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Title Strengthened currents override the effect of warming on lobster larval dispersal & survival

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Abstract

Human induced climate change is projected to increase ocean temperature and modify circulation patterns, with potential widespread implications for the transport and survival of planktonic larvae of marine organisms. Circulation affects the dispersal of larvae, whereas temperature impacts larval development and survival. However, the combined effect of changes in circulation and temperature on larval dispersal and survival has not been studied in a future climate scenario. Such understanding is crucial to predict future species distributions, anticipate ecosystem shifts, and design effective management strategies. We simulate contemporary (1990s) and future (2060s) dispersal of lobster larvae using an eddy-resolving ocean model in south-eastern Australia, a region of rapid ocean warming. Here we show that the effects of changes in circulation and temperature can counter each other: ocean warming favours the survival of lobster larvae, whereas a strengthened western boundary current diminishes the supply of

larvae to the coast by restricting cross-current larval dispersal. Furthermore, we find that changes in circulation have a stronger effect on connectivity patterns of lobster larvae along south-eastern Australia than ocean warming in the future climate so that the supply of larvae to the coast reduces by ~ 4% and the settlement peak shifts poleward by ~270km in the model simulation. Thus ocean circulation may be one of the dominant factors contributing to the climate-induced expansion of species ranges.

Introduction

The combined effect of ocean boundary current intensification and ocean warming driven by human-induced climate change has led to poleward displacement of ocean surface isotherms in recent decades (Sen Gupta *et al.* 2014), which has in turn influenced the distribution of marine organisms (Poloczanska *et al.* 2013). Changes in circulation affect the transport of larvae whereas changes in temperature influence their survival (Cowen & Sponaugle 2009, Lett *et al.* 2010) with potential impacts on marine ecosystems (Doney *et al.* 2012). In addition, changes in water bio-geochemistry and consequently on the availability of planktonic prey or predator distributions may play an additional role in modifying future dispersal patterns (Harley *et al.* 2006). Colonization by new species and increases in the abundance of tropical species has indeed been observed at temperate latitudes, particularly along (e.g. Fodrie *et al.* 2010, Yamano *et al.* 2011), and downstream (Last *et al.* 2011) of western boundary currents. Such changes may facilitate critical ecosystem shifts (Verges *et al.* 2014). Thus, thorough understanding of the mechanisms by which the intensification and warming of western boundary currents causes species redistribution is necessary to project the impacts of future climate change on marine ecosystems.

Poleward range extension of species along the southeast coast of Australia has been attributed to larval advection from lower latitudes by stronger poleward excursions of the warm East Australian Current (EAC), as well as regular settlement into habitats that, due to changes in temperature, became suitable for settlement for some species (e.g. Ling *et al.* 2009, Johnson *et al.* 2011). However, although studies have shown an increase in poleward transport by the EAC (Cetina-Heredia *et al.* 2014) and a dramatic temperature increase east of Tasmania in recent decades (Hill *et al.* 2008), long-term changes in planktonic larval dispersal have not been quantified in this region. Furthermore, it is unknown to what extent the observed poleward extension of species is facilitated by either warmer temperatures favourable for survival of larvae, juveniles and adults after settlement or ocean circulation acting as a vector of dispersal into new areas. Because climate projections and downscale modelling show that further increases of poleward transport of the EAC and ocean surface temperature are expected in the future climate (e.g. Matear *et al.* 2013), understanding the impact of both these factors on larval dispersal is crucial for predicting likely ecosystem changes and designing adaptive management strategies (Koehn *et al.* 2011).

A handful of studies have used bio-physical models to explore the effect of climate change on the dispersal of larvae; for example, by modelling the dispersal of larvae with a shortened pelagic phase (e.g. Munday *et al.* 2009, Ayata, *et al.* 2010). Such parameterization of climate change is based on the impacts of projected temperature rise on larval development. These and similar studies have provided a preliminary framework to study and understand climate change impacts on larval dispersal. Recent studies (Brochier *et al.* 2013, Andrello *et al.* 2015) have shown the importance of exploring the combined effects of climate-induced changes in hydrodynamics and environmental variables (e.g. oxygen concentration, temperature mediating the onset of spawning) on dispersal. However, the effect of spatial and temporal (throughout larval dispersal) variation of hydrodynamics and environmental variables in the

response to climate change has rarely been considered (Lett *et al.* 2010) or examined using outputs from a downscaled climate change model.

In this study, we use an eddy-resolving ($1/10^\circ$ horizontal resolution) numerical oceanic circulation model, downscaled for contemporary (1990s) and future (2060s) climate under the IPCC SRES A1B greenhouse gas emission scenarios. We investigate how circulation and temperature in the future climate modify lobster larval distribution and survival along the southeast coast of Australia. Specifically, we use modelled velocity and temperature fields to virtually transport larvae and quantify the supply of larvae competent to settle to the coast, based on changes in temperature and changes in circulation. The simulated larvae represent eastern rock lobster, *Sagmariasus verreauxi* (see methods section), an ecologically and economically important species. Lobster play a major role in the trophic structure of temperate marine ecosystems (Johnson *et al.* 2013) and *S. verreauxi* represents the most economically valuable fishery in southeastern Australia (Montgomery & Craig 2005).

Materials and methods

Ocean and particle tracking models

Simulations of idealised lobster larval transport are conducted using the Connectivity Modelling System (Paris *et al.* 2013) and outputs from the Ocean Forecasting Australian Model (OFAM) representing the contemporary (1990's) and future (2060's) ocean state (e.g. Chamberlain *et al.* 2012, Sun *et al.* 2012). The hydrodynamic model in the contemporary scenario is forced with climatology of present atmospheric conditions. In the future scenario, air-sea flux anomalies are added from the CSIRO Mk3.5 climate model under the A1B emissions scenario (Chamberlain *et al.* 2012, Sun *et al.* 2012). Downscaling a coarse climate

model (~1° spatial resolution, monthly fields) to a higher resolution model (~1/10° spatial resolution, daily fields) is necessary to resolve the western boundary current jet, separation, and mesoscale eddy field. These dominant circulation features are key drivers of transport along southeastern Australia (Cetina-Heredia *et al.* 2014) and are likely to determine connectivity patterns. For instance, the EAC can act as a physical barrier to onshore dispersal (Roughan *et al.* 2011), and the prevalence of mesoscale eddies can induce patchy dispersal patterns rather than linear trends in connectivity with distance along a current's path (Siegel *et al.* 2008). Therefore, using a downscaled eddy-resolving ocean circulation model is crucial for this study. Matear *et al.* (2013) showed that the EAC, its separation, and the eddy field are well depicted in OFAM outputs, and a quantitative assessment of a range of climate models (Irving *et al.* 2011) shows that CSIRO MK3.5 performs well at simulating key climate metrics making the OFAM downscaled product ideal for this study.

Particles representing idealised lobster larvae are advected with OFAM's 3D velocity fields and diffused using the CMS scheme. Specifically, at every time step particles are moved by the velocity explicitly solved by OFAM plus a random velocity associated with diffusion.

The 'diffusion velocity' is equivalent to:

$$\left(\frac{2 * K_h}{\Delta t}\right)^{0.5} * X \sim N(0,1)$$

Where Δt is the time step, K_h is the horizontal diffusion coefficient, and $X \sim N(0,1)$ is a random number drawn from a normal distribution with mean zero and a standard deviation of one. A horizontal diffusion coefficient of $8.8 \text{ m}^2\text{s}^{-1}$ was chosen to capture the effect of flow occurring at spatial scales smaller than that explicitly solved by the hydrodynamic model (i.e. 1/10°) following Okubo *et al.* 1971.

Virtual larvae

The length of an organism's larval phase is species and temperature dependent (e.g. Cowen & Sponaugle 2004, O'Connor *et al.* 2007). The eastern rock lobster (*Sagmariasus verreauxi*) has one of the longest pelagic larval durations (PLDs, 8-12 months), and spawns from October to January along the coast of southeastern Australia (Montgomery & Craig 2005). Therefore, using lobster as a case study gives a clear signature of climate driven changes in the pelagic realm that is unconstrained by seasonal signals. In addition, because *S. verreauxi* is both ecologically and economically important (e.g. Montgomery & Craig 2005, Fitzgibbon & Battaglene 2012), larval survival rates as they age have been quantified over a range of temperatures (17-31°C) (Fitzgibbon & Battaglene 2012). This temperature range spans those occurring in contemporary and future climate scenarios along southeastern Australia. Hence, the effect of contemporary and future temperature on *S. verreauxi* larval survival can be adequately incorporated using sound empirical data. Some species of lobster larvae are known to migrate vertically reaching depths of 100m (e.g. western rock lobster (*Panulirus cygnus*), Feng *et al.* 2011); however, there is a paucity of data regarding the vertical distribution of *S. verreauxi* larvae. Thus, our larval transport simulations do not incorporate a vertical migration pattern but allow vertical displacement of passive larvae using 3D velocity fields for advection and an initial distribution of larvae through the water column. The simulated larvae represent *S. verreauxi* larvae life traits; they are released at 91 locations from 24-33°S (where sexually matured lobsters have been observed, Montgomery & Craig 2005); seeded every 10km latitudinally, between the coastline and the longitude of the 85m isobath. Preliminary simulations showed no significant changes in the spatial distribution of larvae after dispersal when seeding 5, 10, or 20 larvae at each of the 91 release latitudes. Conservatively, each release site along the coastline is seeded with larvae in 25 locations evenly distributed across shore and with depth between the coast and the longitude of the

85m isobath. Larvae are released every day during the spawning season (October-January, Montgomery & Craig 2005). This yields approximately 300,000 larvae for each spawning season. Larvae are released over 4 spawning seasons, in oceanic conditions representative of contemporary and future circulation scenarios. Larval positions are recorded every 6 hours and considered to reach the coast leading to settlement if they are located between the coastline and the 50 m isobath at the time they are competent to settle (i.e. after 8-10 months after the beginning of the spawning season as observed by Montgomery and Craig (2005) as the time when recruitment peaks).

Sensitivity of climate change impacts on larval dispersal to PLD

PLDs are greatly affected by temperature (Cowen & Sponaugle 2009). In particular, the larval stage may decrease as a consequence of higher temperatures, accelerated metabolism, and faster growth (O'Connor *et al.* 2007). Because changes in growth rate of *S. verreauxi* with temperature are not documented, we examine the sensitivity of climate change impact on larval settlement to variations in PLD; that is, we simulate PLDs between 4-6, 6-8, 8-10, and 10-12 months encompassing the lifespan of *S. verreauxi* (Montgomery & Craig). When accounting for the effect of temperature, settlement depends both on the location of larvae at the end of the PLD and on their survival (see section below: *Effect of temperature on larval survival*). The same response curve of survival as a function of age and temperature was used for all PLDs explored.

Effect of temperature on larval survival

To incorporate the effect of temperature on larval survival, temperature time series are constructed retrieving the ocean temperature at the 3D positions of the larvae. We use laboratory data (Fitzgibbon & Battaglene 2012) to interpolate the proportion of surviving larvae or probability of survival up to that moment at each time step (6 hours) depending upon the temperature experienced by the larvae and its age. The probability of survival up to a time, the rate of change of the probability of survival, and a number drawn from a standard uniform distribution between zero and one are used to determine if the larvae dies or survives at every time step during dispersal.

Fitzgibbon & Battaglene (2012) measured the proportion of surviving larvae of *S. verreauxi* as they aged at different temperatures. Such proportions can be interpreted as the probability of survival up to a time. For instance, Fitzgibbon and Battaglene experiments (2012) showed that after 44 days at 17°C approximately 14% of the larvae survived; this means that the probability of a larva to survive 44 days at 17°C is 0.14 (Fig. S1). Their experiments were divided in three stages as larvae grew (early, middle and late), and the survival percentage at the beginning of each stage was considered to be 100. In order to obtain an equal or smaller proportion of surviving larvae throughout *S. verreauxi* larval stage, we consider that the proportion of surviving larvae at the beginning of the middle and last stages are equivalent to the proportion of surviving larvae at the end of the early and middle stages respectively (Fig. S1). We use a Delauny triangulation to linearly interpolate these data across time (every 6 hours for 365 days which encompasses *S. verreauxi* larval stage), and temperature (every degree spanning 17-29°C). Figure S1a shows the data provided by Fitzgibbon & Battaglene (2012), the same data after scaling the survival percentages across stages (Fig. S1b), the interpolated product (Fig. S1c), and an example of the temperature experienced by a larva

and the corresponding time series of proportion of surviving larvae or probability of survival up to every time during its dispersal (Fig. S1d).

When advection moves larvae to a location where temperature is more conducive for survival, the probability of survival up to that time is higher than the previous probability of survival. Conversely, if advection moves larvae to a location where temperature is less conducive for survival the probability of survival up to that time is lower than the previous. To incorporate the benefit of being advected into locations with favourable temperatures and vice-versa, larvae do not undergo a survival test unless the probability of survival up to that time ($P(t)$) is smaller than any probability of survival previously experienced (P_{min}). A record of the minimum probability of survival experienced by the larvae is therefore kept throughout its advection and compared to the probability of survival at each time step (Fig. S2a).

When the probability of survival ($P(t)$) of a larva is smaller than any probability of survival previously experienced (P_{min}), it goes under a survival trial. The absolute value of the rate of change of the probability of survival ($|dP/dt|$), calculated as $P(t) - P_{min}$, is compared against a number drawn from a standard uniform distribution between zero and one ($X_s \sim N(0,1)$, Fig. S2b). If $X_s \sim N(0,1) > |dP/dt|$ the larva survives, and if $X_s \sim N(0,1) < |dP/dt|$ the larva dies.

Effect of climate driven changes in circulation and temperature on larval dispersal

Modelled trajectories for each spawning season (i.e. 4 contemporary and 4 future years) are used independently to construct connectivity matrices. Connectivity matrices are first computed using all trajectories of larvae that reach the coast (without considering survival affected by temperature); these results represent the effect of circulation alone. Secondly, connectivity matrices are computed using modelled trajectories of larvae that survive the

pelagic phase (temperature dependent); these results represent the combined effect of circulation and temperature. Mean connectivity matrices are obtained for each scenario (contemporary and future) across spawning seasons (4 years for each scenario); the across year mean and standard deviation of the total number of larvae that settle is computed for each climate scenario.

Climate driven changes in the amount of larvae that reach the coast are obtained by subtracting contemporary from future connectivity matrices (i.e. 16 realizations, all pair combinations from the 4 contemporary and 4 future spawning seasons). The resulting matrices of changes in connectivity are then normalized by the total number of larvae that settle (mean of the number of larvae of the contemporary and future connectivity matrices used to compute the subtraction), and averaged to obtain a mean matrix of changes in connectivity considering circulation alone and considering changes in circulation and temperature.

The effect of climate driven changes in temperature on connectivity is obtained by subtracting the normalized matrix of changes in connectivity caused by circulation to the normalized matrix of changes in connectivity caused by circulation and temperature. The values across the columns of the matrices of changes in connectivity (i.e. driven by circulation only, driven by circulation and temperature, and their difference) are summed to obtain a % of climate driven change in connectivity at each destination latitude.

Results

Contemporary and future larval dispersal and connectivity patterns

The circulation along the southeast coast of Australia is dominated by the poleward flowing EAC and mesoscale eddies that form continuously where the EAC separates from the continent at around 31°S; southwards, a weaker and meandering EAC extension continues flowing polewards (Cetina-Heredia *et al.* 2014). Importantly, simulated contemporary larval distributions along the coast (Fig. 1c) are in qualitative agreement with observations of *S. verreauxi* recruit abundances conducted at 4 different locations along south-east Australia (i.e. Coffs Harbour at ~30°S, Tuncurry at ~32°S, Sydney at ~34°S and Ulladulla at ~35°S) over a 6 month period ten months after the start of the spawning season (October - January) for several years (Montgomery & Craig 2004). Observations show large inter-annual variability but a consistent and significantly smaller number of recruits in the two northern locations (30°S and 32°S, Montgomery & Craig 2004). Our results show the same pattern: inter-annual variability is evident but larvae are least abundant between 24°S and 32°S and most abundant between 32.5°S and 38°S where the northern/southern sampling sites are located. Specifically, the proportion of larvae that reach the coast relative to the total amount of larvae that settle is less than 2% in the northern locations at least 2% in the southern locations (Fig. 1c).

Under climate change, the volume transports of the EAC, and EAC extension are projected to increase, and the mean latitude at which the EAC separates from the coast is expected to be displaced polewards (e.g. Matear *et al.* 2013, Oliver & Holbrook 2014). Our results show that in both the contemporary and future climate scenarios, regions where the EAC is coherent with low cross-shore variability, (e.g. 26-31°S) receive fewer larvae than latitudes where the current direction is more variable (high cross shore variability) due to either separation from

the continent, or the prevalence of mesoscale eddies (e.g. 32-35°S Fig. 1a,b,c). The connectivity matrix for the 2060s scenario (Fig. 2c) reflects projected climate driven changes in circulation, i.e. a poleward transport intensification (Matear *et al.* 2013) and a poleward shift in the mean current separation latitude (Oliver & Holbrook 2014), as well as regions with high eddy energetics (Fig. 3). Specifically, the EAC strengthening causes the number of larvae reaching the coast to decrease in the future climate scenario at most latitudes upstream of 35°S (Fig. 3a 4d), and shifts the region of peak larval arrival approximately 270 km south (from 32.8°S, near Newcastle, to 35.2°S near Jervis Bay, Fig. 3a). Similarly, by the end of the PLD, most of the larvae have been advected an additional ~130km further between release and destination latitudes in the future climate scenario with a swifter EAC (Fig. 5). In addition, an increase in the number of larvae arriving between 36-38°S in the future (Fig. 3a) corresponds with an apparent increase in the presence of eddies in the region (Fig. 3b) which are, in turn, likely to enhance the retention of larvae and consequent larval supply into locations where they dominate the circulation. Larval supply at ~27°S appears to increase.

Effect of circulation and temperature

In addition to transporting larvae, ocean currents transport heat, consequently influencing temperature distributions. Our results show that contemporary and future connectivity patterns, as well as projected changes in connectivity, are similar irrespective of the effect of temperature on larval survival (Fig. 2). This suggests that temperatures experienced by larvae transported into the coast are adequate for their survival. An expected ~1-2°C rise in ocean temperature favours the survival of lobster larvae along most of southeastern Australia; particularly, a rise in annual mean depth averaged temperatures adjacent to the coast of southeast Australia (30°-38°S) from ~22°C to ~23-24°C (not shown) corresponds to an

increase in the mean survival probability across 365 days from ~43% to 45-48% (Fig. S1). Our results show that this induces an ~19% increment in the amount of larvae supplied to the coast (Fig. 4c). However, changes in circulation can instigate a decrease in the amount of larvae supplied to the coast by ~23% (Fig. 4a). In fact, a comparison between the effect of changes in circulation versus changes in temperature between contemporary and future climate scenarios on the abundance of larvae reaching the coast at each destination latitude, shows that the impact of circulation often counteracts, at some latitudes by up to 400%, the impact of temperature (Figure 4d, e, f) leading to a ~4% decrease in total settlement (Fig. 4b).

Sensitivity of climate change impact on larval dispersal to PLD

Our results show that changes in circulation decrease the total amount of larvae that reach the coast over a wide range of PLDs (4-12 months, Fig 6), while changes in temperature increase the amount of larvae that survive and reach the coast. Intuitively an increase in PLD would make the effect of changes in circulation on larval transport, or the effect of changes in temperature on larval survival, more apparent as larvae would for longer periods of time be exposed to ocean currents and have to survive. We find that is the case for the effect of changes in circulation but not for the effect of changes in temperature on larval survival. The impact of changes in circulation on the distribution and number of larvae reaching the coast for long PLDs (10-12months) is double that for short PLDs (4-6 months) while the impact caused by changes in temperature through larval survival remains relatively constant across all PLDs. Although there is large inter-annual variability, our results suggest that the impacts of climate change on larval dispersal is sensitive to the lifespan of larvae, particularly when the effect of climate driven change in circulation rather than that in temperature is considered (Fig. 6).

Discussion

This study compares contemporary and future larval dispersal patterns along southeastern Australia, in a region of rapid ocean warming (Wu *et al.* 2012). The agreement between circulation patterns (flow direction and temporal variability) and the amount of larvae reaching the coast, in both the contemporary and future climate scenarios, highlights the significant role of ocean dynamics in driving larval settlement. Specifically, settlement peaks occur where the EAC separates most frequently from the continent (at 32.8°S in the contemporary scenario, and 270km further south at 35.2°S in the future scenario). Similarly, the supply of larvae is lower where across-shore transport is restricted due to the presence of the along-shore flowing EAC (i.e. upstream of the EAC separation latitude). This corroborates the idea that the EAC might act as a barrier to onshore transport of larvae (Roughan *et al.* 2011).

With the recent emphasis on ocean warming, a number of studies (e.g. Figueiredo *et al.* 2014, Pecorino *et al.* 2013) have investigated the thermal tolerances of a range of marine species in an effort to predict the impact of higher ocean temperatures on larval development and survival. This is crucial information to predict future distributions of larvae after dispersal leading to settlement. However, our findings indicate that predictions of future temperatures alone are insufficient to understand the impacts of climate projections on settlement of marine organisms, particularly those with a long PLD, and that consideration of future temperatures within the context of circulation changes is critical to accurately predict changes in settlement patterns and consequent species range expansions. This can only be achieved through a high-resolution ocean model for climate change scenarios.

Our findings show that, for *S. verreauxi* larvae and species with similar thermal tolerances, although ocean warming likely enhances settlement along the southeast coast of Australia, intensification of currents is expected to counter this effect. The net result is a reduction in the amount of larvae reaching the coast under a future climate scenario. In contrast, Andreello *et al.* 2015 found that in the Mediterranean Sea where currents are generally weaker than western boundary currents like the EAC, temperature driven changes in larval growth rate and timing of spawning have a larger impact on connectivity of the dusky grouper, than changes in circulation. This discrepancy highlights that the dominant factor driving larval dispersal patterns depends upon prevalent hydrodynamics of the region and the species studied. Nevertheless, studies exploring combined effect of currents and water properties have found that both changes in hydrodynamics and environmental variables play an important role on larval dispersal and that their effect can counter each other. For instance, Brochier *et al.* (2013) found that increased ocean stratification leads to higher numbers of retained larvae but also, through decreasing oxygen, reduces the extent of suitable habitat for settlement. This highlights the importance of considering changes in circulation in concert with those in temperature and other water properties to more accurately predict meta-population spatial structure and the consequent potential for future species range shifts. Importantly, we found here that the magnitude of the effect of changes in circulation on lobster larval settlement depends on PLD, so that species with a long larval phase are more affected by changes in circulation. Effects of climate driven ocean circulation changes on larval distributions might, therefore, be less detrimental for species with similar thermal tolerance to that of *S. verreauxi* larvae but with shorter PLDs.

This study shows an overall climate change-induced decrease in the amount of lobster larvae that reach the coast, and a poleward shift in the peak of settlement within the western boundary current of the South Pacific subtropical gyre. Ongoing climate driven

intensification and poleward shifting of western boundary currents is expected to be larger in the South Atlantic than in the South Pacific (Cai *et al.* 2005). In addition, the rate of median poleward movement of isotherms, caused by the heat advection of intensifying currents, is twice as fast in the northern hemisphere (Sen Gupta *et al.* 2014). Thus, our results are likely to be conservative with respect to the impact of climate driven circulation changes within western boundary currents in other ocean basins with likely larger impact on species ranges and ecosystem shifts. Moreover, changes in atmospheric circulation driving the intensification of western boundary currents have been linked to both carbon emissions and ozone depletion resulting from high aerosol concentrations in the atmosphere (Cai *et al.* 2005, Cai *et al.* 2003). In this study we used ocean velocity and temperature fields from a model forced with the conservative A1B carbon emission scenario (Nakicenovic *et al.* 2000). Therefore, the impact of climate change on larval supply to the coastline induced by climate scenarios with higher carbon emissions may be stronger than those found here. Indeed, Fitzgibbon *et al.* 2014 find that by 2050-2100, under A1TF and A2 scenarios, temperatures along southeast Australia are expected to increase above the optimal thermal range for *S. verreauxi* pueruli (i.e. transitional stage between pelagic larvae and juvenile) with the potential to undermine successful recruitment.

Our study reveals that future *S. verreauxi* dispersal patterns are a balance between less larvae reaching coastal habitat due to intensified currents, and enhanced potential settlement due to favourable temperatures for larval survival during dispersal. However, changes in temperature will also affect other physiological aspects of larvae such as their energy budget and consequent swimming performance. Similarly, changes in the water bio-geo-chemistry such as nutrient concentrations, may impact food availability and predator distributions (Lett *et al.* 2011). Hence, the development of coupled ocean-atmosphere and bio-geo-chemistry

models, as well as a thorough understanding of larval physiology, are necessary tools to explore synergistic larval dispersal processes.

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References

- Aiken CM, Navarrete SA, Pelegri JL (2011) Potential changes in larval dispersal and alongshore connectivity on the central Chilean coast due to an altered wind climate. *Journal of Geophysical Research*, **116**, G04026, doi:10.1029/2011JG001731.
- Andreollo M, Mouillot D, Somot D, Thuiller W, Manel S (2015) Additive effects of climate change on connectivity between marine protected areas and larval supply to fished areas. *Diversity and Distributions*, **21**, 139-150.
- Brochier T, Echevin V, Tam J, Chaigneau A, Goubanova K, Bertrand A (2013) Climate change scenarios experiments predict a future reduction in small pelagic fish recruitment in the Humboldt System. *Global Change Biology*, **19**, 1841-1853.
- Ayata SD, Lazure P, Thiebaut E (2010) How does the connectivity between populations mediate range limits of marine invertebrates? A case study in the NE Atlantic. *Progress in Oceanography* 87:18-36.
21. Cai W, Shi G, Cowan T, Bi D, Ribbe J (2005) The response of the Southern Annular Mode, the East Australian Current, and the southern mid-latitude ocean circulation to global warming, *Geophysical Research Letters*, **32**, L23706, doi:10.1029/2005GL024701.

22. Cai W, Whetton PH, Karoly DJ (2003) The response of the Antarctic Oscillation to Increasing and Stabilized Atmospheric CO₂, *Journal of Climate*, **16**, 1525–1538.
14. Cetina-Heredia P, Roughan M, van Seville E, Coleman MA (2014) Long-term trends in the East Australian Current separation latitude and eddy driven transport, *Journal of Geophysical Research Oceans*, **119**, 4351–4366.
27. Chamberlain MA, Sun C, Matear RJ, Feng M, Phipps SJ (2012) Downscaling the climate change for oceans around Australia, *Geoscientific Model Development*, **5**, 1177–1194.
4. Cowen RK, Sponaugle S (2009) Larval Dispersal and Marine Population Connectivity, *Annual Review Marine Science*, **1**, 443–66.
2. Doney SC *et al.* (2012) Climate Change Impacts on Marine Ecosystems, *Annual Review Marine Science*, **4**, 11–37.
24. Feng M *et al.* (2011) Ocean circulation, Stokes drift and connectivity of western rock lobster population, *Canadian Journal of Fisheries and Aquatic Sciences*, **68**, 1182–1196.
19. Figueiredo J, Baird AH, Harii S, Connolly SR (2014) Increased local retention of reef coral larvae as a result of ocean warming, *Nature Climate Change*, **4**, 498–502.
30. Fitzgibbon QP, Battaglione SC (2012) Effect of water temperature on the development and energetics of early, mid and late-stage phyllosoma larvae of spiny lobster *Sagmariasus verreauxi*, *Aquaculture*, **344–349**, 153–160.
- Fitzgibbon Q, Ruff N, Tracey SR, Battaglione S (2014) Thermal tolerance of the nektonic puerulus stage of spiny lobsters and implications of ocean warming, *Marine Ecology Progress Series*, **515**, 173–186.
9. Fodrie FJ, Heck KL Jr, Powers SP, Graham W, Robinson KL (2010) Climate-related, decadal-scale assemblage changes of seagrass-associated fishes in the northern Gulf of Mexico, *Global Change Biology*, **16**, 48–59.
- Harley CDG, Hughes AR, Hultgren KM, Miner BG, Sorte CJB, Thornber CS, Rodriguez LF, Tomanek L, Williams S (2006) The impacts of climate change in coastal marine systems. *Ecology Letters*, **9**, 228–241.
15. Hill KL, Rintoul SR, Coleman R, Ridgway KR (2008) Wind forced low frequency variability of the East Australian Current, *Geophysical Research Letters*, **35**, L08602.
29. Irving D *et al.* (2011) Evaluating global climate models for the Pacific Island region. *Climate Research*, **49**, 169–187.
13. Johnson CR *et al.* (2011) Climate change cascades: Shifts in oceanography, species' ranges and subtidal marine community dynamics in eastern Tasmania, *Journal of Experimental Marine Biology and Ecology*, **400**, 17–32.

6. Koehn JD, Hobday AJ, Pratchett MS, Gillanders BM (2011) Climate change and Australian marine and freshwater environments, fishes and fisheries: synthesis and options for adaptation, *Marine Freshwater Research*, **62**, 1148-1164.

11. Last PR *et al.* (2011) Long-term shifts in abundance and distribution of a temperature fish fauna: a response to climate change and fishing practices, *Global Ecology Biogeography*, **20**, 58-72.

3. Lett C, Ayata S-D, Huret M, Irisson, J-O (2010) Biophysical modelling to investigate the effects of climate change on marine population dispersal and connectivity, *Progress in Oceanography*, **87**, 106–113.

12. Ling SD, Johnson CR, Ridgway K, Hobday AJ, Haddon A (2009) Climate-driven range extension of a sea urchin: inferring future trends by analysis of recent population dynamics. *Global Change Biology*, **15**, 719-731.

16. Matear RJ, Chamberlain MA, Sun C, Feng M (2013) Climate change projection of the Tasman Sea from an Eddy-resolving Ocean Model, *Journal of Geophysical Research Oceans*, **118**, 1-16.

17. Montgomery SS, Craig JR (2014) Distribution and abundance of recruits of the eastern rock lobster (*Jasus verreauxi*) along the coast of New South Wales, Australia, New Zealand *Journal of Marine and Freshwater Research*. **39**, 619–628 (2005).

Munday PL, Leis JM, Lough JM, Paris CB, Kingsford MJ, Berumen ML, Lamberchts J (2009) Climate change and coral reef connectivity. *Coral Reefs* 28:379-395.

23. Nakicenovic N *et al.* (2000) Special Report on Emissions Scenarios, IPCC, Nakicenovic N & Swart R (Eds) pp 570 (Cambridge Univ. Press, 2000).

25. O'Connor MI *et al.* (2007) Temperature control of larval dispersal and the implications for marine ecology, evolution, and conservation, *Proceedings of the National Academy of Science, USA*, **104**, 1266-1271.

Okubo A (1971) Oceanic diffusion diagrams, *Deep-Sea Research*, **18**:789-802.

18. Oliver ECJ, Holbrook NJ (2014) Extending our understanding of South Pacific gyre “spin-up”: Modeling the East Australian Current in a future climate, *Journal of Geophysical Research Oceans*, **119**, 2788-2805.

26. Paris CB, Helgers J, van Sebille E, Srinivasan A (2013) Connectivity Modelling System: A probabilistic tool for the multi-scale tracking of biotic and abiotic variability in the ocean, *Environmental Modelling & Software*, **42**, 47–54.

20. Pecorino D, Lamare MD, Barker MF, Byrne M (2013) How does embryonic and larval thermal tolerance contribute to the distribution of the sea urchin *Centrostephanus rodgersii* (Diadematidae) in New Zealand?, *Journal of Experimental of Marine Biology and Ecology*, **445**, 120-128.

8. Poloczanska ES *et al.* (2013) Global imprint of climate change on marine life, *Nature Climate Change*, **3**, 919-925.

Roughan M, Macdonald HS, Baird ME, Glasby TM (2011) Modelling coastal connectivity in a Western Boundary Current: seasonal and inter-annual variability, *Deep-Sea Research II*, **58**, 628-644.

7. SenGupta A *et al.* (2014) Episodic and non-uniform shifts of thermal habitats in warming Ocean, *Deep-Sea Research II*, <http://dx.doi.org/10.1016/j.dsr2.2013.12.002i>.

Siegel DA, Mitarai S, Costello CJ, Gaines SD, Kendall BE, Warner RR, Winters KB (2008) the stochastic nature of larval connectivity among nearshore marine populations, *Proceedings of the National Academy of Science USA*, **105**(26), 8974-8979.

28. Sun C *et al.* (2012) Marine Downscaling of a Future Climate Scenario for Australian Boundary Currents, *Journal of Climate*, **25**, 2947–2962.

5. Vergés A *et al.* (2014) The tropicalization of temperate marine ecosystems: climate-mediated changes in herbivory and community phase shifts, *Proceedings of the Royal Society of London, series B Biology*, **281**, 20140846. <http://dx.doi.org/10.1098/rspb.2014.0846>.

10. Yamano H, Sugihara K, Nomura K (2011) Rapid poleward expansion of tropical reef corals in response to rising sea surface temperatures, *Geophysical Research Letters*, **38**, L04601.

Wu, L. *et al.* Enhanced warming over the global subtropical western boundary currents. *Nature Climate Change*, **2**, 161-166 (2012).

Figure 1. Contemporary lobster connectivity matrix (effect of circulation). a) Mean velocity field (arrows) and variability ellipses computed from all trajectories of larvae that settle in the contemporary scenario. b) Across years mean connectivity matrix of the contemporary scenario, the matrix is normalized by the total amount of larvae that settle; the black diagonal line highlights self-recruitment. c) Across years mean and standard deviation of the percentage of larvae arriving at each destination latitude relative to the total amount of larvae that settle of the contemporary scenario. These results represent the effect of circulation; they are computed using all particle trajectories without considering the effect of

temperature in larval survival. See methods section: effect of climate driven changes in circulation and temperature on larval dispersal for computation details.

Figure 2. Contemporary and future lobster connectivity matrices (effect of circulation, effect, and simultaneous effect of circulation & temperature) and climate driven changes. Normalized mean (across years) connectivity matrix for contemporary (left column) and future (right column) scenarios considering the effect of circulation (top row) and the simultaneous effect of circulation & temperature (bottom row). See methods section: effect of climate driven changes in circulation and temperature on larval dispersal for computation details.

Figure 3. Changes in the % of lobster settlement across destination latitudes driven by enhanced eddy activity. a) contemporary (grey) and future (black) across years mean and standard deviation of the percentage of larvae arriving at each destination latitude relative to the total amount of larvae that settle. These results represent the effect of circulation; they are computed using all particle trajectories without considering the effect of temperature in larval survival. b) Map of the change in eddy activity between climatic scenarios (future – contemporary) as determined from the frequency with which absolute spin parameters (Ω) larger than 0.2 occur (Cetina-Heredia *et al.* 2014). Positive/negative values indicate a higher/lower eddy activity in the future.

Figure 4. Climate driven changes in lobster connectivity matrices and in the % of lobster settlement across destination latitudes (effect of circulation, simultaneous effect of circulation & temperature, and effect of temperature). Top row) matrices of changes in connectivity driven by change in: a) circulation, b) circulation & temperature, and c) temperature, amongst climatic scenarios. See methods section: effect of climate driven changes in circulation and temperature on larval dispersal for computation details. Bottom

row) across years mean (thick line) and standard deviation (shaded area) of the percentage of change in larval abundance arriving at each destination latitude relative to the total larvae settled (mean among contemporary and future climate scenarios) driven by changes in d) circulation, e) circulation & temperature, and f) temperature. See methods section: effect of climate driven changes in circulation and temperature on larval dispersal for computation details.

Figure 5. Lobster contemporary and future dispersal kernels. Across years mean and standard deviation of the % of larvae, relative to the total amount of larvae settled, as a function of the distance between release and destination latitudes for the contemporary (grey) and future (black) climate scenarios.

Figure 6. Climate driven changes in % of lobster total settlement for different PLDs (effect of circulation, simultaneous effect of circulation & temperature, and effect of temperature). Mean and standard deviation (across years) of changes in larval abundance caused by changes in circulation & temperature (green), changes in circulation (grey), and changes in temperature (pink) for different pelagic larval durations. The y-axis shows percentage of change relative to the total amount of larvae that settle in each case (i.e. circulation & temperature or circulation). The percentage of change in larval abundance caused by temperature is obtained subtracting the effect of circulation to the effect of circulation & temperature.

Supporting Information

Figure S1. Proportion of surviving lobster larvae (%) as a function of temperature and larvae age.

Figure S2. Probabilities of survival experienced by a larva throughout dispersal.