** Annual sea surface temperature difference (from 1988 to 2007)–(from 1950 to 1969) showing **a** 0.3°C contour interval and **b** significant difference in means (red warmer, blue colder). Data from British Atmospheric Data Centre



2006). There are also suggestions that surface currents may tend to increase as a result of increased thermal stratification of the ocean surface layer (Steinberg 2007). On the other hand, models indicate that climate change is likely to weaken the Atlantic Meridional Overturning Circulation (AMOC) (Meehl et al. 2007). A decrease in the AMOC could change the eddy activity in the Caribbean Ocean, causing more North Brazil Current Rings (NBCR) to impinge the eastern Caribbean (Goni and Johns 2001). Increased frequency of NBCRs could increase low-salinity intrusions into the Caribbean as most of these eddies entrain water from the Amazon River (Paris et al. 2002; Cowen et al. 2003). Such large-scale changes to circulation patterns clearly have the potential to influence the dispersal and survival patterns of marine larvae, but there is still the need to downscale such information to spatial scales relevant to the complex water movement that occur within and between reefs before it would be possible to adequately predict the effects on population connectivity.

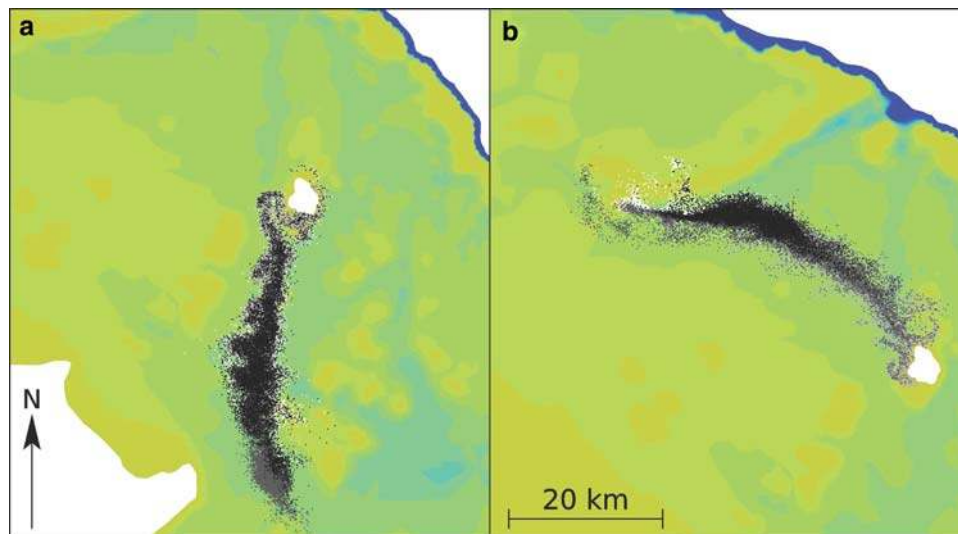
To illustrate the potential influence that changes in major ocean currents could have on the dispersal of marine larvae, we modelled the dispersion of passive particles around Lizard Island (14° 40'S) on the northern Great Barrier Reef (GBR) in response to a shift in the position of the South Equatorial Current's (SEC) inflow to the GBR. We applied this model because global warming is expected to cause a southerly shift in the average position of the SEC inflow (Cai et al. 2005; Steinberg 2007). The model included tides and Coral Sea circulation, but not wind forcing, in order to isolate the potential influence of large-scale ocean circulation patterns on local hydrodynamic patterns. When the model had the SEC inflow situated between 13°S and 19°S, particles were slowly advected towards the south of Lizard Island (Fig. 3a). A simulated 2° southerly shift in the position of the SEC inflow caused significant changes to current patterns, resulting in particles

being advected towards the north-west (Fig. 3b). This indicates that changes to major current systems could potentially have substantial and unexpected impacts to local current patterns.

Changes to ocean circulation could also influence population connectivity through impacts on ocean productivity. Increased thermal stratification of the ocean surface layer is expected to reduce the mixing of cool nutrient-rich waters from below the thermocline into warmer surface waters (Bindoff et al. 2007; Poloczanska et al. 2007), with consequences for the productivity and structure of plankton communities (Hays et al. 2005; Richardson 2008) that are food for the larvae of most coral reef organisms. Changes to the strength of major ocean currents and the locations where they intercept shallow tropical seas could also affect the location, intensity and duration of upwelling, with further implications for planktonic productivity near coral reefs (McKinnon et al. 2007; Steinberg 2007). As with other prediction related to ocean circulation, the effects of climate change on planktonic productivity near coral reefs remains highly uncertain.

#### Ocean chemistry

An insidious effect of enhanced greenhouse gas concentrations is a progressive change in ocean chemistry. About 30% of the excess carbon dioxide (CO<sub>2</sub>) released into the atmosphere in the past 250 years has been absorbed by the oceans (Sabine et al. 2004). Increasing the amount of CO<sub>2</sub> dissolved in the oceans lowers ocean pH and decreases the availability of carbonate ions used by calcifying organisms to form shells and skeletons (Kleypas et al. 1999, 2006; Hoegh-Guldberg et al. 2007). Global ocean pH is estimated to have already dropped by 0.1 and is projected to fall another 0.3–0.4 units by the end of this century (Royal Society 2005).



**Fig. 3** Simulated advection of passive particles around Lizard Island, Great Barrier Reef (GBR) in relation to the position of the South Equatorial Current (SEC) inflow and bifurcation point. **a** Corresponds to oceanographic conditions on 5 Dec 1995 with the SEC bifurcation between 13°S and 19°S. **b** Models a 2° shift of the SEC bifurcation point, with the inflow zone situated from 14°30'S to 22°S. In both cases, 80,000 simulated particles were released at time 0 from the northern (*light grey dots*), southern (*dark grey dots*), eastern (*white dots*) and western (*black dots*) extremities of Lizard Island. The

particles were allowed to diffuse for 7 days at  $0.1 \text{ m/s}^2$  and with a mortality rate of  $0.1 \text{ day}^{-1}$ . Simulations used the SLIM model applied to the GBR (Lambrechts et al. 2008). This model captures hydrodynamic features from scales of a few hundred metres near the coast, islands and reefs to large-scale circulation over the whole GBR. Wind forcing was not included in the simulation in order to investigate the potential effect of a shift in the position of the SEC alone. The simulations are not intended to represent real dispersal patterns around Lizard Island for any particular time

Experiments have also shown that growth and skeletal calcification of some invertebrate larvae is reduced at  $\text{CO}_2$  concentrations predicted to exist by 2100 (Shirayama and Thornton 2005). Disrupted skeletal development has the potential to affect the survival and dispersal patterns of larvae of susceptible species. In addition to affecting calcification rates, increased levels of dissolved  $\text{CO}_2$  and reduced pH could potentially affect the reproductive success or physiological performance of some marine larvae (Ishimatsu et al. 2004; Pörtner et al. 2004; Havenhand et al. 2008), especially at the higher water temperatures that will be experienced in the future (Pörtner et al. 2005). Another concern for coral reef organisms is that changes to ocean chemistry may affect the development of sensory capabilities that help larvae locate coral reefs when they are ready to settle (Munday et al. 2008a, 2009). Understanding the full range of consequences that changing ocean chemistry is likely to have on coral reef organisms is extremely limited at present and this is a serious knowledge gap.

### Tropical cyclones

Warming oceans might be expected to increase the intensity and frequency of tropical cyclones; however, their formation depends on factors other than just water temperature. There is increasing evidence that the destructive potential of tropical cyclones has increased in recent decades (Emanuel 2005; Webster et al. 2005; Trenberth et al.

2007). Although there is no clear indication as to whether climate change will affect the preferred locations of cyclones, several studies now suggest that there could be fewer tropical cyclones in a warmer world, but those that do occur are likely to be more intense (Meehl et al. 2007; Gutowski et al. 2008).

Cyclones are short-duration events that could affect the localized dispersal patterns and survival probability of coral reef larvae, but which are unlikely to affect dispersal at most other times or places. Tropical storms have been linked to strong recruitments pulses of some marine organisms (Shenker et al. 1993; Eggleston et al. 1998), but whether severe cyclones have the same positive effects as weaker tropical storms and cyclones is unknown. A more likely consequence of stronger tropical cyclones is increased physical disturbance to coral reefs (Dollar 1982; Massel and Done 1993), which could compound the impacts of bleaching and ocean acidification, leading to greater habitat loss and fragmentation of coral reef communities.

### Rainfall and freshwater runoff

Coral reefs exist in a range of environments with some regularly influenced by low salinity and turbid waters from adjacent land masses. For most tropical locations, projections of changes in average rainfall and river flow are not well defined. There is, however, a general consensus that

the intensity of extreme flood and drought events are likely to increase (Meehl et al. 2007). Although little is known about the effects of floods on reef fish recruitment, more extreme floods and droughts could potentially influence temporal patterns of coral reef connectivity on nearshore reefs, especially if such events differentially affect the survival and dispersal pattern of larvae, or the production of the planktonic food that larvae need during their pelagic phase. For example, changes in nutrient availability associated with runoff can change the composition of plankton communities that are food for larvae (McKinnon et al. 2007) and changes in salinity can alter the direction of currents or cause larvae to modify their vertical position in the water column (Paris et al. 2002; Cowen et al. 2003).

### Sea level

Average sea level has risen ~20 cm over the past century, due to thermal expansion and melting of land-based ice (Trenberth et al. 2007), and is projected to be another ~60 cm higher by 2100 (Meehl et al. 2007). This may be a conservative estimate because as it does not allow for changes in the loss rate of the vast Greenland and Antarctic ice sheets (e.g. Howat et al. 2007). Gradual sea-level rise may not be a major source of stress to coral reefs; nevertheless, flooding of shallow reef flats may affect local current patterns, especially around enclosed or semi-enclosed lagoons. Changes to local current patterns could influence the likelihood that newly hatched larvae are retrained in or near lagoons.

### Inter-annual (ENSO events) and multi-decadal climate variability

The ENSO is the major source of short-term climate variability relevant to coral reefs. The two phases of ENSO, El Niño and La Niña are typically associated with distinct anomalies of the tropical atmospheric and oceanic climate (McPhaden 2004). Maximum SSTs are likely to be significantly warmer than usual during an El Niño event and

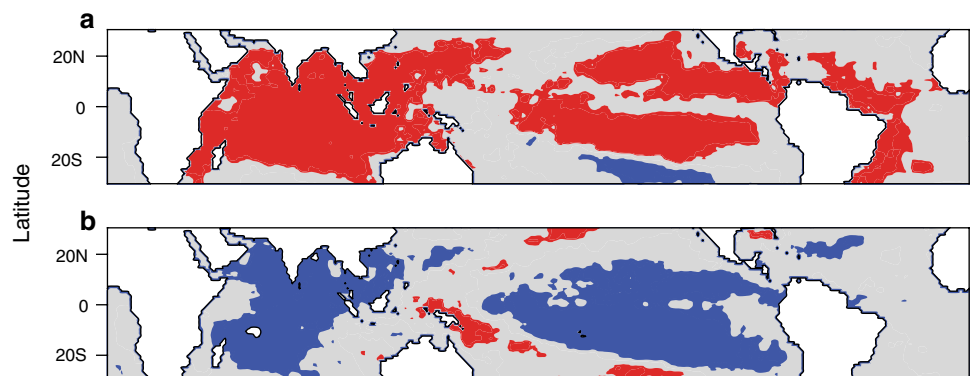
significantly cooler during a La Niña event (Fig. 4). There is currently no consistent picture as to how ENSO amplitude and frequency will be affected by global warming, although there is some suggestion amongst global climate models of a more El Niño-like Pacific climate in a warmer world (Meehl et al. 2007). It should be assumed, therefore, that these events will continue to be a source of short-term climate variability superimposed on the overall warming of the tropical oceans.

There are also internal decadal to multi-decadal oscillations that modify tropical climates. For example, the strength of ENSO teleconnections in the Pacific is modulated by the Pacific Decadal Oscillation and SST gradients and rainfall in the Indian Ocean are modulated by the Indian Ocean Dipole (Trenberth et al. 2007). Exactly how these longer-term sources of climate variability may alter in a warming world is still unclear but they are likely to continue to operate and may well make it difficult to discern, for example, changes in ENSO activity (Christensen et al. 2007; Meehl et al. 2007).

### Effects of climate change on adult and larval biology

Like most coral reef organisms, fishes are ectotherms and temperature changes of a few degrees celsius can influence key physiological processes, such as developmental rate, growth rate, swimming ability and reproductive performance (Munday et al. 2008a) (Table 1). Physiological responses to temperature typically exhibit a dome-shaped relationship, where rates increase with temperature up to an optimum level (thermal optimum) and then decrease rapidly as further temperature increase become deleterious. The thermal optimum for any particular physiological process can differ between species. It may also differ within a species as a result of acclimation or adaptation to local temperature regimes (Hawkins 1996). Fishes appear to be particularly sensitive to temperature variation while breeding and during their early life history (eggs and larvae) (Wood and McDonald 1997), which are also the key

**Fig. 4** Tropical regions with significantly warmer (red) or significantly cooler (blue) maximum SSTs during typical El Niño (a) and La Niña (b) events. Data from British Atmospheric Data Centre



**Table 1** Predicted changes in the global climate and potential effects on coral reef organisms that might affect population connectivity

Variable	Consequences	Likely impact on population connectivity
Warmer waters	Shifts to the timing of reproduction (HC)	Changed temporal connectivity patterns (MI)
	Reduced reproductive output (MC)	Reduced magnitude of connectivity (HI)
	Shorter pelagic larval duration (HC)	Reduced spatial scale of connectivity, but increased magnitude of recruitment (MI)
	Earlier reef-seeking behaviour by larvae (MC)	Reduced spatial scale of connectivity (MI)
	Increased swimming efficiency for larvae (MC)	Increased or decreased scale of connectivity (LI)
	More variable larval survival (MC)	Greater variability in recruitment and connectivity patterns (HI)
Changes to ocean currents	Coral bleaching causing habitat loss and fragmentation (HC)	Reduced connectivity between populations (HI)
	Altered patterns of larval advection (MC)	Changes to spatial scale and patterns of connectivity (HI)
	Changes to planktonic food resources (LC)	More recruitment variability and possible changes to connectivity patterns (HI)
Ocean acidification	Reduced coral calcification causing habitat loss and fragmentation (HC)	Reduced connectivity between populations (HI)
	Possible consequences for formation of calcareous structures in larvae (LC)	Reduced survival and disrupted orientation (HI)
	Possible effects on sensory capacity (MC)	Reduced recruitment and connectivity (HI)
More intense tropical cyclones	Increased physical disturbance to reefs contributing to habitat loss and fragmentation (HC)	Localized reduction in connectivity in affected areas (MI)
	Short-duration changes to currents, vertical mixing, salinity and water temperature (HC)	Localized changes to connectivity patterns and possible favourable effects on recruitment (LI)
More extreme floods and droughts	Temporal shifts in coastal plankton communities leading to more variability in larval survival (MC)	More variability in connectivity patterns (MI)
Rising sea level	Changes to currents in some lagoonal areas leading to changes in patterns of larval dispersal (HC)	Possible changes to local connectivity patterns (LI)

The level of certainty associated with the prediction (low LC; moderate MC; high HC) and the likely importance of the impact for coral reef connectivity (low LI; moderate MI; high HI)

life stages involved in population connectivity. Therefore, we consider the consequences that the projected 1–3°C increase in SST over the next 50–100 years is likely to have on adult and larval life stages.

#### Adult performance and reproduction

Increased sea temperature could have either a positive or negative effect on individual performance, depending on the current temperatures experienced by individuals relative to their thermal optimum for physiological activities and the availability of additional food to fuel higher metabolic rates. Since basal metabolic rate increases with increasing temperature (Wood and McDonald 1997), individuals must consume more food to maintain the same level of growth and reproduction at higher temperatures. Some reef fish populations appear to be food limited (Jones and McCormick 2002), which suggests that they may not be able to compensate for increased temperatures by consuming more food and, thus, may have less surplus energy available for growth or reproduction at higher sea temperatures.

Even where additional food is available, higher temperatures may have a negative effect on growth and reproduction if they exceed thermal optimums. For example, adults of the spiny damselfish, *Acanthochromis polyacanthus*, lost weight when reared at 3°C above average summer temperatures regardless of the amount of food they consumed (Munday et al. 2008b). This indicates that populations of this species are living close to their thermal optimum and even relatively small temperature increases could have a deleterious effect on adult body condition, which will ultimately lead to fewer and smaller offspring being produced (Donelson et al. 2008). Determining the proportion of species that appear to be living close to their thermal optimums and, thus, might be expected to exhibit similar responses to *A. polyacanthus* will be important for assessing the broader consequences of increases temperatures for reef fish communities. Such data are scarce, however, a recent comparative analysis by Nilsson et al. (2009) found that although some other species of damselfish were less temperature sensitive than *A. polyacanthus*, several cardinalfish species exhibit even stronger declines in performance with increasing temperature. At Lizard Island on the Great Barrier Reef,

the capacity for aerobic activity by two cardinalfishes, *Ostorhinchus cyanosoma* and *Ostorhinchus doederleini*, was nearly halved with just a 2° increase in sea surface temperature above the summer average (Nilsson et al. 2009). These results indicate that thermal sensitivity differs significantly among species and, perhaps, even families of reef fishes.

Reproduction in marine fishes typically occurs within a narrow temperature range (Van der Kraak and Pankhurst 1997) and an increase of 2–3°C can be sufficient to reduce reproductive activity (Ruttenberg et al. 2005) or increase egg mortality (Gagliano et al. 2007). Consequently, warmer sea temperatures are likely to have a negative effect on reproductive success, unless populations shift the timing of breeding to match favourable temperatures. At higher latitudes, shifts in reproductive timing could easily be achieved by commencing the breeding season earlier, when temperatures are still increasing from winter minima. Shifting the breeding season might not be effective in equatorial regions, where temperatures are generally more stable and may be favourable for reproduction nearly year-round (Srinivasan and Jones 2006). Elevated temperatures at these low latitude locations could cause an overall decline in reproductive output if water temperature rises above the optimum for reproduction for large parts of the year (Munday et al. 2008a). A reduction in reproductive effort would clearly have implications for population connectivity by reducing the number of offspring available to disperse to neighbouring reefs. In contrast, shifts in the timing of reproduction might alter the timing of dispersal, but not the absolute numbers of larvae produced. Population connectivity would be seriously affected, however, if a shift in the breeding season caused a mismatch between the timing of reproduction and the optimal conditions for survival of larvae in the plankton (Edwards and Richardson 2004).

Although the effects of elevated water temperature on adult reproduction are likely to have significant consequences for the population connectivity, very little is known about how reproductive performance of most coral reef organisms responds to elevated temperature, and even less is known about the potential for acclimation or adaptation of reproductive processes to increased temperatures.

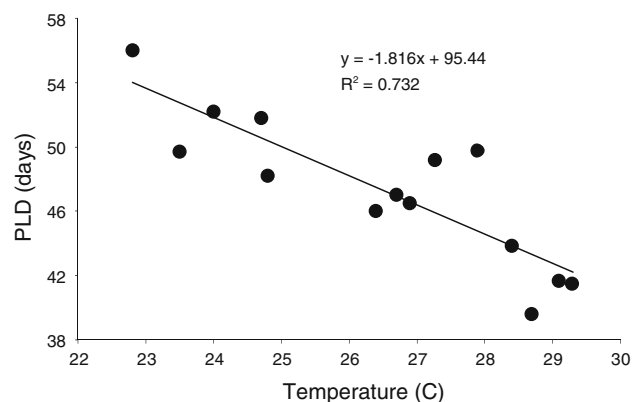
#### Larval biology and performance

Increased water temperature is expected to accelerate physiological processes in larvae, provided temperatures do not exceed thermal optima for this life stage (Munday et al. 2008a). Studies of growth and developmental rates of larval coral reef fishes in relation to existing natural variation in water temperature, or experimental manipulations of rearing temperature, have generally found more rapid

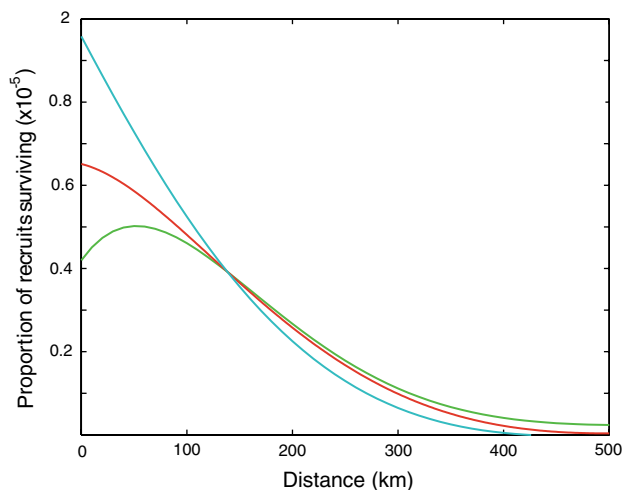
development and faster growth in warmer water (McCormick and Molony 1995; Wilson and Meekan 2002; Meekan et al. 2003; Green and Fisher 2004; Sponaugle et al. 2006), both of which could have important implications for larval dispersal and connectivity between populations.

Increased developmental rate at higher temperatures will mean that larvae reach ontogenetic milestones earlier, and thus will be competent to settle earlier. Using the relationship between PLD and temperature derived by O'Connor et al. (2007), based on 69 species of invertebrates and fish of mostly temperate distribution, an increase of 1°C from 30 to 31°C should decrease PLD by ~1.5% and a 3°C temperature increase from 30 to 33°C should decrease PLD by 4.2–15.5%. The few studies that have examined the relationship between PLD and temperature for coral reef fishes indicate that there is considerable variation in the relationship, and that values extrapolated from temperate species tend to underestimate the effects on tropical species. For example, PLD of *Thalassoma bifasciatum* decreased by ~4% for every 1°C increase in temperature between 23 and 29°C (Fig. 5) (Sponaugle et al. 2006). PLD of *Upeneus tragula* decreased by 25% between 25 and 30°C (5% per 1°C) (McCormick and Molony 1995) and PLD of *Amphiprion melanopus* decreased by 25% between 25 and 28°C (8.3% per 1°C) (Green and Fisher 2004). Overall, the limited evidence suggests that PLD of larval reef fishes is likely to decrease by between 12 and 25% if sea temperature increases 3°C.

A decrease in PLD is expected to decrease the spatial scale of larval dispersal and, thus, decrease the scale of connectivity. Model simulations support the hypothesis that reduced PLD tends to decrease the scale of dispersal and increase the level of self-recruitment (Fig. 6). A 20% reduction in PLD of *T. bifasciatum* changed the modal dispersal distance predicted by simulations from ~50 km to mostly self-recruitment (10 s km) and also reduced the



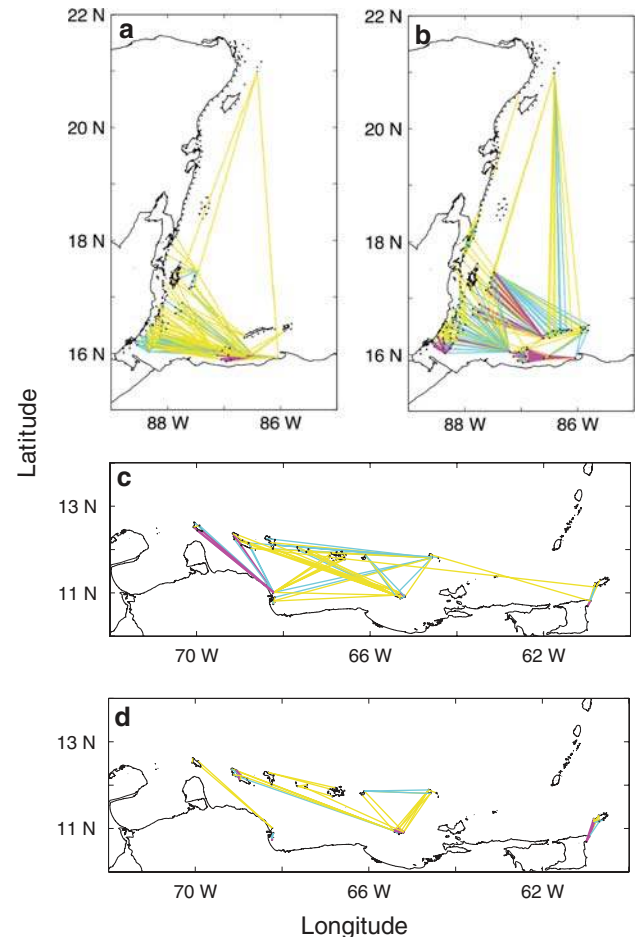
**Fig. 5** Relationship between average PLD and the sea temperature experienced by different cohorts of *Thalassoma bifasciatum* (from data in Sponaugle et al. 2006)



**Fig. 6** The influence of reduced PLD on dispersal kernels. Mean probability of successful dispersal distances for *Thalassoma bifasciatum* populations (each occupying a 10-km reef patch) at current-day temperature and PLD (green line), with a 10% reduction in PLD (red line) and a 20% reduction in PLD (blue line). The simulations were based on an area of barrier reef with 667 reef patches and where recruitment frequency was calculated in 10 km bins. Simulations were produced with a coupled biophysical individual-based model using the 3D Hybrid Coordinate Ocean Model (HYCOM 1/12°) forced by daily winds for the years 2003–2004 and with a monthly release frequency of 100 particles per reef patch. Ontogenetic vertical behaviour, reef-seeking behaviour (5 km sensory zone at competence), and plasticity of pelagic duration of larval *T. bifasciatum* were simulated in the particle-tracking scheme as described by Paris et al. (2007)

number of larvae dispersing long distances. However, the effect of reduced PLD on connectivity patterns was also strongly affected by the dispersion of habitat patches (Fig. 7). In areas of high-reef density, simulations predicted that local connectivity networks would strengthen with decreased PLD because more larvae would be exchanged between nearby reefs (Fig. 7a, b). In contrast, connections between reefs were weakened and lost in areas of low reef density (Fig. 7c, d). Therefore, the precise effect of reduced PLD on connectivity patterns is likely to differ between locations with contiguous tracks of reef, such as barrier reefs, and locations with a more fragmented distribution of reefs.

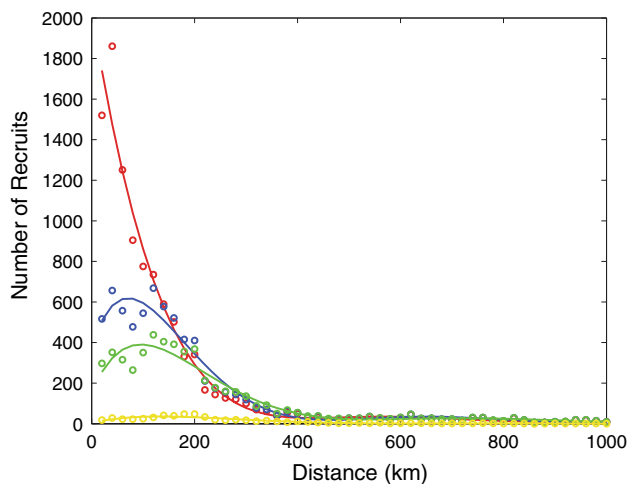
A corollary of accelerated development is that behavioural milestones will be reached sooner at higher temperatures. It is well established that fish larvae have behavioural capabilities that are sufficient to influence dispersal outcomes (Stobutzki and Bellwood 1997; Kingsford et al. 2002; Leis 2006). Behavioural ability increases with development (e.g. Fisher and Bellwood 2000), so it would be expected that the gradual transition from relatively passive plankton to very active nekton would take place sooner at higher temperatures. It is unclear to what extent larval fishes use their behavioural



**Fig. 7** Simulated larval fluxes of *Thalassoma bifasciatum* between population patches using current-day PLD (a, c) and with a 20% reduction in PLD (b, d) in a location with high reef density (a, b) and a location with much lower reef density (c, d). In the location with a dense distribution of reefs, more larvae are exchanged and more links are made when PLD is reduced (b). In contrast, connections are lost when PLD decreases where reefs are less densely distributed (d). The coupled biophysical IBM has the same characteristics described in Fig. 6

capabilities to alter passive dispersal trajectories, however, recent evidence of very local self-recruitment in reef fishes (Swearer et al. 2002; Jones et al. 2005; Almany et al. 2007) suggests that larval behaviour often restricts dispersal, rather than enhances it. Importantly, larval fishes have the capacity to orient towards reefs near the end of their pelagic phase (e.g. Simpson et al. 2005; Gerlach et al. 2007) and the ontogenetic timing of such behaviour is expected to significantly affect dispersal outcomes (Armsworth 2000). Model simulations also suggest that an earlier onset of reef-seeking behaviour at higher temperatures should greatly reduce the modal scale of dispersal (Fig. 8).

Fish muscle operates more efficiently at higher temperatures, therefore, warmer waters might enable larvae to swim faster or more efficiently (Wieser and Kaufman



**Fig. 8** Effect of earlier seeking behaviour on dispersal patterns of marine larvae in the Caribbean. The probabilities of successful dispersal distances are simulated for a generic coral reef organism with a 30-day PLD. Larvae (particles) are transported passively in the currents until they are capable of actively searching for suitable settlement habitat. The onset of reef-seeking behaviour was varied from 4 to 30 days. Red = 4 days, blue = 10 days, green = 15 days, yellow = 30 days. The simulation uses the mixed-layer currents of the Miami Isopycnal Coordinates Ocean Model forced by daily winds for the year 1984 and with a monthly release frequency of 500 particles from 260 spawning locations around the Caribbean. The model assumes larvae could sense reefs up to 9 km away and would be attracted by the first reef detected after active reef-seeking behaviour had developed. Each point is an estimated mean number of larvae settling from the 260 locations at 12 times

1998). Unfortunately, little research has been done on muscle physiology of larval coral reef fishes, so it is not yet possible to quantify the direct effect that increased temperatures might have on swimming efficiency. Water also becomes less viscous as it warms, thus enabling larvae to move into a more efficient inertial hydrodynamic environment at a smaller size (Fuiman and Batty 1997; Leis 2006). Although the effect would be relatively small for the temperature increases predicted in tropical areas ( $\sim 2\%$  decrease in both kinematic and dynamic viscosity per  $1^\circ\text{C}$  increase between 20 and  $30^\circ\text{C}$ ) it would lead to more efficient swimming sooner during the PLD and, thus, more behavioural influence on dispersal by larvae earlier in their development. Viscosity is more important for small, slow swimming larvae than for larger, faster larvae such as the late-stage larvae of many coral reef fishes (Fuiman and Batty 1997). Nevertheless, larvae may have a lower net cost of swimming at higher temperatures due to increased muscle efficiency and decreased viscosity, and this might partly compensate for increased energy demands from temperature-induced increase in metabolic rates.

Although there is evidence that larval swimming speed and temperature are positively correlated in temperate fishes (Wieser and Kaufman 1998; Batty et al. 1991), only one study has examined this in coral reef fishes. Contrary to

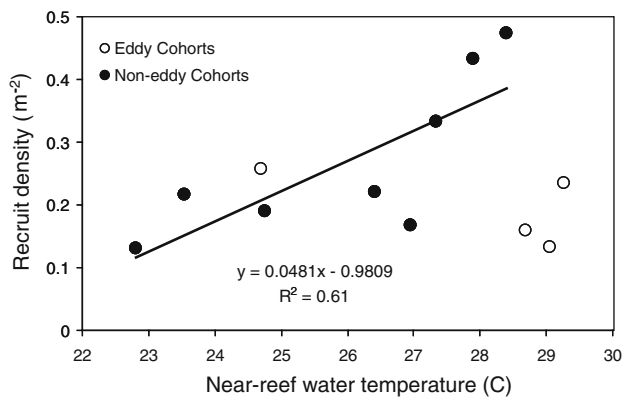
expectations, larvae of *A. melanopus* did not swim faster at  $28^\circ\text{C}$  than at  $25^\circ\text{C}$  (Green and Fisher 2004). They did, however, reach the same speed at an earlier age in the warmer temperature, thus supporting the expectation that behaviours capable of influencing dispersal develop sooner at higher temperatures.

It is clear from the rather limited information available that much more research is needed into the effects of elevated temperature on larval ontogeny, physiology and behaviour to reliably predict the effects of climate change on larval dispersal. However, the balance of evidence suggests that these factors will act to decrease the spatial scale of dispersal and connectivity in coral reef systems.

### Larval supply and recruitment dynamics

The effects of climate change on adult reproduction and the performance and survival of larvae described above will flow-on to influence the spatial and temporal patterns of recruitment to benthic populations of coral reef organisms. Within the temperature range currently experienced by reef fishes, warmer years generally appear to favour good recruitment events for a variety of coral reef fishes (Meekan et al. 2001; Wilson and Meekan 2002; Cheal et al. 2007). Numerous studies have found a positive correlation between water temperature and larval growth rate (McCormick and Molony 1995; Wilson and Meekan 2002; Meekan et al. 2003; Sponaugle et al. 2006) and there is increasing evidence that the survival of larval fishes is often positively correlated with faster growth (Searcy and Sponaugle 2000; Bergenius et al. 2002; Wilson and Meekan 2002; Meekan et al. 2003). Together, these observations suggest that small increase in temperature might tend to have a favourable influence on larval survival and recruitment, provided optimal thermal conditions are not exceeded. Furthermore, reduced PLD at higher temperatures might increase larval survivorship, because mortality rates are usually very high during the larval phase. Even a small reduction in larval duration could have a positive influence on the number of larvae surviving to settlement (Houde 1989; O'Connor et al. 2007). Higher survival rates would increase the magnitude of settlement and might be expected to increase the spatial scales over which dispersal of demographic significance takes place. Such an increase in the scale of demographic connectivity due to increased survivorship might tend to offset some of the reductions in the scale of connectivity that come from accelerated larval development and earlier reef-seeking behaviours.

Faster metabolic rates at higher temperatures, which are responsible for increased growth rates and accelerated developmental schedules, also require larvae to increase their energy intake at higher temperatures (Pepin 1991).



**Fig. 9** Relationship between mean water temperature experienced during larval life and recruitment density for *Thalassoma bifasciatum* in the Florida Keys, USA. Cohorts that were exposed to Florida Current frontal eddies are shown in open circles. Cohorts not exposed to frontal eddies are shown in filled circles. Reproduced from Sponaugle et al. (2006) with permission

Higher energetic demands mean that larvae have a greater chance of starving before encountering favourable patches of food. Furthermore, climate change is expected to cause greater fluctuations in the quality and quantity of planktonic communities that are food for larval fishes (Hays et al. 2005; Richardson 2008). Consequently, warmer temperatures could increase the spatial and temporal variation in larval mortality, and thus cause greater variability in recruitment to reef-based populations. Larval survival and recruitment at higher temperatures may generally be improved when food supply is abundant, but may be less successful at higher temperatures when food supply is limited (Munday et al. 2008a). In an example of this effect, Sponaugle et al. (2006) found that average size of recruitment pulses of *T. bifasciatum* increased with increasing temperature, but also became more variable at higher temperatures (Fig. 9). In this case, recruitment was not enhanced by increased water temperature when larvae were exposed to different oceanographic conditions that could affect either their dispersal patterns or mortality rates.

More variation in patterns of larval survival and recruitment will mean more variation in patterns of connectivity between reefs. Furthermore, while small increase in water temperature might tend to favour recruitment in many instances, larger increases in water temperature could lead to widespread recruitment failure due to reproductive failure of adults and this would clearly have severe consequences for population connectivity.

### Habitat degradation and fragmentation

Corals, whose larvae are subject to many of the same effects as those described above for fish, are the primary

builders of the physical habitat upon which of the most other reef organisms depend. Mass coral bleaching, ocean acidification and more intense cyclones due to climate change will cause fundamental changes to the reef habitat, including reduced coral cover, changes to the composition of coral assemblages and reduced structural complexity (Hughes et al. 2003; Aronson and Precht 2006; Hoegh-Guldberg et al. 2007). All the available evidence suggests that widespread and persistent degradation of coral communities is likely to lead significant reductions in the abundances of many reef fishes (Wilson et al. 2006; Pratchett et al. 2008). Coral-dependent species will be most seriously affected (Munday 2004), but many other species could suffer long-term population declines due loss of settlement habitat (Jones et al. 2004) and loss of essential habitat structure for post-settlement survival (Syms and Jones 2000; Gratwicke and Speight 2005; Graham et al. 2006). While the exact patterns of habitat fragmentation that might occur are unknown, reef fish populations are expected to become more fragmented as patches of suitable habitat become more degraded and isolated due to the continuing impacts of bleaching and acidification. Population connectivity is expected to decline if population sizes decrease and the metapopulation becomes more fragmented.

Habitat degradation could also affect the number of larvae produced by some species. For example, changes in resource availability similar to that caused by coral bleaching have been shown to decrease the body condition of adults that are dependent on corals for food (Pratchett et al. 2004; Berumen et al. 2005). Reduced maternal body condition can lead to the production of fewer, smaller offspring with a reduced chance of survival (e.g. Donelson et al. 2008). Therefore, habitat degradation may have additional effects on population connectivity through impacts on the number and quality of larvae produced by adults in poorer physical condition.

Whilst habitat degradation is expected to have negative effects on the populations of many reef fish, some generalist species and rubble dwellers may become more abundant as their preferred habitats become more common (Bellwood et al. 2006). For these species, population connectivity may increase in the future.

### Connectivity and adaptation to climate change

Climate change will alter patterns of population connectivity on coral reefs; at the same time the patterns of connectivity between populations will influence the ability of coral reef organisms to adapt to rapid climate change (Munday et al. 2008a). Many coral reef fishes have geographic ranges that span a large latitudinal extent (Jones

et al. 2002) and the temperature gradient across this latitudinal range can be considerable. For example, populations in equatorial zones may experience maximum summer SST at least 3–4°C higher than population on high-latitude reefs (Lough 2000). This indicates that there should be some potential for acclimation or adaptation to climate change by fish populations, either by existing phenotypic plasticity within populations (promoted by existing high levels of gene flow) or by exchange of favourable genotypes from populations already living at higher temperatures. The scales of larval dispersal relevant to demographic connectivity are likely to be different to those that could be relevant for genetic adaptation; population connectivity of demographic significance will mostly depend on the modal scale of dispersal, whereas the tail of the dispersal pattern might also be relevant to connectivity of genetic significance.

High levels of gene flow have been reported among populations living on essentially contiguous tracks of reef such as the GBR (e.g. Doherty et al. 1995; Bay et al. 2006). Gene flow from low- to high-latitude populations should favour some degree of adaptation to increasing SST among populations living in these highly connected habitats. More isolated populations, such as those on island groups in the central Pacific or Indian Oceans, or separated by unfavourable habitat, have less opportunity to receive favourable genotypes from other populations (Planes 2002, Rocha et al. 2007). Reef fish populations on isolated islands are at greater risk of adverse effects from rapid climate change because they are more likely to be adapted to local environmental conditions than are genetically connected populations along latitudinal gradients. The problem for these species is that, in the absence of gene flow from low latitude populations, they may not be able to adapt quickly enough to rapid climate change, especially if existing local adaptation has removed genetic variants that would be favoured under changed environmental conditions (Visser 2008). Determining the potential for acclimation and adaptation to rapid climate change is critical for understanding the long-term impacts of climate change on coral reef connectivity.

### Utility of models for predicting effects of climate change on connectivity

Given the difficulties of directly observing small pelagic larvae, several indirect methods (e.g. plankton surveys, otolith tagging and genetic analyses) have been developed to estimate dispersal patterns. Although these empirical methods can provide dispersal information relevant to specific populations, there are limitations to the spatial and temporal scales at which they can be applied. Numerical

modelling approaches are unique in being able to generate a spectrum of estimated dispersal and connectivity patterns (Botsford et al. 2009). Importantly, numerical models can be applied at spatial and temporal scales not possible in empirical studies and can be used to forecast future dispersal patterns given predicted effects of climate change on specific biological or physical features.

Coupled biological–physical models have the greatest relevance to climate change questions because connectivity patterns of marine organisms are usually determined by both physical and biological processes (Werner et al. 2007). Assimilation of near-real time ocean remote sensing observations together with increased computational abilities has greatly contributed to a better understanding of ocean processes and improved 3D dynamical ocean models. On the biological side, the computation of individual-based trajectories is the best-recommended practice as it permits simulating natural ranges of life history parameters (Paris et al. 2007). These methods enable a suite of different physical and biological variations to be compared to better understand the relative importance of predicted climate impacts on dispersal and connectivity.

The coupling of ocean general circulation models (OGCM) with stochastic particle-tracking tools (including biological traits of larvae) allows preliminary biophysical models to be conducted rapidly for a range of spatial and temporal scales. However, nested shelf-scale models that better resolve the local topography of individual reefs and the initial dispersion patterns of larvae are needed to adequately model the scales of larval exchange which may be in the order of just a few kilometres for some populations (e.g. Jones et al. 2005, Almany et al. 2007). Furthermore, assessing climate change impacts can require extensive computing power and sophisticated models. For example, coupled climate-OGCM models are necessary to forecast the effect of temperature change on the stratification of the oceans. The capacity to run these coupled climate-OGCM models at the high spatial resolution required to adequately assess effects on larval dispersal patterns, and to incorporate relevant biological processes, is currently lacking.

The dispersal kernels estimated earlier (Figs. 6, 7, 8) demonstrate some of the utility of numerical models for assessing the impact of climate change on population connectivity. The projected decrease in PLD and earlier reef-seeking behaviour as a result of increased water temperature caused a general trend towards increased self-recruitment and higher total recruitment. However, these simulations do not consider potential changes in mortality rates which could significantly affect recruitment levels and possibly change connectivity patterns (Paris et al. 2007). The simulations also suggested that reduced PLD might have a greater impact on connectivity where reefs are less densely distributed. This has two implications: first, a loss

of reef habitat will cause isolation and conceivably local extinction in places where subsidies from distant sources are significant. Secondly, conservation efforts may need to consider the level of habitat fragmentation because regions that are naturally fragmented might be at higher risk according to relatively simple models used here.

### Implications for the management of coral reef ecosystems

Marine-protected areas are increasingly being used as a fisheries management tool and in efforts to conserve marine biodiversity. The optimal size and spacing of protected areas should differ between networks established for fisheries purposes (where the goal is to maximize recruitment into non-reserve areas) versus biodiversity conservation (where the goal is to maximize recruitment of many species within and between reserve areas) (Hastings and Botsford 2003). Nevertheless, in both cases, designing an effective MPA network depends on some understanding of the dispersal patterns of the organisms being managed (Botsford et al. 2001, 2003, 2009). Although the effects of climate change on the dispersal patterns of coral reef fishes are far from certain, most of the evidence suggests that average dispersal distances are likely to be reduced, rather than increased, and this could have implications for the efficacy of MPA networks in the future.

Most existing MPAs have been designed on the premise that the ecosystem we see today will not change markedly, and considerable emphasis is placed on protecting iconic sites and achieving a high representation of biodiversity. However, biodiversity is not static and rapid climate change is causing populations and communities to change in unexpected ways (Pressey et al. 2007). Given that coral reef communities will be strongly affected by climate change, it is difficult to predict which sites will remain iconic or representative in the future. We do know, however, that population connectivity will continue to be a key process in effective reserve networks and this strengthens the case for including connectivity as an important element in designing MPAs for the future.

The reduced scales of dispersal for coral reef organisms predicted due to climate change might tend to increase population self-recruitment and, therefore, decrease the minimum size of protected areas needed to sustain a population of any particular target species. At the same time, reduced dispersal would tend to reduce the spatial scale of larval connectivity between protected areas, or between protected areas and fished areas. Consequently, protected areas may need to be spaced more closely together in the future to retain connectivity patterns between the different components of the network similar to that experienced

today. Increasing habitat degradation and fragmentation will complicate the effectiveness of MPA networks in the future (Jones et al. 2007). As populations become smaller and more isolated due to habitat loss and fragmentation, it may be necessary to both increase the size of reserves to ensure they maintain viable populations within their boundaries and adjust the placement of reserves to ensure that populations remain connected by sufficient dispersal. Connectivity does not just involve populations within MPAs; maintaining larger populations of key species outside of MPAs would also be effective in sustaining connectivity among populations as the climate changes.

Whether changes to the scale of dispersal brought about by climate change are critical to the optimal design of reserves will depend, to a large degree, on the relative importance of these changes, compared to the existing spatial and temporal variation in dispersal kernels. Estimating dispersal kernels and their variances remains an important challenge for marine ecology (Sale et al. 2005), but now, we also need to consider how dispersal kernels will be affected by a rapidly changing climate.

Another issue for the management of coral reef fishes is the potential that already variable recruitment might become more variable in the future, especially in locations where dispersal patterns and planktonic food supply change substantially in response to oceanographic features. More extremes of recruitment would make reef fisheries inherently more difficult to manage and increase the risk of overfishing during periods of poor recruitment, especially for short lived species. Future management strategies for reef fisheries and biodiversity conservation may need to incorporate additional safeguards to account for greater fluctuations in adult numbers. Fisheries may also need to adjust to changes in the suite of species available for capture, because it is almost certain that the composition of local reef-fish communities will change as the climate changes (Munday et al. 2008a; Nilsson et al. 2009).

### Knowledge gaps and conclusions

It is clear that climate change could alter patterns of population connectivity of coral reef organisms through a range of effects on adult and larval life stages. All the available evidence suggests that the spatial scales of population connectivity might tend to be reduced in the future due to the effects of climate change on adult reproduction, larval dispersal and habitat fragmentation. However, we are still a long way from predicting the significance of these effects for the sustainability of reef fish populations. There are major gaps in our knowledge about how the tropical marine climate will change, how fishes and other organisms will respond to these changes and the relative

magnitude of these changes in comparison to existing variation in patterns of population connectivity. Furthermore, the effects of a rapidly changing climate on population connectivity are likely to vary greatly among locations due to regional differences in the physical effects of climate change and differences in the responses of populations, depending on such things as geographic isolation, latitudinal position and community composition. Numerical simulation and sensitivity models can generate hypotheses and predictions about climate change impacts, but these models are simplifications of the real world and rely on relevant empirical data for parameterizing variables. To further understand and predict the likely impacts of climate change on marine population connectivity, a range of additional information is needed, including:

- Reliable estimates of how major oceanic currents and patterns of productivity will respond to global warming across a range of climate mitigation scenarios.
- Reliable downscaling of changes in major oceanographic features to spatial scales relevant to larval dispersal.
- Spatial and temporal integration of climatic parameters relevant to connectivity of marine organisms (e.g. SST, ocean circulation and ocean chemistry) to provide holistic predictions about climate change in marine systems as scales relevant to coral reef organisms.
- A greater understanding of the relative importance of different environmental and biological variables to the survival and dispersal of coral reef organisms. For example, predictions about how ocean circulation might change are highly speculative, especially at the scales relevant to coral reef connectivity, however, establishing the relative importance of local current patterns on dispersal compared to other factors, such as reef-seeking behaviour, will help determine how much effort should focus on predicting localized circulation patterns for the future.
- A much better understanding of how increased temperature will affect adult reproduction and the development, survival and behaviour of larvae because extrapolations from temperate water species are unlikely to be reliable.
- Investigations of how ocean acidification will affect the development, survival and behaviour of larvae of coral reef organism.
- Much more research is needed on the capacity for coral reef organisms to adapt to rapid climate change because the potential for adaptation will ultimately determine the consequences of climate change for all ecological communities. Our rudimentary understanding of the potential for rapid adaptation by coral reef organisms to novel environmental variation is one of the most

serious gaps in our knowledge and must be a priority area for future research.

Addressing these knowledge gaps will help to generate more reliable predictions about the different effects of climate change on coral reef connectivity. The improved predictions can then be used to assess the relative importance of climate change impacts compared to other threats faced by coral reefs and how these various stressors will interact with the effects of climate change into the future.

**Acknowledgements** This article is a product of a joint ARC Centre of Excellence for Coral Reef Studies and Coral Reef Targeted Research and Capacity Building for Management Program workshop on coral reef connectivity. The authors thank G. Jones, P. Sale, G. Russ and B. Steneck for organizing the workshop and the participants for stimulating discussions and suggestions. J. Lambrechts acknowledges the Belgian Fund for Research in Industry and Agriculture where he is working within the project “A second-generation model of the ocean system” funded under contract ARC 04/09-316 by the Communauté Française de Belgique.

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