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NOTE

How Much Do Marine Connectivity Fluctuations Matter?

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ABSTRACT: There is growing awareness that fluctuations in larval flux (connectivity) depress the long-run growth of marine metapopulations, but by how much is unclear. Here, we explore how reproductive schedule and larval behavior affect how much connectivity fluctuations depress growth. We combine larval dispersal simulations from the Florida Keys with theoretical results to calculate the effect of fluctuations on bicolor damselfish (*Stegastes partitus*). We find that fluctuations depress growth only slightly (~2%), but the effect would be much stronger for an organism that spawned only part of the year. Larval behavior can also matter, as vertical migration allows larvae to become entrained in eddies. Eddies synchronize connectivity fluctuations, further decreasing growth. However, here, they also divide the Keys into largely independently fluctuating regions, mitigating the effects of local synchrony. Therefore, in situations where connectivity fluctuations matter, the presence of independently fluctuating regions due to larval behavior may be important.

Keywords: connectivity, larval behavior, larval dispersal, metapopulation dynamics, mesoscale eddies, stochasticity.

Introduction

Many sessile and benthic marine species go through a pelagic larval phase in which recently hatched individuals drift until they have developed enough to swim, settle to the bottom, and attempt to establish themselves as adults. The tiny larvae begin life as drifters but quickly develop the ability to ride different ocean currents, mostly by controlling their vertical position in the water column (Paris and Cowen 2004). Later on, they can orient and swim directionally (Leis 2006). Nonetheless, their control over dispersal is partial: ocean currents play a role in where larvae end up (Paris et al. 2007). Ocean currents thus connect one habitat patch to another and influence larval connectivity—the flux of larvae from one place to another

(Cowen et al. 2006). The time-averaged connectivity is a key determinant of metapopulation success or failure (Armsworth 2002; Hastings and Botsford 2006). However, coastal currents are typically highly variable, and there is increasing awareness that long-run metapopulation growth is determined not only by mean connectivity but by fluctuations in connectivity (Berkley et al. 2010; Hogan et al. 2012; Watson et al. 2012; Williams and Hastings 2013).

There is widespread recognition in terrestrial ecology that in the absence of nonlinearity, environmental variability will tend to depress long-run growth (Lewontin and Cohen 1969; Tuljapurkar 1990). Terrestrial systems have been used to examine the demographic buffering hypothesis (Sæther and Bakke 2000), which states that there should be selection against variability in demographic rates, especially in rates to which growth is highly sensitive (Gillespie 1977; Pfister 1998). The fitness cost of variability also produces bet-hedging strategies, meant to reduce variability in year-to-year growth (Cohen 1966), and here, too, evidence has often been sought in terrestrial systems (Venable 2007; Childs et al. 2010). However, ecologists are just beginning to consider the consequences of connectivity fluctuations in marine systems.

Watson et al. (2012) recently investigated the effect of connectivity fluctuations for two fish species in the California Bight (CB). They found that the reduction in metapopulation growth rate is potentially large, especially if pelagic larval duration is long and a population spawns at a time of year with strong current reversals. To understand how important connectivity fluctuations are likely to be in other locations, we need not just a measure of relative current variability but also a deeper understanding of how biological processes determine the influence of fluctuations.

As shown in the next section, the expression for long-run metapopulation growth contains a penalty term that is proportional to the covariances in connectivity fluctuations. We expect positive covariances (reduced growth) because larvae leaving from nearby locations are likely to

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be entrained by similar currents. In particular, mesoscale eddies extending tens of kilometers and lasting weeks to months have the potential to create similar fluctuations in dispersal paths over large areas. While surface water layers tend to be dominated by wind forcing and wave action, many benthic marine larvae descend into progressively deeper layers as they mature (ontogenetic vertical migration; Paris and Cowen 2004), which influences their drift trajectory (Vikebø et al. 2007). In these deeper layers, geostrophic and shear flows dominate, and larvae can be trapped into coastal eddies or swept along frontal systems (Limouzy-Paris et al. 1997). We therefore expect larval behavior to have an important effect on the degree to which connectivity fluctuations depress long-run growth.

We also expect life-history aspects such as spawning seasonality to affect the importance of connectivity fluctuations. In many places, water circulation is more variable in some seasons than in others. In addition, if the population spawns at some times of year but not others, this adds an additional source of variability: larval connectivity drops all the way to zero outside of the spawning season instead of varying between the bounds set by changing circulation patterns.

In this study, we explore how reproductive schedule and larval behavior affect the importance of connectivity fluctuations. We also help generalize earlier work by changing location, using larval dispersal simulations from the Florida Keys (FK) to calculate the effect of stochasticity on a hypothetical population of *Stegastes partitus* (bicolor damselfish). *Stegastes partitus* is a representative coral reef fish with well-studied reproductive and larval behavior. The model used here successfully represents settlement (Spongaugle et al. 2012). We find that connectivity fluctuations have very little effect on metapopulation growth for our system. However, this is mostly due to *S. partitus*'s year-round spawning, not the location; greater seasonality in spawning would have produced a greater reduction in growth. Growth rate reductions are similar whether larvae engage in vertical migration or float passively on the surface, but the physical drivers of that reduction are quite different. When larvae migrate to deeper water layers, they become entrained in mesoscale eddies that synchronize connectivity fluctuations over the extent of the eddy, intensifying the effect of fluctuations on long-run growth. However, eddies also divide the FK into semi-independently fluctuating regions, partially mitigating the effects of local synchrony. If, on the other hand, larvae do not migrate and instead remain in the surface layer, wind forcing synchronizes connectivity fluctuations over a much larger region, with a similar net effect on long-run growth.

Theoretical Background

If we assume that population levels are low enough to ignore density dependence, we can write the dynamics of a metapopulation as $\mathbf{n}_{t+1} = \mathbf{A}_t \mathbf{n}_t$, where \mathbf{n}_t gives the population at each location at time t , and \mathbf{A}_t is a time-dependent transition matrix specifying population growth and dispersal between locations. The long-run growth of the metapopulation is given by the system's dominant Lyapunov exponent, equal to the expected value of $\lim_{t \rightarrow \infty} (1/t) \ln N(t)$, where $N(t)$ is the total population at time t . This involves the product $\mathbf{A}_{t-1} \mathbf{A}_{t-2} \dots \mathbf{A}_0$, and in general, it can't be calculated exactly. However, if fluctuations are small, we can make a Taylor expansion of the matrix product and get something tractable. We write the transition matrix as

$$\mathbf{A}_t = \bar{\mathbf{A}} + \mathbf{Q}_t, \quad (1)$$

where $\bar{\mathbf{A}}$ is the time-averaged transition matrix, and the components of the perturbation matrix \mathbf{Q}_t are assumed to be small. Ruelle and Tuljapurkar independently showed that if the \mathbf{Q}_t are independent and identically distributed, then, to second order in the perturbation matrix \mathbf{Q}_t , the long-run growth rate \bar{r} is given by

$$\bar{r} = \log \lambda_1 - \frac{1}{2\lambda_1^2} \underbrace{\sum_{i,j,k,l} \frac{\partial \lambda_1}{\partial \bar{A}_{ij}} \frac{\partial \lambda_1}{\partial \bar{A}_{kl}} \text{Cov}(Q_{ij}, Q_{kl})}_{\text{fluctuation penalty}}, \quad (2)$$

where λ_1 is the dominant eigenvalue of $\bar{\mathbf{A}}$ and $\text{Cov}(Q_{ij}, Q_{kl}) = \mathbb{E}\{Q(t)_{ij} Q(t)_{kl}\}$ (Ruelle 1979; Tuljapurkar 1990). (Please note that this formulation assumes that we have normalized the eigenvectors so that the dot product of the left and right dominant eigenvectors of $\bar{\mathbf{A}}$ is 1.)

We see that long-run growth is reduced by a fluctuation penalty: increased variance in the components of the transition matrix (increased $\text{Cov}(Q_{ij}, Q_{ij})$) reduces \bar{r} , and if transition matrix components positively covary (positive $\text{Cov}(Q_{ij}, Q_{kl})$), then that increases the penalty. In the present context, fluctuations in the transition matrix are caused by fluctuations in larval connectivity.

Williams and Hastings (2013) consider a case where covariances are negative, and so fluctuations inflate the long-run growth rate. However, as discussed in the introduction, we expect positive covariances here because larvae leaving from nearby locations are likely to be entrained by similar currents.

Methods

We used detailed larval dispersal simulations (particle tracking models) to create monthly transition matrices for a hypothetical population of *Stegastes partitus* in the Florida Keys from 2004 to 2008. We then found the time-

averaged transition matrix and the fluctuations away from that time average to calculate the penalty term in the small noise approximation (eq. [2]). We checked the validity of this approximation using an empirical estimate of the Lyapunov exponent and examined the effects of mesoscale circulation features by performing a spatial cluster analysis. The details follow.

Larval Dispersal Simulations

To simulate spawning, larval transport, and recruitment, we used the open-source, coupled biophysical connectivity modeling system (CMS; Paris et al. 2013). This multiscale simulation relies on nested hydrodynamic models, which are three different implementations of the hybrid coordinate ocean model (HYCOM) covering the study domain with different horizontal resolutions from 1 to 7 km and using different climatological forcing from daily to 6 hourly hindcasts from 2004 to 2008. This configuration, detailed in Spongaugle et al. (2012), captures the appropriate scales of the eddy field circulation that is known to influence reef fish larval dispersal in the FK (Limouzy-Paris et al. 1997). For the purposes of modeling recruitment of *S. partitus* and generating a connectivity matrix, coral reef space is divided into 38-unit reef-polygons of ~10 km long, which includes a 5-km sensory envelope (Paris et al. 2005). Larvae can settle anywhere within the polygon. Demersal spawning occurs daily in each reef-polygon from January to November, and subsequent daily hatching is scaled by observed lunar cyclic hatching (Spongaugle et al. 2012), releasing a maximum of 1,400 particles around the third quarter moon. Larvae are subjected to daily natural mortality following a half-life ontogenetic function measured in situ (Paris 2009) and are competent to settle between 22 and 32 days, 32 days being the maximum pelagic larval duration. Settlement occurs if larvae enter a habitat polygon within that competency period. From these simulations, we obtained monthly dispersal matrices, the components of which specify the probability of larvae migrating from one polygon to another.

Larval Behavior. Like many marine species, *S. partitus* larvae are found at different depths at different life stages. In our simulation with larval behavior, larval vertical distribution has a stage-specific center of mass and vertical spread (Paris and Cowen 2004). For the simulations without migration, *S. partitus* larvae float passively in the surface layer.

Seasonal Spawning. While *S. partitus* spawns nearly year-round, spawning levels are seasonal. The fraction of annual larval production that occurs in each month come from year-round samples of *S. partitus* in the Barbados (Dorsey 1999; Cowen 2002). For the model without sea-

sonal spawning, the annual larval production is divided equally among all months.

Model

From the simulation, we have monthly dispersal matrices \mathbf{D}_t , where the ij th component represents the probability that a larva spawned at j will arrive at i during month t . Each dispersal matrix \mathbf{D}_t is multiplied by either a constant fecundity f or a monthly fecundity f_t that reflects seasonal spawning levels (the same for each year). After also multiplying by a constant recruitment probability r , $rf_t\mathbf{D}_t$ gives us the number of larvae traveling from j to i . We let $\mathbf{B}_t = rf_t\mathbf{D}_t$ and refer to \mathbf{B}_t as the (realized) connectivity matrix at time t . We use these to create an age- and space-structured model with a monthly time step. The reef habitat is divided into 38 locations, and we assume that no individual lives more than 24 months. The population vector \mathbf{n}_t therefore has 38×24 entries, where the first 38 give the populations of 1-month-olds in each of the 38 locations, the second 38 give the populations of 2-month-olds, and so forth. We assume that fish begin spawning at 13 months and that the monthly survival probability is $0.5^{1/12}$ for all ages. The update rule is then $\mathbf{n}_{t+1} = \mathbf{A}_t\mathbf{n}_t$, where the transition matrix \mathbf{A}_t takes the form

$$\mathbf{A}_t = \begin{pmatrix} \mathbf{0} & \mathbf{0} & \dots & \mathbf{B}_t & \mathbf{B}_t & \dots \\ \mathbf{S} & \mathbf{0} & \dots & & & \\ \mathbf{0} & \mathbf{S} & \mathbf{0} & \dots & & \\ \vdots & & & & & \\ \mathbf{0} & \dots & \dots & \dots & \dots & \mathbf{S} \end{pmatrix}, \quad (3)$$

and where the survival submatrix \mathbf{S} is a 38×38 diagonal matrix containing the monthly survival probability.

We have no data on fecundity or recruitment probability, so we choose rf such that the time-averaged \mathbf{A} has dominant eigenvalue 1; that is, the population neither grows nor shrinks in the absence of fluctuations.

Additional Mathematical and Statistical Analysis

Empirical Estimate of the Lyapunov Exponent. Equation (2) assumes that the monthly transition matrices are independent and identically distributed. This is almost certainly not the case. At a minimum, there will be greater variability during the winter than in the summer. As a check on our approximation, we also made empirical estimates of the long-run growth rate. We began with a population distributed according to the stationary stage distribution in the absence of fluctuations (i.e., according to the dominant right eigenvector of $\bar{\mathbf{A}}$). We then created a 1,000-year time series by sampling years with replacement from our original time series. (We sampled years

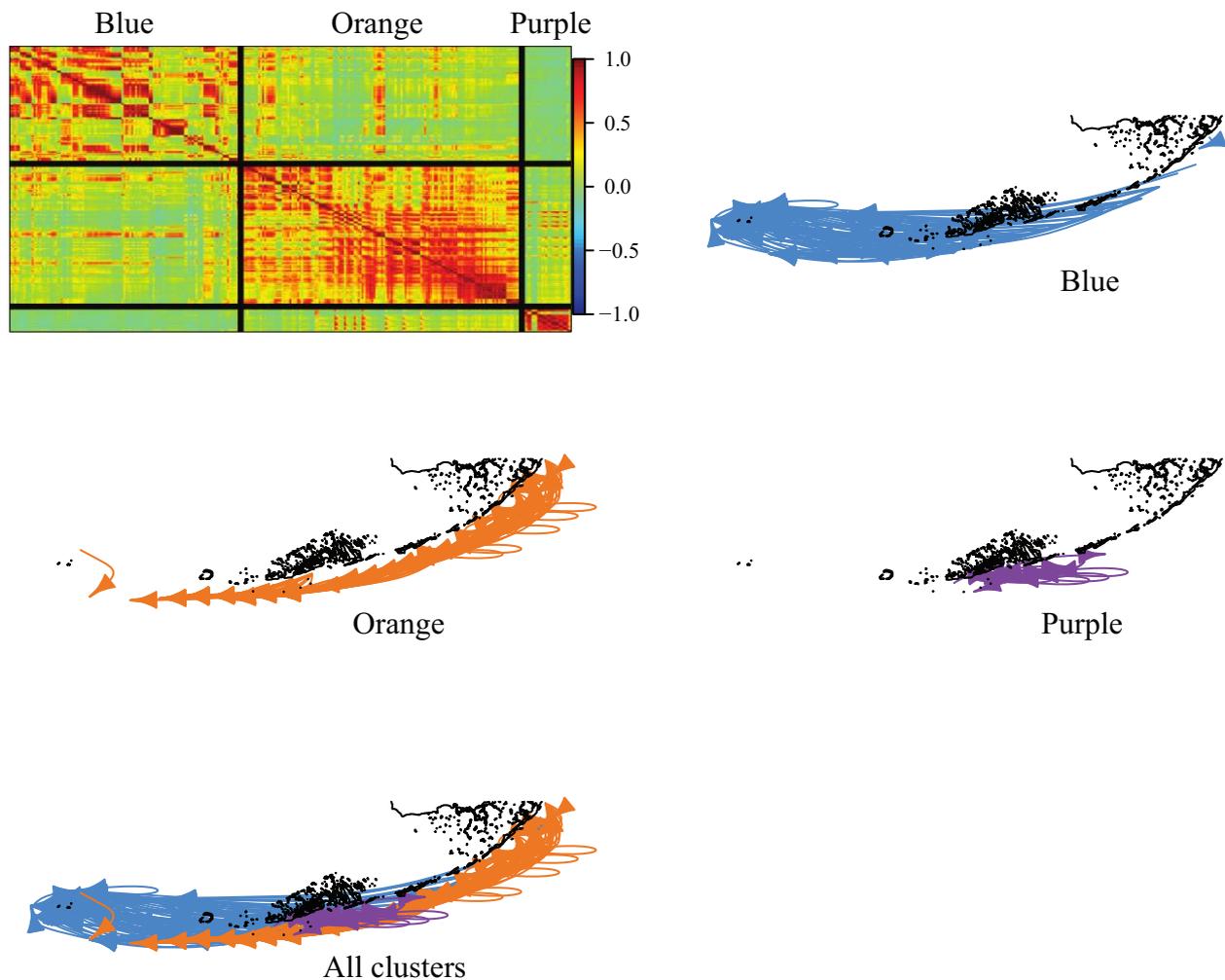


Figure 1: Clustering for the most variable routes (top 20%) with larval migration and seasonal spawning. The upper-left figure shows the correlation matrix of the most variable entries of the connectivity matrix (routes) and a hierarchical clustering partitioning into three clusters. The maps of the Florida Keys show the routes in each of the three clusters independently as well as all together. The spatial segregation of the clusters suggests that the Pourtales Gyre, located at the purple cluster, is dividing routes into upper and lower clusters that fluctuate roughly independently.

instead of months to keep within-year correlations intact.) We applied the first monthly transition matrix, recorded the growth, renormalized the population vector to have the original population size (but kept the new distribution), applied the next month's transition matrix, and recorded the population growth, and so on. The empirical estimate of the Lyapunov exponent is simply the time average of the log of the monthly growth rates, and we converted this to a yearly rate by multiplying by 12. We estimate the standard deviation of the long-run growth rate using the method presented in Cohen (1986).

Spatial Clustering. The long-run growth rate is reduced by variances and positive covariances among the elements of the connectivity matrices \mathbf{B}_r . (Note that the

\mathbf{B}_r are the only components of the transition matrix that vary.) We call the elements of the \mathbf{B}_r "routes," as the ij th element represents larvae that dispersed along some route from j to i . In order to determine what oceanographic processes might be causing connectivity fluctuations to covary, we applied hierarchical clustering with Ward's method, as implemented in the `hclust` function of R (R Development Core Team 2008), to the routes with variances in the top 20%, using the correlation matrix as a distance metric (i.e., the distance between routes B_{ij} and B_{kl} was equal to $1 - \text{Cor}(B_{ij}, B_{kl})$). Ward's method creates clusters that minimize within-cluster variance in the distance metric, in our case, creating clusters of routes that were positively correlated within the cluster and typically

weakly correlated between clusters. We chose the number of clusters subjectively by plotting the resulting correlation matrix (e.g., fig. 1, *upper left*) to see what gave a good partitioning.

Results

Seasonal Spawning

With or without seasonal spawning, the effects of connectivity fluctuations were small: after normalizing the transition matrices so that the annual growth rate was zero in a constant environment, the long-run metapopulation growth rates were around -0.02 with seasonal spawning and -0.01 without, whether larval behavior was included or not (table 1). Given the standard deviations on the empirical estimates, the differences are not statistically significant. Nonetheless, we might well expect seasonal spawning to lower growth more than nonseasonal spawning, as it adds variable fecundity to variable dispersal probability. Then again, if the variability in ocean circulation is itself highly seasonal, then seasonal spawning can be a way to avoid the most variable circulation periods and might actually decrease the reduction in long-run growth.

We also note that our study shows a smaller effect of stochasticity than Watson et al. (2012) found for many of the parameter combinations in their study of the CB. There, many of the long-run growth rates were in the range of -0.05 to -0.15 , and some were lower than -0.3 .

We next altered the reproductive schedule so that all spawning was concentrated in a 3-month interval, similar to the kelp bass and sheephead that were simulated by Watson et al. (2012). This change intensifies the variation due to spawning seasonality. Depending on what time of year the spawning took place, stochasticity reduced the growth rate to between -0.0702 and -0.1256 , confirming our intuition that increased spawning seasonality can decrease growth rate. These effect sizes are also on a par with those reported by Watson et al. (2012), though it is important to remember that Watson et al. (2012) uses a yearly time step and cannot fully consider within-year variability.

Larval Behavior

Other research has shown that larval vertical migration can substantially increase mean connectivity by reducing the number of larvae being swept offshore (Paris and Cowen 2004; Paris et al. 2007; Morgan and Fisher 2010; Huebert et al. 2011; Robins et al. 2013). We expected vertical migration to have a similarly large effect on the degree to which fluctuations depress long-run growth. After all, vertical migration allows larvae to become entrained in eddies, which in addition to enhancing larval retention (increasing mean connectivity) should also create positive covariances between route fluctuations (increasing the fluctuation penalty). However, we found that connectivity fluctuations depressed long-run growth by similar amounts, with or without larval behavior.

To explore why, consider components of the dispersal submatrix with variances in the top 20%. Covariances among these highly variable routes are responsible for most of the reduction in long-run growth: if we set all dispersal submatrix components to their temporal mean save for these high-variance routes, we find that the covariances among these routes are responsible for 74% of the reduction in long-run growth with larval behavior and 80% without. The spatial pattern of covariances is quite different with and without larval behavior, however.

We clustered routes into groups such that fluctuations were positively correlated within a group but only weakly correlated, if at all, between groups. When larval behavior is included, the routes fall into an upper cluster and a lower cluster, overlapping in the Middle Keys, and a third cluster centered on the overlap zone (fig. 1). The overlap zone/third cluster occurs at the location of the Pourtales Gyre, a mesoscale eddy lasting ~ 1 month created by the offshore meandering motion of the Florida Current (Lee et al. 1992). The Pourtales Gyre has already been hypothesized to aid in larval retention for a number of species (e.g., Yeung and McGowan 1991; Lee et al. 1992). Here, the convergence zone created by the gyre appears to be acting to isolate fluctuations in one region from another. Figure A1 (figs. A1, A2 are available in the online appendix) shows the same figure without spawning seasonality. We see the same division into upper and lower clusters, although without a third cluster at the overlap zone.

Table 1: Long-run stochastic growth rates

	Small-noise approximation	Empirical estimate (SD)
With seasonality, with migration	$-.0189$	$-.022$ (.034)
With seasonality, without migration	$-.021$	$-.039$ (.008)
Without seasonality, with migration	$-.0078$	$-.012$ (.013)
Without seasonality, without migration	$-.0091$	$-.0098$ (.009)

Note: Transition matrices are normalized so that the long-run growth rate in a constant environment is zero.

If, on the other hand, larvae float passively on the surface, the routes form a single correlated cluster plus some additional routes that are mostly weakly correlated with both routes in the cluster and each other (fig. 2). Mapping this group onto the Florida Keys, the routes are distributed broadly. Here, presumably, neustonic larvae are not deep enough in the water column to be entrained by eddies and instead are wind driven and swept along fronts. Thus, correlations in connectivity fluctuations reduce long-run growth by a similar amount whether there is larval behavior or not, but the sources of those correlations are different, and those different sources produce different spatial patterns of correlation. Figure A2 shows a similar pattern in the absence of spawning seasonality.

Location and Simulation Methods

It is possible that we found much smaller effects than Watson et al. (2012) not because of *Stegastes partitus*'s less seasonal spawning schedule, but because the circulation in the CB may be more variable and/or our particle tracking systems are different. To account for the differences in particle tracking systems and location, we used Watson et al.'s (2012) connectivity simulation data for the CB with

S. partitus's pelagic duration and reproductive schedule. Their particle tracking system releases fewer larvae and therefore might be expected to produce higher variability in connectivity. The small-noise approximation with the CB data gave us a stochastic growth rate of -0.0431 . This approaches the lower range of Watson et al.'s (2012) results but is still a very modest reduction. We therefore believe that the differences in our findings are largely the result of differences in spawning schedule. (See table A1 in the online appendix, however, for a more complete summary of the differences in particle tracking systems.)

Discussion

Researchers are only just beginning to consider the effects of marine variability: it is still not clear when and where connectivity fluctuations will have a large effect on the growth of marine metapopulations. Here, we have explored how spawning seasonality and larval behavior affect the importance of connectivity fluctuations. We also estimated the effect of fluctuations on growth in a new location: the Florida Keys.

We found that connectivity fluctuations had only a small effect on the long-run growth of *Stegastes partitus* in the FK

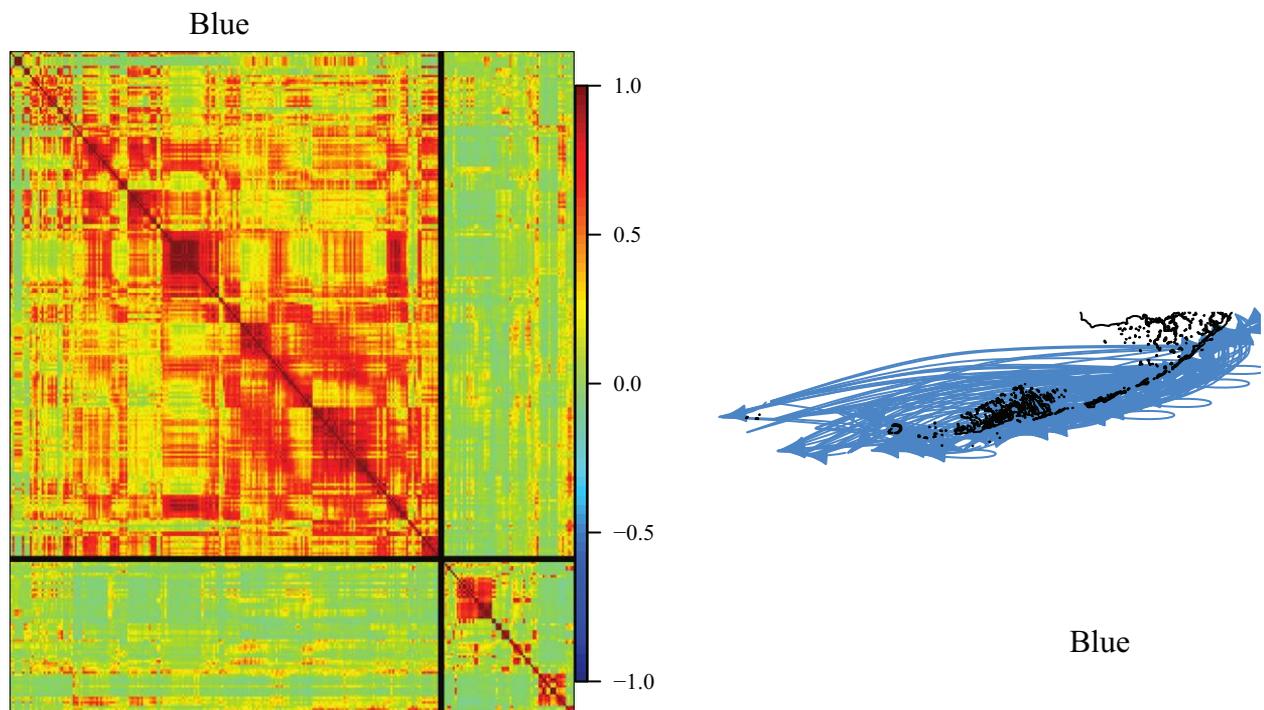


Figure 2: Clustering for the most variable routes (top 20%) without larval migration and with spawning seasonality. The left figure shows the correlation matrix of the most variable entries of the connectivity matrix (routes) and a hierarchical partitioning into a single cluster and a group of largely uncorrelated routes. The map of the Florida Keys (FK) shows the routes in the cluster. The lack of spatial segregation suggests that in the absence of larval migration, connectivity fluctuations are driven by wind, which has a similar effect across the FK.

(a reduction from zero to about -0.02). This is in contrast to the effects found by Watson et al. (2012) for the CB, where connectivity fluctuations reduced growth from zero to -0.05 or -0.15 , and in a few instances lower than -0.3 . While some of the difference is undoubtedly due to different oceanographic conditions and different particle tracking systems, more appears to be the result of *S. partitus*'s spawning schedule: when we concentrated spawning into a 3-month interval instead of spreading it across the year, the long-run growth rate was reduced to between -0.07 and -0.12 , depending on spawning timing.

It is tempting to conclude that connectivity fluctuations will be more important for seasonal spawners and less important for year-round spawners, and indeed, this is likely true in many cases. However, if ocean turbulence were highly seasonal, then seasonally restricted spawning could potentially reduce connectivity fluctuations if spawning took place during times with low variability in larval transport. That is not the case here. While connectivity is more variable in winter and less in summer, the reduction in growth created by winter connectivity fluctuations is less than the reduction that would be produced by letting the flux of larvae drop to zero for part of the year.

Larval behavior also matters, though not in the way we anticipated. Larval behavior has previously received attention for its effects on time-averaged connectivity, with presumed consequences for long-run growth (e.g., Paris et al. 2007; Morgan and Fisher 2010; Huebert et al. 2011; Robins et al. 2013). We found that larval behavior affects connectivity fluctuations also, but the demographic consequences are unexpected. Connectivity fluctuations reduced growth by roughly the same amount whether there was larval behavior or not, but they did so for different reasons. If larvae engage in vertical migration, they can become entrained in eddies, which cause fluctuations to positively covary over extended areas. Without vertical migration, larvae float near the top of the water and fluctuations covary because wind drives surface water movements over large areas.

It would be possible to create an even more detailed model of larval behavior, incorporating diel migration, say, or more capacity for horizontal swimming. It is not clear how these refinements would affect our results.

It is important to remember that we have not accounted for all sources of connectivity fluctuations in this study, and therefore, fluctuations may be more important than we suppose. Connectivity fluctuations are the net result of fluctuations in larval production, transport, settlement, and recruitment, and we have only modeled fluctuations in transport and settlement.

Furthermore, our estimates of connectivity fluctuations may increase if larval production is limited in some areas. The particle tracking systems that we use release large

numbers of "larvae" that saturate the system, ensuring that every location that can be reached is reached. However, actual larval production may be much lower in some areas, in which case, realized larval transport is the result of limited sampling from the dispersal kernel and we must add sampling effects to the sources of variability (Simons et al. 2013).

Even without better information about exactly how much connectivity fluctuates, the current study provides some useful insight about how ocean circulation features influence the effects of those fluctuations. The spatial clustering analysis confirmed our intuition that mesoscale eddies help synchronize connectivity fluctuations across wide areas. In particular, a convergence zone created by the Pourtales Gyre divides the FK into largely independent upper and lower regions, with a small zone around the gyre itself that fluctuates independently of both. For *S. partitus* in the FK, connectivity fluctuations do not substantially reduce long-run growth. However for species/locations where connectivity fluctuations are a greater concern, it may be important to include multiple independently fluctuating regions when designing marine reserves, so that fluctuation penalties within regions are partially offset. Knowing how coastal circulation patterns partition water movement will help provide information about how to achieve that goal.

In conclusion, we examined the effects of spawning seasonality and larval vertical migration on the reduction in growth caused by stochastic ocean circulation. We found that seasonal spawning can add to the negative effects of stochastic ocean circulation. In this study, we saw a similar reduction in growth whether larvae underwent vertical migration or floated passively on the surface. It is interesting to note, however, that the growth penalty with larval migration can be partially offset, as it is here, because eddies divide the area into independently fluctuating regions. It is possible that without this subdivision, the spatial correlations produced by larval migration might produce a larger penalty. While the growth penalty is small in this region for this organism, the mitigating effects of such subdivisions may prove important in other circumstances.

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