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Inverse approach to estimating larval dispersal reveals limited population connectivity along 700 km of wave-swept open coast

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Demographic connectivity is fundamental to the persistence and resilience of metapopulations, but our understanding of the link between reproduction and recruitment is notoriously poor in open-coast marine populations. We provide the first evidence of high local retention and limited connectivity among populations spanning 700 km along an open coast in an upwelling system. Using extensive field measurements of fecundity, population size and settlement in concert with a Bayesian inverse modelling approach, we estimated that, on average, *Petrolisthes cinctipes* larvae disperse only 6.9 km (± 25.0 km s.d.) from natal populations, despite spending approximately six weeks in an open-coast system that was once assumed to be broadly dispersive. This estimate differed substantially from our prior dispersal estimate (153.9 km) based on currents and larval duration and behaviour, revealing the importance of employing demographic data in larval dispersal estimates. Based on this estimate, we predict that demographic connectivity occurs predominantly among neighbouring populations less than 30 km apart. Comprehensive studies of larval production, settlement and connectivity are needed to advance an understanding of the ecology and evolution of life in the sea as well as to conserve ecosystems. Our novel approach provides a tractable framework for addressing these questions for species occurring in discrete coastal populations.

1. Introduction

A paradigm shift is under way in marine ecology. A long-standing assumption has been that minute, weakly swimming larvae of most nearshore species are transported far from natal populations by ocean currents, suffering high mortality along the way [1,2]. Consequently, recruitment (the addition of individuals to a population) was assumed to be decoupled from local production and populations were assumed to be demographically open [3–5]. A long history of notoriously poor stock–recruitment relationships for ecologically and commercially important species has supported this view [6,7]. However, the recent advent of powerful new techniques, such as elemental fingerprinting and parentage analysis, is overcoming the challenge of determining natal origins of larvae, revealing substantially less dispersal and the possible return of more larvae to natal populations than was widely expected [8–12].

A focus of recent studies has been estimating self-recruitment, the number of larvae returning to a particular natal population relative to the number of

recruits arriving from all sources. However, self-recruitment is essentially a measure of isolation and is of limited relevance in understanding marine population dynamics [13]. Fully understanding connectivity among populations (and self-replenishment of any individual population) requires estimating both larval production and the probability of dispersal from patch to patch [13]. Measuring both quantities can be logistically challenging, but it is essential for understanding metapopulation dynamics and effective management and conservation of resources in the sea [13,14].

In the absence of larval production data, larval connectivity patterns have been estimated from surface circulation data, settlement patterns and chemical or genetic signatures in larvae, with the usual assumption that larval production is equal in all habitat patches [13–16]. However, larval production can vary considerably among populations, potentially affecting metapopulation dynamics [17,18]. Some investigators have addressed spatial variation in larval production by using population or habitat size as a proxy [19–21], though one study revealed that population size was not a good proxy [18]. Additionally, most empirical studies of larval dispersal and connectivity have been conducted at small spatial scales (several to tens of kilometres) in neighbouring insular or discrete systems, such as coral reefs, estuaries and bays [11,13]. Consequently, we know little about marine population connectivity at large spatial scales and in other potentially more connected marine environments.

To quantify connectivity over large scales, one must assess heterogeneity in both larval production and settlement over space. We quantified larval production and settlement in a metapopulation that spanned 700 km of open coast in central and northern California, where coastal oceanography is characterized by seasonal upwelling and strong, persistent advection [22]. Larvae and eggs in this region have long been considered susceptible to offshore and alongshore transport, limiting the number of recruits returning to coastal communities [4,23]. The ability of larvae to regulate transport has been widely underestimated in this region of strong current flow and it is now evident that larvae regulate depth in stratified currents, thereby controlling rates and directions of cross-shore transport [24–28]. Larvae of most nearshore invertebrates complete development in a coastal boundary layer of slower flow close to shore (less than 6 km) by either remaining beneath faster-moving surface currents or ascending only at night (diel vertical migration) after winds have subsided and currents have slowed [26,27,29–32]. These behaviours reduce alongshore transport and population connectivity [24,33]. Therefore, we expected to find more limited connectivity than one would predict from passive dispersal alone.

We chose one of the species in this region whose larvae develop in the nearshore zone, the porcelain crab *Petrolisthes cinctipes*, to determine the degree of connectivity between larval production and settlement across discrete subpopulations within the coastal metapopulation. Adult *P. cinctipes* are planktivorous and live in high densities in the mid-intertidal zone of discrete cobble fields and mussel beds. Females brood clutches of embryos that hatch during the upwelling season (April–July). Larvae then spend approximately 4–6 weeks in the water column, where they complete their development less than 6 km from shore [29,34]. Larvae settle gregariously in response to chemical cues emitted by adults, which is typical of many sedentary marine invertebrates [35,36].

We quantified larval production and larval settlement at 11 subpopulations of *P. cinctipes*, and just larval production at an additional 33 of the largest subpopulations across the study region. We used these data to estimate a one-dimensional dispersal kernel, a simple representation of larval settlement along a linear coastline. The kernel is a probability density function that describes the probability of dispersal from a natal site to any other location along the coast [33,37–39]. The parameters of a dispersal kernel (mean and standard deviation of dispersal distance) could be estimated directly from observing the movement and settlement of propagules in the coastal ocean, either real or simulated via Lagrangian circulation models (e.g. [38,39]). Alternatively, when it is not possible to observe propagule movement directly or when uncertainty about larval behaviour makes Lagrangian simulations unreliable, the kernel can be inferred indirectly from the spatial patterns of larval production and settlement. This is called ‘solving the inverse problem’ when applied to dispersing terrestrial plant seeds [40,41]. We developed a prior estimate for the larval dispersal kernel based on measured current velocities and previously documented larval behaviour and duration. Using a Bayesian modelling approach, we then updated the prior using the empirically determined production and settlement estimates for all 44 populations in addition to a fitted larval mortality rate to obtain a posterior estimate of the kernel. The resulting posterior estimate of the dispersal kernel provides a description of metapopulation connectivity in this system that accounts for spatial heterogeneity in larval production along the coast.

2. Material and methods

(a) Sampling

We surveyed 28 populations of *P. cinctipes* inhabiting cobble fields and 16 populations inhabiting mussel beds between the species’s southern range limit in central California and the California–Oregon border (electronic supplementary material, table S1). These sites represent all of the cobble fields and mussel beds we could find through reviewing the literature, assessing sites included in coast-wide monitoring programmes of rocky shore communities, searching aerial imagery of the coastlines through Google Earth (Google, Inc., Mountain View, California) and visiting accessible portions of the coastline. At each site, we attempted to estimate total larval production, and at a subset of sites, we estimated larval settlement. These data were used to estimate the empirical dispersal kernel using the inverse method. We first describe the field sampling used to estimate production and settlement.

To estimate larval production, we estimated total habitat area, population density and *per capita* fecundity in each population, then multiplied those three quantities to obtain overall larval production. However, sampling of these quantities differed among populations due to logistical constraints (electronic supplementary material, table S2). For the 28 populations in cobble fields, all sampling occurred between 2008 and 2011. For 21 of these populations, we directly measured habitat size and we assigned the remaining seven to qualitative size categories. We estimated population density directly using quadrat sampling at 11 focal sites, sampling large cobbles at 14 of the sites, and we used the mean density at these 25 sites as a proxy for the remaining three sites. For the 11 focal cobble sites where we measured population density in quadrats, we also determined the sex ratio and the number of embryos

produced per female (fecundity; see the next section for details on fecundity calculations). The mean of these fecundity estimates was used as a proxy value for the other sites. Approximately six weeks after sampling habitat, population density and fecundity, we counted the number of settlers—colourless post-larvae and pigmented first instars [42]—in 10 randomly placed quadrats (0.25 m²) at the 11 focal sites.

We sampled the 16 populations of *P. cinctipes* in mussel beds in 2014. Although sampling these populations in a different year than the cobble field populations was not ideal, surveys of central and northern California mussel beds across 2 decades revealed that the cover, depth and biomass of these mussel beds did not change [43], and we expect that the adult population of this fairly long-lived crab species—at least 8 years in the laboratory [44]—is fairly stable. We estimated habitat size, population density and *per capita* fecundity in these populations using methods similar to those used in cobble fields; the means of direct field estimates from two of the populations were used as proxies for the remaining 14 populations. Settlement was not quantified in mussel beds. The details of all field sampling and estimation are given in the electronic supplementary information.

(b) Fecundity estimation

To estimate larval production per square metre in each population, we used linear regression to determine the relationship between carapace width and number of brooded embryos for female crabs in 10 of the 11 focal cobble habitat populations for which these data were collected (electronic supplementary material, figure S1), based on an earlier finding that *P. cinctipes* carapace width and clutch size are correlated [45]. We then calculated larval production per square metre by multiplying the estimated number of embryos per brood for each of four adult size classes (carapace width 5–8 mm, 8–11 mm, 11–14 mm and more than 14 mm) by the average number of females of each size class per square metre. Because we only found one gravid female in our southern-most focal population (Kirk Creek), we calculated larval production per square metre by employing the linear relationship between carapace width and number of embryos from the other 10 cobble habitat populations from which we collected gravid crabs in conjunction with the female size class distribution and population size at Kirk Creek.

To estimate larval production of each population for use in dispersal kernels (see 'Bayesian estimation of dispersal kernel'), we first divided the estimates of larval production per square metre at the 11 focal cobble sites and 2 focal mussel bed sites by the average number of crabs (m⁻²) to obtain estimates of *per capita* fecundity. We assumed that *per capita* fecundity at the remaining 17 cobble field sites and 14 mussel bed sites was equal to the mean *per capita* fecundity across all other sites of the same habitat type. We then estimated the larval production from each population by multiplying *per capita* fecundity by the product of population density and habitat area.

(c) Production-settlement analysis

We used linear regression to determine the relationship between larval production and settlement at the 11 focal cobble sites at which both quantities were measured. Larval production per square metre data were log-transformed because the original data spanned an order of magnitude and the few large values had unduly high leverage. We tested for spatial autocorrelation in both variables with Moran's *I*. These analyses were performed using R v. 3.2.0 [46].

(d) Bayesian estimation of dispersal kernel

To characterize the spatial pattern of larval dispersal, we combined data on settlement at the 11 focal sites and estimated

total larval production at all 44 populations to estimate the parameters of a dispersal kernel. Based on the results of idealized oceanographic simulations [38], we assumed the kernel followed a Gaussian distribution and thus had two primary dispersal parameters: the mean dispersal distance and the standard deviation around the mean (i.e. the mean and standard deviation of the Gaussian distribution). In order to estimate these parameters, we took a Bayesian approach similar to that used by terrestrial ecologists studying seed dispersal [40,41]. In seed dispersal parlance, this is the inverse problem: given a pattern of propagule production and propagule settlement, what is the underlying dispersal process?

The inverse method calculation works as follows: for a given value of the mean and standard deviation of the dispersal kernel, one can calculate the probability of a larva dispersing from each site to every other site. This dispersal probability depends on the distance between sites. Then the total larval production at each site, multiplied by the dispersal probabilities and the larval mortality rate, gives the number of larvae expected to disperse and settle at each of the sites. We compared this predicted number of larval settlers at the 11 focal sites to the observed settlement at those sites to calculate the likelihood of the kernel parameters and the larval mortality rate, given the data.

We undertook a Bayesian analysis of the kernel because we had prior knowledge of the physical processes likely to affect dispersal in this system, namely estimates of current velocities in the nearshore region where *P. cinctipes* spend their larval period. We developed a prior estimate for the mean and standard deviation of the dispersal kernel based on continuous measurements of ocean currents throughout the water column at the 30 m isobath, 1.2 km off Bodega Head, California (38°18'42.5" N, 123°04'58.9" W), made by a moored acoustic Doppler current profiler (ADCP) and a high-frequency radar array [47,48]. We assumed that *P. cinctipes* larvae undertake diel vertical migrations [29] but are otherwise transported passively for six weeks (see the electronic supplementary material for details on oceanographic data). This was the only time series of current data of which we were aware that spanned the typical spawning season of *P. cinctipes* and was collected in the relevant depth and alongshore position for *P. cinctipes* larvae. We assumed that this was a reasonable first-order estimate of the circulation patterns likely to affect dispersal. Therefore, we placed only moderate confidence in the prior estimate of the mean and lower confidence in the prior estimate of the standard deviation and the larval mortality rate. The prior for the larval mortality rate was derived from literature estimates [49].

Using the inverse method to calculate the likelihood, we used a Markov chain Monte Carlo (MCMC) algorithm to update our prior and estimate the posterior distribution of the two kernel parameters, the larval mortality rate and an observation error term associated with the likelihood calculation. MCMC estimation was performed in MATLAB v. 8.4 (R2014b). Full details of the kernel estimation procedure and all model code are provided in the electronic supplementary material.

Once we obtained a posterior estimate of the kernel parameters, we predicted patterns of connectivity among the populations. We multiplied expected larval production in each population (based on habitat quality, patch size, female size structure, density and fecundity) by the dispersal kernel and the larval mortality rate to estimate larval export to each other population (as well as locally produced settlers). We then calculated the proportion of predicted settlement in each population that was spawned in every other population.

Our kernel calculations relied upon a large number of underlying data to obtain the predicted larval production at each site (habitat area, population size, fecundity, etc.), all of which contain measurement error. Therefore, we undertook a sensitivity analysis. Because the kernel estimation relied on a

computationally intensive MCMC algorithm, it was not practical to evaluate the sensitivity of kernel parameters to every component of the underlying production calculation. Instead, we created 100 new datasets in which we added a random deviation to both the *per capita* fecundity and total population size estimates for each population. The random deviation was drawn from a normal distribution with mean 0 and coefficient of variation 0.1; essentially this represents uncertainty of 10% in the baseline estimates. We then calculated the posterior distributions of the kernel parameters for each of the 100 datasets and compared the results to the original baseline value.

We also conducted two additional sensitivity analyses. First, we estimated the kernel posteriors with a dataset that only included the 11 populations for which we estimated both larval production and larval settlement. This second run revealed what happens to our estimate when there are unknown populations contributing to recruitment (for example if there were additional *P. cinctipes* populations along the coast that we did not identify or sample). Second, we evaluated the sensitivity of the posterior to our choice of prior by varying the level of confidence in the prior on the mean dispersal distance. We did this by varying the coefficient of variation of the prior distribution of the mean from 0.25 (high confidence) to 2 (low confidence); the baseline value was 1 (uncertainty in the mean is of the same order as the magnitude of the mean; see the electronic supplementary material for more detailed description).

3. Results

Larval production per square metre of habitat and settlement per square metre of habitat were weakly coupled in the 11 populations for which we measured both quantities ($r^2 = 0.27$, $n = 11$, $p = 0.099$; figure 1). Neither variable exhibited spatial autocorrelation (larval production per square metre, Moran's $I = -0.138$, $p = 0.68$; settlement per square metre, Moran's $I = -0.021$, $p = 0.54$).

The Bayesian analysis of production and settlement patterns yielded a posterior estimate of the dispersal kernel predicting that most larvae recruited close to home (figure 2a). The prior dispersal kernel had a mean displacement of 153.9 km poleward with a standard deviation of 430.1 km, based on empirical observations of nearshore depth-stratified alongshore flow and diel vertical migration by larvae. The posterior dispersal kernel, obtained after including larval production and settlement data from *P. cinctipes* populations (electronic supplementary material, figure S2) and fitting a larval mortality rate, had a mean dispersal distance of only 6.9 km (± 25.0 km s.d.) poleward with a standard deviation of 22.7 km (± 28.2 km s.d.) around that mean (figure 2a; electronic supplementary material, figure S3). A mortality rate of 1.28 d^{-1} provided the best fit with the data. There was good agreement between the observed settlement at each of the 11 focal sites and the settlement predicted by the model ($r^2 = 0.34$; electronic supplementary material, figure S4).

The short mean distance and narrow standard deviation of the posterior estimate of dispersal implies high local retention and predicts that exchange of propagules occurred only among nearby populations. This can be visualized in two ways. First, we visualized the dispersal pattern in terms of the proportion of larvae predicted to arrive from other sites at each of the 11 focal sites (figure 2b). The posterior dispersal kernel can also be visualized as a matrix of dispersal probabilities among sites, illustrating the low probability

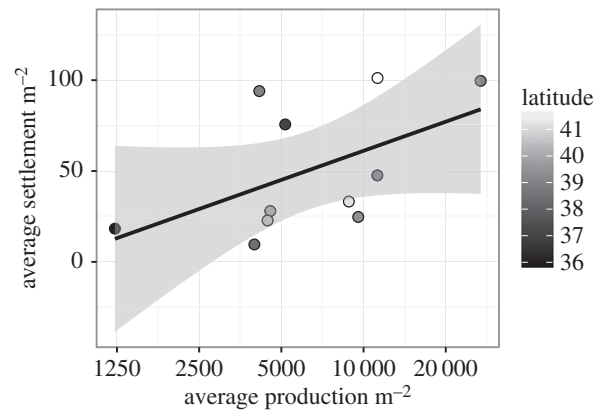


Figure 1. In *Petrolisthes cinctipes* populations along the California coastline ($n = 11$), larval production per square metre correlates weakly with post-larval settlement per square metre (linear regression, $r^2 = 0.27$, $p = 0.099$). Points, representing populations, are shaded by latitude and reveal no latitudinal or autocorrelated trends. The grey region represents the 95% CI for fit.

of dispersal across long gaps in the habitat (figure 3a). When the dispersal probabilities are multiplied by the estimated larval production in each site (figure 3b), the resulting matrix of connectivity among patches shows that closely spaced patches are predicted to have high connectivity with their neighbours, while isolated patches are predicted to receive larvae from only a few sites or be primarily self-recruiting (figure 3c).

The kernel estimate was not highly sensitive to measurement error in the underlying larval production calculations (electronic supplementary material, table S5). The coefficient of variation (CV) in estimates of the mean dispersal distance in the 10 randomly varied datasets was only 0.081, less than the CV of 0.1 in the underlying production data (the range of posterior values estimated was 6.0–7.9 km; electronic supplementary material, table S5). The posterior estimates were also relatively insensitive to restricting the analysis to the 11 focal sites (electronic supplementary material, table S6). The posterior was not strongly influenced by the prior estimates based on nearshore current velocities (note the large difference between prior and posterior in figure 2a), and this held true unless very high confidence (CV = 0.25) was placed on the prior (electronic supplementary material, table S7).

4. Discussion

We were able to estimate the larval dispersal kernel and connectivity patterns within the crab metapopulation due to our extensive sampling effort, which involved estimating the population size of most populations spanning 700 km of coastline, quantifying larval production for 13 of them, and quantifying settlement for 11 of them. Connectivity is typically assessed at much smaller scales [13], but expansive and thorough studies of marine metapopulations are essential for assessing population connectivity given the potential for widespread dispersal. The inverse approach used in terrestrial ecology [40,41] is a novel means of tackling this problem for a marine metapopulation.

Although we did not detect strong coupling between larval production and settlement, we estimated a short-distance dispersal kernel for a species with a six-week planktonic larval duration: a mean dispersal distance of

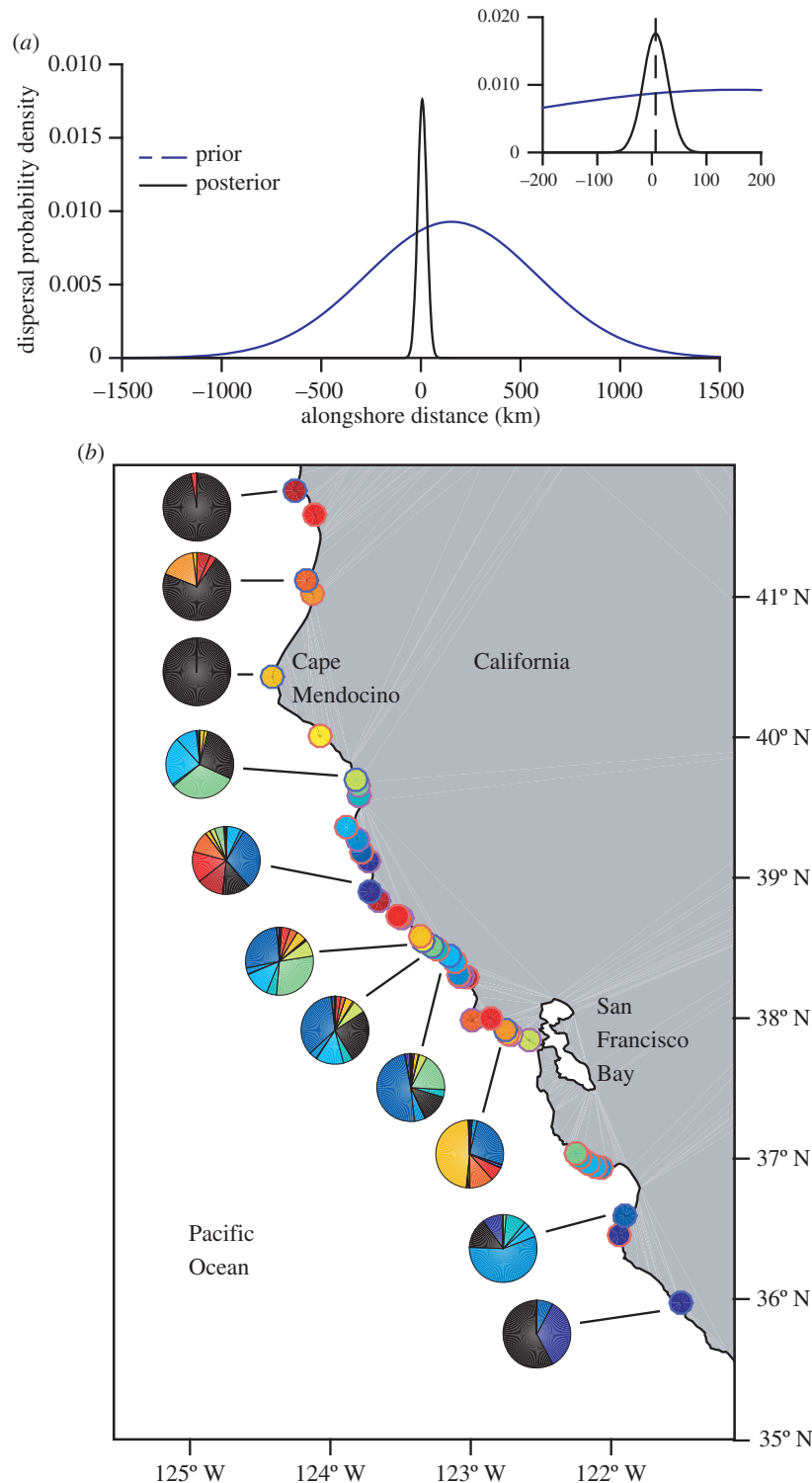


Figure 2. Modelled larval dispersal kernels and estimated population connectivity. (a) The prior dispersal kernel (blue curve), based on depth-stratified flow near shore, larval duration and diel vertical migration by *Petrolisthes cinctipes* larvae, and posterior dispersal kernel (black curve) after including demographic data and fitting larval mortality. Inset shows the same curves, zoomed in for detail, as well as the mean of the posterior distribution (vertical dashed line). (b) Pie charts depict the estimated proportion of settling larvae from each natal site for the 11 populations for which we quantified settlement based on the posterior dispersal kernel. Pie slices indicate proportional contribution to recruitment from sites of the corresponding colour. The contributing sites are ordered from north to south, moving clockwise from 12 o'clock. Black indicates local retention. Note that site colours repeat along the coast, but dispersal to any site was only from the nearest site of a particular colour. The edge of each site marker indicates the level of sampling at that site: full habitat size, population density, fecundity and settlement (blue); full population density but not fecundity or settlement (purple); or relative estimates of site size and density only (red; see electronic supplementary material, table S2 for different sampling methods).

only 6.9 km (± 25.0 km). This mean dispersal distance estimate is half as long as the shortest reported dispersal distance (estimated by invasion spread) for an invertebrate species with planktonic durations of six weeks in an open-coast environment [50,51]. However, our dispersal estimate

is consistent with an empirical study of cross-shore transport by *P. cinctipes* larvae in this region [34]; larvae of this species remained very close to shore (within 6 km) after strong upwelling events. Short-distance dispersal is probably typical, even in upwelling systems, due to larval behaviours

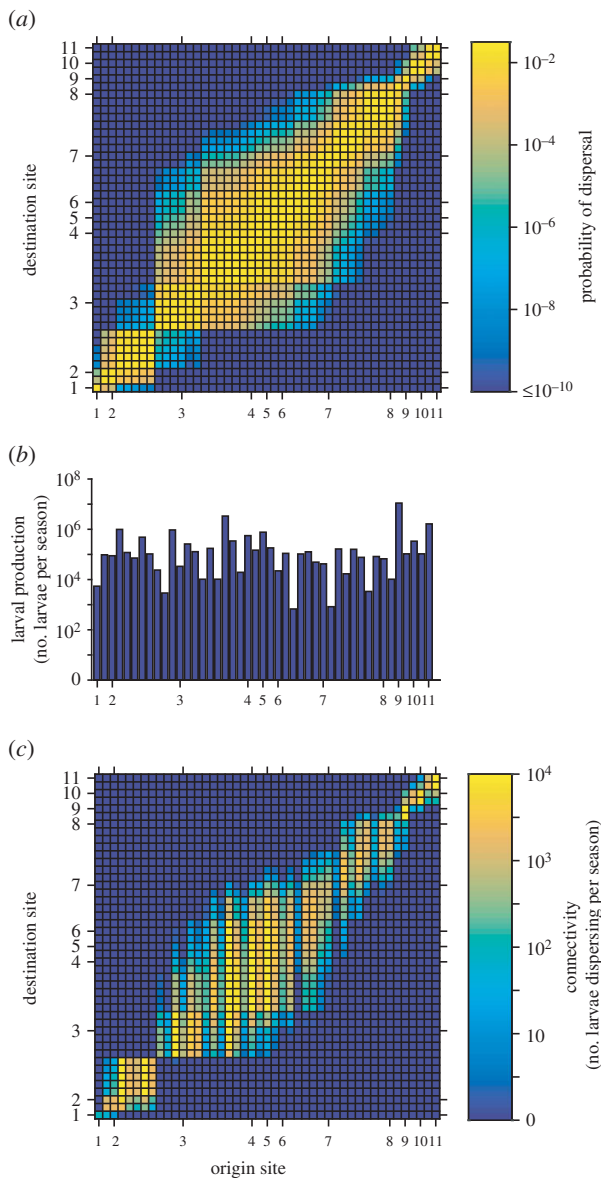


Figure 3. Matrices depicting estimated dispersal patterns among sites. (a) Probability of larval dispersal among sites as predicted by the posterior dispersal kernel. The colour of a cell indicates the probability of dispersal from the site on the column to the site on the row. The 11 focal sites depicted in figure 2b are indicated by number, from south to north. (b) Estimated larval production at each site. (c) Larval connectivity among sites, as calculated by multiplying the probability of dispersal by larval production and larval mortality. The interpretation is the same as (a), but the units are total number of larvae per spawning season. (Online version in colour.)

facilitating retention in slower flows close to shore [26,28,32]. Larvae of most nearshore invertebrates develop in the slow-moving, highly retentive coastal boundary layer by either remaining beneath the fast-moving surface layer or undertaking diel vertical migrations to the surface at night after winds have subsided [25,26,29,31,52].

To evaluate connectivity among populations, all demographic data ideally would be collected during the same reproductive season and year. Production and settlement data for the 11 focal cobble habitat sites were indeed all collected from the same reproductive season and year (2011). However, production and population size data for all other populations were collected in 2008, 2009 and 2014, making interannual variation in these demographic data potentially confounding. Where population data were based on habitat

size alone (17 populations), we do not expect our data from different years to introduce much interannual variation, because the cobble and mussel bed habitats are stable in size across years [43]. An additional source of uncertainty is the limited demographic data that we collected from *P. cinctipes* populations living in mussel beds: we collected population density and production data for only 2 of the 16 populations in mussel beds. We recognized that more complete demographic data from these populations, collected in the same reproductive season as those collected from populations in cobble habitats, would have improved our ability to detect a relationship between production and settlement, but logistical considerations constrained further sampling.

Our estimate of larval dispersal could be refined further by accounting for spatial variation in advection, diffusion and larval mortality. Given our access to alongshore velocities measured from only one location, we used a relatively simple, spatially invariant Gaussian dispersal kernel [37,38,53] to describe dispersal along the linear California coastline. A Gaussian dispersal kernel is not necessarily the most realistic possible description of dispersal patterns; a skewed distribution may better characterize dispersal [33,39,54,55], and temporal and spatial variability due to irregularities in the configuration of the shoreline and bathymetry also affect larval dispersal distributions [30,56–59]. This is a useful first approximation, however, that also has the advantage of being directly applicable to idealized models of metapopulation dynamics and marine reserve design along this type of coastline [60,61]. Many studies have used a rough estimate of alongshore current velocity for a region and multiplied it by a planktonic larval duration to estimate a larval dispersal kernel [37,38,57,62]. The subsequent step we have taken by employing the inverse approach is to improve those rough estimates by fitting them to demographic data. While the estimate of larval dispersal used as the prior in our Bayesian model accounted for factors hypothesized to affect dispersal—nearshore currents, larval duration and larval behaviours—the posterior estimate of the kernel that incorporated demographic data from the metapopulation was nonetheless much shorter and narrower. The disparity of the posterior dispersal estimate ($6.9 \text{ km} \pm 25.0 \text{ km s.d.}$) and the prior estimate (153.9 km) reveals the importance of including demographic data to refine estimates of larval dispersal based on oceanographic data alone [51]. We anticipate that our first step in resolving large-scale metapopulation production and connectivity patterns, particularly for species with larvae that complete development in the nearshore coastal boundary layer, will be improved by using recent developments in ocean circulation models, including better resolution of nearshore flow and refined representations of larval behaviour [24].

The estimate of the larval mortality rate derived from the Bayesian model (1.28 d^{-1}) is much greater than the rate obtained for porcellanid crab larvae (including *P. cinctipes*) in another empirical study from the same region (0.095 d^{-1}), which included sampling throughout the water column along three transects in the retentive coastal boundary layer every other day for two months [49,63]. One important consideration is that the mortality rate estimated by White *et al.* [49] explicitly accounts for and excludes advection, while the observed settlement data include mortality as well as losses due to advection, which may contribute significantly to the mortality of open-coast invertebrate larvae [64].

By projecting the consequences of our dispersal kernel for metapopulation dynamics, we estimated the predicted connectivity among all subpopulations in the study. Estimated connectivity depended on reproductive output and proximity, and ranged from being substantial among populations that were closely spaced (within 30 km) to self-contained for the clusters of isolated populations north of Cape Mendocino and south of San Francisco Bay. These results were not an artefact of edge effects, because nearby populations did not occur to the south (a range boundary) and north (nearest population approximately 140 km away) of our study area. Thus, we expect considerable variation in population dynamics within the larger *P. cinctipes* metapopulation, with well-connected subpopulations exhibiting greater synchrony and resilience, and being more likely to persist in the long term than more isolated subpopulations [65–67].

Fecundity was not equal across crab populations, as is assumed in many estimates of population connectivity [16]. The importance of heterogeneity in reproductive output to connectivity estimates can be seen by comparing the sites contributing larvae to the two most isolated subpopulations: the subpopulation at Cape Mendocino and the southern-most subpopulation, Kirk Creek (figure 2b). The former has much higher reproductive output than its distant neighbours and is predicted to be primarily self-seeding, while the latter has low reproductive output, so despite being isolated, most settling larvae are expected to arrive from neighbouring populations (figures 2b and 3c).

Our understanding of population connectivity can be improved by incorporating recently developed empirical approaches. Elemental fingerprinting is still limited to species with larvae that retain calcified structures throughout larval development, such as shells and otoliths, despite our efforts to extend the technique to *P. cinctipes* and other species that do not retain hard parts during larval development [68,69]. Genetic relatedness analysis, however, may be more widely applicable across taxa (e.g. [70]). Over 20 recent studies have used these approaches to determine self-recruitment, but unfortunately, only one study has determined local retention (i.e. the proportion returning relative to all recruits produced in the natal population itself [71]), which is critical to understanding metapopulation dynamics [13]. Such studies are needed to determine the relative importance of local retention and larval immigration in maintaining populations.

In conclusion, our study revealed high local retention and limited dispersal among subpopulations in a system that was once assumed to be broadly dispersive. Comprehensive studies of larval production, settlement and connectivity of metapopulations are needed to advance our fundamental understanding of the ecology and evolution of life in the sea, and management and conservation of its resources and ecosystems [10]. Effective spatial conservation management hinges on understanding population persistence, which requires knowledge of population connectivity [13]. The inverse approach borrowed from terrestrial ecology and applied to a marine metapopulation in this study provides a tractable framework for quantifying connectivity for species that occur in discrete, accessible populations, and provides a key to assessing population persistence.

Data accessibility. The datasets supporting this article and the MATLAB code used in the dispersal kernel estimation have been uploaded as part of the electronic supplementary material.

Authors' contributions. S.O.H., J.W.W. and S.G.M. designed research, S.O.H. and S.H.M. performed research, S.O.H., J.W.W. and K.J.N. analysed data, and S.O.H., J.W.W. and S.G.M. wrote the paper with input from S.H.M. and K.J.N. All authors gave final approval for publication.

Competing interests. We declare we have no competing interests.

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