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Extreme climatic events reduce ocean productivity and larval supply in a tropical reef ecosystem

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Abstract

Increasing ocean temperatures due to global warming are predicted to have negative effects on coral reef fishes. El Niño events are associated with elevated water temperatures at large spatial (1000s of km) and temporal (annual) scales, providing environmental conditions that enable temperature effects on reef fishes to be tested directly. We compared remote sensing data of sea surface temperature (SST) anomalies, surface current flow and chlorophyll-*a* (Chl-*a*) concentration with monthly patterns in larval supply of coral reef fishes in nearshore waters around Rangiroa Atoll (French Polynesia) from January 1996 to March 2000. This time included an intense El Niño (April 1997–May 1998) event between two periods of La Niña (January–March 1996 and August 1998–March 2000) conditions. There was a strong relationship between the timing of the El Niño event, current flow, ocean productivity (as measured by Chl-*a*) and larval supply. In the warm conditions of the event, there was an increase in the SST anomaly index up to 3.5 °C above mean values and a decrease in the strength of the westward surface current toward the reef. These conditions coincided with low concentrations of Chl-*a* (mean: 0.06 mg m^{-3}, SE ± 0.004) and a 51% decline in larval supply from mean values. Conversely, during strong La Niña conditions when SST anomalies were almost 2 °C below mean values and there was a strong westward surface current, Chl-*a* concentration was 150% greater than mean values and larval supply was 249% greater. A lag in larval supply suggested that productivity maybe affecting both the production of larvae by adults and larval survival. Our results suggest that warming temperatures in the world's oceans will have negative effects on the reproduction of reef fishes and survival of their larvae within the plankton, ultimately impacting on the replenishment of benthic populations.

Keywords: chlorophyll-*a*, climate, coral reefs, current, El Niño, ENSO, fish larvae, La Niña, larval supply, settlement, SST

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Introduction

Overwhelming evidence has now accumulated that the Earth is undergoing a warming phase due to anthropogenic factors and much of this excess heat is stored within the oceans (Barnett *et al*., 2005). Over time, this will result in increased environmental variability with serious consequences predicted for marine ecosystems (Harley *et al*., 2006; Brander, 2007; Cheung *et al*., 2010). Coral reefs and their associated fisheries are particularly vulnerable to climate change, yet they provide the major source of protein and livelihoods for many of the poorest people in the world (Munday *et al*., 2008). This gives urgency to the task of determining the impact of climatic phenomena on marine fishes in tropical environments.

Munday *et al*. (2008, 2009) suggested that the consequences of warming trends for coral reef fishes could manifest in a number of ways, but identified two key issues. Firstly, because warmer water temperatures will increase basal metabolic rates, fishes may require higher rates of food intake to support the maintenance of body function. This could make reef fishes more susceptible to starvation. Secondly, ocean warming could affect local and regional current patterns, both altering the supply of food and nutrients to reefs and modifying the dispersal patterns of larvae. Because these larval stages undergo a period (weeks to months) of planktonic development away from reefs, changes in dispersal might affect the numbers returning to replenish benthic

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populations of adults. Until now, testing these hypotheses has been difficult due to a paucity of long-term data available for tropical environments that has prevented the comparison of patterns in temperature, currents and planktonic food with the supply of larvae to reefs.

The effects of any changes in climatic and oceanographic factors are likely to be most clearly expressed on the larvae of coral reef fishes, due to their fast growth, small initial size and lack of body reserves (Houde, 1987; Pepin, 1991; Sponaugle *et al.*, 2006; Munday *et al.*, 2008). Evidence to support this idea comes from long-term (decadal) monitoring studies that examine pelagic food chains and ichthyoplankton assemblages in temperate coastal environments. These show clear links between the abundance of larvae and climatic phenomena at multidecadal, decadal and interannual scales (Smith & Moser, 2003; Brodeur *et al.*, 2008). However, there has been little comparable research in tropical systems, principally due to the difficulties involved in capturing, identifying and enumerating the pelagic young of reef fishes, particularly older forms (Sampey *et al.*, 2004; Meekan *et al.*, 2006a; Vilchis *et al.*, 2009). At relatively small spatial and temporal scales (1–10s of km and months to years), a number of studies have shown clear links between water temperature, growth and survivorship of the larvae of coral reef fishes (e.g. Bergenius *et al.*, 2002, 2005; Meekan *et al.*, 2003; Sponaugle *et al.*, 2006), although to date there has been no attempt to test predictions about the effects of anomalous sea surface temperatures (SSTs) driven by a warming climate on these larval traits.

Because it involves warming of the oceans at large spatial (thousands of km) and temporal (annual) scales, the El Niño-Southern Oscillation (ENSO) cycle offers the opportunity to examine the predicted effects of climate change on coral reef environments. The ENSO cycle is one of the most pervasive and important climatic and oceanographic phenomena, affecting marine and terrestrial ecosystems throughout the world. The El Niño phase occurs at intervals of 3–7 years and is typified by a warming of the ocean in the tropical Pacific basin in association with a weakening of the trade winds. Events vary in duration and intensity, with effects observed in a great variety of ecosystems including reef corals, pelagic food chains, fish communities, seabird and mammal populations (McPhaden, 1999a, b; Garcia *et al.*, 2003; Wang & Fiedler, 2006).

Here, we relate patterns of larval supply of coral reef fishes to physical (surface current, SST) and biological [chlorophyll-*a* (Chl-*a*) concentration] factors during an El Niño event at a coral reef ecosystem in the central Pacific. Patterns occurring during this warming phase were compared with those experienced by larvae during the more typical and cooler neutral and La Niña phases of the ENSO cycle. Larval supply was sampled intensively on the atoll of Rangiroa (French Polynesia) from January 1996 to March 2000. This time period encompassed a strong El Niño event (April 1997–May 1998) in between two periods of La Niña (January–March 1996 and August 1998–March 2000) conditions. The occurrence of these events during our study allowed us to test predictions about the likely effects of a warming ocean on the larval survivorship and replenishment of populations of coral reef fishes and disentangle the relative effects of physical (currents) and biological (productivity) factors on patterns of larval supply.

Methods

Remote sensing data

The strength of ENSO events from 1996 to 2000 was taken from Niño Region 3.4 SST anomalies (using the May 2008 algorithm based on SSTs for 1950–1979 averaged from 5°N to 5°S over the longitudinal range 170–120°W, data available from http://www.cgd.ucar.edu/cas/catalog/climind/TNI_N34/index.html#Sec5). A positive SST anomaly index of $>0.4\,^{\circ}$C that prevails for more than 1 month indicates El Niño conditions, whereas La Niña conditions occur during periods (>1 month) with a negative index $<-0.4\,^{\circ}$C (Trenberth, 1997). Rangiroa is situated at 147°38.79′W 14°57.48′S, 10° outside of the range of Niño Region 3.4 that is centred on the equator. The Niño Region 3.4 SST anomaly correlated closely (Pearson's correlation, $r=0.49$, $P<0.001$) with a local anomaly that we calculated using a short time series (50 months) of SST data from temperatures adjacent to Rangiroa (pathfinder AVHRR data, averaged over 147.9–147.5°W and 14.9–14.5°S, available from http://podaac.jpl.nasa.gov/PRODUCTS/p102.html). The local SST anomaly had reduced amplitude (2.04 °C) compared with that of the equatorial anomaly (5.48 °C), suggesting that a $\pm 0.4\,^{\circ}$C cut-off for defining La Niña/El Niño conditions (Trenberth, 1997) might be overly conservative for higher-latitude reefs. The strength of the correlation between local and regional data was greatest (Pearson's correlation, $r=0.61$) when the regional anomaly was compared with the local anomaly with a 3-month time lag, suggesting that changes in SST occur at Rangiroa ahead of equatorial locations at a similar longitude. We used the Niño Region 3.4 SST anomaly to define El Niño events and La Niña conditions, and used both in our analysis of SST anomaly with other physical data.

The Ocean Surface Current Analyses Real-time (OSCAR) product was used to estimate horizontal currents in the upper layer integrated from the surface to the Ekman depth (up to 150 m depth in the open ocean and the zone within the water column in which the majority of the pelagic larvae of reef fish larvae are found; Lo-Yat *et al*., 2006) and currents were estimated using remotely sensed data of sea surface height, wind stress and SST (*in situ* measurements were also used for SST) (Bonjean & Lagerloef, 2002; http://www.oscar.noaa.gov). Current estimates from the OSCAR product were validated using *in situ* observations of velocities within the subregion 120–180°W, 10–30°S during the period of this study (January 1996–March 2000) using drifter records (World Wide Buoy Deployment data). There was a close relationship between zonal currents derived from OSCAR and *in situ* measurements (Pearson's correlation, $n = 5363$, $r = 0.8$, $P < 0.001$). Data were available at 5-day intervals on a 1/3° grid, and for this study the zonal (east–west, denoted as Uzo) component of current flow was investigated as, unlike the north–south component, this is strongly modulated by ENSO events.

As Chl-*a* is the main pigment contained in phytoplankton, concentrations of this pigment provide an estimate of the biomass of phytoplankton and act as a proxy for the biomass of planktonic consumers such as copepods that rely on it as a food source (Platt *et al*., 2003). Copepods are themselves prey for fish larvae and dominate the gut contents of young larvae of a diverse suite of tropical shorefish families (Sampey *et al*., 2007). Chl-*a* concentration is derived from ocean colour obtained from remote sensing by the SeaWIFS sensor and maps of ocean colour have been provided for the world's oceans since September 1997. Here, we used the product on a 0.1° grid (Level-3 standard Mapped Image product available on http://oceancolor.gsfc.nasa.gov). Both remote sensing-derived current and Chl-*a* data were averaged on a monthly basis for a 1° cell centred on 147°W, 14.3°S from September 1997 to March 2000.

Larval supply

We used a crest net to monitor larval supply on the north coast of Rangiroa Atoll, French Polynesia (147°38.79′W 14°57.47′S). This technique samples the late-stage larvae of coral reef fishes in the process of, or immediately before, settlement to the reef (Dufour & Galzin, 1993) and provides an accurate estimate of larval supply to reef habitats (Doherty *et al*., 2004). At Rangiroa, the net had a rectangular mouth (1.5 m wide, 0.8 m height) and was made of a 1 mm mesh, which was fine enough to retain all incoming fish larvae (Dufour & Galzin, 1993). For simplicity, catches were recorded as numbers of larvae per metre of net-width per day rather than numbers per m^2 (which would require continual measurement of the height of tide), or numbers per m^3 (which would require continual measurement of the flow of water through the net). The cod-end was attached to the net in the afternoon to minimize the accumulation of debris in the net during daylight hours when few fish larvae are usually captured (Dufour & Galzin, 1993) and the net was cleared of catches in the hours just after sunrise. Catches were sorted and fishes identified using the guide provided by Leis & Trnski (1989). All fishes were recorded with the exception of very small larvae (standard length <5 mm, mostly Gobiidae, Blenniidae, Scaridae and Labridae) due to difficulties in identification. As newly settled reef fishes are present on Rangiroa Atoll throughout the year, settlement was sampled for 10 nights centred around the new moon in each month from January 1996 to March 2000. This 10-day sampling window captures the peak period of settlement within a lunar month (Dufour & Galzin, 1993). As the crest net technique depends on both current flow and directed swimming of fish larvae over the reef crest, fishes that settled on the outer slope or pelagic species that resided in nearshore waters around the reef were not captured.

Linear regression was used to investigate the effects of SST anomalies on environmental variables (Chl-*a* concentrations and the west–east surface current vector) and on the numbers of larvae arriving in the crest nets. Data was pooled into monthly intervals for this comparison and regressions calculated at 0-, 1- and 2-month lags between current flow and catch data and 0–6-month lags for Chl-*a* concentrations and catch data. In the former comparison, the 1–2-month lag represented the approximate average time (1–2 months) likely to have been spent in the plankton by the pelagic larvae of reef fishes where they would have been susceptible to current flows. In the latter, food availability may have affected not only larval survivorship but also parental condition before spawning and thus the quantity and quality of larval output. For this reason, we explored correlations between these variables over a 6-month time frame.

Results

Physical and biological conditions

A regional El Niño event occurred in the 14 months from April 1997 to May 1998, during which time the monthly Niño Region 3.4 SST anomalies were >0.4 °C above the monthly averages (max: $+3.5$ °C in October 1997). La Niña conditions (negative index <-0.4 °C below the monthly averages) prevailed for 23 months,

in two periods: January–March 1996 and August 1998–March 2000; min: −2.0 °C in January 2000 (Fig. 1a).

By convention, the west–east vector (Uzo) for sea surface currents is negative when westward and positive when eastward. At Rangiroa, the prevailing current typically flows westward, so that an increasing Uzo value, as seen during the El Niño event, indicated a reduction in flow (or even reversal) of the westward current (Fig. 1b). In contrast, during La Niña conditions, a decrease in the Uzo value showed a strengthening of the westward surface current.

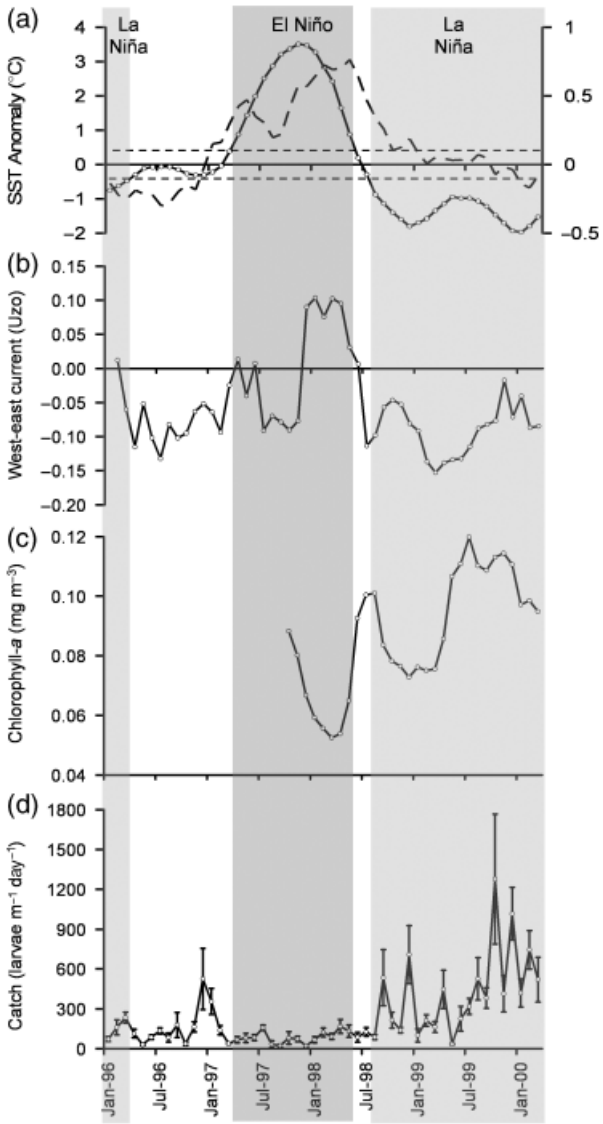

Fig. 1 Physical data and larval catches at Rangiroa. (a) Sea-surface temperature anomalies, showing Niño Region 3.4 SSTa (solid line, left axis) and local anomaly (dashed line, right axis), both 5-month moving averages, horizontal dashed lines and vertical shading through the figure indicate cut-off (± 0.4 °C) in Niño Region 3.4 SST that if surpassed for >1 consecutive month were defined as El Niño or La Niña conditions; (b) west–east sea surface current vector, Uzo; (c) chlorophyll-*a* data from SeaWIFS indicating patterns in primary production (data only available from October 1997); and (d) larval supply of coral reef fishes measured as monthly means (± SE) of daily catches.

Chl-*a* data were only available from October 1997 onwards, so that productivity before the 1998 El Niño event was unknown. However, the lowest values of Chl-*a* concentration in the SeaWIFS data appeared during the latter part of the El Niño event (Fig. 1c), and the trend was inversely correlated with the Uzo values during the period for which data were available (Pearson's correlation, $n = 30$, $r = -0.643$, $P < 0.001$). Chl-*a* declined rapidly from September 1997 to March 1998 during the El Niño, with a sudden rise in values just before the end of the event around April 1998. Chl-*a* concentration during the July 1999 peak (0.12 mg m^{-3}) was approximately twice that seen during the El Niño event (0.06 mg m^{-3}).

Larval supply

A total of 221 439 larvae from 131 taxa (most identified to species, Table S1, see Supporting Information) representing 30 families (Table S2; see Supporting Information) were collected during the 51 months of the study. Larval settlement averaged 240 individuals m^{-1} day^{-1} (SE ± 36) with settlement peaks occurring in December 1996–March 1997, October 1998–May 1999 and September 1999–March 2000. No peaks in settlement occurred from late 1997 to early 1998 (Fig. 1d).

Effects of physical and biological conditions on larval supply

A significant relationship existed between the SST anomalies and the catches in the crest nets (linear regressions throughout, $n = 51$; Niño Region 3.4 SST: $r = 0.63$, $P < 0.001$; Rangiroa local anomaly: $r = 0.33$, $P = 0.017$; Fig. 2a), with greater numbers of larvae collected during La Niña conditions (defined as SST anomaly values more than 0.4 °C below the monthly means for >1 month using the Niño Region 3.4 SST) than during the El Niño event (*t*-test, $t = 2.61$, df = 49, $P = 0.012$). The mean catch during the El Niño event was 119 larvae m^{-1} day^{-1} (SE = 27) compared with 307 larvae m^{-1} day^{-1} (SE = 51) during La Niña conditions. A significant relationship was also found between both of the SST anomalies and Chl-*a* concentrations ($n = 30$; Niño Region 3.4 SST: $r = 0.58$, $P = 0.001$; Rangiroa local anomaly: $r = 0.54$, $P = 0.002$; Fig. 2b), with higher productivity in cooler months, and between both of the SST anomalies and the west–east vector ($n = 50$; Niño Region 3.4 SST: $r = 0.52$, $P < 0.001$; Rangiroa local anomaly: $r = 0.61$, $P < 0.001$; Fig. 2c), with warm condi-

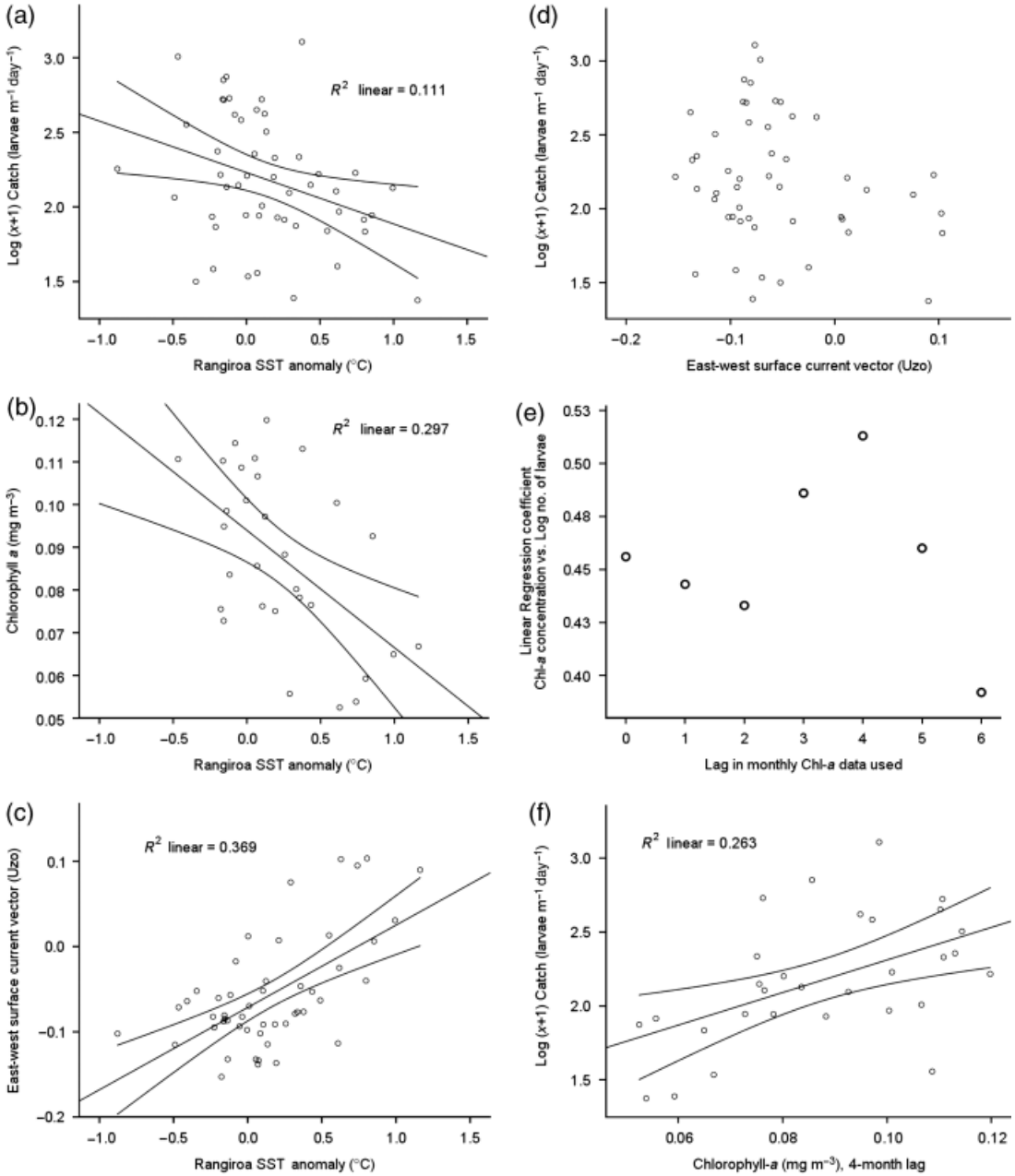

Fig. 2 Comparisons of physical and catch data. (a) Regression of sea-surface temperature (SST) anomaly vs. log ($x + 1$) abundance of larvae in crest net catches; (b) regression of SST anomaly vs. primary productivity estimated using chlorophyll-*a* concentration data from SeaWIFS; (c) regression of SST anomaly vs. west–east sea surface current vector, Uzo; (d) no significant relationship between west–east sea surface current vector and abundance of larvae in crest net catches; (e) Regression coefficients for relationship between chlorophyll-*a* concentrations and abundance of larvae in crest net catches using different lags in the analysis (4-month lag is the best predictor of catch); and (f) regression between chlorophyll-*a* concentration with a 4-month lag and abundance of larvae in crest net catches. Where significant relationships were found, regression trends are shown with 95% confidence intervals and R^2-values. (a)–(c): Relationships are shown using the locally derived SST anomaly, which are similar to those using the Niño Region 3.4 SST anomaly (statistics in text).

tions sometimes associated with a switch in the current from the prevailing eastward to a westward direction.

Since both Chl-*a* and the current vector changed in association with the SST anomaly, further analysis was conducted to disentangle the effects of these two potential drivers on larval supply. There was no relationship between the current vector and crest net catches (Fig. 2d), whether the data were analysed for the

month of capture or with a 1- or 2-month lag to account for the period when the larvae would have been in the open ocean. In contrast, Chl-*a* concentrations did relate to catches, and analysis of different time lags identified the greatest effect of Chl-*a* concentrations occurred 3–4 months before the arrival of larvae in the nets (Fig. 2e and f).

Discussion

Between January 1996 and March 2000, we obtained the longest continuous record of larval supply to any coral reef, which spanned a period of major climatic and oceanographic variability in the Pacific. Our study site at Rangiroa Atoll was affected by an intense El Niño from April 1997 to May 1998 and as SST increased during this event, both ocean productivity (as measured by Chl-*a*) and larval supply to the atoll declined. In contrast, during La Niña conditions (January–March 1996, August 1998–March 2000), productivity and supply increased as SST declined.

There are a number of potential explanations for the correlations between warming SST driven by the El Niño event, ocean productivity and larval supply. Because larvae are poikilotherms, higher than average temperatures during the planktonic stage can increase growth rates, but relatively high rates of food intake are required to support this growth (Houde, 1987). Satellite measurements of Chl-*a* suggested that ocean productivity was relatively low during the El Niño event, possibly due to a reduction of the depth of the mixed layer in the ocean surface, in turn caused by slackening of trade winds. When stratification increases, fewer nutrients are upwelled from depth to the surface and the growth of phytoplankton declines (Rougerie & Rancher, 1994; Messie *et al.*, 2006). This combination of increasing SST and declining productivity may have increased mortality of larvae in the plankton due to insufficient food, resulting in lower rates of larval supply to reefs. This idea is supported by evidence from a range of marine ecosystems that show that food availability can influence larval survival (Heath, 1992; Platt *et al.*, 2003). Conversely, during La Niña conditions, surface water temperatures were lower and food availability for larvae was higher, possibly due to greater mixing and upwelling of nutrients. These factors would promote survival of fish in the plankton and ultimately lead to greater levels of larval supply to the atoll.

We found little evidence that alterations to current flows during the El Niño had a major influence on our catches. During this event, the westward surface current in the region declined in strength and countercurrents appeared from December 1997 to June 1998 (Martinez *et al.*, 2009). Although this might have acted to reduce retention and disperse larvae and their food away from the atoll (Lo-Yat *et al.*, 2006), it did not appear to have this effect, as when current flows reverted to normal strengths and directions for some months before the end of the El Niño event, this change was not accompanied by an increase in larval supply.

The effects of warming SST are not likely to be limited to the larval stages of reef fishes. Higher water temperatures can negatively affect spawning of adults (Munday *et al.*, 2008, 2009; Donelson *et al.*, 2010), so that the lower rates of larval supply we recorded might also reflect lower spawning output (Meekan *et al.*, 2001; Sampey *et al.*, 2004). This might explain why there was a 3- to 4-month lag between the rebounding of ocean productivity (as measured by Chl-*a*) towards the end of El Niño conditions and an increase in larval supply. Such a lag may represent the time required by adults to attain suitable condition to re-commence or increase spawning output, in combination with the average planktonic duration of larvae (somewhere between 2 weeks and a month for most reef species, Leis, 2002). The idea that adult condition may determine larval supply and recruitment is supported by studies in temperate systems where condition of adult spawning haddock (*Melanogrammus aeglefinus*) was strongly correlated with levels of recruitment in the following year (Friedland *et al.*, 2008).

Evidence from synchronous changes in abundance of geographically separated populations of clupeids (Lluch-Belda *et al.*, 1993; Klyashtorin, 1998), salmonids (Mantua *et al.*, 1997; Hare *et al.*, 1999; Mueter *et al.*, 2002), gadoids (Brunel & Boucher, 2007), coral reef fishes (Cheal *et al.*, 2007) and other species (Klyashtorin, 1998) has confirmed that the dynamics of stocks of marine fishes must, to some extent, be linked to and driven by large-scale (100s–1000s of km) atmospheric and oceanographic phenomena. The ENSO is a pervasive and major climatic cycle that has far-reaching effects on both temperate and tropical marine ecosystems; however, the effect of global warming on this phenomenon is uncertain. Outcomes of future climate projections on circulation models for the oceans are contradictory, with some models predicting a shortening of the ENSO cycle with more frequent El Niño events, while others predict that cycles will remain unchanged (Cane, 2005). Irrespective of these forecasting difficulties, across the wider Indo-Pacific the effects of any alteration to ENSO cycles on reef fishes may be even harder to predict. Meekan *et al.* (2003) and Sampey *et al.* (2004) examined the growth, survivorship and abundance of larval reef fishes during El Niño and La Niña cycles on the tropical North–West Shelf of Western Australia. Both studies found that larvae were more abundant during La Niña than El Niño events, although

in contrast to the present study, La Niña conditions were characterized by warmer water temperatures and lower primary productivity than the El Niño event. Yet another pattern was described by Cheal *et al*. (2007), who found that abundances of adult reef fishes on the Great Barrier Reef displayed synchronous patterns of increase over broad spatial scales (100s of km) in the year immediately following El Niño events. If such increases were due to patterns of larval supply, this implies that El Niño events favored the survivorship of planktonic larvae, in contrast to the situation in French Polynesia. Similarly, strong year classes following El Niño events were recorded for Galapagos damselfishes (Meekan *et al*., 2001) and for some labrids (Victor *et al*., 2001) in the eastern tropical Pacific when conditions in the plankton were characterized by relatively high SST and low productivity. Together, our work and the outcomes of these earlier studies suggest that the effect of climatic phenomena such as ENSO cycles on reef fish assemblages may be species, context and location-specific and therefore extremely difficult to predict.

The late-stage larvae such as those captured by our study are the survivors of the processes that occur in the plankton, thus are more informative than the newly hatched and very young larvae typically collected by studies that use nets to sample ichthyoplankton, since these have yet to undergo much of the dispersal and mortality that will occur during larval life (Meekan *et al*., 2006b). Owing to their relatively high trophic level, these older larval fishes integrate the effects of both physical and biological variables and this might account for some of the inconsistencies noted above in the effects of climatic forcing. Lower trophic levels of zooplankton can act as weak links/strong filters (*sensu* Runge, 1998) that alter the influence and outcomes of changes in primary production and environmental signals depending on their species composition, abundance and circumstances. A better understanding of the relationship between climate and the process of replenishment of reef fish communities may thus require a holistic approach that examines not only the inputs (physical variables and primary productivity) and outputs (larval supply to reef environments) in the system, but also the links in the chain of events that allow energy to flow within pelagic food chains of the tropics.

Climate-envelope models based on thermal tolerances of adult fish predict a gradual 40–50% decline in the productivity of fish populations in coastal tropical areas over the next century due to increasing sea temperatures (Cheung *et al*., 2010). This study suggests that extreme climatic events may, intermittently, have even more devastating effects on fish populations, with complete cessation of the replenishment of populations. This highlights the importance of including larval processes in the next-generation of models to enable better predictions of the effects of climate change on fish populations.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Monthly average of fish larval settlement (no m^{-1} d^{-1}) at Rangiroa atoll as measured by crest nets from January 1996 to March 2000. Taxa are ranked by abundance.

Table S2. Monthly average of fish larval settlement (no m^{-1} d^{-1}) in Rangiroa from January 1996 to March 2000 as measured by catches in crest nets. Families are ranked by abundance. For Blennidae, only representatives of the *Aspidontus*, *Petroscirthes*, and *Plagiotremus* were included in the data set as these were the only genera that could be reliably identified.

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Electronic appendices:

Table1. Monthly average of fish larval settlement (no.m^{-1}.d^{-1}) at Rangiroa atoll as measured by crest nets from January 1996 to March 2000. Taxa are ranked by abundance

Rank	Taxa	Average monthly larval settlement (no.m^{-1}.d^{-1})	Rank	Taxa	Average monthly larval settlement (no.m^{-1}.d^{-1})	Rank	Taxa	Average monthly larval settlement (no.m^{-1}.d^{-1})
1	*Chromis viridis*	82.89	45	*Chaetodon ephippium*	0.26	89	*Aspidontus dussumieri*	0.017
2	*Bothus pantherinus*	18.45	46	*Pomacentridae spp.*	0.26	90	*Cantigaster janthinoptera*	0.015
3	*Scopaenidae spp.*	16.14	47	*Abudefduf spp.*	0.22	91	*Canthigaster cf.solandri*	0.015
4	*Chrysiptera glauca*	15.18	48	*Grammistes sexlineatus*	0.19	92	*Plectropomus laevis*	0.014
5	*Acanthurus triostegus*	14.33	49	*Lethrinidae spp.*	0.18	93	*Choeroichthys cf. sculptus*	0.014
6	*Corythoichthys sp.*	11.81	50	*Chaetodon ulietensis*	0.17	94	*Acanthurus lineatus*	0.014
7	*Chrysiptera leucopoma*	10.77	51	*Chaetodon trifascialis*	0.17	95	*Chaetodon quadrimaculatus*	0.014
8	*Synodontidae spp.*	10.60	52	*Scomberoides lysan*	0.16	96	*Zanclus cornutus*	0.013
9	*Pomacentrus pavo*	6.06	53	*Pseudobalistes flavimarginatus*	0.14	97	*Heteropriacanthus cruentatus*	0.013
10	*Neoniphon argenteus*	5.91	54	*Gymnapogon urospilotus*	0.13	98	*Chaetodon pelewensis*	0.012
11	*Pleuronectiforms spp.*	5.15	55	*Monotaxis grandoculis*	0.12	99	*Carangidae spp.*	0.012
12	*Fistularia commersonii*	4.77	56	*Cephalopholis argus*	0.12	100	*Chaetodon vagabundus*	0.011
13	*Bothus mancus*	4.03	57	*Lutjanus monostigma*	0.12	101	*Chaetodon mertensii*	0.010
14	*Apogon exostigma*	3.10	58	*Lactoria cornuta*	0.11	102	*Centropyge sp.*	0.009
15	*Naso brevirostris*	2.43	59	*Sphyraenidae*	0.11	103	*Taenianotus triacantus*	0.007
16	*Antennaridae spp.*	2.35	60	*Chaetodon spp.*	0.11	104	*Balistapus undulatus*	0.006
17	*Neoniphon sammara*	2.13	61	*Arothron spp.*	0.10	105	*Pomacanthus imperator*	0.006
18	*Mulloidichthys flavolineatus*	2.07	62	*Zebrasoma scopas*	0.092	106	*Serranidae spp.*	0.006
19	*Dascyllus aruanus*	1.48	63	*Mullidae spp.*	0.090	107	*Kuhlia marginata*	0.006
20	*Apogonidae spp.*	1.47	64	*Acanthurus nigricauda*	0.084	108	*Neoniphon opercularis*	0.005
21	*Ctenochaetus striatus*	1.14	65	*Ostracion cubicus*	0.083	109	*Parupeneus pleurostigma*	0.004

Rank	Taxa	Average monthly larval settlement ($no.m^{-1}.d^{-1}$)	Rank	Taxa	Average monthly larval settlement ($no.m^{-1}.d^{-1}$)	Rank	Taxa	Average monthly larval settlement ($no.m^{-1}.d^{-1}$)
22	*Chaetodon auriga*	1.05	66	*Arothron hispidus*	0.075	110	*Heniochus chrysostomus*	0.004
23	*Myripristis spp.*	1.03	67	*Acanthurus olivaceus*	0.072	111	*Caracanthus unipinna*	0.003
24	*Mugilidae*	1.02	68	*Caranx melampygus*	0.072	112	*Chaetodon unimaculatus*	0.003
25	*Tetraodontidae spp.*	1.01	69	*Hemiramphidae spp.*	0.071	113	*Pygoplites diacanthus*	0.002
26	*Aulostomus chinensis*	0.86	70	*Aspidontus taeniatus*	0.071	114	*Chaetodon trichrous*	0.002
27	*Parupeneus multifasciatus*	0.75	71	*Gnathodentex aurolineatus*	0.067	115	*Ctenochaetus strigosus*	0.002
28	*Chaetodon trifasciatus*	0.69	72	*Centropyge flavissimus*	0.065	116	*Zebrasoma rostratum*	0.002
29	*Zebrasoma veliferum*	0.69	73	*Naso annulatus*	0.055	117	*Epinephelus socialis*	0.002
30	*Carapidae spp.*	0.68	74	*Canthigaster benetti*	0.055	118	*Kuhlia mugil*	0.001
31	*Stegastes cf. fasciolatus*	0.63	75	*Lutjanidae spp.*	0.052	119	*Chaetodon reticulatus*	0.001
32	*Stegastes nigricans*	0.62	76	*Acanthurus xanthopterus*	0.052	120	*Monacanthidae sp.*	0.001
33	*Rhinecanthus aculeatus*	0.58	77	*Lutjanus kasmira*	0.050	121	*Rhinecanthus triangulus*	0.001
34	*Parupeneus barberinus*	0.52	78	*Dascyllus trimaculatus*	0.050	122	*Siganus argenteus*	0.001
35	*Lutjanus fulvus*	0.49	79	*Epinephelus polyphekadion*	0.049	123	*Syngnathidae sp.*	0.001
36	*Sargocentron spiniferum*	0.47	80	*Naso vlamingii*	0.048	124	*Alectis ciliaris*	0.001
37	*Apogonichthys ocellatus*	0.43	81	*Acanthurus spp.*	0.045	125	*Gnathanodon speciosus*	0.001
38	*Sargocentron microstoma*	0.41	82	*Pterois sp.*	0.040	126	*Heniochus monoceros*	0.001
39	*Canthigaster valentini*	0.39	83	*Pterois cf. radiata*	0.039	127	*Polydactylus sp.*	0.001
40	*Chaetodon lunula*	0.38	84	*Plagiotremus cf. tapeinosoma*	0.036	128	*Platax orbicularis*	0.001
41	*Naso unicornis*	0.33	85	*Parupeneus cyclostomus*	0.030	129	*Canthidermis maculata*	0.0005
42	*Sargocentron punctassimus*	0.32	86	*Naso lituratus*	0.026	130	*Ostracion meleagris*	0.0005
43	*Chaetodon citrinellus*	0.31	87	*Naso spp.*	0.021	131	*Mulloidichthys cf. vanicolensis*	0.0001
44	*Dactyloptena orientalis*	0.28	88	*Corythoichthys cf. flavofasciatus*	0.018			
							Total :	**240.6**

Table 2 Monthly average of fish larval settlement (no.m^{-1}.d^{-1}) in Rangiroa from January 1996 to March 2000 as measured by catches in crest nets. Families are ranked by abundance. For Blennidae, only representatives of the *Aspidontus*, *Petroscirthes*, and *Plagiotremus* were included in the data set as these were the only genera that could be reliably identified.

Rank	Family	Average of fish larval settlement (no.m^{-1}.d^{-1}) per month	Rank	Family	Average of fish larval settlement (no.m^{-1}.d^{-1}) per month
1	POMACENTRIDAE	118.16	19	LETHRINIDAE	0.37
2	PLEURONECTIFORMES	27.62	20	DACTYLOPTERIDAE	0.28
3	ACANTHURIDAE	19.43	21	CARANGIDAE	0.24
4	SCORPAENIDAE	16.23	22	OSTRACIIDAE	0.20
5	SYNGNATHIDAE	11.84	23	GRAMMISTINAE	0.19
6	SYNODONTIDAE	10.60	24	SERRANIDAE	0.19
7	HOLOCENTRIDAE	10.28	25	BLENNIIDAE*	0.12
8	APOGONIDAE	5.12	26	SPHYRAENIDAE	0.11
9	FISTULARIDAE	4.77	27	POMACANTHIDAE	0.08
10	MULLIDAE	3.47	28	HEMIRAMPHIDAE	0.07
11	CHAETODONTIDAE	3.20	29	ZANCLIDAE	0.01
12	ANTENNARIDAE	2.35	30	PRIACANTHIDAE	0.01
13	TETRAODONTIDAE	1.66	31	KUHLIIDAE	0.01
14	MUGILIDAE	1.02	32	CARACANTHIDAE	0.0035
15	AULOSTOMIDAE	0.86	33	MONACANTHIDAE	0.0013
16	BALISTIDAE	0.73	34	SIGANIDAE	0.0010
17	LUTJANIDAE	0.70	35	POLYNEMIDAE	0.0009
18	CARAPIDAE	0.68	36	EPHIPPIDAE	0.0005
				Total :	240.6