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## Research

### Individual variation in marine larval-fish swimming speed and the emergence of dispersal kernels

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Dispersal emerges as a consequence of how an individual's phenotype interacts with the environment. Not all dispersing individuals have the same phenotype, and variation among individuals can generate complex variation in the distribution of dispersal distances and directions. While active locomotion performance is an obvious candidate for a dispersal phenotype, its effects on dispersal are difficult to measure or predict, especially in small organisms dispersing in wind or currents. Therefore, we analyzed the effects of larval swimming on dispersal and settlement of coral-reef fish larvae using a high-resolution biophysical model. The model is, to date, the only biophysical model of marine larval dispersal that has been statistically validated against genetic parentage estimates of larval origin and destination, and incorporates empirically-estimated larval behaviors and their ontogeny. Larval swimming, in combination with depth, orientation and navigation behaviors, actually reduced dispersal distances compared to those of passive larvae. Swimming had no consistent effects on long distance dispersal, but increased the spread of settlement locations. Swimming speed, in contrast, did not consistently affect median dispersal distances, but faster swimming larvae had greater mean and maximum dispersal distances than slower swimming larvae. Finally, faster larval swimming speeds consistently increased the probability of settlement. Our analysis shows how larval swimming differentially affects multiple properties of dispersal kernels. In doing so, it indicates how selection could favor faster larval swimming to increase settlement and local retention, which may actually result in longer dispersal distances as a by-product of larvae trying to locate habitat rather than to disperse greater distances.

Keywords: condition-dependent dispersal, dispersal kernel, marine, phenotype-dependent dispersal

#### Introduction

Dispersal distributes alleles and individuals in space. As a result, dispersal is an important determinant of variation in the genetic and demographic structure within and



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between species (Clobert et al. 2012). Dispersing individuals often vary in their morphological, physiological and behavioral traits as well as in their responses to external cues (Howard 1960, Clobert et al. 2009, Nanninga and Berumen 2014, Baines et al. 2019). However, the effects of such individual variation in small animals subject to advective and diffusive processes in air (Zera and Denno 1997, Bonte et al. 2007, Leitch et al. 2021) or water (Leis 2010, Nanninga and Berumen 2014, Shima et al. 2015) are difficult to measure and predict. Furthermore, because dispersal in marine systems is to a large extent driven by water currents during developmental stages before larvae are developmentally competent to settle (Cowen and Sponaugle 2009), the traditional view was that the behavior of larvae did not exert a meaningful influence on dispersal (Leis 2006, Swearer et al. 2019). Though it is now well-recognized that larvae have behaviors, it remains less clear how exactly those behaviors affect dispersal kernels. Therefore, understanding how the characteristics of individuals interact with different physical properties of air and water to influence movement and life in each medium is a crucial prerequisite for generating predictions about how dispersal kernels emerge and vary within populations.

Dispersal kernels are often defined as the density of individuals that settle, or the probability that individuals settle, a certain distance from their natal location (Hovestadt et al. 2012, Nathan et al. 2012, D'Aloia et al. 2015). They emerge as a consequence of phenotype  $\times$  environment interactions. In terrestrial systems, phenotypes like the sex, mass, wing shape, wing muscle strength, leg length, speed performance, orientation, the readiness to emigrate or the timing of dispersal, are relatively well-studied in this context (Saastamoinen et al. 2018, Tung et al. 2018, Baines et al. 2019, Leitch et al. 2021). In marine systems, traits such as pelagic larval duration (PLD), vertical position in the water column, ontogeny of swimming and orientation capability, horizontal swimming speed and the timing and frequency of propagule release have been hypothesized as important ways that marine life histories interact with ocean currents to influence dispersal (Marshall and Keough 2003, Shanks and Eckert 2005, Leis 2006, Fiksen et al. 2007, Gerlach et al. 2007, Shima and Swearer 2009, D'Alessandro et al. 2010, Sundelöf and Jonsson 2012, Paris et al. 2013, Morgan 2014, Pringle et al. 2014, Faillettaz et al. 2018). Nonetheless, the estimation of dispersal kernels and the role of individual variation in dispersal traits in marine systems lags that in terrestrial systems because of the relative difficulty of direct observation and tracking individuals in marine systems (Buston et al. 2012, Harrison et al. 2012, Nanninga and Berumen 2014, D'Aloia et al. 2015, Williamson et al. 2016, Almany et al. 2017).

Larval swimming speed is a trait that could strongly influence the emergence of larval dispersal kernels in demersal marine fishes. Especially in perciform fishes towards the end of their pelagic larval phase, individual larvae are able to directly influence their dispersal by horizontal swimming (Leis 2006). Swimming speeds measured in situ vary among and within species, and within tropical species can range from  $\sim 2$

to  $65 \text{ cm s}^{-1}$ , or  $\sim 4$  to  $38$  body lengths  $\text{s}^{-1}$  (Leis and Carson-Ewart 1999, 2001, Leis et al. 2006, 2009). For perspective,  $28 \text{ cm s}^{-1}$  is  $1 \text{ km h}^{-1}$  and Olympic swimmers can manage two body lengths  $\text{s}^{-1}$  in a 50 m race. In the laboratory, larvae nearing the end of their PLD can swim nearly constantly for several days to a week or more (Stobutzki and Bellwood 1997) and, if given access to food, still grow and begin to metamorphose (Leis and Clark 2005). Larvae typically exhibit consistent directional swimming orientations in open water and near reefs, and larvae competent to settle often actively move towards reefs (Leis and Carson-Ewart 1999).

Predicting how exactly larval swimming affects dispersal is not straightforward. Much of the transport is likely to occur before larvae are developmentally competent to settle, or even to swim in a manner that can influence dispersal outcomes. The effects of horizontal swimming also depend on other traits such as swimming orientation, vertical positioning, when swimming and settlement competency develop during the pelagic stage, and the ability to sense and locate settlement habitat (Trembl et al. 2015, Leis 2020). Demersal fish taxa, that are either ovoviviparous or brood their eggs in the demersal habitat, avoid drift during the egg stage in contrast to taxa that spawn eggs into the water column. However, after hatching, larvae are not immediately capable of swimming and navigating, so still spend several days drifting prior to swimming (Leis 2010). Nonetheless, several hypothesis have been proposed to explain how swimming speed could influence dispersal and settlement. For example, faster swimming speeds could lead to greater dispersal distances if faster swimming larvae simply cover more area than slower swimming larvae (Nanninga and Manica 2018, Majoris et al. 2019). Alternatively, swimming could decrease dispersal distances (Trembl et al. 2015). If faster swimming larvae are better able to swim towards suitable settlement habitats, especially once developmentally competent, then they could increase local retention and avoid advection and further displacement that might occur in slower swimming larvae. Finally, swimming speed could show no association with dispersal distances, but still increase the probability of supply of competent larvae to settlement habitat (Drake et al. 2018), or have no effect on supply at all.

Evaluating hypotheses for how larval swimming affects dispersal are prohibitively challenging to address empirically for a series of reasons. To begin with, it is difficult to assess the larval phenotypes in the field (Leis and Carson-Ewart 1999, Paris et al. 2013) and to track individual larvae throughout their entire pelagic stage. Furthermore, estimating the effect of larval traits requires not only knowing the larval traits of settlers (Shima and Swearer 2009), but also the traits of larvae that were unsuccessful at settling. Finally, hydrodynamic forcings in marine environments vary greatly at a range of spatial and temporal scales. To detect a signal of swimming ability through this large amount of stochasticity requires the measurement of a very large number of larvae. Biophysical simulation models can, however, be analyzed in such a way to provide model-based estimates of these quantities (Mullon et al. 2002, Huebert and Sponaugle

2009, Sponaugle et al. 2012, Faillettaz et al. 2018). However, most biophysical models are developed to explore spatial patterns of population connectivity and their proximate causes, and though some studies have compared observed and modelled distributions of larvae or recruits (Jenkins et al. 1999, Burgess et al. 2007, Huebert and Sponaugle 2009, Sponaugle et al. 2012) or compared observed estimates of self-recruitment with modelled estimates of local retention (Nanninga et al. 2015), only one has, to date, statistically validated a biophysical model against direct empirical estimates of larval origin and destination (Bode et al. 2019).

Therefore, our overall goal was to use the empirically-validated high-resolution biophysical model of Bode et al. (2019) to answer three important, broadly applicable questions that are prohibitively challenging to address empirically. First, how does larval swimming, in combination with other realistic larval behaviors, affect dispersal distances and the spread of settlement locations, compared to dispersal of passive larvae? Second, what is the effect of larval swimming speed on dispersal distances? Third, how does larval swimming speed affect the probability of settlement? Settlement

is a crucial component of fitness in marine biphasic life cycles, which larval swimming speed is likely to affect. The model we use describes larval dispersal for the bar-cheek coral grouper *Plectropomus maculatus* (family Serranidae) among coral reefs distributed across a broad seascape in the southern Great Barrier Reef, Australia (Fig. 1). Importantly, the model explicitly incorporates empirically-derived estimates of spawning location and timing by adults and behavior by larvae, including swimming abilities.

The advantage of using this particular biophysical model is that it provides higher confidence that the predicted effects of swimming on dispersal reflect what would happen in nature if those effects were able to be estimated, compared to more generalized models with unrealistic assumptions and not based on any specific species. Bode et al. (2019) compared patterns of connectivity estimated from several biophysical models parameterized with different values of multiple larval traits against high-quality genetic parentage data that assigned individual settlers to parents in order to directly estimate dispersal origin and destination (Williamson et al. 2016). Several different types of formal statistical comparisons were used, including event matching, model likelihood and aggregate estimates of dispersal distance and direction. Bode et al. (2019) found that the dispersal distances calculated from positive parentage assignments reported in Williamson et al. (2016) could plausibly have been generated by a specific set of empirically-determined larval behavior parameters in the context of the regional hydrodynamic regime. The goodness of fit was strengthened by the fact that the parentage dataset was powerful enough to statistically exclude alternative behavioral parameterizations of the model. The poor fit of the passive model in Bode et al. (2019) confirms the importance of larval traits in influencing dispersal, and the poor fit of models with different parameterization of larval behaviors emphasizes the importance of the specific larval behaviors, which we focus on in our analysis here.

## Methods

### Biophysical model

The biophysical models we used are fully described in Bode et al. (2019). Only the features relevant to our purposes are described here. The model simulates larval dispersal among the inshore and mid-shelf reefs of the southern Great Barrier Reef (GBR) (Fig. 1), parts of which include *Plectropomus maculatus* habitat and the region where a genetic parentage dataset was sampled (Williamson et al. 2016). The hydrodynamic component of the model was based on a temporally implicit 3D barotropic scheme, built from three nested computational grids with resolutions of 1.85 km (1 nautical mile) for the whole GBR, 370 m for three focal regions where larvae were released from in the model, and 74 m around reefs within focal regions. The model incorporated a subgrid scale parameterization of hydrodynamic impedance around reefs that results in more accurate modelling of currents passing

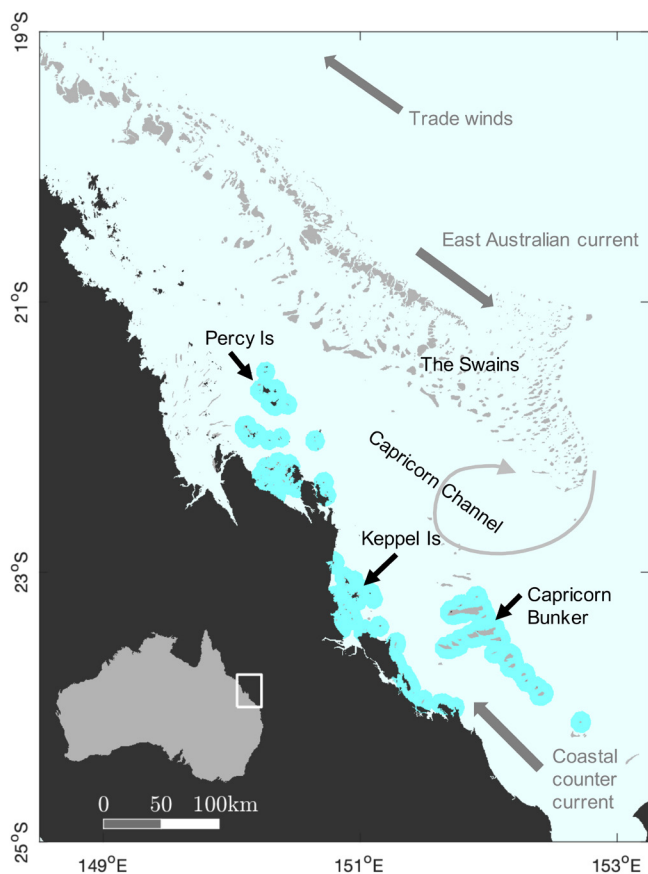


Figure 1. Map of the study region in the southern Great Barrier Reef, Australia, showing the location of reefs (potential settlement habitat, grey), locations of larval releases (blue highlight), which reflect the habitat of *Plectropomus maculatus* (Barcheek Coral Grouper; Serranidae) and land (black). Grey arrows depict dominant current and wind directions.

through the complex reef matrix. Currents were determined hourly. The hydrodynamic component of the model captures the dominant flows in the study region: northwest flowing surface currents that are predominantly driven by trade winds; variable flows during the austral summer when *P. maculatus* spawning is most intense and when tropical lows can cause southward current reversals; and a south-flowing boundary current (the East Australian Current) along the eastern edge of the outer reefs of the GBR that flows strongest during the austral summer, and periodically generates cyclonic eddy structures that create mesoscale recirculation patterns in the Capricorn Channel (Fig. 1). The numerical results have been validated with data from current meters.

The biological component of the model was an individual-based model that tracked each particle (virtual larva) in 5-min time steps from spawning to settlement. Two variants of the model were used, which we call the ‘swimming’ model and the ‘passive’ model. The swimming model used here is the ‘consistent’ behavior model of Bode et al. (2019), which reflected consistent differences among individuals and which provided the best fit to a contemporaneous genetic parentage dataset. It should be noted that the swimming model includes multiple larval behaviors in addition to swimming. We refer to it as the swimming model here because we are specifically interested in the effect of swimming by larvae on dispersal in the presence of other realistic, empirically determined, larval behaviors (Supporting information).

In both models, the timing and location of spawning was the same. Eggs were released at spawning locations in the middle of the water column, on the basis that, in spawning aggregations, *P. maculatus* start their upward spawning rushes near the bottom and release the eggs before reaching the surface. The vertical position of pelagic eggs thereafter was determined by a combination of positive buoyancy, that moved eggs towards the surface, and vertical turbulence in the water column that moved eggs upwards or downwards (see Table S2.1 of Bode et al. 2019 for further details). Eggs hatched within 27 hours. Planktonic eggs were input at the edges of reefs in three focal reef clusters where *P. maculatus* are typically found and where the model has been validated: the high-island archipelagos of the Keppels and Percy Islands, as well as the platform reefs of the Capricorn Bunker group (Fig. 1). Eggs were released each day for  $\pm 5$  days around each new moon between July 2011 and July 2013, reflecting empirical observations in *P. maculatus*, and which encompassed all dispersal events in the parentage dataset. There were, therefore, 24 releases from which dispersal matrices describing the origin and destination of virtual larvae were calculated for the swimming model and the passive model, respectively. Larvae were competent to settle by day 24, and were removed from the model if they had not settled by day 33 (based on observations of otoliths from 107 *P. maculatus* juveniles, where about 75% settled within 24–29 days of hatching, and where PLDs of longer than 34 days were not observed, Williamson et al. 2016). In both models, settlement-stage larvae were considered to have settled when competent larvae encountered a reef, following Bode et al. (2019). We assume that the very

high mortality that usually occurs in the field during and shortly after the period of transition between the pelagic and demersal environments (Almany and Webster 2006) is random with respect to larval swimming capability or speed, and is not spatiotemporally biased.

In the passive model, larvae were assumed to follow the same vertical distribution dynamics as passive eggs (i.e. subject to vertical turbulence), but acting as neutrally buoyant particles. The passive model was considered as a null model against which the swimming model can be compared to in order to estimate the specific effect of larval behavior on dispersal.

In the swimming model, the behavioral parameters were based on empirical data for *P. maculatus* (pelagic larval duration, spawning times, spawning locations and vertical distribution) or the most closely related and ecologically similar grouper species for which the required information was known (typically *P. leopardus* or *Epinephelus coioides*, see Table S2.2 in Bode et al. 2019 for complete details). The statistical fit of the biophysical model to genetic parentage data reported in Bode et al. (2019) in spite of these substitutions is therefore encouraging. The larval behavioral parameters include realistic sensory abilities, vertical migration, preferred depth, swimming speed and orientation, all in an ontogenetic context. All larval behavioral parameters were based on diver observation of larvae in situ, as well as plankton-net, light-trap and lab-based studies (Leis and Carson-Ewart 1999, Leis et al. 2009).

Behavioral parameters of larvae exhibited among-individual variation, in addition to diel, spatial and ontogenetic variation (Supporting information). Age based ontogenetic change in the model was conditioned on a linear growth assumption and the conversion of size-based behavioral information from the literature into age-based information (Supporting information). Among-individual variation was included by randomly sampling the behavior for each individual larva from cumulative probability distribution functions (CDFs) based on field measures, and which were defined for four different ontogenetic stages (Supporting information). The sampled value for each behavior was maintained throughout the ontogenetic stage, and was then resampled at the beginning of each subsequent stage from its CDF. Therefore, the model preserved rank orders among larvae for each behavior, but not between behaviors. See Bode et al. (2019) for further details.

## Vertical distribution

After eggs hatch, larvae in the swimming model were vertically distributed through the water column according to a relative depth distribution that changed with their ontogenetic stage. Larvae also exhibited different distributions during the day and night (diel variation). The location of a larva in the water column was randomly allocated at the beginning of each ontogenetic stage from the relative depth distribution. The relative depth distributions were stretched or compressed according to the local water column depth. That is, where the

water depth was less than 10 m, the deepest larvae occurred at half of the full depth. Between 10 and 35 m water column depth, the deepest larvae occurred at the full depth. For water depth greater than 35 m, the deepest larvae occurred at 35 m. The depth distributions of larvae were constructed from plankton-net and light-trap studies and diver observation of larvae in situ (see Table S2.2 of Bode et al. 2019 for complete literature sources).

### Larval orientation

Larval orientation was modelled using two parameters. The first was  $0 \leq \theta < 2\pi$ , which describes the angle of an individual's mean orientation, with  $\theta=0$  indicating a northward bearing. The second parameter,  $0 \leq r \leq 1$ , measures the precision of the larva's orientation as measured over the observation period (stochastic variation). A value of  $r=0$  corresponds to a uniform distribution of bearings – that is, a larva that moves in all directions with equal probability. A value of  $r=1$  indicates the opposite – that the larva consistently travels in the  $\theta$  – direction. Each larva was randomly allocated a particular location-independent ( $r, \theta$ ) pair from two independent CDFs. Most larvae swam directionally in situ (the within-individual mean value of  $r$  was  $0.59 (\pm SE 0.045)$ , based on data in Leis et al. 2009). There was no relationship between  $r$  and the size of the larvae.

At 24 days after hatching, larvae reached settlement competency (i.e. were developed enough to settle to demersal habitat). Once competent to settle, larvae inside a reef detection radius sensed, navigated and swam directly towards the nearest reef within their detection radius in their attempt to reach settlement habitat. The detection radius was 4 km, and was based on hearing abilities and the propagation of reef-based sound measured in GBR waters (4 km may even be conservative Radford et al. 2011). When outside a reef detection zone, orientation was determined in the same manner as in ontogenetic stage 4 (Supporting information).

### Swimming speed

Larval swimming speed increased throughout ontogeny at an overall rate of  $1.4 \text{ cm s}^{-1}$  for every millimeter increase in larval standard length (Leis and Carson-Ewart 1999, Leis et al. 2009). Importantly, a larva's swimming speed relative to other larvae was similar throughout ontogeny (i.e. rank was maintained). In addition, rank orders among larvae were not maintained between behaviors – that is, swimming speed was uncorrelated with other behaviors, such that faster swimmers differed in orientation in the same manner as poorer swimmers. Therefore, the effects of swimming on settlement are not confounded with other traits, and are estimated independently of any effects of body size or growth rate on swimming speed.

The measure of swimming speed used in our analyses was the swimming speed of each larva discounted by its within-individual orientation precision. Swimming speed therefore reflects the net displacement between each 5 min timestep,

rather than the speed along the swimming path of a larva between timesteps (the former being more relevant to dispersal and is similar to how swimming speed and orientation are measured in situ (Leis and Carson-Ewart 1999, Leis et al. 2009)). For larvae swimming at the same speed along their swimming path, a more variable swimming direction (lower  $r$ ) will result in slower net movement in the dominant direction  $\theta$ , hence slower discounted speed. Swimming speed is presented in the figures as the speed ( $\text{m s}^{-1}$ ) in the fourth ontogenetic stage, though it is important to remember that the effects of swimming speed reported here reflect the accumulated effects of swimming throughout ontogeny where rank is maintained (that is, some individuals are consistently faster swimmers than others).

### Analysis of the model to estimate the effects of larval swimming on dispersal

We assessed the effect of larval swimming on dispersal in multiple ways. First, we estimated the effect of larval swimming in the context of all larval behaviors by comparing population-level dispersal outcomes for the swimming model to those for the passive model. Second, we analyzed how variation in swimming speed among larvae relates to dispersal distance in the swimming model. Third, we specifically analyzed how variation in swimming speed among larvae relates to the probability of settlement in the swimming model. Analyses were based on a random selection of 10 000 virtual larvae from each of the 24 monthly releases, which covered the same time period as the parentage dataset used to validate the model (Bode et al. 2019).

We calculated the effect of larval swimming in the context of all larval behaviors as the difference between the mean, median, modal and maximum dispersal distances in the swimming model compared to the passive model for each release. The modal distance was calculated to the nearest kilometer. The maximum distance was calculated as the distance beyond which 1% of settlers dispersed. We also calculated differences in the spread of the 2-dimensional dispersal kernels, where the spread in each release was calculated as the sum of variances ( $\sigma^2$ ) along the east–west axis ( $X$ ) and north–south axis ( $Y$ ) as  $\sigma_X^2 + \sigma_Y^2 + 2\sigma_{X,Y}$  (where  $\sigma_{X,Y}$  is the covariance). In each release, we also calculated the percent local retention using different scales for 'local' ([the number of settlers within a certain radius from the natal site/the number of larvae released]  $\times 100$ ) and the percent settlement ([the number of settlers anywhere in the domain/the number of larvae released]  $\times 100$ ). We calculated the effect of larval behavior on local retention as the percent local retention in the swimming model minus the percent local retention in the passive model. The effect of larval behavior on percent settlement was calculated as the percent settlement in the swimming model divided by the percent settlement in the passive model.

To estimate the effect of larval swimming speed on dispersal distance of settlers, we calculated the mean, median and maximum dispersal distance for different swimming speeds using a rolling window approach. The window size was 0.04

$\text{m s}^{-1}$  and progressed by  $0.01 \text{ m s}^{-1}$ . Distances in each window were subtracted from the overall mean distance for that particular release to create mean standardized distances. The mid-point swimming speed for each window was plotted against the mean-standardized mean, median or maximum dispersal distance for each window.

To estimate the effect of larval swimming speed on the probability of settlement, we fit a binomial generalized linear model, with a logit link function. Each larva was assigned a 1 if settled, or a 0 if did not settle by day 33 or had been washed out of the domain. Larval swimming speed was fitted as a second order polynomial to allow for any curvature (on the logit scale). Separate models were fit for each monthly release in the swimming model.

## Results

### The effect of larval swimming and other behaviors on population dispersal kernels

The mean, median and modal dispersal distances in the swimming model were less than in the passive model in 22 (92%), 24 (100%) and 20 (83%), respectively, of the 24 releases (Fig. 2a). For example, in the middle 50% of releases (i.e. the box in Fig. 2a), the median dispersal distance was between 36 km and 88 km less in the swimming model compared to the passive model. Similarly, in the middle 50% of releases, the modal dispersal distance was between 10 km and 135 km less in the swimming model compared to the passive model. There was no consistent effect of larval behaviors on the maximum dispersal distance. For example, larval behavior decreased the maximum dispersal distance by between 1 km and 63 km in eight (33%) releases, and increased the maximum dispersal distance by between 3 km and 96 km in 16 (67%) releases. The variance in settlement locations was greater in the swimming model compared to the passive model in 23 out of 24 releases (Fig. 2b, Supporting information).

Local retention was almost always higher in the swimming model compared to the passive model for a range of local retention scales (Fig. 2b). For example, local retention within a 5 km radius of the natal site was between 0.65 and 10 percentage points higher in 20 (83%) of the 24 releases. The percent of larvae that settled at all was between 1.60 and 5.82 times higher in the swimming model than in the passive model in 23 (96%) of the 24 releases (Fig. 2c).

The spatial spread of settlement locations relative to the natal site was greater in the swimming model compared to the passive model (Fig. 2b, 3a–c, Supporting information). In the swimming model, larvae settled at reefs to the north–west, but also at reefs to the north–east of their natal site (Fig. 3b). In the passive model, larvae generally settled at reefs in a north–west direction from their natal reef, reflecting the direction of the dominant current (Fig. 3c). In both models, settlement patterns were influenced by the spatial distribution of potential settlement locations. Settlement in

the north–east and south–east quadrants in the swimming model reflected larvae that crossed the Capricorn Channel to settle on mid-shelf reefs in the Swains because they had reached the eastward-flowing portion of the eddy current in the channel (Fig. 1). This created the second minor peak in the one-dimensional dispersal kernel (Fig. 3a).

### The effect of larval swimming speed on dispersal distance

Faster swimming speeds led to a greater mean (in all but one release) and maximum dispersal distance compared to slower swimming speeds (in the exceptional release, the mean declined with swimming speed, Fig. 4a, c). However, swimming speed did not consistently affect the median dispersal distance (Fig. 4b). Therefore, larvae that settled the furthest from their natal site tended to be the faster swimmers, but swimming speed did not affect the distance up to which 50% of the larvae dispersed. In essence, slower swimming larvae settled at shorter distances, while faster swimming larvae settled in higher numbers at all distances and greater distances (Fig. 4d–f). Faster swimming also reduced the mean and median pelagic larval duration of settlers (Supporting information).

### Effects of larval swimming speed on settlement

The probability of settlement increased with larval swimming speed (Fig. 5). For the slowest swimming speed, the probability of settlement ranged from 0.17 to 0.49 in all but one release. For the fastest swimming speed, the probability of settlement ranged from 0.85 to 0.91 in all but one release. In release 12 (the lowest line in Fig. 5), overall settlement probability was relatively low, but the probability of settlement still increased from 0.01 for the slowest larval swimming speed to 0.36 for the fastest larval swimming speed.

## Discussion

Dispersal kernels emerge as a consequence of phenotype  $\times$  environment interactions. While it is increasingly recognized that small spiders and insects dispersing in wind currents (Bonte et al. 2007, Leitch et al. 2021), or marine larvae dispersing in water currents, are not completely at the whims of stochastic forcings, it has been difficult to predict how individual variation in phenotypes affects the emergence of population dispersal kernels (D'Aloia et al. 2015). For marine larvae in particular, much of the transport is likely to occur before larvae are developmentally competent to swim or to settle. Our analysis of a high resolution, empirically-validated, biophysical model with realistic adult and larval behaviors has generated clear predictions for how larval swimming can influence dispersal distances in an ecologically and economically important coral-reef fish. Individuals with different swimming speeds, including passive movement, contributed differentially to the emergence of the overall dispersal kernel for the population. Such phenotype-dependent

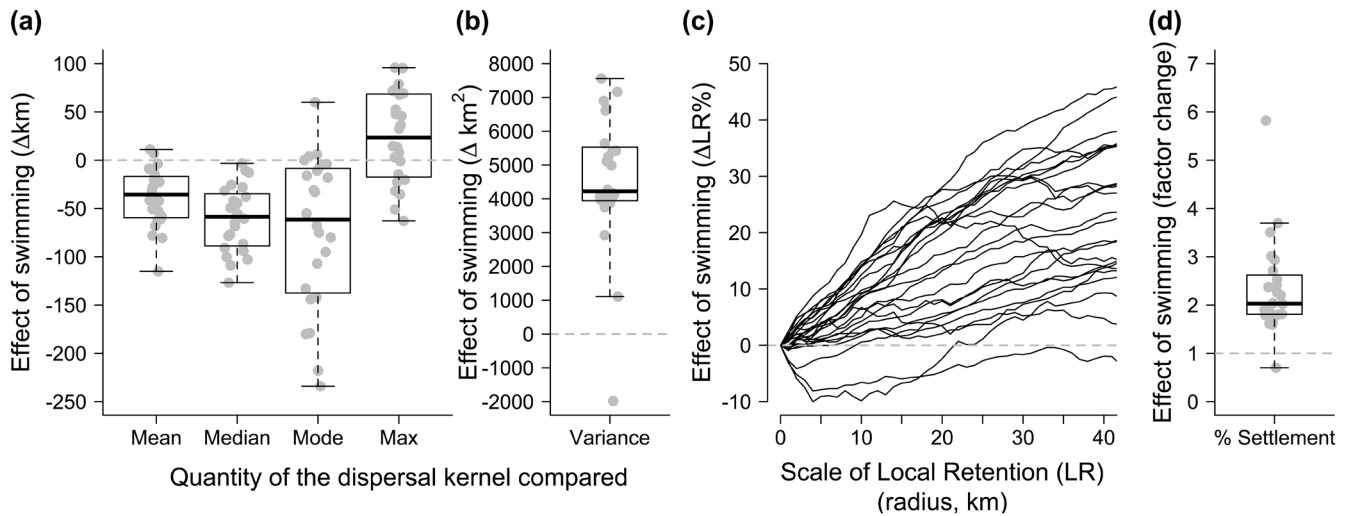


Figure 2. (a) The difference in the mean, median, mode and maximum dispersal distance ( $\Delta km$ ) between the biophysical model with and without larval swimming. (b) The difference in the 2-dimensional variance (spread) of dispersal distances ( $\Delta km^2$ ) between the biophysical model with and without larval swimming. (c) The difference in the percent local retention ( $\Delta LR\%$ ) for a given radius (km) around the natal site between the biophysical model with and without larval swimming. (d) The factor change in % Settlement in the biophysical model with swimming relative to the model without larval swimming. Each dot or line represents one of 24 monthly releases over a 2 year time period.

dispersal is important because it means that changes in composition of larval behaviors in the population will alter the distribution of dispersal distances in the same oceanographic regime. Furthermore, the composition of larval behaviors will differ across dispersal distances, which has important implications for adaptation and range expansion through natural selection and spatial sorting (Shine et al. 2011, Phillips and Perkins 2019).

Swimming had complex effects on dispersal. Despite intuition that swimming should lead to greater dispersal distances than simply remaining passive, larval swimming tended to increase local retention (reduce dispersal) but had no consistent effects on long-distance dispersal, compared to those of

passive larvae. Faster swimming larvae, in contrast, did not have greater median dispersal distances than slower swimming larvae, but did have greater mean and maximum dispersal distances, and settled sooner (i.e. younger). So although faster swimming larvae could settle at greater distances from the natal site than slower swimming larvae with otherwise similar behaviors, passive larvae dispersed even further in a third of the releases. Active larval behavior, including the ability to swim, acted to limit dispersal by facilitating navigation towards reefs within detection zones when larvae were competent to settle. Larval behavior also increased the dispersion of settlement locations from the natal site compared to that in releases with passive larvae because swimming

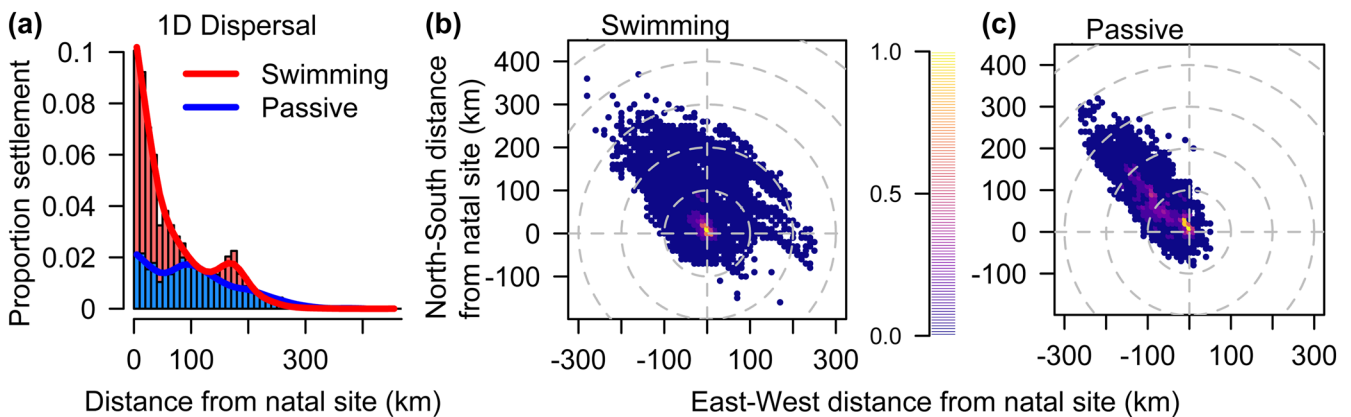


Figure 3. (a) One-dimensional dispersal kernels for biophysical models with (red) and without (blue) larval swimming. (b) Two-dimensional distribution of dispersal distances for the biophysical model with larval swimming. (c) Two-dimensional distribution of dispersal distances for the biophysical model without larval swimming (passive model). In (b) and (c), the color scale represents the relative density of settlers in  $10 \times 10$  km grid cells (proportion of settlers in each grid cell/maximum proportion of settlers in any grid cell, where proportion of settlers = number that settle/total released). Data shown here are all 24 releases from inner and mid shelf reefs in the southern GBR pooled. See Supporting information for the individual monthly releases.



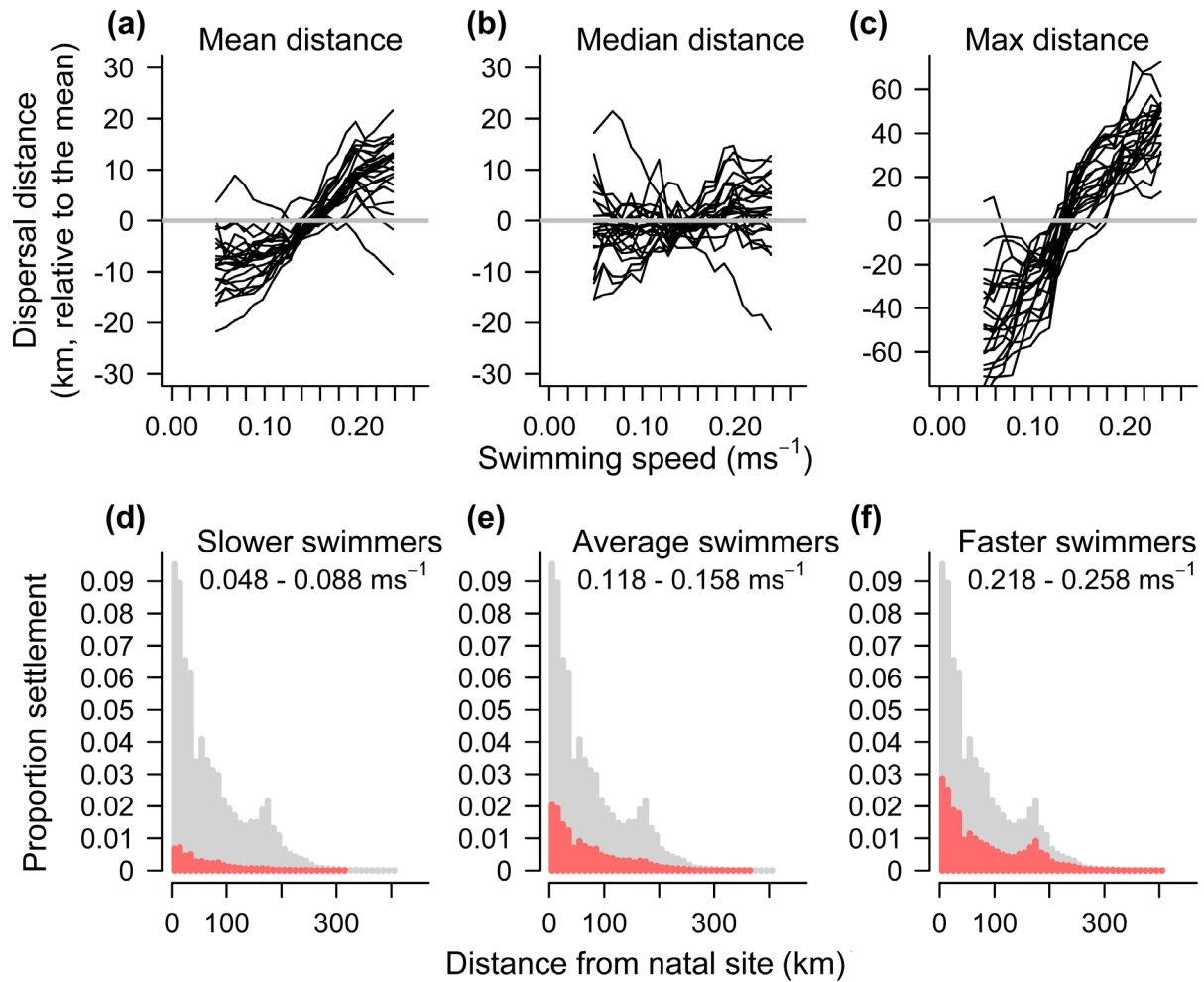


Figure 4. Top: the relationship between discounted swimming speed ( $\text{m s}^{-1}$ ) and the (a) mean, (b) median and (c) maximum mean-standardized dispersal distance for each release, using a rolling window. Each black line represents one of 24 releases over a 2 year time period. The grey line indicates the mean. Bottom: dispersal kernels (all releases combined) for nominally chosen (d) slower swimming larvae, (e) average swimming larvae and (f) faster swimming larvae. The grey bars represent all individuals (and are the same as that shown in Fig. 3a–b), while the red bars show the subset of larvae with a given swimming speed.

orientation varied among individuals and ontogenetically. Faster swimming led to greater maximum distances than slower swimming because larvae tended to swim directionally (i.e. relatively high precision, which was based on field data) without regards to current direction or the location of reefs prior to settlement competency, and when reefs were not within detection zones during competency. Larval swimming speed effectively stretched the tail of the dispersal kernel without affecting the distance up to which 50% of individuals dispersed.

We found that faster swimming larvae, which all had orientation and navigation capabilities, had a higher probability of reaching settlement habitat after attaining competency. Our model-based estimate of the effect of larval swimming on settlement is also likely to be conservative. Instantaneous daily larval mortality rates are estimated to be up to approximately 50% per day (D’Alessandro et al. 2010), but the model did not include larval mortality. The inclusion of larval mortality

in the model would only increase the steepness of the relationship between swimming speed and settlement probability, because slower swimming larvae spent about a day longer in the pelagic environment before settling than faster swimming larvae (Supporting information). It is unclear whether larval swimming, or other behaviors that consume energy, decrease physiological condition to the point where it would decrease survival before or after settlement (Leis and Clark 2005, Leis 2006). Larvae in situ feed while swimming (Leis and Carson-Ewart 1998), and variation in physiological condition of larvae is most often attributed to variation in food availability (Shima and Swearer 2009). Once the caudal fin forms, larvae of tropical reef fishes appear to swim efficiently in an inertial hydrodynamic environment, rather than at a high cost in a viscous environment (Leis 2006). If anything, larvae that swim faster may encounter more food in the plankton and have faster escape response from predators (Fuiman and Cowan Jr. 2003), which would also increase the

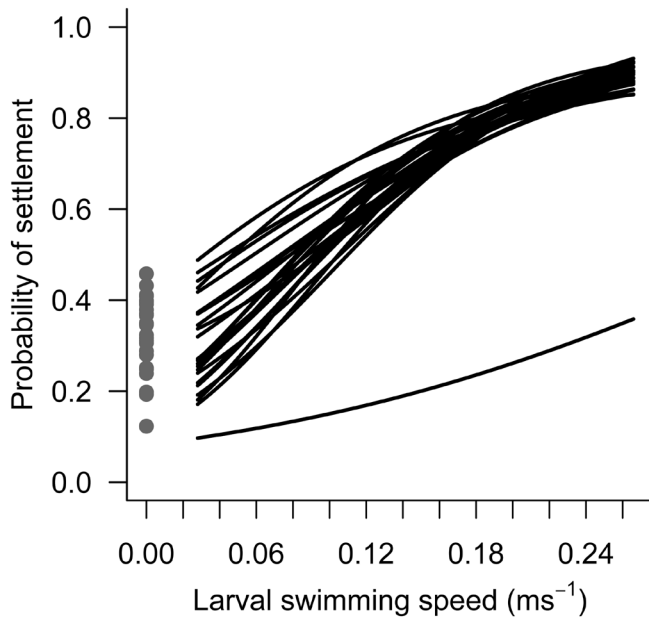


Figure 5. The relationship between discounted swimming speed and the predicted probability of settlement. Each line represents the fit from a binomial generalized linear model in each of the 24 monthly releases. The dots indicate the probability of settlement in the passive model without larval swimming.

steepness of the relationship between swimming speed and settlement probability.

Any effect of larval swimming speed on dispersal distance could be influenced by the spatial distribution, size and density of habitat patches. For example, the greater spread of settlement locations in the swimming model could occur if swimming larvae were better at crossing larger gaps between reefs, facilitating settlement at reefs in the Swains that are separated by a ~60 to ~160 km expanse of water (without reefs) from the natal site (Fig. 1). As a test of the potential effect of reef structure, we repeated our analyses by releasing virtual larvae from reefs in the Swains section of the GBR (Fig. 1, Supporting information). The Swains has a much higher reef density than the inshore reefs in our focal area. *Plectropomus maculatus* is less abundant in these mid-outer reef habitats, where it is replaced by congener species *P. leopardus* and *P. laevis*. We found that, in direct contrast to the releases from the inshore locations, faster larval swimming tended to reduce both the mean and median dispersal distance (Supporting information). The reduction of the mean and median dispersal distance for faster swimming larvae relative to slower swimming larvae in the Swains releases was due to a combination of factors. First, the slower net current speeds as a result of the dense reef matrix of the Swains reduced the NW displacement of larvae prior to the ontogenetic onset of swimming. Second, faster swimming larvae, especially during the second ontogenetic stage when larvae tended to swim south into the prevailing NW current flow, were displaced downstream less than slower larvae. In the Swains, the displacement was less than inshore because of the stronger prevailing current inshore. Third, the relatively low orientation

precision in the third ontogenetic stage caused larvae to generally swim away from reefs beyond their sensory zone in inshore releases (where there are large gaps between settlement habitat) but not in the Swains releases where there are reefs in all directions. As a consequence, larvae in the Swains releases largely remained within the reef matrix so were closer to settlement habitat when competent than in the inshore releases, so faster larvae settled sooner than slower larvae.

All biophysical models are necessarily specific for the particular region and the particular way behavior was parameterized, much like the results from any empirical field study. All species and locations are different in important ways. Furthermore, empirically studying how swimming speed affects dispersal and settlement would require thousands of tiny larvae to be phenotyped and tracked in the water column until they settled or died. Our results, therefore, are best interpreted as a test of a broadly applicable hypothesis in a setting where the underlying assumptions are clear, realistic, and have been validated against empirical data, which has led to more refined understanding for how larval swimming can affect dispersal. Any generalizations on how exactly larval fish swimming affects dispersal will only emerge after more studies like ours, and it will be informative to understand the extent to which the predictions generated here apply in other settings.

That said, aspects of our predictions are broadly similar to previous modelling studies in other locations, but where the combination of behavioral parameters used was not based on any specific species. For example, the modelling study by Treml et al. (2015) found that increased larval swimming speed decreased median dispersal distances in a semi-enclosed temperate marine bay (Port Phillip Bay, Victoria, Australia), and this outcome depended on when swimming develops, when directionality and sensing was used, and the distribution of habitat (Treml et al. 2015). The modelling study by Drake et al. (2018) concluded that shoreward swimming increased nearshore larval supply along an exposed coastline dominated by upwelling (the central Californian coast). The strength of this effect also depended on other larval behaviors and the ontogeny of swimming, but the spatial patterns of larval connectivity were similar with and without shoreward swimming.

Previous empirical studies have suggested that larval swimming speed relates to increased dispersal distance in a generalized way, but some predictions contrast with ours. For example, Nanninga and Manica (2018) found the population genetic differentiation (measured using  $F_{ST}$ ) was lower, and geographic range size was greater, in demersal marine fish species with faster, compared to slower, laboratory-derived prolonged swimming speeds (measured as  $U_{crit}$ , the most widely used measure of swimming capabilities in the laboratory for fish larvae; Downie et al. 2021) in settlement-stage larvae. Despite the low correlation between  $U_{crit}$  and swimming speeds measured in situ (Leis 2020), their result across species suggests that higher species-specific larval swimming abilities increases long-distance dispersal over timescales that influence gene flow. We found that faster swimming larvae

were capable of dispersing further than slower swimming larvae, but passive larvae frequently dispersed even further and both slow and fast swimmers settled at short distances. Similarly, Majoris et al. (2019) found that one species (*Plectropomus leopardus*) with a faster average larval swimming speed (again measured as U-crit), had a greater mean and maximum dispersal distance when measured directly with genetic parentage data, than two other, quite different, species of coral reef fish in different locations. Modal distances were unaffected by species-specific swimming speeds. We found similar outcomes when considering variation in swimming speed within a species while all else was equal, but in the context of other realistic behaviors, swimming of any ability decreased the mean, median and modal distances, and had no consistent effect on maximum distances, compared to passively dispersed larvae.

Our result leads us to a set of hypotheses. First, we hypothesize that selection favors faster larval swimming speed to increase settlement probability, but alters the distribution of dispersal distances as a by-product, in ways that depend on the distribution of suitable habitat and the presence of other larval behaviors that vary ontogenetically. For example, when reef density beyond the immediate vicinity of the natal reef is low, larvae that remain near natal reefs are more likely to encounter suitable habitat when competent than larvae that move far from natal reefs prior to competency. Once competent, faster swimming larvae reach reefs sooner if they are not swimming into the current. However, when reef density is relatively low, larvae must travel further to find reefs, and faster swimming larvae reach distant reefs quicker. Under this first hypothesis, there is nothing inherently better about natal sites, other than staying close to a reef increases the chance of settlement. Similarly, swimming faster would not be selected for its ability to increase dispersal distance as such, but would affect dispersal distance as a by-product of trying to locate reefs once larvae are competent to settle. Increasing the period of competence could be another way of increasing the likelihood of encountering suitable habitat without swimming, but a longer pelagic period would lead to an increase in cumulative mortality (Leggett and DeBlois 1994, D'Alessandro et al. 2010), so would be riskier than swimming faster. In fact, faster swimming reduced PLD relative to slower swimming. A second hypothesis is that selection favors larval behaviors that reduce displacement from natal sites at the same time as increasing the number of different settlement locations in all directions, not simply along the axis of the prevailing currents. While it reduced average dispersal distances from the natal site, the full behavioral repertoire increased the spread of settlement locations compared to that of passive larvae, consistent with that expected when dispersal functions to spread risk in unpredictable environments or avoid negative kin interactions. To test these hypotheses, one would need to know what the spatial and temporal scales of environmental variation and relatedness are relative to the scale of dispersal (Duputié and Massol 2013).

Even when dispersal is driven by complex winds and currents, individual traits of small animals can still regulate their dispersal (Clobert et al. 2009, Leitch et al. 2021), and individual

variation in traits provides the scope for selection and adaptation (Tung et al. 2018). Our analysis suggests that selection favors faster larval swimming by increasing settlement, which may actually result in longer dispersal distances as a by-product of larvae trying to locate habitat rather than to disperse as such (Burgess et al. 2016). Estimating the extent of heritable variation in larval swimming speed and covariation between swimming and other larval traits will therefore be important (Johnson et al. 2010). Because larval swimming speed has the consequence of altering the patterns of larval dispersal, rapid evolutionary changes in larval swimming speed could have observable ecological consequences (Johnson et al. 2014). An appreciation of larval behavior, not just in the sense that larvae have behaviors, but that individuals vary in their behaviors, will be important for future work on marine larval dispersal, and for organisms that move in wind or currents more generally.

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### Author contributions

**Scott C. Burgess:** Conceptualization (lead); Formal analysis (lead); Methodology (lead); Visualization (lead); Writing – original draft (lead); Writing – review and editing (lead). **Michael Bode:** Conceptualization (supporting); Formal analysis (supporting); Methodology (equal); Writing – review and editing (supporting). **Jeffrey M. Leis:** Conceptualization (supporting); Methodology (equal); Writing – review and editing (supporting). **Luciano B. Mason:** Methodology (equal); Software (lead).

### Data availability statement

Data are available from the Dryad Digital Repository: <<https://doi.org/10.5061/dryad.kwh70rz3j>> (Burgess et al. 2021).

### Supporting information

The supporting information associated with this article is available from the online version.

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