

# Reports

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## Currents connecting communities: nearshore community similarity and ocean circulation

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**Abstract.** Understanding the mechanisms that create spatial heterogeneity in species distributions is fundamental to ecology. For nearshore marine systems, most species have a pelagic larval stage where dispersal is strongly influenced by patterns of ocean circulation. Concomitantly, nearshore habitats and the local environment are also influenced by ocean circulation. Because of the shared dependence on the seascape, distinguishing the relative importance of the local environment from regional patterns of dispersal for community structure remains a challenge. Here, we quantify the “oceanographic distance” and “oceanographic asymmetry” between nearshore sites using ocean circulation modeling results. These novel metrics quantify spatial separation based on realistic patterns of ocean circulation, and we explore their explanatory power for intertidal and subtidal community similarity in the Southern California Bight. We find that these metrics show significant correspondence with patterns of community similarity and that their combined explanatory power exceeds that of the thermal structure of the domain. Our approach identifies the unique influence of ocean circulation on community structure and provides evidence for oceanographically mediated dispersal limitation in nearshore marine communities.

**Key words:** larval dispersal; marine biodiversity; marine community structure; ocean circulation.

### INTRODUCTION

The decay of similarity with geographic distance has long been identified (Tobler 1970), yet reasons why this relationship exists in ecological communities are still debated (Menge et al. 1997, Nekola and White 1999). Spatial patterns in biodiversity and community similarity reflect the influence of multiple processes, broadly categorized as either niche based, through species sorting and the effect of environmental gradients on individual species demography (Armstrong and McGehee 1980, Leibold 1995), or by neutral processes, namely, dispersal limitation (Hubbell 2001). In most ecological systems, because there is often strong correspondence between patterns of dispersal and

environmental variables, quantifying the relative contribution of niche and neutral processes in determining community composition remains a challenge (Gilbert and Lechowicz 2004). Our aim is to identify the unique influence of dispersal on spatial patterns of community similarity for nearshore marine species in the Southern California Bight (SCB). In order to address this challenge, we have developed novel metrics of dispersal using ocean circulation models.

In benthic marine systems, the role of dispersal in determining community dynamics, population demography and genetic structure has had a long and rich history (Hjort 1914, Gaines and Roughgarden 1985, Alberto et al. 2010, White et al. 2010). As adults, many nearshore marine species are sedentary, with limited home ranges (e.g., <10 km). It is primarily during their larval stage that they disperse further, potentially hundreds of kilometers (Kinlan and Gaines 2003,

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Watson et al. 2010). During this stage, ocean currents play a vital role creating, at the same time, barriers to dispersal and highly connected regions (Cowen et al. 2006). It is unknown whether this seascape structure exerts control on community similarity through dispersal limitation. Recently, Lagrangian particle simulations have been used to capture the spatial complexity of oceanographically mediated dispersal and have provided insight into the potential scales of population connectivity (e.g., Cowen et al. 2006, Mitarai et al. 2009) and in understanding the drivers of genetic structure (e.g., Galindo et al. 2006, Kool et al. 2010, Selkoe et al. 2010, White et al. 2010). Here, we use Lagrangian particle simulations to investigate the influence of ocean circulation on the community similarity of nearshore marine species in the SCB.

The SCB is a region on the west coast of North America that stretches from Point Conception to the U.S.-Mexican border (Fig. 1a). It is characterized by the meeting of two major water masses at Point Conception: the relatively cool, offshore, equatorward flowing California Current and the warmer, near coastal, poleward-flowing Southern California Counter Current (Fig. 1a). Spatial patterns in intertidal community similarity have been shown to correspond strongly with the thermal structure of the SCB (Blanchette et al. 2008), suggesting that species are adapted to this thermal gradient. However, environmental variables such as temperature will correspond with patterns of oceanographically mediated dispersal because both quantities are strongly influenced by ocean currents. Hence, it remains an open question whether the thermal structure of the SCB is the primary force shaping community structure in the SCB. The goal of this work is to partition the statistical contribution of oceanographically mediated dispersal from that of the thermal structure of the SCB. In order to do so, we use simulations of Lagrangian water mass trajectories and develop novel metrics of dispersal based on the complex ocean circulation of the SCB.

#### METHODS

We analyzed spatial patterns in marine community composition (i.e., species identity and abundance) from two empirical sources: in 2004, subtidal rocky reef communities were surveyed using underwater visual census as part of the Cooperative Research Assessment of Nearshore Ecosystems Program (CRANE 2004), and intertidal communities were surveyed as part of the Community Biodiversity Survey conducted by the Partnership for the Interdisciplinary Study of Coastal Oceans (PISCO), an ongoing project that started in 2001 (Blanchette et al. 2008). Subtidal surveys were conducted with trained divers counting all fish species observed and key invertebrate species on replicate  $30 \times 2$  m transects stratified by depth. Percent cover of intertidal taxa was calculated from point contact data collected on a rectangular grid at each site measuring 30 meters on

the landward and seaward sides; the length of the two remaining sides was determined by the slope of the intertidal gradient. At least 11 000 points were sampled at each intertidal site (Blanchette et al. 2008). Fifty-nine subtidal rocky reef sites and 39 intertidal sites in the SCB were sampled, spanning the mainland and the Channel Islands (Fig. 1a). We analyzed a total of 204 species (98 subtidal and 106 intertidal species, see Appendix A for details). Spatial distributions of species richness can be found in Appendix B. The data were square-root transformed to reduce the influence of highly abundant species and, at each site, normalized to the interval [0,1]. A community similarity matrix was then calculated using the Bray-Curtis similarity coefficient. We tested the influence of different transformations and community similarity metrics, for example the presence/absence Jaccard coefficient, on our results and found them to be robust to these choices.

Lagrangian particle simulations were used to quantify the movement of water parcels, between nearshore regions. More than 50 million passive Lagrangian particle trajectories were released from a total of 135 circular patches (5 km in radius), distributed uniformly throughout the nearshore of the SCB, over the period 1 January 1996–31 December 2002 (see Mitarai et al. 2009 for more information on the Lagrangian particle simulations). The size of these patches reflects resolution limitations in the Lagrangian particle simulations. Lagrangian particles advect passively with velocity fields produced from a Regional Oceanic Modeling System (ROMS) solution to the SCB (Dong et al. 2009, Mitarai et al. 2009; see Fig. 1b). This solution is three dimensional with a horizontal spatial resolution of 1 km and 40 vertical levels, with all eight islands in the Southern California Bight are resolved. The ROMS model solutions reproduce specific oceanographic features such as persistent eddying motions and upwelling events, as well as the general circulation of the SCB (Dong et al. 2009) and near-surface Lagrangian particle dispersion (Ohlmann and Mitarai 2010).

Lagrangian particle transit times, between all pairs of nearshore sites, provide a quantification of spatial separation based on ocean currents (Mitarai et al. 2009; Fig. 1c) and describe patterns of passive larval dispersal. An important property of Lagrangian particle transit times is their inherent asymmetry, that is, Lagrangian particles traveling from patch A to B may have a different mean transit time than those particles traveling from B to A. Thus the first metric used here, termed the *oceanographic distance*, is the average of the two-way Lagrangian transit times. The second metric is termed the *oceanographic asymmetry* and is defined as the absolute difference in the two-way Lagrangian particle transit times. Both oceanographic distances and asymmetries are measured in units of time (days).

The thermal environment of the empirical sampling sites was assessed using monthly sea surface temperatures from the Pathfinder 5 Advanced Very-High

Resolution Radiometer (Kahru and Mitchell 2002). Data at a spatial resolution of 4 km was averaged over the period 1997–2008. Spatially, values were then smoothed using a two-dimensional, 5 km radius, Gaussian filter. These values were then linearly interpolated to the subtidal and intertidal sampling sites. Smoothing and interpolation created a better representation of the local sea surface temperatures than the empirical (community) sampling sites was then defined as the difference in SST ( $\Delta$ SST). Unlike Lagrangian transit times,  $\Delta$ SST is a symmetric quantity.

Univariate and multivariate linear models of community similarity were made using oceanographic distance, asymmetry and  $\Delta$ SST as independent variables. The Mantel correlation statistic ( $r$ ) and its permutation test of significance ( $P$  value) were used to describe univariate relationships. In the multivariate case, multiple linear regression on distance matrices was used to explore the influence of each independent variable (Legendre and Legendre 1998). Further, multivariate models were created for different regions of the SCB: a full model (using all sampling sites) and a regional model (comparing island with mainland sites only). Standard regression coefficients and semi-partial correlation coefficients (Legendre and Legendre 1998) were used to describe the multivariate models. Standard regression coefficients are produced using the z-score of the independent variables, which controls for differing units among terms and allows for direct comparisons of their influence; larger standard regression coefficients identify those independent variables with more influence. Confidence intervals on these values were estimated with a bootstrap procedure. Semi-partial correlation coefficients were used to quantify the relative contribution of each independent variable in a given model. These are determined as the reduction in  $R^2$  when a given independent variable is left out of a multivariate model. Values are reported as fractions of the original  $R^2$ . For all models, the key assumptions of linear regression were met: the distribution of community similarities was approximately normal (assessed with quantile–quantile plots), community similarity and all independent variables correspond linearly and collinearity among independent variables, quantified using the variance inflation factor, was negligible (all variance inflation factors were found to be less than five).

## RESULTS

The univariate analysis revealed a significant, negative, linear relationship between community similarity and  $\Delta$ SST for both the subtidal and intertidal communities ( $r = -0.59$  and  $-0.25$ ,  $P < 0.01$ , Fig. 2a and b respectively). For both, variability in community similarity is largest at small mean differences in SST. This could simply be a result of fewer data points at greater SST differences or it may indicate the spatial scales over which  $\Delta$ SST has explanatory power. For instance,  $\Delta$ SST

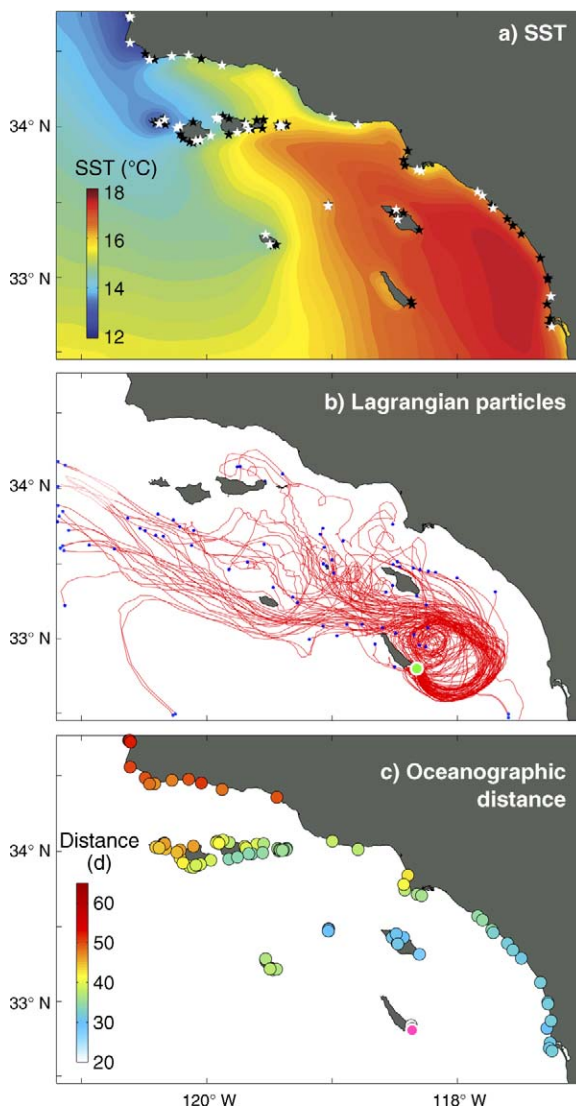


FIG. 1. (a) The Southern California Bight with average sea surface temperature (SST, for the period 1997–2008). Empirical intertidal (white stars) and subtidal (black stars) sampling locations are shown. (b) Example 30-day simulated Lagrangian particle trajectories. Particles were released within the green circle on 1 September 1997. Their locations 30 days after passive advection by ocean currents are identified by blue dots. (c) Example oceanographic distances (the number of days, on average, for a Lagrangian particle to travel from the pink site to all others).

can explain differences in species composition at the extremes of the SCB, the very warm ( $\sim 17^{\circ}\text{C}$ ) compared to the very cold ( $\sim 12^{\circ}\text{C}$ , Fig. 1a). However, in the center of the SCB, where the temperature gradient is less steep, there is less significance to  $\Delta$ SST's explanatory power.

Oceanographic distance shows a stronger, more significant, negative relationship with subtidal and intertidal community similarity ( $r = -0.73$  and  $-0.38$ , both  $P < 0.01$ , Fig. 2c and d respectively). This indicates that those local communities that are far apart, based on

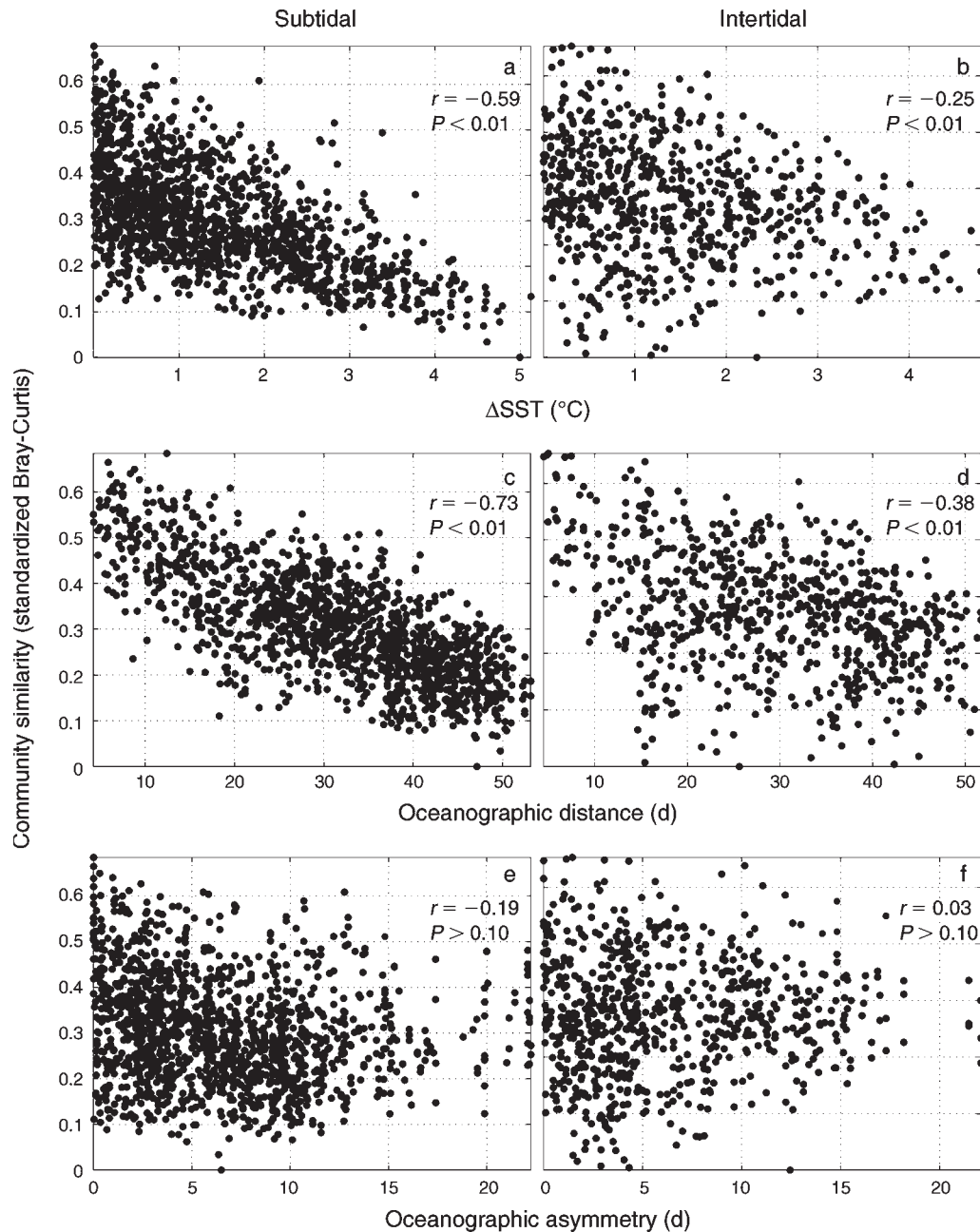


FIG. 2. Univariate comparison of community similarity with change in sea surface temperature ( $\Delta$ SST), oceanographic distance, and asymmetry for the (a, c, e) subtidal and (b, d, f) intertidal sites. Mantel correlation ( $r$ ) and  $P$  values are shown.

ocean circulation, are less similar than those closer together. Further, in contrast to  $\Delta$ SST, the variability in the relationship between community structure and oceanographic distance is homogenous throughout the domain. The significance and strength of the relationship indicate that oceanographic distance is a better predictor of community similarity than  $\Delta$ SST. Oceanographic asymmetry was found to have a negative relationship with subtidal community similarity ( $r = -0.19$ ,  $P < 0.01$ , Fig. 2e). Asymmetry did not produce a

significant relationship with intertidal community similarity ( $r = 0.03$ ,  $P > 0.10$ , Fig. 2f) and hence, from a univariate analysis, it is difficult to draw any conclusions as to the influence of asymmetry on community similarity.

Between all sampling sites (the full model), multivariate linear models using oceanographic distance, asymmetry and  $\Delta$ SST as independent variables explained 58% ( $P < 0.01$ ) and 18% ( $P < 0.01$ ) of the variance in subtidal and intertidal community structure (Figs. 3a

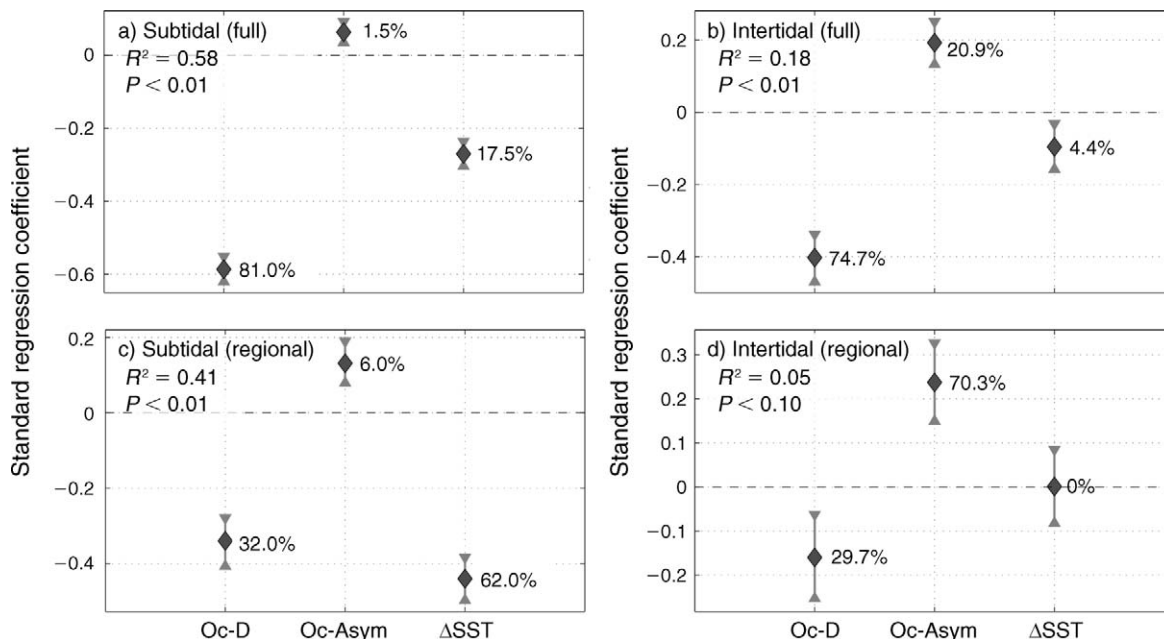


FIG. 3. Standardized regression (diamonds) and semi-partial correlation coefficients (percentages) for the multiple linear regression models. Independent variables are on the  $x$ -axis: oceanographic distance (Oc-D), oceanographic asymmetry (Oc-Asym), and the difference in sea-surface temperature ( $\Delta$ SST). Error bars describe the 95% confidence interval for the regression coefficients. (a, b) Full models, using all sampling sites for the (a) subtidal and (b) intertidal. (c, d) Regional models comparing community similarity between only islands and mainland sites for the (c) subtidal and (d) intertidal communities.

and b), respectively. For both communities, oceanographic distance was most influential with the largest standard regression coefficient and semi-partial correlation coefficient (81.0% and 74.7%).  $\Delta$ SST and asymmetry swap importance between the subtidal and intertidal communities with  $\Delta$ SST being more influential on subtidal community similarity and less so for intertidal community similarity. For the subtidal community,  $\Delta$ SST then has the second largest semi-partial coefficient (17.5%) and oceanographic asymmetry has the smallest (1.5%), suggesting that asymmetry has little influence in this model. In contrast, asymmetry has more unique explanatory power than  $\Delta$ SST for the intertidal community (20.9% compared to 4.4%, respectively).

We found notable differences between the subtidal and intertidal groups when comparing only pairs of sites between the mainland and the islands (the regional model, Figs. 3c and d, respectively). In both cases the explanatory power ( $R^2$ ) of the multivariate models decrease, from 0.58 to 0.41 in the subtidal community model and from 0.18 to 0.05 in the intertidal community. In particular, the intertidal model is not as significant ( $P < 0.1$ ). For the subtidal community,  $\Delta$ SST now has the largest influence with the largest standard regression coefficient and semi-partial correlation coefficient (62.0%, Fig. 3c). Relative to full model, the influence of oceanographic asymmetry increased (from 1.5% to 6.0%) and the oceanographic distance dropped (from 81.0% to 32.0%). For the intertidal community, asymmetry has the largest standard regres-

sion coefficient (70.3%). The influence of oceanographic distance decreased from 74.7% in the full model to 29.7% in the regional model. Interestingly,  $\Delta$ SST's contribution to the regional model is zero.

#### DISCUSSION

Here, we present evidence for the influence of oceanographically mediated dispersal on spatial patterns of nearshore marine species community similarity. We developed two metrics of dispersal, oceanographic distance and asymmetry, using high-resolution ocean circulation simulation results. Both metrics describe spatial separation between nearshore locations based on the complex patterns of ocean circulation of the SCB. Oceanographic distance was defined as the mean of the two-way Lagrangian particle transit times and asymmetry as their absolute difference. In the multivariate models, oceanographic distances better explained community similarity than the thermal structure of the SCB, and oceanographic asymmetry, a quantity unique to ocean dispersal, was found to be a statistically significant predictor variable. In contrast, a difference in any environmental variable, such as SST, is intrinsically symmetric. Therefore, the statistical significance of oceanographic asymmetry provides direct evidence for the influence of oceanographically mediated dispersal on patterns of community similarity in the SCB.

The explanatory power of the multivariate models is a result of the interaction between oceanographic distances and asymmetries; respectively, oceanographic dis-

tances and asymmetries were negatively and positively associated with community similarity. For example, take two pairs of sites [A, B] and [C, D] and assume that the oceanographic distance, the average of the two-way Lagrangian transit times, is 20 days for both. Now consider that the Lagrangian transit times for the [A, B] pair are 20 days each way, but between [C and D] the two-way times are different, say 30 and 10 days. In the case of the [C, D] pair the minimum oceanographic distance is 10 days. This lower bound to the oceanographic distance, captured by our metric of oceanographic asymmetry, results in greater ocean connectivity and hence community similarity. Essentially, larger values of asymmetry result in a smaller minimum oceanographic distance. Note that using the minimum and maximum oceanographic distance in place of the mean created essentially the same result. Oceanographically, the weak explanatory power of oceanographic asymmetry, relative to oceanographic distance, indicates that dispersal between regions is dominated by bidirectional mesoscale eddy dynamics rather than unidirectional persistent currents (Siegel et al. 2008). These results are complimented by metapopulation theory (e.g., Kawecki and Holt 2002, Vuilleumier and Posingham 2006) and population genetic structure (e.g., Vuilleumier and Fontanillas 2007), where asymmetric dispersal has been found to play an important role.

Our analysis assumes an implicit relationship between ocean circulation and patterns of larval dispersal. This assumption could be inaccurate as many marine species' larvae are thought to be able to influence dispersal patterns through vertical behavior or late-larval period active swimming (e.g., Leis 2007, Shanks 2009). This larval behavior could have a large effect on dispersal patterns. However, although our metrics of oceanographic distance and asymmetry were derived from passive Lagrangian particle simulations, it is likely that they describe long-term patterns of dispersal in the SCB (Mitarai et al. 2009). Further, other than patterns of ocean circulation and dispersal, there are numerous physical and demographic factors that alter community similarity, for example wave exposure, air temperature (especially for intertidal species), larval mortality in the water column, settlement behavior and post-settlement processes. Thus, we may not expect these two quantities to be closely linked. Indeed, the low explanatory power of the intertidal multivariate models reveals that intertidal community similarity will be predominantly shaped by factors not included in this analysis. However, our key finding is not the absolute explanatory power of the multivariate models, rather it is the significance of the independent variables; the existence of a statistically significant relationship between our metrics of dispersal, oceanographic distance and asymmetry, and community similarity indicates that oceanographically mediated dispersal is important to spatial patterns of community similarity.

We found that subtidal community similarity was better explained by oceanographic distance and asymmetry, relative to their predictions of intertidal community similarity. There are several potential reasons for this. First, although our Lagrangian particle simulations accurately capture regional patterns of ocean circulation (Mitarai et al. 2009), surf-zone currents are not represented by the 1-km ROMS solutions. Hence, patterns of intertidal larval dispersal may not be well described by our calculations of oceanographic distance and asymmetry. Indeed, surf-zone hydrodynamics and their effect on dispersal is an area of active debate; surf-zone currents could act to retain dispersing larvae and limit long distance dispersal (Shanks 2009). Second, in our data sets there are many more subtidal species, for example fish and invertebrates, which have long pelagic larval durations and the potential for long distance dispersal. Oceanographic distance and asymmetry metrics describe patterns of dispersal on scales greater than 1 km, rather than dispersal over short distances (i.e., <1 km), and therefore are expected to show a stronger relationship with the subtidal species examined.

Neutral theory suggests that spatial autocorrelation in dispersal will create a decline in compositional similarity between communities as the distance between sites increases (Hubbell 2001, Gilbert and Lechowicz 2004). It is important then that the appropriate spatial basis, by which 'distance' is measured, be identified. The predictive power of our multivariate models decreases only slightly when geographic distance is used in the place of oceanographic distance and asymmetry (subtidal and intertidal  $R^2$  values drop to 0.54 and 0.15 from 0.58 and 0.18, respectively). This reveals that if prediction is the goal, then it is reasonable to use geographic distance as a proxy for more process based measures of larval dispersal such as oceanographic distance and asymmetry. However, patterns of larval dispersal, at the temporal and spatial scales of this investigation, do not necessarily correspond with geographic distance. This is revealed in the variance of the relationships between geographic distance and oceanographic distance and with oceanographic asymmetry (Appendix C: Fig C1a and C1b, respectively, note the regional differences identified by colors). Further, asymmetry is not captured by geographic distance and hence it cannot be used to quantify a critical aspect of dispersal in the ocean.

Spatial patterns in biodiversity and community similarity are inherently dynamic. There is significant evidence suggesting that key oceanographic phenomena, such as El Niño events, are vital to larval recruitment and demographic processes of nearshore marine species in the SCB (Cowen 1985, Selkoe et al. 2007). However, most analyses of community similarity are confined to static descriptors of spatial separation (i.e., geographic distance) and hence do not account for such dynamism. In contrast, oceanographic distances and asymmetries are derived from multiyear simulations of ocean

circulation patterns and hence quantify spatial separation as a dynamic property. In the SCB, there is significant interannual and seasonal variation in patterns of ocean circulation (Dong et al. 2009, Mitarai et al. 2009, Watson et al. 2010) and these are reflected in our estimates of oceanographic distances and asymmetries. For example, some nearshore sites are effectively “closer” together during El Niño conditions than during La Niña conditions (Appendix D). Given the results of this paper, it is expected that such changes in ‘distance’ will result in corresponding changes in community similarity for these years.

Understanding the processes that drive spatial patterns in community similarity is crucial to spatial fisheries management and conservation. The knowledge generated from quantitative investigations secure adequate representation of biodiversity in, for instance, marine protected areas (Lubchenco et al. 2003). For example in the SCB, knowledge of spatial patterns of community structure has already proven informative to spatial fisheries management (California Department of Fish and Game 2008). Further, making use of real-time simulation data products will greatly improve our ability to account for changes in patterns of community similarity driven by climate change. Ultimately, incorporating modeled oceanographic products, like those used here, will improve decision-making processes and our governance of nearshore living resources.

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#### APPENDIX A

Intertidal and subtidal species lists (*Ecological Archives* E092-098-A1).

#### APPENDIX B

Spatial patterns in species richness (*Ecological Archives* E092-098-A2).

#### APPENDIX C

Comparisons with geographic distance (*Ecological Archives* E092-098-A3).

#### APPENDIX D

Temporal changes in oceanographic distance (*Ecological Archives* E092-098-A4).