# Larval dispersal in a changing ocean with an emphasis on upwelling regions

Samuel M. Bashevkin,[1,2,3],† Connor D. Dibble,[1,2] Robert P. Dunn,[1,4] Jordan A. Hollarsmith,[1,2,5] Gabriel Ng,[2,6] Erin V. Satterthwaite,[1,2,7,8] and Steven G. Morgan[1,2]

[1]Department of Environmental Science and Policy, University of California, Davis, One Shields Avenue, Davis, California 95616 USA
[2]Coastal and Marine Sciences Institute and Bodega Marine Laboratory, University of California, Davis, 2099 Westshore Road, P.O. Box 247, Bodega Bay, California 94923 USA
[3]Delta Science Program, Delta Stewardship Council, 980 9th Street, Suite 1500, Sacramento, California 95814 USA
[4]Coastal and Marine Institute & Department of Biology, San Diego State University, 4165 Spruance Road, San Diego, California 92182 USA
[5]Department of Biological Sciences, Simon Fraser University, 8888 University Drive, Burnaby, British Columbia V5A 1S6 Canada
[6]Department of Evolution and Ecology, University of California, Davis, One Shields Avenue, Davis, California 95616 USA
[7]National Center for Ecological Analysis and Synthesis, University of California Santa Barbara, 735 State Street, Suite 300, Santa Barbara, California, USA
[8]Future Earth, School of Global Environmental Sustainability, Colorado State University, 108 Johnson Drive, Fort Collins, Colorado 80523 USA

**Abstract.**   Dispersal of benthic species in the sea is mediated primarily through small, vulnerable larvae that must survive minutes to months as members of the plankton community while being transported by strong, dynamic currents. As climate change alters ocean conditions, the dispersal of these larvae will be affected, with pervasive ecological and evolutionary consequences. We review the impacts of oceanic changes on larval transport, physiology, and behavior. We then discuss the implications for population connectivity and recruitment and evaluate life history strategies that will affect susceptibility to the effects of climate change on their dispersal patterns, with implications for understanding selective regimes in a future ocean. We find that physical oceanographic changes will impact dispersal by transporting larvae in different directions or inhibiting their movements while changing environmental factors, such as temperature, pH, salinity, oxygen, ultraviolet radiation, and turbidity, will affect the survival of larvae and alter their behavior. Reduced dispersal distance may make local adaptation more likely in well-connected populations with high genetic variation while reduced dispersal success will lower recruitment with implications for fishery stocks. Increased dispersal may spur adaptation by increasing genetic diversity among previously disconnected populations as well as increasing the likelihood of range expansions. We hypothesize that species with planktotrophic (feeding), calcifying, or weakly swimming larvae with specialized adult habitats will be most affected by climate change. We also propose that the adaptive value of retentive larval behaviors may decrease where transport trajectories follow changing climate envelopes and increase where transport trajectories drive larvae toward increasingly unsuitable conditions. Our holistic framework, combined with knowledge of regional ocean conditions and larval traits, can be used to produce powerful predictions of expected impacts on larval dispersal as well as the consequences for connectivity, range expansion, or recruitment. Based on our findings, we recommend that future studies take a holistic view of dispersal incorporating biological and oceanographic impacts of climate change rather than solely focusing on oceanography or physiology. Genetic and paleontological techniques can be used to examine evolutionary impacts of altered dispersal in a future ocean, while museum collections and expedition records can inform modern-day range shifts.

† **E-mail:** smbashevkin@ucdavis.edu

## INTRODUCTION

Dispersal drives the exchange of genetic material among populations, with diverse ecological and evolutionary consequences including species range limits, connectivity, and the potential for local adaptation. Dispersal is especially important in the context of climate change since adaptation and range shifts may prove essential to persistence (Davis and Shaw 2001). Thus, insights into the interplay between climate change, dispersal, and the ecological or evolutionary consequences of dispersal shifts will prove essential to understanding the complex impacts of climate change on marine, aquatic, and terrestrial environments.

The majority of marine benthic and demersal animals have a biphasic life cycle in which early development is spent as a free-swimming pelagic larva (Thorson 1950). Pelagic larval stages are vitally important for population and community dynamics of marine species because these developmental stages are the primary agents of dispersal that connect populations, supply recruits, and colonize new habitats (Underwood and Fairweather 1989, Chesson 1998, Burgess et al. 2016). Population genetic connectivity can be maintained by the exchange of very few larvae (Strathmann et al. 2002, Swearer et al. 2002, Burgess et al. 2016), rendering it extremely sensitive to disruptions in larval dispersal. Furthermore, larval supply is an important supply-side factor that affects population dynamics, interaction strengths, and the resilience of communities (Menge et al. 1997, Navarrete et al. 2005, Palardy and Witman 2014). However, the journey of tiny pelagic larvae is fraught with danger, as they contend with strong currents, patchy food supplies, predators, and environmental variation before finding a suitable nursery or adult habitat (Morgan 1995, Llopiz et al. 2014). Furthermore,

larvae are generally more sensitive to stressors than adults (Byrne 2011, Harvey et al. 2013, Kroeker et al. 2013, Pandori and Sorte 2019), making them especially vulnerable to global climate change.

The global climate has been changing at an unprecedented rate since the industrial revolution as atmospheric carbon dioxide has both increased at the fastest rate and reached the highest level on record for the past 800,000 yr (IPCC 2013), and expected increases will exceed levels observed on earth in the previous tens of millions of years (Doney and Schimel 2007). Increasing atmospheric $CO_2$ raises global temperature through the greenhouse effect (IPCC 2013) and lowers the pH and carbonate ion concentrations of oceans, which have absorbed one-third of all atmospheric $CO_2$ emissions (Sabine et al. 2004). Rising atmospheric and oceanic temperatures directly or indirectly alter ocean pH, salinity, stratification, circulation, long-term climatic cycles, storms, upwelling, ultraviolet radiation (UVR), and dissolved $O_2$ (DO; Fig. 1).

Climate change exposes larvae to an environment that is novel on evolutionary timescales, affecting the phenology of their release, as well as their feeding, growth, development, behavior, mortality, habitat selection, and transport. Taken together, these impacts on larvae will likely influence dispersal from the site of spawning (for free-spawners) or larval release (for brooders) to the site of settlement. However, larval dispersal will not be altered uniformly by climate change due to interspecific differences in behavior, physiology, and life histories. Marine animals exhibit considerable behavioral and physiological diversity, such as the presence or absence and method of calcification, ability to cope with physiological stress and adjust their internal chemistry, and swimming behavior and speed. In addition, larval exposure to oceanographic conditions differs
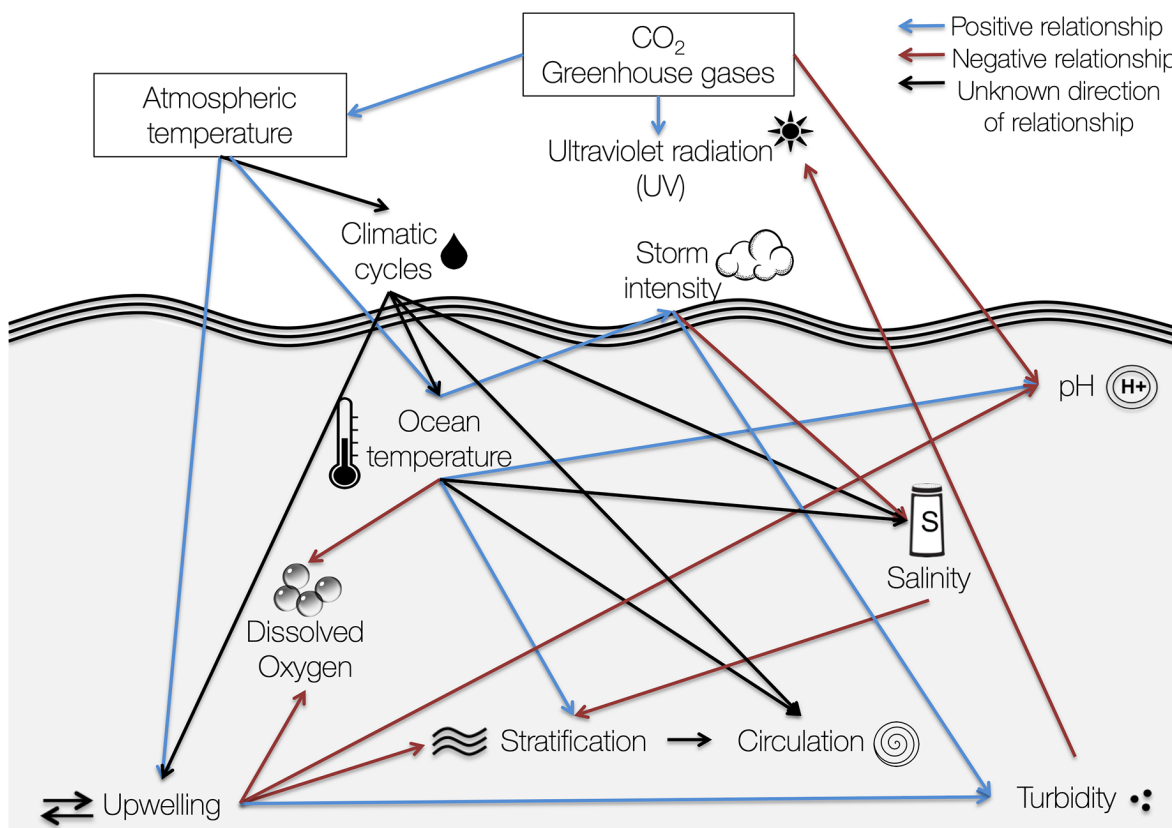
Fig. 1. Important ocean changes associated with climate change. Higher concentrations of greenhouse gases in the atmosphere have caused a cascading array of abiotic changes in the global oceans. Linkages between variables indicate a direct effect of one factor on another and were obtained from a literature search. Blue lines indicate positive relationships between variables, red lines indicate negative relationships between variables, and black lines indicate a known relationship, but the direction of change is unknown or has no clear direction.

by life history, which can be divided into three broad categories: direct development (no pelagic phase, not discussed in this paper), lecithotrophy (non-feeding), and planktotrophy (feeding; Thorson 1950). The pelagic larval duration (PLD) of lecithotrophs and planktotrophs ranges from minutes to months, affecting exposure to pelagic sources of mortality. Lecithotrophs generally have shorter PLDs due to their reliance on internal energy reserves supplied by the mother.

Marine dispersal is a complex process involving aspects of life history strategies, physiology, behavior, and oceanography, which are likely to be impacted by changing ocean conditions (Llopiz et al. 2014, Chan et al. 2018). Yet, the effects of climate change on all determinants of

dispersal as well as its ecological and evolutionary consequences have not been reviewed as an integrated whole. Without a conceptual framework incorporating all of these elements, predicting the effects of climate change on dispersal is challenging and yields inconsistent results. A thorough understanding of future changes to larval dispersal is critical to predict how species will be affected by climate change since larval dispersal both replenishes adult populations and exchanges individuals among populations, thereby driving patterns of genetic variation impacting local adaptation. To address this gap and encourage and enable future researchers to incorporate biology and oceanography when forecasting impacts of climate change on dispersal, we synthesized predicted impacts of

anthropogenic climate change on the dispersal of benthic or demersal, fully marine (unless otherwise noted) organisms with biphasic life cycles in the coastal ocean. We comprehensively searched for the following terms in the Web of Science, Biosis, and Google Scholar: all combinations of each climate factor (temperature, ocean acidification [OA], salinity, stratification, circulation, El Nino Southern Oscillation [ENSO], Pacific Decadal Oscillation [PDO], North Pacific Gyre Oscillation [NPGO], storm, upwelling, UVR, hypoxia) with organismal factors (phenology, larval release, spawning, feeding, growth, development, behavior, swimming, mortality, settlement, recruitment, transport), along with the word "larva."

We examined the full extent of the pelagic larval phase, starting at fertilization for free-spawning organisms or larval release for internally fertilizing organisms, and ending at the onset of a primarily benthic habitat association (settlement), the endpoint of dispersal. Most examples were drawn from highly dynamic upwelling regions that are already characterized by extreme environmental variability and encompass some of the most productive fisheries in the world. Select examples are drawn from other (especially tropical) regions to illustrate the global significance of these concepts. We detail how oceanic changes will directly alter the transport of larvae as well as impact aspects of larval organismal biology critical for their dispersal, such as phenology, feeding, growth, mortality, and behavior. We then evaluate the expected implications of altered dispersal for population dynamics and evolutionary adaptation. We conclude by predicting which life history traits related to dispersal may confer evolutionary advantages in a changing ocean and illustrate the use of our framework with three case studies. We do not attempt to provide a generalized answer regarding how larval dispersal will be affected by climate change. This question has no general answer due to conflicting directionalities of effects among regions and taxa. Instead, we provide a synthesis of the important factors to consider when conducting region- and taxon-specific studies of climate change and marine dispersal, with a discussion of the implications of altered dispersal.

## THE IMPACTS OF CLIMATE CHANGE ON LARVAL TRANSPORT AND ORGANISMAL BIOLOGY

Climate change can have direct effects on larval transport and organismal biology as well as indirect effects through changes to predation pressure or food supply. Direct effects on larval transport involve oceanographic changes that move or hinder the movement of larvae while the organismal impacts include changes to larval phenology, feeding, growth and development, swimming, mortality, and habitat detection (Table 1). Transport impacts influence the potential dispersal of larvae, that is, where they could go, while organismal impacts interact with transport to influence realized dispersal, that is, where larvae actually end up (Fig. 2). Climate factors may be antagonistic or synergistic (Fig. 1), and their effects on larvae may have conflicting directions (Fig. 3), but their combined effects on larval dispersal are simpler since many of these organismal and transport factors are interrelated (Fig. 2). We start by outlining impacts of broad oceanographic changes then narrow to individual environmental factors.

### Direct Effects

*Circulation.*—Climate change will directly affect larval dispersal by altering circulation or water movement. Ocean circulation patterns will shift through changes in pressure gradients and seawater density from surface heating, evaporation, and freshwater inputs, as well as changing winds and sea-level height (Fig. 1; Carless et al. 2016, Wilson et al. 2016). The net effect of climate change on circulation will be idiosyncratic due to the patchwork of large- and small-scale processes involved, though some generalities emerge. Because groups of larvae spread out through diffusion as they are transported and the rate of spread of groups of larvae increases as they separate, the duration of exposure is critical to the shape of the probability distribution curve describing transport distances (Largier 2003, Cowen et al. 2007). Advection dominates dispersal in the pelagic environment where the Peclet number is high, except in very high shear zones (Largier 2003). Intensifying (weakening) advective currents increase (reduce) the mean, variance, and maximum distance that clutches of

Table 1. The direct effects of each climate change factor on the transport and organismal biology of marine larvae.

| Factor | Transport | Phenology | Feeding rate | Growth, development, PLD | Swimming behavior | Larval survival | Habitat detection |
|---|---|---|---|---|---|---|---|
| Altered ocean circulation | Non-directional | | | | | | |
| Altered climatic cycles | Non-directional | | | | | | |
| Increased upwelling | Non-directional | | | | | | |
| Increased storm intensity | Non-directional | | Inconsistent directions | | Non-directional | Inconsistent directions | Inconsistent directions |
| Increased stratification | Non-directional | | **Increased** | | Non-directional | | Inconsistent directions |
| Increased Ocean temperature | | Non-directional | Inconsistent directions | **Increased** | Non-directional | *Decreased* | **Increased** |
| Decreased ocean pH | | | *Decreased* | *Decreased* | Non-directional | *Decreased* | *Decreased* |
| Altered salinity | | Non-directional | *Decreased* | *Decreased* | Non-directional | *Decreased* | Non-directional |
| Increased hypoxia | | Non-directional | *Decreased* | *Decreased* | Non-directional | *Decreased* | Inconsistent directions |
| Increased ultraviolet radiation | | Non-directional | Inconsistent directions | *Decreased* | Non-directional | *Decreased* | *Decreased* |
| Increased turbidity | Non-directional | Non-directional | Inconsistent directions | Inconsistent directions | Non-directional | *Decreased* | *Decreased* |

*Notes:* PLD, pelagic larval duration. Filled boxes indicate documented effects on organismal or transport processes in negative (italics), positive (bold), or in an unclear direction. Non-directional impacts include those where an organismal impact is altered with no clear directionality, for example, changes in swimming behavior or habitat preference. The directionality of climate factors is represented as the most common predicted change, but some factors may change in different directions in certain regions, often with the opposite predicted effect on larvae. See Appendix S2: Table S1 for references.

larvae travel. Thus, changes in the magnitude and inter- and intra-annual variation in currents may have profound impacts on the distribution of larval dispersal directions and distances.

Latitudinal (i.e., equatorward or poleward) transport patterns will determine whether dispersal trajectories track (through poleward transport) shifting latitudinal climate envelopes that partially determine species range limits (Sorte 2013, Pringle et al. 2017). In most eastern boundary current systems, intensifying gyres will strengthen equatorward-flowing currents (Stock et al. 2011), especially in the Northern Hemisphere where intensified equatorward currents in the sub-polar North Atlantic may extend the maximum dispersal distance (the extreme tail end of the dispersal kernel) by 7°–10° latitude per 6 months of larval exposure to currents (van Gennip et al. 2016). Poleward-flowing western boundary currents and the higher latitude components of some eastern boundary current systems are also rapidly warming and intensifying, especially in the Southern Hemisphere (Sun et al.

2011, Hogg et al. 2015), potentially extending the range of extreme dispersal events near southern Chile, Uruguay, and Tasmania by 7°–10° latitude per 6 months of exposure (van Gennip et al. 2016). Poleward dispersal is expected to weaken near northern New Zealand and the eastern United States and Caribbean, while equatorward dispersal should weaken along the coast of Brazil, in all cases reducing extreme dispersal by 7°–10° latitude per 6 months of exposure (van Gennip et al. 2016). Furthermore, in the Southern Hemisphere, eastern boundary currents are expected to increase in poleward flow, potentially enabling more dispersal toward the poles in present-day flow regimes that are predominantly equatorward (van Gennip et al. 2016).

Where longitudinal environmental gradients exist (e.g., near the equator and at high latitudes (van Gennip et al. 2016, Wilson et al. 2016), projected changes in longitudinal circulation will affect dispersal. Changing longitudinal transport patterns will track or counter changing climate envelopes where projected impacts to water
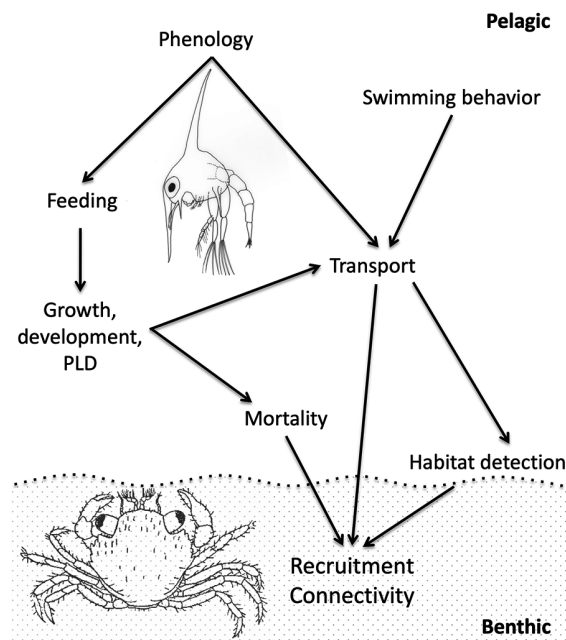
Fig. 2. The inter-relationships among organismal factors and current-mediated transport and their eventual impacts on recruitment and connectivity through altered dispersal. Recruitment and connectivity will be directly impacted by larval mortality, transport, and habitat detection, which are in turn determined by upstream impacts on larval phenology, feeding, growth, development, pelagic larval duration (PLD), and swimming behavior.

properties (e.g., temperature) vary across longitude, as in the equatorial Pacific (DiNezio et al. 2009, Popova et al. 2016). Connectivity patterns and larval colonization rates among tropical Pacific islands, for example, may be altered by weaker currents and enhanced equatorial warming depending on the direction of transport, which varies in time and space (DiNezio et al. 2009, Munday et al. 2009, van Gennip et al. 2016).

Smaller scale circulation structures that are mostly responsible for transporting larvae generally occur within 10 km of shore (Morgan et al. 2009, 2018) and are driven by gyre currents and their interactions with coastal topography, the seafloor, and local forces like land breezes and riverine inputs. Larval transport in these small-scale structures strongly depends on spatial and temporal variation in gyre currents. For example, during strong equatorward flows in eastern boundary current systems, larvae may be entrained in eddies that slow their equatorward transport rates, but local variation in wind stress modifies the gyre circulation and reduced or

reversed currents may disrupt these accumulation zones and potentially transport larvae quickly poleward (Wing et al. 1998; S. G. Morgan et al., *unpublished manuscript*) sometimes resulting in net poleward dispersal (Hameed et al. 2016). Thus, future changes in the magnitude, direction, and variability of gyre circulation may affect larval transport directly via shifts in basin-scale latitudinal and longitudinal currents but also indirectly by changing the conditions that generate smaller scale nearshore flow structures impacting larval transport.

*Long-term climatic cycles.*—Climate change is expected to alter both the magnitude and variability of multi-annual (ENSO) and multi-decadal (PDO, NPGO) climatic oscillations. Oscillations from one phase to another profoundly change precipitation patterns, temperature, primary productivity, and the strength of major currents (Fig. 1; Chavez et al. 1999, McPhaden et al. 2006, Menge et al. 2009, Keister et al. 2011). Though preliminary evidence suggests that ENSO and NPGO will change in periodicity, amplitude of the oscillations, and

skewness with climate change (Timmermann et al. 1999, Van Oldenborgh et al. 2005, Di Lorenzo et al. 2008), multiple drivers of these oscillations will be affected, often in opposing manners rendering projections difficult. For instance, increasing temperature could diminish ENSO amplitudes by weakening Walker Circulation (Vecchi and Soden 2007, DiNezio et al. 2009, Collins et al. 2010), whereas expected reductions in Pacific equatorial upwelling will induce temperature anomalies that favor increasing ENSO oscillation magnitudes (Collins et al. 2010). ENSO amplitudes are predicted to increase slightly at most (Van Oldenborgh et al. 2005, Collins et al. 2010, Cai et al. 2015), and the effect of interactions between climate change and the PDO and NPGO remains unclear.

Climatic cycles alter ocean currents potentially transporting larvae across oceanographic barriers to unfavorable habitats (Le Port et al. 2014) or to new or newly favorable habitats (Yamada et al. 2015, Wood et al. 2016). For instance, a particularly strong positive phase of ENSO (El Niño) in the early 1990s strengthened northward currents along the coasts of the northeast Pacific, transporting larvae beyond their geographic range (Sorte et al. 2001) and spreading introduced species to new habitats (Yamada et al. 2015). In addition, changes in the intensity of ENSO will influence the strength and direction of the east–west flowing equatorial currents (Neelin et al. 1998, Cai et al. 2015) with implications for longitudinal dispersal distances (Lo-Yat et al. 2011). The different phases of ENSO, PDO, and NPGO can also influence the strength of upwelling, potentially altering patterns of advection and stratification that affect transport or larval development (Macias et al. 2012, Yamada et al. 2015).

*Upwelling.*—Recent observations and global model projections indicate that global warming very likely will affect atmospheric pressure gradients, intensifying winds that drive coastal upwelling (Fig. 1; Bakun et al. 2015, García-Reyes et al. 2015). Prevailing equatorward winds interact with the rotation of the Earth to advect surface water offshore (Ekman transport), causing sea level to drop, and pulling cold, nutrient-rich, acidified, low $O_2$ water to the surface (Hickey 1998). Coastal upwelling is strongest and most persistent at lower latitudes

along eastern boundaries of ocean basins and headlands.

In a warming ocean, upwelling seasons are predicted to begin earlier, last longer, and intensify more at higher latitudes on upwelling coasts, homogenizing upwelling gradients within those regions (Wang et al. 2015). However, increased stratification may reduce nutrients and increase temperature in upwelled waters (Wang et al. 2015). Stronger upwelling could increase offshore and alongshore transport of embryos and larvae in the surface layer and onshore transport below the surface layer. In the absence of strong stratification, increased upwelling could increase food for larvae (by spurring phytoplankton blooms) and physiological stress from low pH and hypoxic water (see *Ocean acidification* and *Hypoxia* sections; García-Reyes et al. 2015, Hollarsmith et al. 2019). Potential losses of embryos and larvae from offshore transport may have selected for latitudinal differences in reproductive strategies of fishes and crustaceans in the California Current System (Parrish et al. 1981, Shanks and Eckert 2005), raising the possibility of increased selective pressure for reduced time in the plankton due to climate change. Unlike eggs, larvae can limit transport even in highly advective upwelling regimes by regulating depth in a sheared water column to migrate offshore in seaward-flowing surface currents before returning onshore in landward-flowing bottom currents late in development (Queiroga and Blanton 2005, Morgan 2014). Depth regulation may continue to be effective at limiting transport under future conditions, because increases in offshore Ekman transport should be balanced by onshore current flow at depth, though larvae would be exposed to more acidified and hypoxic water. Increased offshore transport may diminish the ability of postlarvae to use directed horizontal swimming to navigate onshore to adult habitats using hierarchies of acoustic, chemical, visual, and celestial cues (Kingsford et al. 2002, Drake et al. 2018; Bashevkin and Morgan, *in press*).

*Storms.*—The number and intensity of tropical and subtropical cyclones rose from 1970 to 2004, likely in association with increases in sea surface temperature (SST). The largest increases occurred in the Pacific and Indian Oceans (Webster et al. 2005), and this trend is projected to continue (Knutson and Tuleya 2004). Future increases in
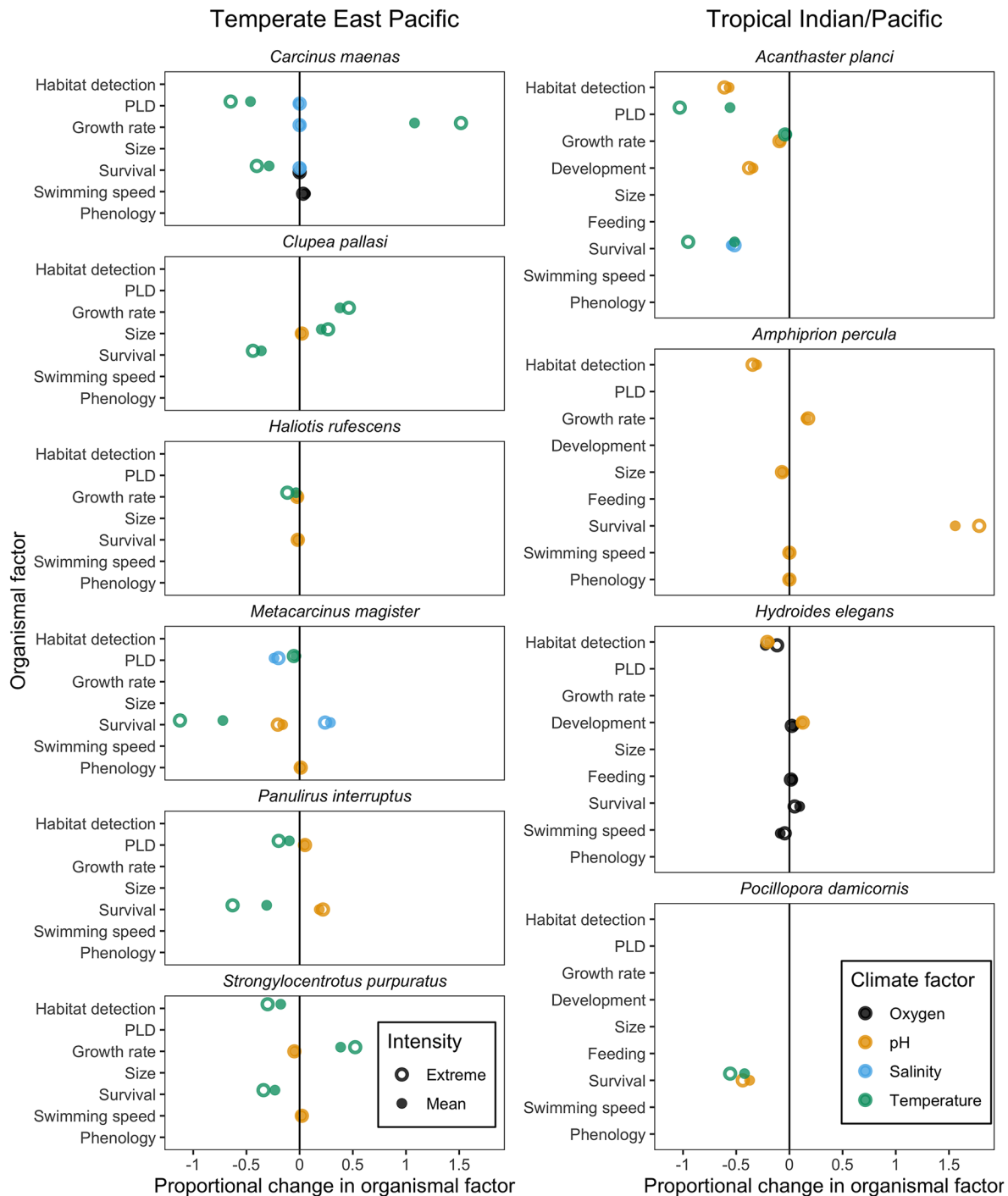
Fig. 3. Quantitative case studies demonstrating the expected proportional effects of climate change factors on organismal traits in 10 well-studied or important species across two bioregions. Effects vary widely across region and different climate factors may have conflicting effects, illustrating the importance of species- and region-specific studies to determine the net effects of climate change on dispersal. Effects were calculated from proportional changes obtained from the literature scaled to the expected change in each climate factor by 2096 from the CMIP5

(Fig. 3. *Continued*)

(Climate Model Intercomparison Project Phase 5) global coupled atmosphere–ocean model outputs for the IPCC (Intergovernmental Panel on Climate Change) warming scenario RCP6 (Representative Concentration Pathway 6). The Temperate East Pacific climate values were pulled from two locations off the coasts of Monterey and San Diego, California. The Tropical Indian/Pacific climate values were from Lizard Island, Australia. Extreme values represent extreme warming, low salinity pulses, pH reductions, and dissolved oxygen reductions calculated by adding (temperature) or subtracting (salinity, pH, oxygen) the model-predicted SD of each climate factor to/from the mean projected climate values. The organismal factor "size" indicate sizes where no growth rate could be calculated (e.g., size at hatching). More detailed methods and citations are available in Appendix S1.

storm intensity will be accompanied by reduced frequency, though this pattern is variable among ocean basins (Kang and Elsner 2015). In the coastal ocean, storms will increase wave height (Young et al. 2011) as well as rapidly reduce salinity and increase turbidity regionally following heavy rains (Fig. 1; IPCC 2013).

Changes in storm frequency and strength may affect larval transport by disrupting persistent oceanographic features, such as fronts, which otherwise can act as barriers to dispersal (Gillespie et al. 2007, Yamada et al. 2017). Strong storms can alter nearshore circulation through reduced salinity or by shifting predominant wind patterns, creating short-term windows of opportunity for invading larvae, altering species distributions in some cases (Table 2; Yamada et al. 2017). For example, a change in wind direction during storms can force postlarvae of blue crabs, *Callinectes sapidus*, into bays increasing recruitment (Etherington and Eggleston 2003), and strong cyclones typically increase recruitment of this species by expanding the nursery habitat for settlers (Eggleston et al. 2010). Thus, the predicted increase in cyclone strength (Kang and Elsner 2015) could increase the abundance of species that rely on these extreme events for strong recruitment years.

Increasingly intense storms should stimulate primary production through nutrient enrichment of the coastal zone and, through storm-induced turbulence, increase encounter rates between predatory larvae and zooplankton prey (Rothschild and Osborn 1988), enhancing larval feeding. However, turbulence can also reduce feeding by predatory fish larvae by decreasing capture success (MacKenzie and Kiørboe 2000) and induce or hasten settlement in some invertebrates (Denny and Shibata 1989, Gaylord et al. 2013).

*Stratification.*—Climate change may affect larval dispersal by creating barriers to larval movement. Stratification will be strengthened by both surface salinity decreases and surface temperature increases and weakened by surface salinity increases as well as stronger storms and upwelling that will mix the water column (Fig. 1). Sharp pycnoclines (strong vertical density gradients) associated with stratified water columns may prevent the vertical movement of larvae and embryos (Lougee et al. 2002, Arellano et al. 2012). Strongly swimming larvae are more impeded by haloclines (strong vertical salinity gradients) than thermoclines (strong vertical temperature gradients; Young 1995; Bashevkin and Morgan, *in press*). A pycnocline could inhibit diel vertical migrations undertaken by larvae to forage in productive surface waters or exploit tidal currents under the cover of darkness. On the other hand, stratification can concentrate food making it easier for larvae to feed (Metaxas and Young 1998).

*Temperature.*—Global SST has risen by an average of 0.11°C per decade since the 1970s, with an additional 3–5°C of warming expected by 2100 (IPCC 2013). Increases in seawater temperature due to anthropogenic climate change occur to depths >2000 m, though the most severe and variable warming is near the surface (Gleckler et al. 2016). Surface warming is faster in some regions than others. For example, the ocean in the Southern Hemisphere is heating at four times the rate of the ocean in the Northern Hemisphere (Wijffels et al. 2016), and surface waters have cooled in some strong upwelling regions over the past 50 yr (Belkin 2009). Brief temperature anomalies (marine heatwaves) will intensify with global change across most regions (IPCC 2013, 2019, Frölicher et al. 2018), while changing frequencies of climate oscillations will alter oceanic

Table 2. Examples of the ecological and evolutionary implications of altered larval dispersal due to climate change.

| Scenario | Background | Current status | Future predictions |
| --- | --- | --- | --- |
| Range expansion driven by larval physiology and extreme events | The invasive green crab *Carcinus maenas* (Fig. 4A, B) had been unable to enter the Salish Sea due to cool surface waters inhibiting larval development and estuarine outflow preventing larval entry. Without invading larvae from nearby populations, *C. maenas* was never observed in the Salish Sea in any life stage despite extensive surveys (Yamada et al. 2017) | Anomalously high water temperatures during the "warm blob" oceanographic event, combined with major storms that reversed the predominant current, enabled *C. maenas* to finally invade the Salish Sea (Yamada et al. 2017) | Both warm temperature events and storms are expected to increase in the future (The impacts of climate change on larval transport and organismal biology), potentially enabling similar population expansions in comparable systems as other barriers to invasion are lifted |
| Local adaptation impacted by reduced pelagic larval duration (PLD) and connectivity | An important recreational fishery species, the red abalone *Haliotis rufescens* (Fig. 4C, D) has a short PLD but maintains a well-connected population from Monterey, California to the Oregon border (De Wit and Palumbi 2013). Adults are large and slow moving (Ault and Demartini 1987) relative to larvae entrained in currents moving 10–50 cm/s, so population connectivity is principally via larval dispersal | Despite high connectivity, local selective pressures have induced genetic differentiation between subpopulations (De Wit and Palumbi 2013) | In the future, rising sea temperatures should shorten PLD (Leighton 1974), decreasing connectivity and potentially enhancing local adaptation to existing oceanographic differences. On the other hand, decreased connectivity may limit adaptation to changing ocean conditions by reducing the immigration of well-adapted genotypes from other regions, as well as reducing the probability of recolonizing disturbed habitats |
| Fishery affected by changes in the Pacific Decadal Oscillation (PDO) and upwelling through larval supply and settlement | Recruitment of the important commercial fishery species Dungeness crab *Metacarcinus magister* (Fig. 4E, F) increases in negative phases of the PDO and with earlier spring transitions of the California Current (Shanks and Roegner 2007, Shanks 2013). Enhanced southward flow of the California Current during negative phases of the PDO is the likely mechanism increasing Dungeness recruitment in Oregon and northern California by transporting more larvae to the south. Only during large larval settlement events at negative PDO phases are recruits subject to density-dependent mortality (Shanks 2013) | An earlier spring transition increases recruitment by helping larvae reach shore as the California currents moves nearshore (Hickey 1979) and by increasing larval food supply as this transition corresponds with the beginning of upwelling (Lynn et al. 2003, Bakun et al. 2015) | Long-term directional shifts in PDO patterns due to climate change are difficult to predict (The impacts of climate change on larval transport and organismal biology: Direct effects: Long-term climatic cycles); however, the spring transition of the California Current has trended later since the late 1960s (Bograd et al. 2009), potentially driving lower *M. magister* recruitment. Upwelling is expected to increase in intensity at higher latitudes (Sydeman et al. 2014), which may provide more food for larvae after the spring transition. Shifts in the date of the spring transition and upwelling strength, in addition to potential alterations to PDO variability, will interact to determine the fate of Dungeness crab populations |

*Note:* See Fig. 4 for images of each species.

water temperatures at large scales (Fig. 1; Feng et al. 2013, Di Lorenzo and Mantua 2016).

Warmer temperatures generally increase organismal metabolic rates until developmental abnormalities and death ensue (Byrne 2011). A faster metabolism increases demand for food (per unit time) and speeds development rates, thereby reducing PLD, and increasing the probability that larvae will settle closer to natal populations (Kendall et al. 2013, Figueiredo et al.

2014). Furthermore, seasonally abnormal temperatures can induce adults to release larvae at suboptimal times (Tlusty et al. 2008; R. Dunn, *personal observation*) when food is not available (Cushing 1990), environmental conditions are intolerable (Pörtner and Farrell 2008), or perhaps when seasonal dispersal pathways are inactive. Alternatively, increasing variability in the timing of larval release in a population could increase the potential for reproductive success (Cowan et al. 2007). Oxygen demand sets the lethal limits of rising temperatures (Pörtner and Knust 2007), which could interact with hypoxia arising from climate change (Doney et al. 2012). Long-term exposure to higher temperatures can reduce settlement (Randall and Szmant 2009), but short-term exposure can increase settlement and recruitment as long as cooler temperatures resume before temperature-induced mortality (Nozawa and Harrison 2007).

*Ocean acidification.*—The average pH of ocean surface waters has decreased by 0.1 since industrialization due to the absorption of anthropogenic $CO_2$ (Sabine et al. 2004, Orr et al. 2005) and the resulting decrease in carbonate ($CO_3^{2-}$) ion concentrations and increase in $H^+$ ion concentrations. Low concentrations of carbonate ions eventually result in the undersaturation of aragonite and calcite, the two main biological forms of calcium carbonate ($CaCO_3$). Aragonite is already undersaturated ephemerally in surface waters of temperate coastal upwelling systems (Feely et al. 2008). At the current rate of emissions, aragonite is projected to be undersaturated throughout the water column of the Southern Ocean by 2100, and carbonate is projected to decrease by 45% in the tropics (Orr et al. 2005).

Ocean acidification can damage organ tissue (Frommel et al. 2012, 2016) and has especially severe effects on larvae that create aragonite or calcite structures which can experience severe deformations, erosion, and altered mineralization (Dupont and Thorndyke 2009, Albright 2011). Though rare, severe skeletal deformation can be lethal (Dupont et al. 2008). Skeletal or shell deformations can affect dispersal by altering feeding or swimming capabilities (Pimentel et al. 2014, Espinel-Velasco et al. 2018) and increasing vulnerability of larvae to predation (Gaylord et al. 2011).

In low pH conditions, some larvae avoid or fail to detect auditory or olfactory cues that indicate good settlement conditions or swim toward predator cues (Nagelkerken and Munday 2016, Ashur et al. 2017). Vision can compensate for compromised olfaction though it can come with trade-offs, such as increasing vulnerability to visual predators by foraging in brighter light (Devine et al. 2012). Reduced sensory ability combined with reduced swimming ability for many species could effectively result in passive dispersal (Leis 2018). Changes in chemical cue or cue source can reduce settlement success, such as changes in the algal community and cue integrity reducing coral settlement (Albright 2011, Nagelkerken and Munday 2016, Espinel-Velasco et al. 2018).

*Salinity.*—As ocean temperatures rise, salinity will likely change due to melting sea ice and altered precipitation and evaporation patterns (Fig. 1). Sea surface salinity of oceans is expected to change by as much as 1–1.5 psu over the next 100 yr, generally increasing in already saltier regions (e.g., Western Atlantic) and decreasing in fresher regions (e.g., Tropical Western Pacific; IPCC 2013). Freshwater discharge from increasingly intense storms and melting sea ice in the Arctic will further reduce surface salinity (IPCC 2013).

Alterations to predictable salinity cues may impact larval release timing and vertical migrations. Salinity fluctuations during storms induce barnacles to release larvae (Cawthorne and Davenport 1980, Gyory and Pineda 2011), and salinity changes over tidal cycles cue tidal rhythms of larval release and vertical migrations by estuarine crabs (Forward et al. 1986).

Though large changes in salinity often do little to slow larval development, except above or below critical salinity levels (Pechenik 1987), low salinity can induce developmental abnormalities (Holliday 1969, Pia et al. 2012) and alter the swimming behaviors of larvae (Vázquez and Young 1996, Arellano et al. 2012). In addition, salinity stress can induce mortality depending on parental conditions, stage of exposure, acclimation, genetics, and other factors (Holliday 1969, Pechenik 1987). Susceptibility to salinity stress can vary during larval development (Holliday 1969, Pechenik 1987, Richmond and Woodin 1996) and may not manifest until later stages

(Pechenik 1987). Low salinity guides crustacean postlarvae to settlement sites in estuaries (Boehlert and Mundy 1988), and thus, changes to salinity regimes may interfere with larvae using salinity as a cue.

*Hypoxia.*—Warmer water holds less DO; therefore, DO in the global oceans is predicted to decline 1–7% by 2100 (Fig. 1; Keeling et al. 2009). Increasing stratification between DO-rich surface waters and low DO subsurface waters prevents mixing, expanding the DO minimum zone (OMZ). An expanding OMZ is of particular concern for larvae in upwelling regions where upwelled waters are increasingly hypoxic or anoxic (Chan et al. 2008, Chavez and Messié 2009). Anthropogenic nutrient addition and warming also increase hypoxia by causing large phytoplankton blooms that subsequently decay (Altieri and Gedan 2015).

The effects of hypoxia on larvae appear to be environment-, taxon-, and life stage-specific. Hypoxia cues hatching in some species (Dimichele and Taylor 1980, Ehlinger and Tankersley 2003), so more frequent hypoxia could result in earlier hatching. Hypoxia can also reduce larval feeding (Widdows et al. 1989, Wang and Widdows 1991) and shift distributions of larvae avoiding hypoxic bottom water (Johnson-Colegrove et al. 2015). Hypoxia has only induced mortality of crab larvae among several taxa tested (Stalder and Marcus 1997, Eerkes-Medrano et al. 2013, Vanderplancke et al. 2015) though fish larval growth was depressed (Vanderplancke et al. 2015). Hypoxic conditions have delayed settlement of diverse taxa, potentially altering settlement patterns and habitat choice (Baker and Mann 1992, Powers et al. 2001, Lagos et al. 2015). Furthermore, low oxygen can reduce the visual sensitivity of larval cephalopods and crustaceans (McCormick et al. 2019), which could have severe consequences for their ability to feed, avoid predators, and detect settlement habitats.

*Ultraviolet radiation.*—The intensity of UVR penetrating the ocean is expected to shift with climate change, but the intensity and direction of this change differs geographically. Penetration of UVR through the atmosphere to reach the ocean surface depends on ozone, clouds, aerosols, and ice coverage, while penetration of UVR through ocean waters mainly depends on turbidity

(Fig. 1). The success of the Montreal Protocol in reducing ozone depletion is expected to reduce sea-level UVR worldwide, with the greatest reduction (40%) over Antarctica and lesser reductions over other regions (<10%; Bais et al. 2014), but projected greenhouse gas emissions will cause further ozone depletion in the tropics (Watanabe et al. 2011). Projected increases in cloud cover will decrease UVR at high latitudes in the Northern Hemisphere, but reductions in aerosols from improved air quality near populated areas will increase UVR by 10–20%, and even more in China (Bais et al. 2014). Finally, melting polar ice will dramatically increase UVR exposure in areas of the ocean that were once covered by a layer of ice (Bais et al. 2014). Overall, sea surface UVR is expected to increase globally, largely driven by increases expected in the tropics (Watanabe et al. 2011). Increased turbidity in regions with increasing storm intensity and freshwater discharge will locally reduce UVR penetration into the oceans (Fig. 1).

Many fishes, especially the larval stages of tropical species, rely on UV vision to detect prey (Job and Bellwood 2007), so localized increases in UVR may increase their feeding efficiency. On the other hand, high doses of UVR can induce eye and brain lesions, which may inhibit their ability to feed and to detect and avoid UVR (Hunter et al. 1981, Chiang et al. 2007). Larval development and growth generally slow upon exposure to UVR, and effects on embryos are stronger (Bancroft et al. 2007). Though a number of species can detect and avoid UVR by descending from surface waters (Pennington and Emlet 1986, Speekmann et al. 2000, Chiang et al. 2007), doing so will likely alter dispersal in vertically stratified currents.

Ultraviolet radiation can substantially increase larval mortality, often changing nonlinearly with life stage and maternal investment (Hunter et al. 1982, Gleason and Wellington 1995). Since UVR attenuates rapidly with depth, effects are expected to be strongest for larvae inhabiting surface waters, although these larvae may be the best protected from UVR damage. For example, many surface-inhabiting fish and crab larvae are heavily pigmented, which may protect them from UVR damage (Bashevkin et al. 2019, Hunter et al. 1982). Rising UVR may reduce available settlement sites since coral larvae preferentially

settle where UVR exposure is low (Gleason et al. 2006), and UVR compromises the effectiveness of biofilms in inducing settlement (Hung et al. 2005).

*Turbidity.*—Large rainfall events associated with increasing storm intensity will increase turbidity nearshore. Increasing turbidity can trigger release of larvae by adult barnacles (Gyory et al. 2013), which can cause a mismatch between ideal conditions for barnacle nauplii and the timing of their release. Studies have repeatedly shown that increased sedimentation causes increased larval mortality for a wide range of taxa (Davis 1960, Fichet et al. 1998, Phillips and Shima 2006) and interferes with growth through exposure to adsorbed toxic materials (Fichet et al. 1998). Higher turbidity can also clog the feeding structures of benthic, filter-feeding invertebrates (Lohrer et al. 2006) and filter-feeding holoplankton (permanent members of the plankton; Carrasco et al. 2013) and may similarly affect filter-feeding larvae (Davis 1960). However, sediments can act as a secondary source of food for filter-feeders, such as echinoderm larvae (plutei), if organic matter adheres to the sediment (Hart 1988, Phillips and Shima 2006). For fish larvae that use vision to capture prey, an increase in turbidity enhances contrast between prey and the darkened water increasing feeding rates of the larvae (Boehlert and Morgan 1985, Naas et al. 1992; but see Cobcroft et al. 2001). On the other hand, turbidity can also act as a refuge for larvae because visual predators, such as larval fish, can have trouble detecting or capturing prey in low visibility (Lehtiniemi et al. 2005). Lower visibility can be a double-edged sword, however, if larvae use visual cues to detect and escape their own predators (Lehtiniemi et al. 2005). The net effect of turbidity on predator–larvae interactions is likely determined by individual species sensitivity to loss of visual cues (Weissburg et al. 2014). Sedimentation also reduces settlement by coral and oyster larvae by inhibiting larval attachment to solid substrates (Fabricius 2005, Tamburri et al. 2008).

*Generalities.*—Some organismal factors will clearly be impacted in a consistent direction (e.g., reduced survival), while others are not so clear (e.g., PLD decreased by rising temperatures but increased by lowering pH; Table 1). Furthermore, the magnitudes and directions of impacts

will depend on the species and region of interest. To visualize these dependencies and conflicting effects, we developed 10 quantitative case studies (Fig. 3) of important or well-studied species from two regions (the Temperate East Pacific Ocean and Tropical Indian/Pacific Oceans). We calculated standardized impacts on various organismal factors of mean and extreme climate changes at year 2096. As expected, the directions and magnitudes of effects were highly variable and sometimes conflicting (Fig. 3). Methods are detailed in Appendix S1.

### Interactions and Indirect Effects

There have been a number of recent reviews covering the interactive effects of multiple stressors on marine organisms (Harley et al. 2006, Crain et al. 2008, Przeslawski et al. 2015, Ramajo et al. 2016, Chan et al. 2018). We focus on a few interactions and indirect biological impacts that may be especially important for larvae in a changing climate.

*Temperature and salinity.*—High temperature and low salinity can co-occur during periods of warm freshwater outflow (Riche et al. 2014). They tend to interact antagonistically such that higher temperature ameliorates the lethal effects of low salinity stress, possibly due to the faster growth rate shortening the time as vulnerable larvae (Przeslawski et al. 2015). However, sublethal impacts (abnormality, growth, development, metabolism, cellular processes) of temperature and salinity tend to interact in a simple additive fashion, though larvae of molluscs and echinoderms are much more strongly affected by combined temperature and salinity stress than resilient crustacean larvae (Przeslawski et al. 2015). More generally, exposure to stresses like low salinity is expected to narrow the thermal window of an organism by reducing performance, especially at extreme temperatures (Pörtner and Farrell 2008).

*Warming and OA.*—Warming and OA often act synergistically to reduce calcification and survival in a range of taxa, especially for early life history stages (Pörtner 2008, Harvey et al. 2013, Przeslawski et al. 2015, Gardner et al. 2018). Temperature may be the primary bottleneck for early larval stages, especially in regions that will warm most rapidly, whereas OA will likely have a greater effect on calcifying larval stages,

especially in rapidly acidifying high latitudes (Orr et al. 2005, Byrne 2011). Furthermore, the prevailing temperature may impact the relative strength of warming and pH changes on larvae. For example, warming-induced reductions in PLD will likely swamp pH-induced increases in PLD in cold water, resulting in a net decrease in PLD. However, the reverse will occur in warm water, where the effect of pH will swamp that of temperature, resulting in a net increase in PLD (Gaylord et al. 2015). In most areas of the world, warming and OA are expected to progress in concert. In contrast, changes in temperature and pH will likely be positively correlated in upwelling systems as increased intensity of coastal winds drives increases in upwelling strength and duration leading to reduced temperatures and reduced pH. This could lead to a net increase in PLD in eastern boundary currents.

*Hypoxia and OA.*—The intensification of low DO with high $pCO_2$ and low pH in coastal waters is rapidly emerging as a focal area for predicting the effects of marine climate change. Hypoxia largely has a negative, additive effect with OA on adult traits (Gobler and Baumann 2016). Few studies have been conducted on larvae, but one found no effect of combined OA and hypoxia on two species of mussels (Frieder et al. 2014), while another found additive negative effects on scallop growth and metamorphosis (Gobler et al. 2014).

*Food availability.*—The effects of climate change on other organisms that are trophically linked to marine larvae could have important cascading effects on larval survival. Climate change is expected to alter the timing and composition of phyto- and zooplankton communities (Tortell et al. 2002, Hays et al. 2005), as well as the nutritional content of phytoplankton (Rossoll et al. 2012, Leu et al. 2013, Wynn-Edwards et al. 2014). Crustacean and fish larvae are especially susceptible to starvation due to their large size, high metabolic rates, carnivorous diets, poor feeding ability at small sizes, and inability to intake dissolved organic matter as food (Olson and Olson 1989, Morgan 1995, Anger 2001, China and Holzman 2014). Moreover, shifts in the relative timing of phytoplankton blooms and larval release could result in a temporal mismatch that deprives larvae of quality food (Cushing 1990), slowing growth and increasing mortality from other stresses arising from climate change (Olson and Olson 1989, Edwards and Richardson 2004, Asch 2015).

*Predator abundance.*—Shifting predator assemblages may affect predation pressure on larvae. For example, warm, acidified waters may favor an increase in gelatinous zooplankters (Brodeur et al. 1999, Attrill et al. 2007, Richardson 2008) that prey heavily on larvae (Morgan 1995; Bashevkin and Morgan, *in press*). In addition, the timing of predator abundance, particularly relative to the timing of food availability, can have a large influence on larval mortality. Early food blooms paired with late predator blooms could lower mortality by speeding larval development so larvae settle before peak predation. Conversely, later food blooms paired with earlier predator booms may dramatically increase larval mortality (Nival et al. 1988).

## POPULATION AND COMMUNITY IMPACTS

### Connectivity and range expansions

Changes in larval dispersal due to climate change could have profound consequences for connectivity and species ranges. Local retention of larvae is likely common (Sponaugle et al. 2002, Morgan 2014) and genetic population connectivity among populations may be maintained by export of just a small number of larvae (Strathmann et al. 2002, Swearer et al. 2002, Burgess et al. 2016), rendering population connectivity susceptible to changes in larval duration, survival, and transport.

In comparisons among species, the link between PLD and dispersal distance is weak at best, likely due to differences among species in larval swimming behaviors and life history traits (Shanks et al. 2003, Shanks 2009). However, within a species with a given suite of life history traits and swimming behaviors, individual larvae that spend a longer time in the pelagic environment should disperse farther, simply because they are spending more time in flow (Siegel et al. 2003), resulting in greater population connectivity (Cowen et al. 2006). Furthermore, increased PLD may induce a mismatch between larval behaviors and oceanographic conditions as the timing of ontogenetic migrations shifts, interfering with the ability of larvae to exploit currents for local retention and pushing them further

from their release site. Thus, increases in PLD, such as those caused by hypoxia, reduced salinity, and low pH, may increase the spatial scale of connectivity, but the quality of settling larvae could be reduced after experiencing difficult environmental conditions during the pelagic phase. Similarly, reductions to PLD, such as those caused by increased seawater temperature, could decrease connectivity, especially between far-flung populations. Moreover, increased larval mortality will reduce the number of larvae available for long dispersal events, thus reducing connectivity.

Altered connectivity due to climate change could dramatically alter the capacity of populations to adapt as environmental conditions shift. Whether increased or decreased connectivity will be favorable depends on the existing connections between populations and current levels of genetic variation. In open, well-connected metapopulations like the red abalone *Haliotis rufescens* (Table 2, Fig. 4C, D), decreased connectivity may be favorable in increasing the likelihood of local adaptation to changing environmental mosaics if selection is strong (Carson et al. 2011, Sanford and Kelly 2011, Paterno et al. 2017, Stuckas et al. 2017). However, increased connectivity among previously disconnected populations may also be advantageous by introducing favorable alleles and thus the capacity for adaptation (Aitken and Whitlock 2013).

Increased dispersal distance driven by changing currents and local abiotic conditions could enable larvae to skirt previously unsurpassable biogeographic breaks. Greater dispersal distances could increase recruitment to sink populations, transforming them into larger populations that could become sources (if fitness is correlated with density, i.e., an Allee effect) and expand populations beyond the old range limit of the species. At the other extreme, reduced dispersal could create new biogeographic boundaries or lead to the extinction of sink populations at range edges. As climate change alters the properties of water masses, species limited in dispersal by larval physiological tolerances to environmental conditions may expand their ranges (e.g., green crab *Carcinus maenas*: Yamada et al. 2017; Table 2, Fig. 4A, B). In general, climate change is expected to induce poleward range shifts by increasing recruitment success beyond the poleward edges of species ranges while decreasing recruitment success at the equatorward limits as temperatures rise and species track climate envelopes (O'Connor et al. 2012, Poloczanska et al. 2013, but see Pinsky et al. 2013), aided by poleward current intensification (Wilson et al. 2016). We have already observed poleward range shifts in species distributions by a mean of 72.0 ± 13.5 km per decade (Poloczanska et al. 2013). For example, the East Australian Current has strengthened and expanded farther south since the 1940s (Ridgway 2007), and temperatures have increased enough since the late 1970s for the range of the sea urchin *Centrostephanus rodgersii* to expand hundreds of kilometers poleward due to successful recruitment of dispersing larvae (Ling et al. 2009).

*Recruitment*

Larval recruitment to the benthos is vital for replenishing populations. Recruitment requires that larvae develop and survive to find appropriate benthic habitat, settle, and metamorphose into their benthic form. Impacts of climate change at any of these steps could reduce recruitment. If adult populations are strongly affected by the abundance of larvae returning to benthic habitats, as opposed to post-settlement processes, variability in recruitment will play a strong role in species and community dynamics (Morgan 2001, Underwood and Keough 2001). Even populations that are not recruitment-limited are affected by the number of settling larvae and spatial and temporal variation in settlement (Menge 1991, 2000). Larval supply is an important bottom-up factor that affects population dynamics, interaction strengths, and the resilience of communities (Menge et al. 1997, Navarrete et al. 2005, Palardy and Witman 2014). Early observations of poor correlation between fish stock (population) size and subsequent recruitment (Hjort 1914, 1926) prompted a long-standing interest in recruitment variation in fisheries. Generally, alterations to larval supply of fisheries species, particularly recruitment-limited species, could have severe economic and ecological implications at both global (Ramesh et al. 2019) and regional scales (e.g., the Dungeness crab *Metacarcinus magister* Table 2, Fig. 4E, F). More detailed, regional-scale models of coastal oceanography in upwelling regions are an area
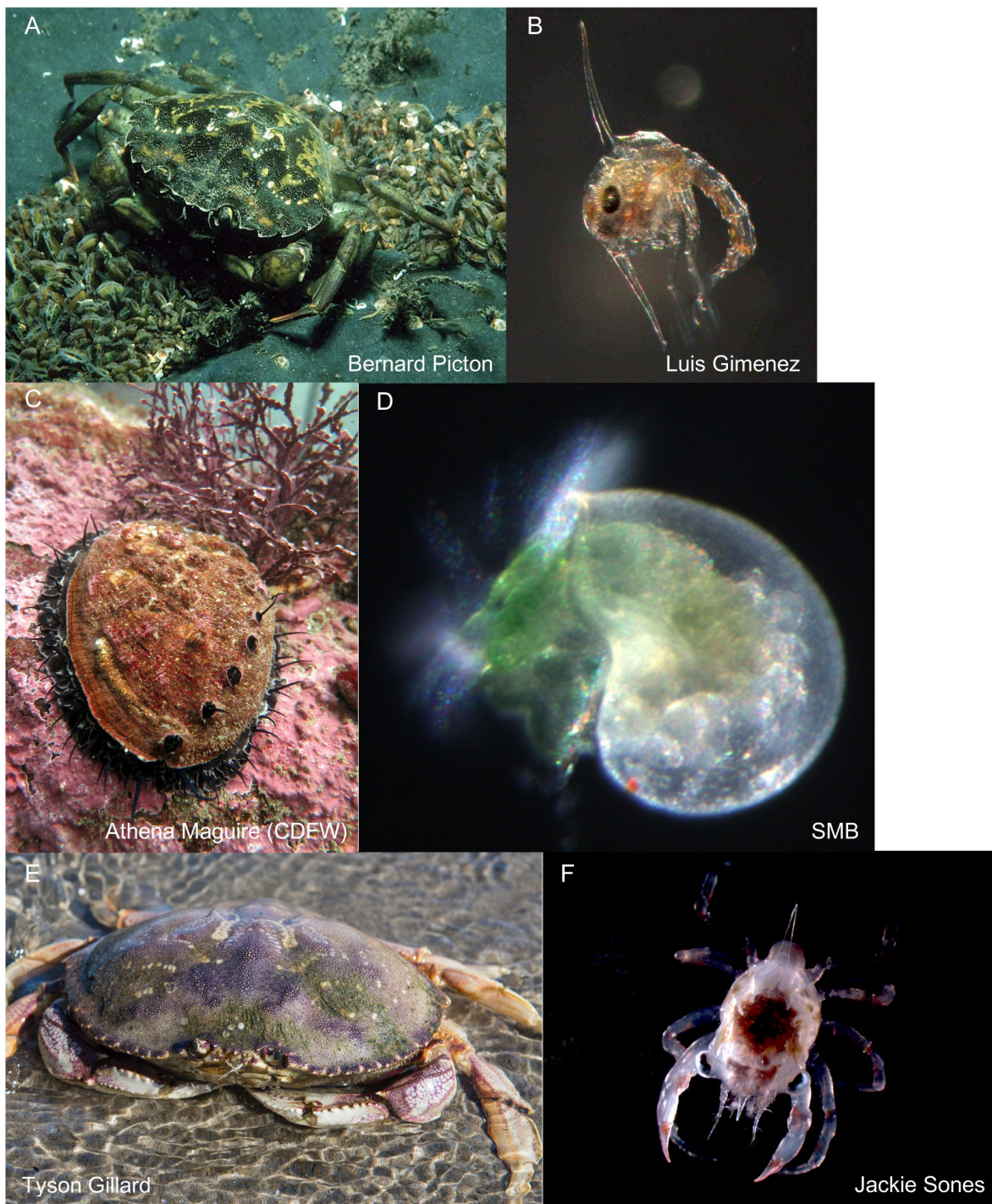
Fig. 4. Benthic adult and dispersing pelagic larval stages of three species of marine invertebrates. Each species is expected to have altered larval dispersal due to climate change with ecological or evolutionary implications (Table 2). (A) Adult green crab *Carcinus maenas* with permission from Bernard Picton, (B) *C. maenas* zoea larva with permission from Luis Gimenez, (C) adult red abalone *Haliotis rufescens* with permission from Athena Maguire (California Department of Fish and Wildlife), (D) *H. rufescens* veliger larva, (E) adult Dungeness crab *Metacarcinus magister* with permission from Tyson Gillard, and (F) *M. magister* megalopa larva with permission from Jackie Sones.

of active research (Bakun et al. 2015) and should provide more highly resolved predictions of climate change impacts on populations affected by recruitment variability.

## WINNERS AND LOSERS

As the climate changes, we expect that certain life history traits will better prepare larvae for successfully completing dispersal in a future ocean (Fig. 5). After settlement, these traits may confer different advantages/disadvantages or other traits may become more important, but here we focus solely on the susceptibility of larval dispersal to disruption from climate change.

Some traits lead to clear predictions on how they may affect the ability of species to disperse in a changing ocean. Larvae with external calcified structures will very likely suffer more extreme physical deformities than non-calcifying larvae or those with internally buffered calcium structures as pH declines, though increasing evidence points to maladaptive behavior in low pH conditions across a range of taxa which could impact dispersal (Espinel-Velasco et al. 2018). Species that release swimming larvae should better adapt to changes in current flow and stratification than free-spawning species that release passive gametes and embryos, particularly in upwelling regions where offshore and equatorward transport is expected to strengthen. Stronger swimmers may regulate depth and navigate onshore better than weak swimmers depending on the extent that declining pH interferes with the ability of larvae to effectively track cues. The onshore navigation capabilities of some species will probably help compensate for the impacts of climate change on larval transport, so species with stronger horizontal swimming abilities may be less affected by changes to their transport. Furthermore, species with specific settlement cues will likely be at a disadvantage as climate change alters cues and shifts benthic community compositions. Species with a wide range of possible settlement cues may be better buffered against the loss of one or more cues.

Other life history strategies, such as long or short PLD, do not necessarily lead to obvious advantages in a changing ocean. Larvae with a long PLD are exposed to ocean currents for a longer time, and as a result, they often express complex behaviors to exploit stratified currents and complete a species-specific dispersal trajectory. These larvae with a long PLD may thus be more sensitive to perturbations in those currents as their complex behaviors become mismatched and dispersal trajectory changes multiply over more time. Furthermore, species with a long PLD will be exposed to future stressors like OA and temperature for a longer duration, potentially increasing the effect on mortality. However, larvae with a long PLD also generally have a longer competency window (Wellington and Victor 1989), so they should have more opportunities to find a suitable habitat, which could mitigate some of these negative effects.

Whether a species has feeding or non-feeding larvae can also influence how it will fare under climate change. Shifts in food supply and the possibility of phenological mismatches place planktotrophic larvae at higher risk of starvation than lecithotrophic larvae, although lecithotrophic larvae may be at risk of starvation if climate change increases metabolic demands without concurrent increases in maternal investment. Shifts in food supply and distribution may even alter the transport of planktotrophic larvae because many larvae track prey through the water column (Metaxas and Young 1998, Sameoto and Metaxas 2008, Bashevkin et al. 2016). However, planktotrophic larvae often remain longer in the larval stage than lecithotrophs, thereby having more time and potentially greater success in locating and settling in favorable habitat.

Although larvae of some species are retained nearshore (e.g., pea crabs, Pinnotheroidea) for the duration of development, others migrate far offshore (e.g., cancrid crabs, Cancroidea) before returning to nearshore adult habitats (Morgan et al. 2009, 2018). Species with larvae that are retained nearshore may face higher mortality in a changing ocean since shallow nearshore waters are expected to change the fastest (IPCC 2013). Furthermore, the future adaptive benefits of retentive behaviors will decrease where transport trajectories for a given population track changing climate envelopes, allowing movement away from deteriorating conditions. Whether dispersal tracks (western boundary currents) or opposes (eastern boundary currents) changing climate envelopes is generally predictable from gyre
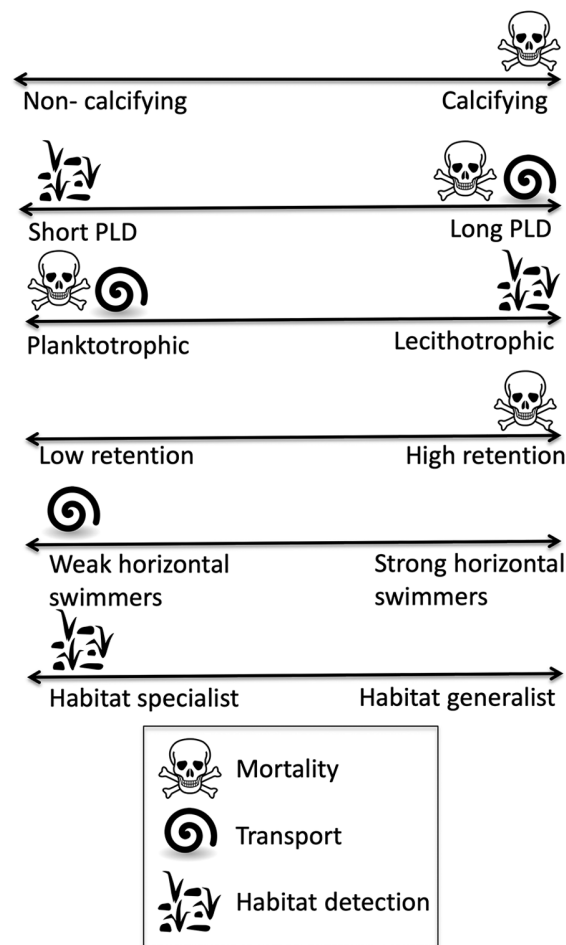
Fig. 5. Vulnerability of different life history traits to climate change impacts on larval mortality, transport, or habitat selection. Axes represent different larval life history traits (e.g., pelagic larval duration [PLD] or swimming ability). Symbols represent factors through which climate change affects larvae either by increasing mortality (skull and crossbones), altering transport patterns (spiral), or reducing their ability to detect suitable habitat within the larval competency window (rocks and plants). Symbols are placed along each axis to denote the larval life history trait that will be most vulnerable to the impacts of climate change. For example, calcifying larvae are more likely to suffer from mortality (skull/crossbones) than non-calcifying larvae. In addition, larvae with long PLD are more likely to be affected by mortality and transport due to climate change, whereas larvae with short PLD will be more affected by habitat availability. See *Winners and losers* for complete explanations of all symbol placements in this figure.

circulation, but impacts are likely to be more localized owing to complex nearshore flow dynamics, changes in pH and hypoxia, and the still poorly understood influence of larval behaviors on alongshore and cross-shore transport.

The variability and extremes of oceanographic conditions currently experienced by species may determine their capacity to acclimate, compensate, or adapt to future ocean changes (Somero 2010). Larvae that are previously adapted to higher variability in environmental conditions or exist in a state farther from their physiological limits may fare better in changing or more variable ocean conditions than species that can only acclimate or are adapted to a very narrow range of conditions. For example, we expect species that exist in highly variable pH and temperature oceanic environments, such as upwelling

systems, may fare better than those existing in a narrower range of oceanographic conditions. It is necessary to couple life history characteristics with the exposure, sensitivity, acclimation, and adaptation of larvae to elucidate the actual degree to which dispersal is vulnerable. It is important to note, however, that the variability or extremes experienced by adults may be unrelated to the conditions experienced by larvae, leading to radically different physiology and environmental tolerances. For example, some hydrothermal vent larvae cannot tolerate adult habitat temperatures and have non-overlapping temperature tolerance ranges with the adults (Pradillon et al. 2001).

## FUTURE DIRECTIONS

To more fully understand the consequences of climate change on marine larval dispersal, future research must include studies on larval behavior, life histories, and historical and fossil records, based in the field and laboratory, as well as models coupling oceanographic processes with larval behavior and physiology. Predictions about the consequences of climate change on larval dispersal will be equivocal until larval behavior is considered, and such predictions are currently only possible for the small minority of well-studied species and systems (Edmunds et al. 2018, but see Bode et al. 2019). A mechanistic understanding of how larvae with different behaviors interact with nearshore ocean processes should improve predictive models of dispersal under current and future conditions, though as with any model, predictions must be validated empirically (Bode et al. 2019, Swearer et al. 2019) prior to their use in a management or conservation context.

Our review highlights the importance of placing future studies in the context of different life history strategies, such as whether species are more or less vulnerable to a given stressor if they produce lecithotrophic or planktotrophic larvae, if the larvae exhibit a particular physiology, or if they occupy a habitat with higher natural variability. Incorporating these nuances will greatly improve the predictive accuracy and applicability of future studies on marine dispersal by placing them in the correct physiological and oceanographic context.

To better understand which life history characteristics are associated with species persistence or extinction during environmental change, we can apply comparative studies to historical or fossil records. These records can be used to assess the frequency of range shifts, speciation, and extinction and begin to associate these changes with life history characteristics and environmental drivers. Investigations of holoplankton (permanent members of the plankton) can also be informative for understanding selective pressures on temporarily planktonic larvae. For example, studies of the fossil record matched to past ocean pH have found that calcifying plankton did not exhibit higher extinction rates (Gibbs et al. 2006), suggesting that OA may not be as detrimental for calcifying larvae as we think. However, the resolution of the fossil record is poor and the speed of past climatic changes is not comparable to current anthropogenic change, so these results must be cautiously applied to predicting impacts of climate change today. Better-resolved historical collections in comparison with modern-day observations and long-term studies may provide more informative results.

To fully understand the impacts of climate change on the dispersal of larvae, future studies should couple physiological changes affecting larval development, swimming speed, or behavior with regional oceanographic transport models under specific climate change scenarios. This would provide specific tests of the impacts on dispersal described in this review, which should then be validated with in situ sampling across temporal or spatial gradients in environmental conditions. Furthermore, new genetic and genomic techniques can be used to evaluate the potential for evolutionary adaptation to changing conditions (Tasoff and Johnson 2019) or identify genes that determine vulnerability to environmental stressors (Benestan et al. 2016). Distribution estimates of these genes integrated into population simulations can quantify the likelihood of population persistence in future ocean conditions (Bay et al. 2017). Adding a biophysical dispersal model to these simulations will enable us to test the role of altered larval dispersal under future ocean conditions in determining whether local adaptation can keep pace with climate change.

## Conclusions

Changing ocean conditions (Fig. 1) will impact marine larval dispersal through effects on larval biology and oceanography (Table 1). While individual effects are complex and often in opposing directions, the key organismal and transport processes involved in dispersal are all interconnected such that they can be distilled and simplified through their net effects on mortality, habitat selection, or transport, which then determine dispersal (Fig. 2). Reduced dispersal distance may make local adaptation more likely in well-connected populations with high genetic variation while reduced dispersal success will lower recruitment with implications for many species including those comprising important fishery stocks. Increased dispersal may spur adaptation by increasing genetic diversity among previously disconnected populations as well as increasing the likelihood of range expansions (Table 2). The effects of climate change on marine dispersal will depend on local oceanography, life history, behavior, and physiology (Fig. 5). For a given taxon and region, the information in this review combined with local knowledge can produce powerful predictions of expected impacts on larval dispersal and their consequences for connectivity, range expansion, or recruitment (Table 2). Overall, we expect the dispersal of some life histories (planktotrophs, calcifiers, poor swimmers, habitat specialists) will be most likely to be affected by climate change. The adaptive value of retentive larval behaviors may decrease where transport trajectories follow changing climate envelopes and increase where transport trajectories drive larvae toward increasingly unsuitable conditions. Future studies should take a holistic view of dispersal incorporating biological and oceanographic impacts of climate change rather than solely focusing on oceanography or physiology. Insights from this synthesis should be helpful to terrestrial researchers tackling similar problems since the ecological and evolutionary consequences will be similar. Marine dispersal mechanisms are different than those on land due to the ubiquity of actively dispersing larval stages, but they are most similar to those in plants with wind or animal driven seed dispersal except that in these cases dispersal is driven either by fluid (air) circulation or behavior/physiology, not both. Our framework could be simplified and applied to these terrestrial systems.

## Acknowledgments

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