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REPORT

Positive spatial autocorrelation in three habitat quality indicators sets the stage for evolution of adaptive dispersal plasticity in a coral reef fish

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Abstract Dispersal, the movement of individuals away from their natal location to another location, is a basic driver of ecological and evolutionary processes. Direct measures of marine fish larval dispersal have shown that individual dispersal distances vary over several orders of magnitude within a species. We currently do not know the causes of this intraspecific variation. One plausible explanation is dispersal plasticity. Dispersal plasticity, especially as an adaptive parental effect where parents alter the dispersal phenotype of their offspring, is widespread in terrestrial systems, but has yet to be described in marine fishes. In this study, we address a key, although often untested, condition for the evolution of dispersal plasticity as an adaptive parental effect: whether parents can reliably predict the environmental conditions that their offspring will encounter. Using a wild population of orange anemonefish, *Amphiprion percula*, we investigate habitat quality predictability by testing for spatial autocorrelation in three habitat quality indicators: anemone size, female size, and egg clutch size. We found strong, positive spatial autocorrelation for all three habitat quality indicators to about 500 m. This suggests selection might favor parents that increase allocation to offspring that stay within 500 m if they are in good habitat and increase allocation to offspring that travel farther if they are in poor habitat. Results from this study lay solid foundations for further investigation of dispersal plasticity in *A. percula* and other marine fishes. Incorporating dispersal plasticity in our investigations of marine fish larval dispersal could contribute to a greater understanding of marine fish metapopulation dynamics, and therefore fisheries recovery and reserve management.

Keywords Adaptive parental effect · *Amphiprion percula* · Dispersal plasticity · Habitat predictability · Larval dispersal · Moran's index

Introduction

A major goal of marine fish ecology is to understand patterns of larval dispersal and causes of variation in these patterns

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(Sale et al. 2005; Berumen et al. 2012; Green et al. 2015). Many marine fishes have a bipartite life cycle composed of a reef resident phase and a dispersive larval phase (Leis and McCormick 2002). The spatial and temporal patterns of larval dispersal describe the rate of exchange of individuals and alleles between populations within a metapopulation, i.e., population connectivity (Botsford et al. 2001; Leis 2006; Cowen and Sponaugle 2009). Population connectivity has major consequences for everything from population persistence in ecological time (Gaines et al. 1985; Hastings and Botsford 2006; Hoegh-Guldberg et al. 2008) to population divergence in evolutionary time (Jablonski 1986; Taylor and Hellberg 2003; Clobert et al. 2009). Understanding the patterns and causes of marine larval dispersal will facilitate marine conservation efforts by informing reserve design (Botsford et al. 2009; Moffitt et al. 2011; Di Franco et al. 2012; Anadón et al. 2013; Green et al. 2015; Abesamis et al. 2017) and fisheries management (Kritzer and Sale 2004; Harrison et al. 2012; Almany et al. 2013).

The spatial pattern of dispersal can be usefully represented as a dispersal kernel, which describes the probability of successful dispersal as a function of distance (Nathan and Muller-Landau 2000; Nathan 2006; Bode et al. 2019). Currently, six marine fishes have had their dispersal kernel empirically estimated using parentage analyses (*Elacatinus lori,* D'Aloia et al. 2015; *Plectropomus maculatus* and *P. leopardus,* Williamson et al. 2016; *Amphiprion percula* and *Chaetodon vagabundus*, Almany et al 2017; *A. clarkii*, Catalano et al. 2021). Two of these estimates have been validated using other genetic methods (*A. percula*, Pinsky et al. 2017; *E. lori*, D'Aloia et al. 2018, Naaykens and D'Aloia 2022) and one using high-resolution biophysical models (*P. maculatus*, Bode et al. 2019). Within species, there are at least four orders of magnitude of variation among individual dispersal distances (e.g., 0.01, 0.1, 1 to 10 km). We still do not know what drives this variation and empirically investigating its causes is a crucial next step.

One plausible explanation for intraspecific variation in individual dispersal distances, above and beyond the effects of advection, diffusion, or simple variation in larval traits (Bode et al. 2019; Burgess et al. 2022), is that larval dispersal distance may be an adaptively plastic phenotype. There are many examples of dispersal plasticity in terrestrial systems in which parents produce offspring with an appropriate dispersal phenotype in response to the parental environment (Bowler and Benton 2005; Clobert et al. 2009). This type of plasticity is considered an adaptive parental effect (Badyaev and Uller 2009). For example, pea aphids exhibit a polymorphism in which clones from the same individual may be winged or unwinged. When a predator or parasitoid is present, or resources are too depleted, a female aphid can switch production to winged offspring that can escape and disperse to other plants (Weisser et al. 1999; Sloggett and Weisser 2002; Sutherland 1969). Although dispersal plasticity as a parental effect has been studied several times in terrestrial systems (e.g., in plants, Imbert and Ronce 2001; birds, Dingemanse et al. 2003; lizards et al. 1995; and insects, Harrison 1980), it has rarely been described in marine systems (e.g., in polychaete worms, Levin 1984; bryozoans, Burgess and Marshall 2011; and, sea slugs, Krug et al. 2012) and has not yet been described in marine fishes. Yet, many marine fishes experience the conditions under which dispersal plasticity might evolve (Warner 1991, 1997; Bowler and Benton 2005; Clobert et al. 2009).

Larval dispersal plasticity, like any phenotypic plasticity, is expected to evolve by natural selection if parents: (i) experience variation in environmental conditions, (ii) can reliably predict the environmental conditions that their offspring will encounter, (iii) can produce offspring with alternative dispersal phenotypes in response to environmental conditions, and (iv) the relative fitness of alternative dispersal phenotypes varies with environmental conditions (West-Eberhard 2003). Of these conditions, the second presents a particular challenge for marine fishes whose offspring disperse from where the parents reside. One way in which environmental conditions could be predictable is if there were positive spatial autocorrelation of habitat quality (Burgess and Marshall 2014). Spatial autocorrelation is an environmental phenomenon in which things that are closer together in space are more similar (Koenig 1999). For example, if there is positive spatial autocorrelation, parents that find themselves in good habitats can predict that they will be surrounded by good habitats up to some distance. Under such conditions, selection might favor parents that produce more short-distance dispersers when they find themselves in good environments and more long-distance dispersers when they find themselves in poor environments. The spatial scale of the positive spatial autocorrelation will indicate the spatial scale at which parents can accurately predict the surrounding environmental quality and thus the spatial scale to which alternative dispersal phenotypes might be adjusted (Burgess and Marshall 2014).

The clown anemonefish, *Amphiprion percula*, has emerged as a model system for investigating patterns of larval dispersal in the marine environment (Jones et al. 2022), and several lines of evidence suggest that conditions (i), (iii), and (iv) for the evolution of dispersal plasticity might be met in this species. Considering condition (i), adult clownfish spend their entire lives living in close association with sessile sea anemones (Elliott and Mariscal 2001; Buston 2003) and there is considerable variation in anemone size which influences female size, clutch size, and lifetime reproductive success (Fautin 1992; Buston and Elith 2011; Salles et al. 2016, 2019; Chausson et al. 2018; Barbasch et al. 2020). Turning to consider condition (iii), larval clownfish vary in their size, physiology, and swimming abilities (Majoris et al. 2019; Kunzmann and Diemel 2020), which could plausibly influence their dispersal distance (Clobert et al. 2009; Buston et al. 2012; Ronce and Clobert 2012; Almany et al. 2017), and new evidence suggests that parents produce different larval phenotypes in response to variation in environmental conditions (Francis et al. in preparation). Finally, considering condition (iv) the relative fitness of alternative larval phenotypes will vary with environmental conditions if there is positive spatial autocorrelation in habitat quality: when conditions are good, short-distance dispersers will fare well relative to long-distance dispersers, and the converse will be true when conditions are poor. The next step is to investigate condition (ii), whether parents can reliably predict the environmental conditions that their offspring will encounter. Although this is a critical step in any investigation of dispersal plasticity as an adaptive parental effect, it is often left untested (Burgess and Marshall 2014).

Here, we investigate whether condition (ii), predictability of environmental conditions, is met in a wild population of orange clownfish, *Amphiprion percula.* First, we test for spatial autocorrelation in habitat quality using three habitat quality indicators: anemone size, which is indicative of resource availability; female size, which is indicative of how long a female has lived and how fast she has grown; and egg clutch size, which is indicative of reproductive success. Second, we determine the scale of spatial autocorrelation by evaluating the relationship between correlations of each indicator between individuals within incrementally increasing distance bands. Finally, we discuss the implications of the observed spatial autocorrelation in indicators of habitat quality for the evolution of larval dispersal plasticity. Results from this study lay solid foundations for further investigation of dispersal plasticity in *A. percula* and other marine fishes, providing a plausible and testable hypothesis for probable causes of individual dispersal distance variation.

Methods

Study population

We conducted this study on nine patch reefs near the Mahonia Na Dari Research and Education Center in Kimbe Bay, Papua New Guinea. *Amphiprion percula* habitat at this site has been previously mapped and studied (Chausson et al. 2018; Rueger et al. 2018; Rueger et al. 2021, 2022; Barbasch and Buston 2018; Barbasch et al. 2020; Branconi et al. 2020). For one lunar month in June 2018, we visited each patch reef every other day to observe 120 breeding pairs of *A. percula* residing in magnificent sea anemones, *Heteractis magnifica*. We exhaustively surveyed every *H. magnifica* hosting *A. percula* at depths up to 20 m while on SCUBA. During our study period, 71 breeding pairs produced at least one egg clutch and were used for analyses.

Spatial information

We recorded the geographic coordinates of each anemone with a handheld GPS (Garmin eTrex 10; Garmin Ltd., USA) towed along the surface while diving. To do this, we recorded the time that the GPS was held taught above each anemone, while it was in the mode to collect track lines. From these tracks, we retrospectively extracted the latitude and longitude coordinates at each recorded time. We uploaded the coordinates of each anemone as XY points in ArcGIS Pro Version 2.9.0 (Esri Inc. 2011) with attributing measures of habitat quality indicators. Points were projected using the WGS 1984 UTM 56 South datum for spatial analyses (Fig. 1).

Measures of habitat quality indicators

We estimated anemone size as the area of its oral surface by measuring both the minor and major diameters to the

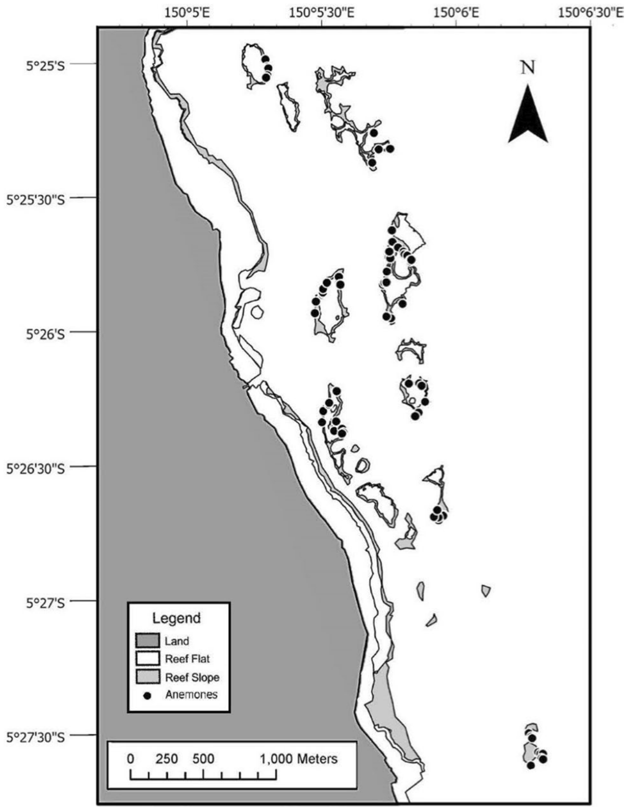

Fig. 1 Map of study site in Kimbe Bay, Papua New Guinea. Black points indicate the 71 anemone locations with breeding pairs of *Amphiprion percula*, found on the reef slope (light gray; 5–20 m deep)

nearest cm using a soft measuring tape underwater, then calculating the area of the oral surface using the formula for an ellipse (e.g., Hattori 1991, 1995; Mitchell and Dill 2005; Holbrook and Schmitt 2005; Barbasch et al. 2020). We measured anemone size twice over the course of the study period and used the average of the two measurements in analyses.

We measured female size as standard length (the length from the tip of the snout to the end of the caudal peduncle). To do this, we individually captured females using hand nets and placed them inside clear plastic bags. While the fish was held flat against a dive slate, we measured her to the nearest 0.1 mm using calipers while underwater and then released back to their anemone. Female size was also measured two times over the study period, and we used the average of the two measurements in analyses.

We surveyed each breeding pair every other day and recorded the presence and age of egg clutches. Egg clutches are easily detectable at the base of the anemone and aged according to the embryos' color and eye development (Buston 2004; Barbasch et al. 2020). We took two photographs of each clutch, at first detection (day 1 or 2), and before natural hatching (day 6 or 7), with an underwater camera (Olympus Tough TG-870; Olympus, Tokyo, Japan). We counted the number of eggs per clutch, or clutch size, from the first of the set of photographs in Image J (Rasband 1997; NIH, USA). In the rare event that we missed a new clutch of eggs and did not get a photograph on day 1 or 2, we counted clutch size from the photo at day 6 or 7.

Spatial statistical analyses

To test for spatial autocorrelation (SA) of habitat quality indicators, we calculated Moran's index (Moran 1948). Moran's index (*I*) is a correlation coefficient that describes whether values of attributes are significantly dispersed, random, or clustered in space (Dale and Fortin 2014). The value of *I* ranges from − 1 to 1, where a negative value signifies a dispersed spatial pattern, 0 signifies a random pattern, and a positive value signifies a clustered pattern. The value of *I* indicates the intensity of the spatial pattern. For example, larger, positive values (closer to 1) indicate more intense clustering of similar values of attributes (Dale and Fortin 2014). *I* is calculated from the following equation,

$$I = \frac{n}{S_0} \frac{\sum_{i=1}^{n} \sum_{j=1}^{n} w_{i,j} z_i z_j}{\sum_{j=1}^{n} z_i^2}$$

where n is the number of features, S_0 is sum of all the spatial weights, i and j denote two features, $w_{i,j}$ is the spatial weight between those features, and z is the deviation of the attribute at that feature from the mean.

To determine the spatial scale of habitat predictability, we used the Incremental Spatial Autocorrelation tool in ArcGIS Pro to calculate *I* for each habitat quality indicator across increasingly larger distance bins. We calculated *I* for anemones that were within each distance bin, starting with anemones that were within 50 of each other, and incrementally increasing the distance threshold by 50 m. In other words, we calculated *I* for anemones that were 0–50 m apart, then 0–100 m apart, 0–150 m apart, etc., until we included our entire sample population.

As a general rule for this calculation, there should be at least 30 features (Cliff and Ord 1981; Legendre and Fortin 1989; Fortin 1990). Any distance less than 50 m resulted in less than 30 anemones, so this informed our shortest distance bin and we made this our resolution for bin size. We investigated alternative bin sizes, but increasing the distance bin increment, e.g., 0–100 m, 0–200 m, etc., does not fundamentally change the results or conclusions and provides less details.

The Incremental Spatial Autocorrelation tool also calculates an expected index value for an absence of spatial autocorrelation (i.e., a random distribution of values for anemones size, female size, and clutch size). Given the number of pairwise anemones within each bin and the variance between the expected and observed index values, the tool computes a *p* value indicating whether the difference is statistically significant. The resulting *I* and *p* value at each incrementally larger distance bin allows us to detect the scale at which there is spatial autocorrelation. This method is used widely by ecologists to describe spatial autocorrelation of biologically relevant environmental conditions in their studies (reviews by Fortin 1990; Koenig 1999; Diniz-Filho et al. 2003; Mathur 2015; Kim 2021).

Importantly, we needed to correct for potentially misleading results from tests of spatial autocorrelation (SA) for multiple habitat quality indicators. Anemone size, female size, and clutch size are highly correlated with one another: larger anemones host larger females, and larger females lay larger clutches (Fautin 1992; Buston and Elith 2011; Chausson et al. 2018; Barbasch et al. 2020). To disentangle SA in female size that might be caused by SA in anemone size from independent SA in female size, and SA in clutch size that might be caused by SA in female size from independent SA in clutch size, we performed the spatial statistical analyses described above on the residuals of these metrics from their known relationship with each other (Koenig 1999). We obtained residuals by performing two linear regression models (*lme4* package in R (Bates et al. 2015)) with female size as the response variable and anemone size as the predictor variable, and with clutch size as the response variable and female size as the predictor variable. We then calculated *I* for both residual female size and for residual clutch size across distance as described above.

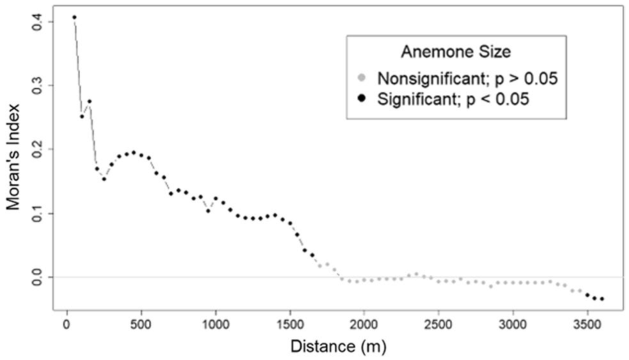

Fig. 2 Autocorrelogram of anemone size. Each point is the calculated Moran's index for all pairs of anemones within a distance class, incrementally increasing by 50 m. Black points indicate positive spatial autocorrelation when greater than 0, while gray points are non-significant, indicating a lack of spatial autocorrelation

Results

Anemone size

The average anemone area (± standard error (SE)) was 56.42 ± 313 cm^2 (Supplemental Fig. S1). Moran's *I* values indicated that anemone size was positively autocorrelated from the 0–50 m bin up to the 0–1,600 m bin (Fig. 2). This relationship is largely driven by the greatest correlation between anemone sizes within 50 m of each other (Moran's Index = 0.408, expected index = – 0.02, variance = 0.022, *z*-score = 2.85, *p*-value = 0.004).

Female size

The average female standard length (± SE) was 54.7 ± 0.7 mm (Supplemental Fig. S2). Moran's *I* values indicated that female size was also positively autocorrelated from the 0–50 m bin up to the 0–1600 m bin (Fig. 3a). This relationship is largely driven by the greatest correlation between female sizes within 50 m (Moran's index = 0.371, expected index = – 0.02, variance = 0.021, *z*-score = 2.71, *p*-value = 0.007).

Anemone size was a positive, significant predicator of female size (Supplemental Figure S4), suggesting that the spatial autocorrelation in female size might be driven by the spatial autocorrelation in anemone size. However, Moran's *I* values indicated that residuals of female size on anemone size were also positively autocorrelated from the 0–300 m bin through the 0–500 m (Fig. 3b). The greatest correlation between residuals occurred between anemones within 450 m of each other (Moran's index = 0.114, Expected index = – 0.015, Variance = 0.003, *z*-score = 2.37, *p*-value = 0.018). This result suggests that there is additional SA in female size from 0 to 300 m through 0 to 500 m that is independent of the SA in female size that might be caused by SA in anemone size.

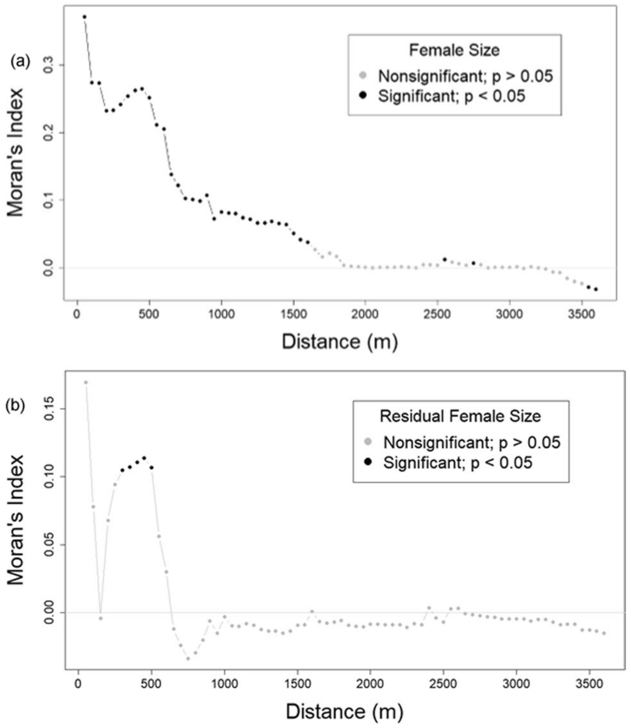

Fig. 3 Autocorrelogram of **a** female size and **b** residual female size. Each point is the calculated Moran's index for all pairs of females within a distance class, incrementally increasing by 50 m. Black points indicate positive spatial autocorrelation when greater than 0, while gray points are non-significant, indicating a lack of spatial autocorrelation

Clutch size

The mean size of the first clutch laid in the lunar cycle (± SE) was 241 ± 16 eggs (Supplemental Fig. S3). Moran's *I* values indicated that clutch size was positively autocorrelated from the 0–100 m bin to 0–2850 m bin (Fig. 4a). This relationship is largely driven by the greatest correlation between clutch sizes within 100 m (Moran's Index = 0.414, expected index = – 0.015, variance = 0.01, z-score = 4.191, *p*-value < 0.001).

Female size was a positive, significant predicator of clutch size (Supplemental Figure S5), suggesting that the spatial autocorrelation in clutch size might be driven by the spatial autocorrelation in female size. However, Moran's *I* values indicated that the residuals of clutch size on female size were also positively autocorrelated from the 0–100 m bin through to the 0–900 m bin, and from the 0–1,800 m bin through to the 0–2,700 m bin. (Fig. 4b). The greatest correlation between residuals occurred between anemones within 100 m (Moran's index = 0.244, Expected Index = – 0.015,

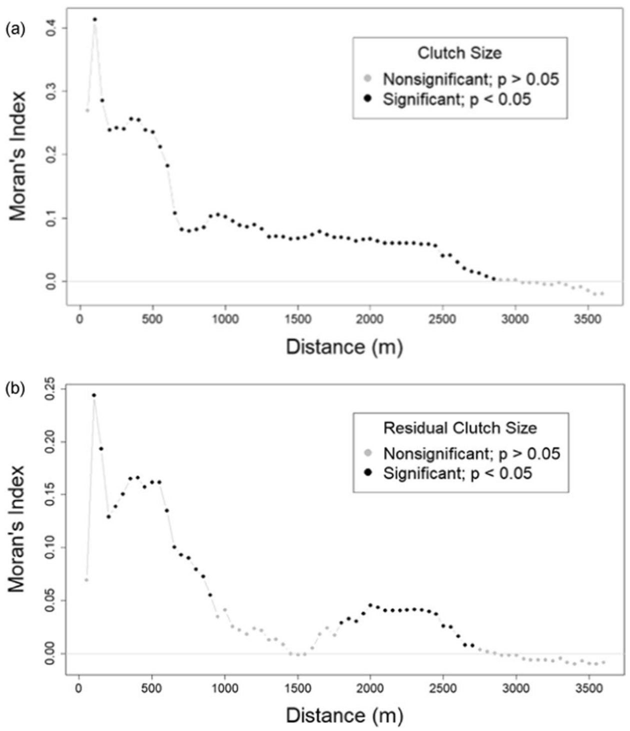

Fig. 4 Autocorrelogram of **a** clutch size and **b** residual clutch size. Each point is the calculated Moran's index for all pairs of clutches within a distance class, incrementally increasing by 50 m. Black points indicate positive spatial autocorrelation when greater than 0, while gray points are non-significant, indicating a lack of spatial autocorrelation

variance = 0.01, z-score = 2.541, *p* value = 0.011). This result suggests that there is additional SA in clutch size from 0–100 m through 0–900 m, and from 0–1,800 m through 0–2,700 m, that is independent of the SA in clutch size that might be caused by SA in female size.

Discussion

Measures of marine fish dispersal using genetic parentage analysis are relatively new, and one remarkable finding is that larval dispersal distance can vary over several orders of magnitude (D'Aloia et al. 2015; Williamson et al. 2016; Almany et al. 2017; Catalano et al. 2021). Currently, we do not know the causes of this substantial variation in individual dispersal distances within species. For reef fishes that have relatively restricted home ranges, it is plausible that larval dispersal distance might be an adaptive, plastic response to variation in parental habitat quality (Warner 1997), since an informed dispersal phenotype is expected to offer an evolutionary advantage over a fixed process (Ronce 2007). While this has never before been demonstrated in a marine fish, dispersal plasticity is widespread in other systems (Bowler and Benton 2005; Arendt 2015), which has motivated our investigation of such a phenomenon in one of the model systems for dispersal in marine fishes: the orange clownfish, *Amphiprion percula* (Jones 2022). When considering the hypothesis that a marine fish could adjust the dispersal distance of its offspring, we must first establish whether parents can reliably predict the quality of habitat that their offspring will encounter (Burgess and Marshall 2014). One obvious way for parents to do this is if there is positive spatial autocorrelation of habitat quality. Although positive spatial autocorrelation is often an inherent property of natural systems (Koenig 1999), establishing this environmental pattern addresses a key criterion for the evolution of dispersal plasticity.

In this study, we found positive spatial autocorrelation (SA) of multiple habitat quality indicators for *Amphiprion percula*. Anemone size, female size, and clutch size are all positively autocorrelated in space—the closer two features are, the more similar their attributes are. This indicates that the environmental conditions that influence habitat quality pertinent to *A. percula* are predictable in space. This result suggests that *A. percula* parents may reliably predict their surrounding habitat. Given this predictability in habitat quality, parents may be able to adaptively alter their offspring's dispersal. Parents that are in large anemones, with large females and greater reproductive output, may reliably predict that they are surrounded by potential homes for their offspring of similarly high quality, and natural selection may favor increased allocation to short-distance dispersal so that their larvae stay within the high-quality habitat. In contrast, parents experiencing a low-quality habitat can reliably predict that the surrounding habitat is also of low quality, and natural selection will favor increased allocation to long-distance dispersal so that larvae increase their chances of finding better quality habitat. Without positive spatial autocorrelation of the environmental conditions that would affect their offspring's future fitness, habitat quality would be unpredictable, and therefore, an adaptive dispersal phenotype would be unlikely. We note that the occurrence of spatial autocorrelation in habitat quality does not necessarily mean that dispersal plasticity will evolve by natural selection because other conditions for the evolution of dispersal plasticity must be met, e.g., parents must be able to produce alternative larval phenotypes, and other evolutionary responses are possible, e.g., parents may produce offspring that are locally adapted to high- or low-quality habitat. However, our results do provide evidence for this key condition for the evolution of dispersal plasticity in *A. percula*.

In addition to the *occurrence* of positive spatial autocorrelation, the *scale* of SA indicates the spatial limits on the parents' ability to predict habitat quality based on the habitat quality in their own home range. Consequently, it will indicate the distance threshold around which dispersal might be adjusted. For a dispersal distance to be favored by selection, the distinction between a relatively short- versus long-distance dispersal phenotype will be defined by the bounds of the area that the parents can predict and respond to. For example, here we found strong positive spatial autocorrelation between anemones that were within about 500 m of each other for all three habitat quality indicators, and weaker positive spatial autocorrelation out to a greater distance that depends on the indicator. This suggests that selection would favor parents that increase allocation to offspring that stay within 500 m if they are in good habitat and increase allocation to offspring that travel farther than this if they are in poor habitat. For our study population, this translates to a decision between staying or leaving the natal reef because each patch reef is about 500 m apart from the next patch reef (Fig. 1). Our results identify a spatial scale to which dispersal plasticity might be tuned over evolutionary time.

In summary, we found predictability of habitat quality by multiple indicators within a natural population of *A. percula*, testing a critical condition for the evolution of adaptive dispersal plasticity in a marine fish. At our study site, parents may reliably predict the qualities of nearby habitat at a scale of 500 m, based on the qualities of their own habitat. Some major caveats to this conclusion are that we only studied (i) one place at (ii) one time. Considering the first caveat, due to the prevalence of SA as an ecological phenomenon (Koenig 1999), we anticipate that since we found positive spatial autocorrelation here, it will be found in other *A. percula* populations elsewhere. Further, while the exact spatial scale of SA might vary from one place to the next, there is no reason to think that it will be orders of magnitude larger or smaller. However, it would be important to evaluate the strength and scale of SA in any population used in future investigations of dispersal distance plasticity. Not only to evaluate the ubiquity of our result, but it would be interesting to see if variation in SA is related to variation in dispersal distance among populations. Moving to considering the second caveat, that we only studied one time, we suggest that our inclusion of multiple indicators of habitat quality that operate on different timescales may address this concern. Clutch size may indicate the habitat quality over previous weeks, because it reflects short-term changes in food availability (Barbasch et al. 2020); female size may indicate the habitat quality over previous years, because it reflects growth over time (Buston 2002; Buston and Garcia 2007); anemone size may indicate the habitat quality over previous decades, because giant tropical sea anemones live for a very long time (Ottaway 1980; Goodfriend 1997). Still, it would be important to investigate temporal autocorrelation explicitly in future investigations because both spatial and temporal habitat predictability are required for dispersal plasticity to evolve in response to selection (Burgess and Marshall 2014). In sum, while our conclusions are limited to our sample population, our comparable results for three different indicators that operate on different timescales suggest that similar results would be possible at other times and places.

While we addressed a key, although often untested, condition for the evolution of dispersal plasticity as an adaptive parental effect (Burgess and Marshall 2014), there are further important steps to take to test the hypothesis that *A. percula* exhibits dispersal plasticity. To explore adaptive dispersal plasticity as a potential explanation for variation in observed larval dispersal, we need to determine whether additional conditions for plasticity to evolve are met. A first step would be to test whether parents have the ability to produce offspring with alternative dispersal phenotypes in response to variation in habitat quality. There is evidence from laboratory studies that parents produce larvae with different body sizes in response to variation in food availability: counterintuitively, compared to parents in high-quality environments (high food availability), parents in poor quality environments (low food availability) produce relatively large offspring potentially increasing the distance their offspring can disperse (Francis et al. in preparation). A second step would be to test whether offspring from different quality environments have different dispersal distance distributions in the wild. We predict that parents living in large anemones, with a large body size, producing large clutches will increase their allocation to larvae that travel short distances and reduce their allocation to larvae that travel long distances, compared to parents living in small anemones, with a small body size, producing small clutches. For now, results from this study suggest dispersal plasticity is plausible in *A. percula*, and importantly, it also gives us a testable prediction for the scale at which dispersal plasticity may occur.

Lastly, there are potentially important broader implications of adaptive dispersal plasticity in marine fishes. Explicitly considering the potential for dispersal plasticity may help us to better predict metapopulation dynamics, enhancing fishery and conservation science. For example, dispersal plasticity may help to explain why certain fisheries collapse. The perceived mortality rates or habitat degradation associated with fishing may be adjusting the dispersal strategies of the offspring of the remaining fish. This could intensify the effect of fishing on local population numbers if offspring disperse elsewhere rather than repopulate the local stock. This feedback loop may work both ways however, which would provide additional support for the use of reserves as a conservation strategy. If habitat quality is improved within a reserve, plasticity of dispersal may drive strategies to remain within the population, re-establishing healthy population levels. While reserves that increase habitat quality may have increased connectivity to other populations due to an increase in larval production, they may, counterintuitively, have reduced connectivity because the larvae are less likely to disperse. In sum, this study's result provides an important, initial step in exploring the possibility of an otherwise overlooked process that could explain variation in marine fish dispersal patterns and potentially could contribute to a greater understanding of marine fish metapopulation dynamics and therefore fishery recovery and reserve management.

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Data availability statement The datasets generated and analyzed during the current study are available in RKF's public GitHub repository, https://github.com/robinkellyfrancis/ApercuIaSpatialAutocorr.

Declarations

Conflict of interests The authors declare no competing interests.

References

Abesamis RA et al (2017) Reef-fish larval dispersal patterns validate no-take marine reserve network connectivity that links human communities. Coral Reefs 36:791–801

Almany GR et al (2013) Dispersal of grouper larvae drives local resource sharing in a coral reef fishery. Curr Biol 23(7):626–630

Almany GR et al (2017) Larval fish dispersal in a coral-reef seascape. Nat Ecol Evol 1(6):0148

Anadón JD et al (2013) Habitat-specific larval dispersal and marine connectivity: implications for spatial conservation planning. Ecosphere 4(7):1–15

Arendt JD (2015) Effects of dispersal plasticity on population divergence and speciation. Heredity 115(4):306–311

Badyaev AV, Uller T (2009) Parental effects in ecology and evolution: mechanisms, processes and implications. Phil Trans Royal Soc B 364:1169–1177

Barbasch TA, Buston PM (2018) Plasticity and personality of parental care in the clown anemonefish. Anim Behav 136:65–73

Barbasch TA et al (2020) Substantial plasticity of reproduction and parental care in response to local resource availability. Oikos 129:1844–1855

Bates, D et al (2015) Parsimonious mixed models. arXiv preprint arXiv:1506.04967

Berumen ML et al (2012) Persistence of self-recruitment and patterns of larval connectivity in a marine protected area network. Ecology and evolution 2(2):444–452

Bode M et al (2019) Successful validation of a larval dispersal model using genetic parentage data. PLoS Biol 17(7):e3000380

Botsford LW et al (2001) Dependence of sustainability on the configuration of marine reserves and larval dispersal distance. Ecol Lett 4(2):144–150

Botsford LW et al (2009) Connectivity and resilience of coral reef metapopulations in marine protected areas: matching empirical efforts to predictive needs. Coral Reefs 28(2):327–337

Bowler DE, Benton TG (2005) Causes and consequences of animal dispersal strategies: relating individual behaviour to spatial dynamics. Biol Rev 80(2):205–225

Branconi R et al (2020) Ecological and social constraints combine to promote evolution of non-breeding strategies in clownfish. Commun Biol 3:649

Burgess SC, Marshall DJ (2011) Temperature-induced maternal effects and environmental predictability. J Exp Biol 214(14):2329–2336

Burgess SC, Marshall DJ (2014) Adaptive parental effects: the importance of estimating environmental predictability and offspring fitness appropriately. Oikos 123(7):769–776

Burgess SC et al (2022) Individual variation in marine larval-fish swimming speed and the emergence of dispersal kernels. Oikos 3:e08896

Buston PM (2002) Group structure of the clown anemonefish *Amphiprion percula*. Cornell University, Ithaca

Buston PM (2003) Size and growth modification in clownfish. Nature 424:145–146

Buston P (2004) Does the presence of non-breeders enhance the fitness of breeders? An experimental analysis in the clown anemonefish *Amphiprion percula*. Behav Ecol Sociobiol 57:23–31

Buston PM, Elith J (2011) Determinants of reproductive success in dominant pairs of clownfish: a boosted regression tree analysis. J Anim Ecol 80:528–538

Buston PM, Garcia MB (2007) An extraordinary life span estimate for the clown anemonefish *Amphiprion percula*. J Fish Biol 70:1710–1719

Buston PM et al (2012) Probability of successful larval dispersal declines fivefold over 1 km in a coral reef fish. Proc R Soc b: Biol Sci 279(1735):1883–1888

Catalano KA et al (2021) Quantifying dispersal variability among nearshore marine populations. Mol Ecol 30(10):2366–2377

Chausson J et al (2018) Host anemone size as a determinant of social group size and structure in the orange clownfish (*Amphiprion percula*). PeerJ 6:e5841

Clobert J et al (2009) Informed dispersal, heterogeneity in animal dispersal syndromes and the dynamics of spatially structured populations. Ecol Lett 12(3):197–209

Cowen RK, Sponaugle S (2009) Larval dispersal and marine population connectivity. Ann Rev Mar Sci 1(1):443–466

D'Aloia CC et al (2015) Patterns, causes, and consequences of marine larval dispersal. Proc Natl Acad Sci USA 112:13940

D'Aloia CC et al (2018) Limited dispersal explains the spatial distribution of siblings in a reef fish population. Mar Ecol Prog Ser 607:143–154

Dale MR, Fortin MJ (2014) Spatial analysis: a guide for ecologists. Cambridge University Press, Cambridge

Di Franco A et al (2012) Dispersal patterns of coastal fish: implications for designing networks of marine protected areas. PLoS ONE 7(2):e31681

Dingemanse NJ et al (2003) Natal dispersal and personalities in great tits (*Parus major*). Proc R Soc Lond Ser b: Biol Sci 270(1516):741–747

Diniz-Filho JAF et al (2003) Spatial autocorrelation and red herrings in geographical ecology. Global Ecol Biogeogr 12(1):53–64

Elliott JK, Mariscal RN (2001) Coexistence of nine anemonefish species: differential host and habitat utilization, size and recruitment. Mar Biol 138:23–36

Esri Inc. 2011. ArcGIS Pro Version 2.9.0. Redlands, CA: Environmental Systems Research Institute

Fautin DG (1992) Anemonefish recruitment: the roles of order and chance. Symbiosis 14:143–160

Fortin MJ et al (1990) Spatial autocorrelation and sampling design in plant ecology. In: Progress in theoretical vegetation science. Springer, Dordrecht

Francis et al. Plasticity of larval dispersal-related traits in response to changes in parental environment in a coral reef fish (**in preparation**)

Gaines S et al (1985) Spatial variation in larval concentrations as a cause of spatial variation in settlement for the barnacle. Balanus Glandula Oecologia 67(2):267–272

Goodfriend GA (1997) Aspartic acid racemization and amino acid composition of the organic endoskeleton of the deep-water colonial anemone Gerardia: determination of longevity from kinetic experiments. Geochim Cosmochim Acta 61(9):1931–1939

Green AL et al (2015) Larval dispersal and movement patterns of coral reef fishes, and implications for marine reserve network design: connectivity and marine reserves. Biol Rev 90(4):1215–1247

Harrison RG (1980) Dispersal polymorphisms in insects. Ann Rev Ecol Syst 11:95–118

Harrison HB et al (2012) Larval export from marine reserves and the recruitment benefit for fish and fisheries. Curr Biol 22(11):1023–1028

Hastings A, Botsford LW (2006) Persistence of spatial populations depends on returning home. Proc Nat Acad Sci 103(15):6067–6072

Hattori A (1991) Socially controlled growth and size-dependent sex change in the anemonefish *Amphiprion frenatus* in Okinawa, Japan. Jpn J Ichthy 38(2):165–177

Hattori A (1995) Coexistence of two anemonefishes, *Amphiprion clarkii* and *A. perideraion*, which utilize the same host sea anemone. Environ Biol Fishes 42:345–353

Hoegh-Guldberg et al (2008) Assisted colonization and rapid climate change. Science 321(5887):345–346

Holbrook SJ, Schmitt RJ (2005) Growth, reproduction and survival of a tropical sea anemone (Actiniaria): benefits of hosting anemone fish. Coral Reefs 24:67–73

Imbert E, Ronce O (2001) Phenotypic plasticity for dispersal ability in the seed heteromorphic Crepissancta (Asteraceae). Oikos 93(1):126–134

Jablonski D (1986) Larval ecology and macroevolution in marine invertebrates. Bull Mar Sci 39(2):565–587

Jones GP et al (2022) Larval Dispersal in. Evolution, Development and Ecology of Anemonefishes: Model Organisms for Marine Science. United States: CRC Press

Kim D (2021) Predicting the magnitude of residual spatial autocorrelation in geographical ecology. Ecography 44(7):1121–1130

Koenig WD (1999) Spatial autocorrelation of ecological phenomena. Trends Ecol Evol 14(1):22–26

Kritzer JP, Sale PF (2004) Metapopulation ecology in the sea: from Levins' model to marine ecology and fisheries science. Fish Fish 5(2):131–140

Krug PJ et al (2012) Seasonal polyphenism in larval type: rearing environment influences the development mode expressed by adults in the sea slug *Alderia willowi*. Integr Comp Biol 52(1):161–172

Kunzmann A, Diemel VC (2020) The effect of spatial position and age within an egg-clutch on embryonic development and key metabolic enzymes in two clownfish species, *Amphiprion ocellaris* and *Amphiprion frenatus*. PLoS ONE 15(1):e0226600

Leis JM (2006) Are larvae of demersal fishes plankton or nekton? Adv. Mar Biol 51:57–141

Leis JM, McCormick MI (2002) The biology, behavior, and ecology of the pelagic, larval stage of coral reef fishes. In: Coral reef fishes: dynamics and diversity in a complex ecosystem, pp 171–199

Levin LA (1984) Multiple patterns of development in *Streblospio benedicti* Webster (Spionidae) from three coasts of North America. Biol Bull 166(3):494–508

Majoris JE et al (2019) Ontogeny of larval swimming abilities in three species of coral reef fishes and a hypothesis for their impact on the spatial scale of dispersal. Mar Biol 166(12):1–14

Massot M, Clobert J (1995) Influence of maternal food availability on offspring dispersal. Behav Ecol Sociobiol 37(6):413–418

Mathur M (2015) Spatial autocorrelation analysis in plant population: an overview. J Appl Nat Sci 7(1):501–513

Mitchell JS, Dill LM (2005) Why is group size correlated with the size of the host sea anemone in the false clown anemonefish? Can J Zool 83:372–376

Moffitt EA et al (2011) The utility and limitations of size and spacing guidelines for designing marine protected area (MPA) networks. Biol Conserv 144(1):306–318

Moran PAP (1948) The interpretation of statistical maps. J R Stat Soc Ser B 37(2):243–251

Naaykens T, D'Aloia CC (2022) Isolation-by-distance and genetic parentage analysis provide similar larval dispersal estimates. Mol Ecol 31(11):3072–3082

Nathan R (2006) Long-distance dispersal of plants. Science 313(5788):786–788

Nathan R, Muller-Landau HC (2000) Spatial patterns of seed dispersal, their determinants and consequences for recruitment. Trends Ecol Evol 15(7):278–285

Ottaway JR (1980) Population ecology of the intertidal anemone *Actinia tenebrosa* IV. Growth rates and longevities. Mar Fresh Res 31(3):385–395

Pinsky ML et al (2017) Marine dispersal scales are congruent over evolutionary and ecological time. Curr Biol 27(1):149–154

Rasband WS (1997–2018) ImageJ, U.S. National Institutes of Health, Bethesda, Maryland, USA

Ronce O, Clobert J (2012) Dispersal syndromes. Disp Ecol and Evol 155:119–138

Ronce O (2007) How does it feel to be like a rolling stone? Ten questions about dispersal evolution. Ann Rev Ecol Evol Syst 38:231–253

Rueger T et al (2018) Reproductive control via the threat of eviction in the clown anemonefish. Proc R Soc B 285:20181295

Rueger T et al (2022) Social rank and species-specific differences influence cooperation and conflict in anemonefish societies. Anim Behav 187:105–116

Rueger T et al (2021) Cooperative and aggressive behaviours vary between ranks in anemonefish social hierarchies. bioRxiv

Sale PF et al (2005) Critical science gaps impede use of no-take fishery reserves. Trends Ecol Evol 20(2):74–80

Salles OC et al (2016) Genetic tools link long-term demographic and life-history traits of anemonefish to their anemone hosts. Coral Reefs 35(4):1127–1138

Salles OC et al (2019) Strong habitat and weak genetic effects shape the lifetime reproductive success in a wild clownfish population. Ecol Lett 23:265–273

Sloggett JJ, Weisser WW (2002) Parasitoids induce production of the dispersal morph of the pea aphid. Acyrthosiphon Pisum Oikos 98(2):323–333

Sutherland O (1969) The role of crowding in the production of winged forms by two strains of the pea aphid. Acyrthosiphon Pisum J Insect Physiol 15:1385–1410

Taylor MS, Hellberg ME (2003) Genetic evidence for local retention of pelagic larvae in a Caribbean reef fish. Science 299(5603):107–109

Warner RR (1997) Evolutionary ecology: how to reconcile pelagic dispersal with local adaptation. Coral Reefs 16(1):S115–S120

Warner RR (1991) The use of phenotypic plasticity in coral reef fishes as tests of theory in evolutionary ecology. In: The ecology of fishes on coral reefs, pp 387–398

Weisser WW et al (1999) Predator-induced morphological shift in the pea aphid. Proc R Soc B 266:1175–1182

West-Eberhard MJ (2003) Developmental plasticity and evolution. Oxford University Press, Oxford

Williamson DH et al (2016) Large-scale, multidirectional larval connectivity among coral reef fish populations in the great barrier reef Marine Park. Mol Ecol 25(24):6039–6054