Plasticity of larval dispersal-related traits in the orange anemonefish

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**ABSTRACT**

A major goal in marine ecology is to understand patterns of larval dispersal and population connectivity. Dispersal plasticity allows for adaptive variation in dispersal phenotypes in response to variation in environmental conditions and may help to explain intraspecific variation in dispersal distances. However, this phenomenon has not yet been investigated in marine fishes. Here, we test the hypothesis that parents produce larvae with different dispersal-related traits in response to variation in environmental quality using the orange anemonefish, *Amphiprion percula.* By experimentally manipulating food rations, we show that parents produce larger offspring on low-food rations than on high-food rations. However, there was no effect of parental diet on larval critical swimming speed. We also found an effect on larval otolith core size which, in combination with parentage analyses, may provide a way to test the dispersal plasticity hypothesis in the field. This study shows that parents can produce different larval phenotypes in response to variation in environmental conditions, demonstrating plasticity in a dispersal-related trait which may help to explain observed variation in *A. percula* larval dispersal distances. Incorporating dispersal plasticity into our understanding of marine dispersal patterns may enhance our understanding of marine metapopulation ecology, fisheries management, and conservation.

**KEYWORDS:** adaptive parental effects, population connectivity, phenotypic plasticity, context dependent strategy, *Amphiprion percula*

**INTRODUCTION**

The movement of individuals from their natal habitat to another, or dispersal, is a fundamental driver of population dynamics and species distributions (Botsford et al. 2001; Hastings & Botsford 2006; Clobert et al. 2004). Dispersal distances traveled by individuals within a species are often highly variable (Bowler & Benton 2005). There are many reasons why individual dispersal distances may vary: passive dispersers may reflect the natural variation in environmental drivers (e.g., wind dispersing seeds; Kuparinen 2006), while active dispersers may reflect adaptive behaviors in response to environmental or social cues (e.g., resource depletion, Baguette et al. 2011; or overpopulation, Sutherland 1969). Currently, the causes of intraspecific variation in dispersal distances for marine fishes are unknown. As one of the largest, and most ecologically and economically significant taxon of organisms, understanding the fundamental drivers of marine fish population dynamics is critical.

Many marine fishes disperse from their natal habitat during the larval stage (Cowen et al. 2007). One useful way to depict the spatial pattern of larval dispersal is using dispersal kernels (Nathan & Muller-Landau 2000). From the six fish species that have had their larval dispersal kernel empirically measured, there appears to be substantial intraspecific variation in dispersal distances among individuals (*Elacatinus lori*, D’Aloia et al. 2015; *Plectropomus leopardus, Plectropomus maculatus*, Williamson et al. 2016; *Amphiprion percula*, *Chaetodon vagabundus*, Almany et al. 2017; *Amphiprion clarkii*, Catalano et al. 2020). Individual larval behavior and morphological traits may be potential causes of this variation (Johnson et al. 2010; Nanninga & Manica 2018; Faillettaz et al. 2018; Burgess et al. 2021; Wu & Seebacher 2022). Marine fish larvae are active dispersers with extraordinary swimming abilities allowing them to outpace local reef currents (Fisher 2005), and with early developmental onset of sensory abilities allowing them to navigate towards suitable habitat (Majoris et al. 2021). Comparisons between multiple marine fish species have shown correlations between larval traits, such as swimming speed and larval body length (Fisher 2005; Majoris et al. 2019), with indicators of population connectivity and dispersal distance (Nanninga & Manica 2018; Majoris et al. 2019). High-resolution biophysical modeling has also linked variation in larval traits, such as swimming speed, to variation in larval dispersal kernels (Burgess et al. 2021). Together, these studies suggest that variation in dispersal distance may be explained by variation in larval dispersal-related traits.

Adaptive plasticity of larval traits is a plausible cause of intraspecific variation in individual dispersal distances. This type of phenotypic plasticity is widespread because a context-dependent dispersal strategy will often have an evolutionary advantage over a fixed phenotype (Bowler & Benton 2005; Ronce 2007; Arendt 2015). Since marine fish dispersal occurs during the larval stage just after hatching, it is likely that marine fish dispersal phenotypes are responsive to cues from the parental environment (e.g., Cortese et al. 2022). Such adaptive parental effects on offspring dispersal distance have been described several times in terrestrial systems (Benard & McCauley 2008; Clobert 2009). For example, parents may respond to predator occurrence (e.g., aphids; Weisser et al. 1999), parasitic load (e.g., lizards; Sorci et al. 1994), nutrient depletion (e.g., plants; Imbert & Ronce 2001) or food availability (e.g., termites; Korb & Katrantzis 2004) by altering offspring traits associated with dispersal distance. These phenotypic changes result in offspring that are either equipped to disperse far from, or remain close to, their natal habitat, depending on which strategy confers a selective advantage. Despite evidence across terrestrial plants, insects and vertebrates, dispersal plasticity has only been hypothesized in marine fishes (Nanninga & Berumen 2014; Francis et al. 2023).

In this study, we investigate whether larval dispersal-related traits are plastic in response to parental habitat quality in a marine fish: the orange anemonefish, *Amphiprion percula*. Anemonefish have become a model system for studying marine fish larval dispersal (Jones et al. 2022), and individual dispersal distances vary over several orders of magnitude (Buston et al. 2012; Almany et al. 2017). Prior evidence supports the hypothesis that dispersal plasticity might underlie this variation in dispersal distance in *A. percula*. Phenotypic plasticity is expected to evolve if individuals (i) experience variation in environmental conditions, (ii) can reliably assess those environmental conditions, (iii) can express different phenotypes in response to environmental conditions, and (iv) if one phenotype has higher relative fitness than the other in one environmental context, and vice versa. In *A. percula*, (i) parents reside in anemones of varying quality (Buston & Elith 2011; Barbasch et al. 2020; Salles et al. 2020), (ii) parents can reliably predict the habitat quality their offspring will encounter due to spatial autocorrelation of multiple habitat quality indicators (Francis et al. 2023), and therefore (iv) different dispersal phenotypes will result in different fitness in different environmental contexts (Buston & Elith 2011; Barbasch et al. 2020; Salles et al. 2020). It remains to be shown whether (iii) parents can produce offspring with different larval phenotypes in response to variation in environmental conditions.

Here, we test the hypothesis that parents in poor-quality environments will produce larvae with traits that will enable them to disperse farther than larvae from parents in high-quality environments. Using a lab population of *A. percula*, we manipulated parental food rations and measured the effect on critical swimming speed and body size of their offspring. Manipulations of food availability have produced plastic responses in *A. percula* reproduction and parental care both in the lab (Barbasch & Buston 2018) and in the field (Barbasch et al. 2020). We predict that in response to a low food ration (i.e., being in a low-quality environment), parents will produce larger larvae with better swimming abilities, enabling them to disperse farther in search of higher-quality environments. Lastly, to provide a way to test the dispersal plasticity hypothesis in the field during future studies, we investigate whether larval otoliths (i.e., ear stones) are markers of parental environment quality by measuring otolith core size in response to parental food availability. Results from this study show that parents can produce different larval phenotypes in response to variation in environmental conditions, demonstrating plasticity in larval dispersal-related traits, which may explain some of the observed variation in *A. percula* larval dispersal distances.

**METHODS**

*Laboratory Population*

This study was conducted in the XXX Lab at XXX from March 2020 to July 2021. The XXX Lab has housed 60 pairs of *Amphiprion percula*, originally wild caught from Papua New Guinea (supplied by Quality Marine), for the past ten years. Individuals in the laboratory population were collected while under 30 mm standard length (SL), ensuring they were nonbreeders and their removal would have no impact on the reproductive output of breeders or local population growth (e.g., Buston 2004). At the start of this experiment, these now adult fish are separated into breeding pairs: one female and one male (Female SL mean ± standard deviation (SD) 5.32 ± 0.17 cm; male SL 4.02 ± 0.20 cm).

Pairs are kept in sixty 120-liter tanks with unique Tank ID’s, connected to an automated, circulating seawater system that maintains conditions of 33-35 ppt salinity, 27°-29° C, and pH 8-8.3. Water quality testing and aquaria maintenance is conducted per Institutional Animal Care and Use protocol (IACUC protocol #17-001; see Schmiege et al. 2017 or Barbasch & Buston 2018 for detailed animal care methods). Each tank contains sand along the bottom, a terracotta tile for the fish to lay eggs on, and a rock that bears anemones, *Entacmaea quadricolor*. At the start of the experiment, 34 of the tanks had consistent and actively breeding pairs and were selected for manipulation.

*Experimental Design*

To manipulate the parental environment, we simulated high- and low-quality conditions with two variations of food ration (Barbasch & Buston 2018; Barbasch et al. 2020). Fish were fed food pellets (Piscine Energetics PE pellets, 1mm slow sinking, manufactured by Mysis) mixed with seawater and a rotating schedule of supplements and vitamins, dispensed from a pipette dropper six days a week. For a high-quality environment, we provided a ‘high ration’ of pellets (0.15 ± 0.006 g). For a low-quality environment, we provided a ‘low ration’ of pellets (0.05 ± 0.005 g).

The 34 breeding pairs were randomly split into two treatment groups. Half were first placed on the ‘high’ ration’ treatment (n = 17 pairs) and the other half were placed on the ‘low ration’ treatment (n=17 pairs). While pairs reproduce on a lunar cycle, we did not collect offspring for measurements until at least 4 months to allow the fish to acclimate to their new diet and ensure that they responded to the treatment. Note that it has previously taken just one month of food manipulation to affect *A. percula* reproduction (Barbasch et al. 2020). After 4 months, we collected and measured offspring from each pair over a three-month sampling period. The fish received the ‘first round’ of food ration treatment for a total of 7 months, and then we switched the treatments.

Pairs that had first received the ‘high ration’ were switched to the ‘low ration’ and vice versa. Pairs that did not reproduce, or from whom we had failed to collect larvae, were removed from the experiment. After another four-month acclimation period, offspring were again collected and measured from each pair over the following 3 months. Collections were discontinued after three months and any pairs that had not reproduced during the ‘second round’ were excluded from the final analyses. Final sample size included 9 breeding pairs that experienced ‘high ration’ then ‘low ration’ and 8 breeding pairs that experienced ‘low ration’ then ‘high ration’. We successfully sampled and measured 15 larvae from each of the final 17 pairs on both rations (n= 510 larvae). This experimental design is powerful because it enables us to compare larvae from the same parents on both diets, controlling for genetic effects while focusing on effects of the parental environment. Additionally, the order of the feeding treatment is reversed for the two groups to control for the effect of order of treatment (‘first round’ or ‘second round’), and seasonal effects.

*Larval Collection and Rearing*

Over the entire 14 months, we surveyed the breeding pairs daily and recorded the presence and age of egg clutches. During the sampling period, we sampled one clutch per pair per treatment. On the night prior to expected hatching, a tile with an individual egg clutch was photographed with an underwater camera (Olympus TG-870). In the field, eggs hatch by day 8 (Buston 2004; Barbasch et al. 2020), however this varies between individual breeding pairs in the lab, so we estimate the hatch day based on the pairs’ previous clutches (7 to 11 days; 9.25 ± 1.00 days). To test the effect of our ‘high ration’ and ‘low ration’ treatments on reproduction, we averaged the number of clutches laid per month (i.e., one reproductive cycle; Seymour et al. 2018) during the sampling period and counted the number of eggs in one sample clutch from photographs in ImageJ (version 1.47; Rasband 1997).

After being photographed, we transferred the tile with the egg clutch to a separate 120-liter rearing tank. Each tank had 50 L of water from the parental tank, 50 L of pre-made saltwater, and 15 rotifers (*Brachionus rotundiformis*) per mL of water to feed the larvae once they hatch overnight. Water quality of the rearing tank was tested and maintained to be the same as the adult tanks (salinity of 33–35 ppt, temperature of 27–28 °C, pH of 8.0–8.3). To keep the eggs oxygenated without their parents to tend them, air was bubbled over the eggs using an aquarium air compressor, tubing, and an air stone. The morning after hatching, we replenished the rearing tanks with rotifers and subsequently collected 15 live individual larvae for measurements.

*Larval Trait Measurements*

To measure critical swimming speed, or Ucrit (cm s-1), a single larva is placed in a swimming flume where it swims against a controlled current speed that is incrementally increased by 2 cm/s every two minutes until the larva fails (see Majoris et al. 2019; modified from the design by Stobutzki & Bellwood 1997). Ucrit is calculated using the following equation:

Ucrit = U + (t/ti × Ui),

where U is the penultimate speed, t is the time spent at the final speed, ti is the time increment and Ui is the speed increment (Brett 1964). The larva is then euthanized with sodium bicarbonate buffered MS-22, soaked in 10% formalin for five minutes to increase the opacity of the fins, and photographed with a dissecting scope on a 1mm graticule slide. Images were captured with a Canon 60D digital SLR camera operated with Helicon Remote version 3.9.10 W (Helicon Soft Ltd. 2000). From photos, we measured standard length (length), body depth (depth), muscle body area (muscle area), and total fin area (fin area) using ImageJ (Figure 1a). Each measurement was made in triplicate and averaged for each individual larva.

Length for Day 0 larvae is measured as notochord length (Roux et al. 2019) from the anterior tip of the lower jaw to the posterior end of the notochord. Depth is measured from the dorsal crest to the ventral side, behind the eye and before the opercle. Muscle area is measured by tracing the visible musculature that starts just behind the head and excludes the gut. Fin area is measured by tracing the extent of the fins. At this age, *A. percula* fins are fused into a single larval fin fold before they develop into the separate dorsal, caudal, and anal fins (Yasir & Qin 2007).

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| (a) | (b) |
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**Figure 1. (a) Larval body morphology metrics and (b) otolith metrics.** (a) Pictured is a Day 0 *Amphiprion percula* larva. Length is illustrated in blue, depth in red, muscle area in purple, and fin area in yellow outlines and labels. (b) Pictured is a larval otolith. Major diameter is illustrated in blue, minor diameter in blue, and measured area in yellow.

To measure otolith core size, 15 additional larvae were collected from either the same clutch or another clutch during the same sampling period. We successfully sampled otoliths from an additional 12-15 larvae from 14 pairs on both rations (n= 414 larvae). These larvae were also euthanized and photographed as previously described. One sagittal otolith was dissected from each larva and photographed with a compound microscope on a 0.01 mm graticule slide. The otolith core is visible in older *A. percula* otoliths by a distinct hatch mark (Berumen et al. 2010) followed by daily incremental growth rings (Raventos & Macpherson 2001). However, the morning after hatching, the otolith is just the core with no growth rings, so the entire extent was measured. The cores were not perfectly symmetrical ovals, therefore we collected multiple measurements. From photos, we measured the otolith’s major diameter, minor diameter, and area in ImageJ (Figure 1b). Each measurement was made in triplicate and averaged for each individual larva. We also estimated the otolith core’s area from the average major and minor diameter using the equation for the area of an ellipse.

*Statistical Analyses*

Statistical analyses were conducted in R (R Core Team 2022, R Version 4.2.2). To determine the effect of parental environment on various metrics, we performed mixed models with treatment (2 categories) as the predictor variable. We also include round (2 categories) to account for differences in offspring produced in the ‘first round’ versus ‘second round’ of the study period (seasonal effects), and the interaction between treatment and round to account for differences in receiving the ‘high ration’ or the ‘low ration’ during the ‘first round’ or ‘second round’ (i.e., order effects). We include ‘tank ID’ of the parents as a random effect to control for the lack of independence of larvae from the same parental pair. We removed variables from the model in a backwards step-wise fashion if they were not statistically significant (alpha 0.05), while blocking for treatment, our variable of interest, and keeping the random effect of ‘tank ID’.

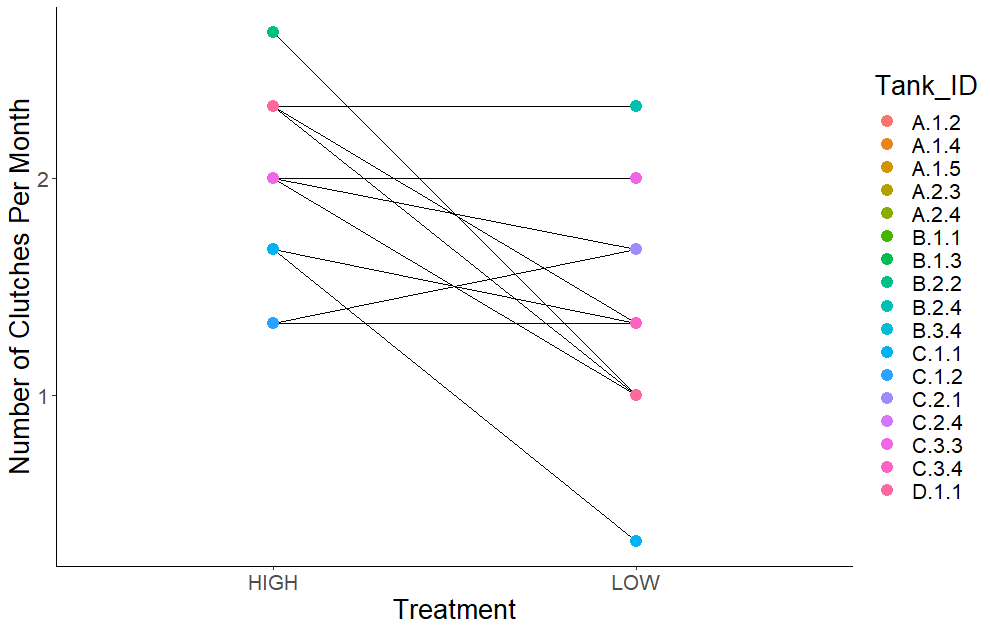
To test whether our treatment influenced reproduction, we used the average ‘number of clutches’ laid per month and the ‘number of eggs’ per clutch as response variables. To determine the effect of treatment on dispersal-related larval traits, we used larval ‘Ucrit’, ‘length’, ‘depth’, ‘muscle area’, ‘fin area’, and otolith ‘major diameter’, ‘minor diameter’, ‘measured area’, and ‘calculated area’ as the response variables. All models were fit using the *lme4* package (Bates et al. 2022). Significance of variables was tested using the *lmerTest* package (Kuznetsova et al. 2020). Assumptions of normality of residuals and heteroscedasticity were assessed visually using diagnostic plots.

**RESULTS**

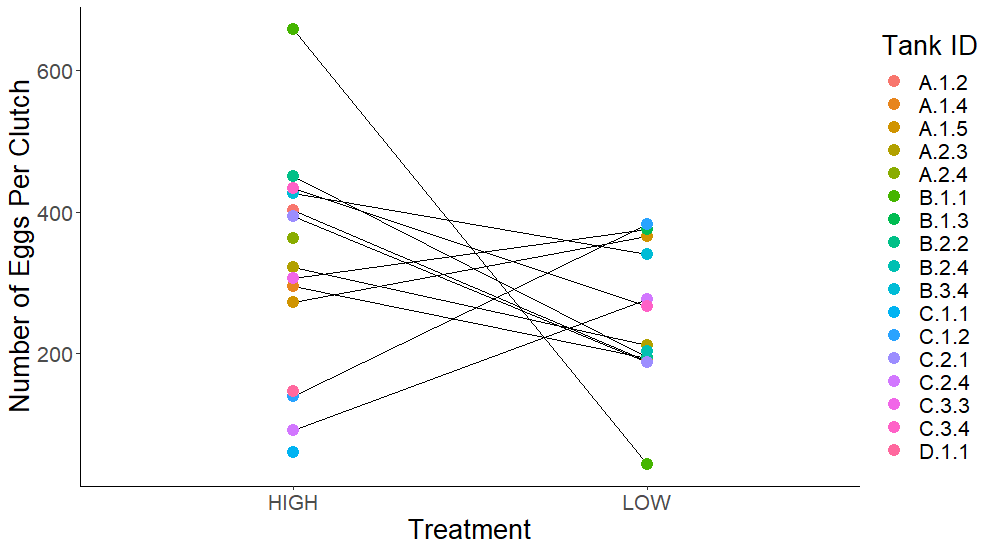
*Experimental Manipulation on Reproduction*

While on the ‘high ration’ treatment, pairs laid up to 3 egg clutches per month (mean ± standard error (SE) of 2.06 ± 0.02 clutches), which is the maximum number of clutches observed in the field (Buston & Elith 2011) as well as the maximum number of clutches possible as a result of plentiful resource availability in the lab (Seymour et al. 2018). The ‘low ration’ treatment was severe enough to lower the number of clutches laid per month to 0 to 2 egg clutches per month (1.37 ± 0.03 clutches), while still enabling some reproduction for the sampling of offspring. The interaction between treatment and round was not a significant predictor and was removed from the final model. However, round had a significant effect on the number of clutches (‘second round’: t = 6.76, DF = 491, p < 0.001). Later in the experiment, during the ‘second round’ of treatment, regardless of treatment, fish laid 0.28 clutches more per month. Treatment had a significant effect on the average number of clutches laid per month (‘low ration’: t = -26.37, DF = 491, p < 0.001). Pairs laid 0.7 clutches less per month while on the ‘low ration’ (Figure 2a).

Pairs responded to the two treatments in a similar way as in a previous study that found plasticity in the number of eggs produced per clutch in response to food availability manipulation in the field (Barbasch et al. 2020). While on the ‘high ration’, pairs produced clutches with a mean of 316.9 ± 9.65 eggs. While on the ‘low ration’, pairs produced clutches with 248.4 ± 6.78 eggs. The interaction between treatment and round was not a significant predictor and was removed from the final model. However, round had a significant effect on the number of eggs (‘second round’: t = 17.41, DF = 346, p < 0.001). Later in the experiment, during the ‘second round’ of treatment, regardless of treatment, fish laid 151.18 more eggs per clutch. Treatment had a significant effect on the number of eggs per sampled clutch (‘low ration’: t = -11.23, DF = 346, p < 0.001). Pairs laid an average of 97.3 fewer eggs while on the ‘low ration’ (Figure 2b). Since the effect of treatment was significant for both the number of clutches laid per month and the number of eggs laid per clutch, we are satisfied that our two feeding rations enabled us to generate the naturally occurring range of variation in *A. percula* reproduction caused by natural variation in environmental quality.

1. 

**(b)**



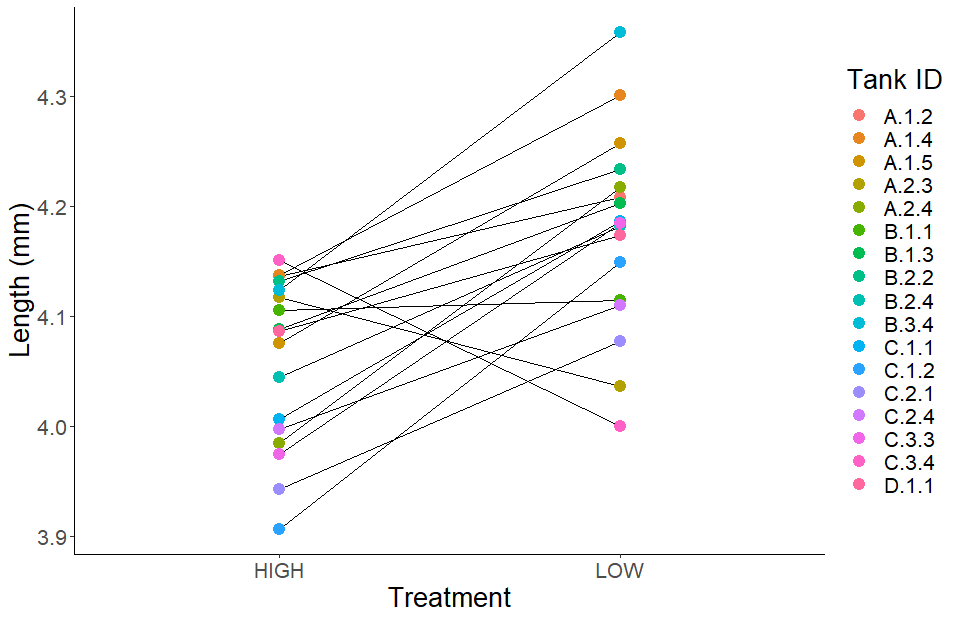
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**Figure 2.** **Individual Pairs’ Reaction Norms of (a) average number of clutches laid per month and (b) number of eggs per clutch.** Each point represents the metric value, per pair, per treatment. Points are individually colored by the unique ‘tank ID’ of each parental pair. The fitted line connects the pair’s measured values and represents the response to the two treatments.

*Standard Length*

Larvae from parents fed the ‘high ration’ had a mean length of 4.06 ± 0.01 mm. Larvae from parents fed the ‘low ration’ had a mean length of 4.18 ± 0.01 mm. Neither round nor the interaction between treatment and round were significant predictors and were removed from the final model. Results from our mixed model show that treatment had a significant effect on length (‘low ration’: t = 11.23, DF = 492, p < 0.001). Larvae were 0.12 mm longer (3% longer) from parents on the ‘low ration’ (Figure 3). Treatment explains 16% of the variation in length (conditional R2 = 0.339, marginal R2 = 0.164). Visually assessing individual pairs’ reaction norm of mean offspring’s length reveals a pattern of a general population level response from one treatment to the next, indicating the presence of plasticity.

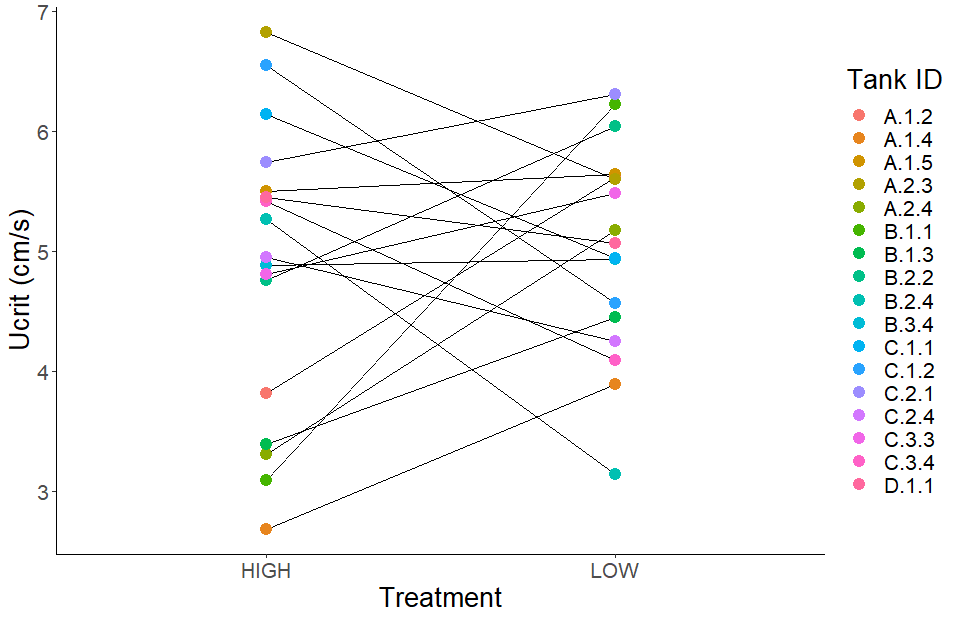
Larval length, depth, muscle area, and fin area were all significantly and positively correlated (Supplemental Figure S1). For brevity, we only report results for length here. The other three body morphology metrics’ final models yielded similar results, showing treatment had a significant effect and that larvae were all-around larger when parents were on the ‘low ration’ (Supplemental Table S1; Supplemental Figure S2).



**Figure 3.** **Individual Pairs’ Reaction Norms for the length of larvae produced.** Each point represents mean length of larvae sampled, per pair, per treatment. Points are individually colored by the unique ‘tank ID’ of each parental pair. The fitted line connects the pair’s offspring means and represents the response to the two treatments.

*Critical Swimming Speed*

Larvae from parents fed the ‘high ration’ treatment had a mean Ucrit of 4.86 ± 0.15 cm/s. Larvae from parents fed the ‘low ration’ treatment had a mean Ucrit of 5.03 ± 0.13 cm/s. The interaction between treatment and round was not a significant predictor and was removed from the final model. Results from our mixed model show that treatment did not have a significant effect on Ucrit (‘low ration’: t = 1.182, DF = 491, p = 0.238). Round did have a significant effect (‘second round’: t = -4.42, DF = 491, p < 0.001). Larvae swam 0.8 cm/s faster on average during the ‘second round’, regardless of treatment. However, treatment and round only describe 4% of the variation in larval Ucrit (conditional R2 = 0.128, marginal R2 = 0.035). Visually assessing individual pairs’ reaction norm of mean offsprings’ Ucrit shows a lack of any general pattern of a population level response from one treatment to the next (Figure 4).

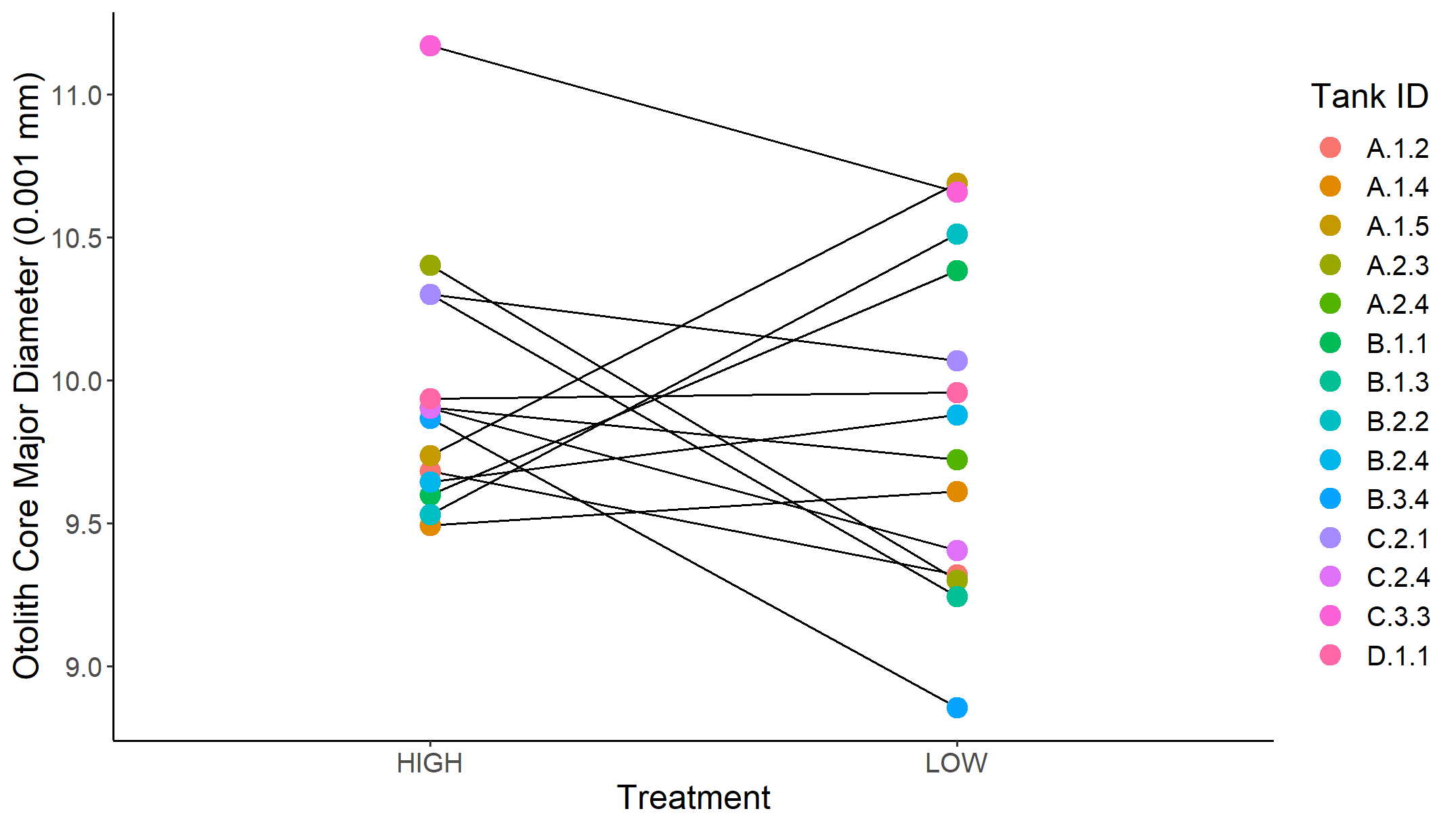


**Figure 4.** **Individual Pairs’ Reaction Norms for Ucrit of larvae produced.** Each point represents mean Ucritof each clutch sampled, per pair, per treatment. Points are individually colored by the unique ‘tank ID’ of each parental pair. The fitted line connects the pair’s offspring means and represents the response to the two treatments.

*Otolith Core*

Larvae from parents fed the ‘high ration’ treatment had otoliths with a mean ± standard error (SE) major diameter of 96.4 ± 0.4 µm. Larvae from parents fed the ‘low ration’ treatment had otoliths with a mean major diameter of 98.3 ± 0.05 µm. Neither round nor the interaction between treatment and round were significant predictors of otolith size and were removed from the final model. Results from our mixed model show that treatment did not have a significant effect (t = -2.22, DF = 399, p = 0.027). The major diameter of larval otoliths were 1.3 µm smaller from parents that were on the ‘low ration’ (Figure 5). However, our model explains less than 0.01% of the variation in otolith size (conditional R2 = 0.287, marginal R2 = 0.009).

Otolith core major diameter, minor diameter, measured area, and calculated area were all significantly and positively correlated (Supplemental Figure S3). For brevity, we only report results for major diameter here. The other three otolith metrics’ final models yielded similar results, showing treatment had a significant effect on the minor diameter and a marginally significant effect on the measured and calculated area (Supplemental Table S2). Otoliths were all-around smaller when parents were on the ‘low ration’ (Supplemental Figure S4).



**Figure 5.** **Individual Pairs’ Reaction Norms for otolith core major diameter of larvae produced.** Each point represents mean otolith core major diamter of each clutch sampled, per pair, per treatment. Points are individually colored by the unique ‘tank ID’ of each parental pair. The fitted line connects the pair’s offspring means and represents the response to the two treatments.

**DISCUSSION**

A major goal in marine population ecology is to determine the causes of variation in larval dispersal distances and consequential population connectivity (Cowen 2002; Cowen & Sponaugle 2009; Buston & D’Aloia 2013). Dispersal plasticity allows for adaptive variation in dispersal phenotypes in response to variation in environmental conditions (Bowler & Benton 2005; Ronce 2007; Arendt 2015) and may help to explain the substantial intraspecific variation we observe in marine fish dispersal distances. For the many demersal spawning reef fishes that provide parental care, it is likely that a plastic response in larval dispersal phenotype would be informed by the parental environment. In this study, we experimentally investigated one of the conditions that must be met for plasticity to occur as an adaptive parental effect: whether parents can produce offspring with different phenotypes in response to variation in the parental environment. By manipulating food availability for *Amphiprion percula* parents, we created variation in reproductive output consistent with the variation seen in high quality and low quality habitats in the field (Buston & Elith 2011; Barbasch et al. 2020). By comparing offspring from the same parents while on a ‘high’ and a ‘low’ food ration, we show a plastic response in body size of *Amphiprion percula* larvae. Counterintuitively, larvae were larger when parents were given the ‘low’ food ration. This counterintuitive result supports the hypothesis that parents in poor quality environments might be producing larvae that can disperse farther, since dispersal ability and body size are positively related in many taxa (Bowler & Benton 2005, Benard & McCauley 2008, and Clobert et al. 2009).

*Evidence of plasticity in body size*

We might expect parents to produce larger offspring when given greater amounts of food (e.g., damselfish, Donelson et al. 2009), perhaps because they have more resources to allocate to gametes as yolk reserves (Valdebenito et al. 2015). Alternatively, selection might favor parents that produce larger offspring when provided with less food, so that the larvae are equipped to disperse out of the poor environment. In accordance with our dispersal plasticity hypothesis, we found parents produced larger larvae during the ‘low ration’ than the ‘high ration’ treatment. Our otherwise counterintuitive result is not anomalous; in a study that used a similar experimental design, Reznick & Yang (1993) found female guppies, *Poecilia reticulte*, produced offspring with greater mass and fat reserves when given lower food rations than females given higher food rations. Such responses to poor diets, in which mothers produce larger eggs (e.g. drosophila flies, Vijendravarma et al. 2010; daphnia water fleas, Gliwicz & Guisande 1992) and/or larvae (e.g., isopods, Brody & Lawlor 1984) has been attributed to adaptive parental effects that may bolster resiliency of offspring born into poor environments (Badyaev & Uller 2009).

Larger body sizes resulting from a poor parental environment may allow offspring to disperse greater distances and have a higher probability of settling in a better environment. Dispersal is a costly life-history trait (Bonte et al. 2012) and many organisms evolved to have condition-dependent dispersal related-traits that result in non-random dispersal syndromes and preferential survival of certain dispersing individuals (reviewed by Bowler & Benton 2005, Benard & McCauley 2008, and Clobert et al. 2009). Body size is a widespread dispersal-related trait (Bowler & Benton 2005, Benard & McCauley 2008, and Clobert et al. 2009). In studies of intraspecific variation in natal-dispersal, generally larger individuals disperse from their natal habitat more than smaller individuals (e.g., damselflies, Anholt 1990; naked mole-rats, O’Riain et al. 1996; screech-owls Belthoff & Dufty 1998; squirrels, Nunes et al. 1998; lizards, Meylan et al. 2002; and flamingos, Barbraud et al. 2003). The current study demonstrates that larval body size varies in response to parental habitat quality and supports the hypothesis of plasticity of a dispersal-related trait in a marine fish.

An alternative way of thinking about the observed plastic response in offspring body size is to consider its consequence on survival. While there are mechanistic reasons why larger offspring may disperse more often or farther (e.g., enhanced walking, swimming, flying), it is widely supported that larger offspring have greater survival (Roff 1992). For marine fishes, mortality rates are especially high during larval dispersal (Bailey & Houde 1989, Leggett & Deblois 1994; Almany & Webster 2005), and larger body sizes at hatch result in greater survival and higher recruitment rates (e.g., salmon, Einum & Fleming 2000; damselfish, Vigliola & Meekan 2002; wrasse, Raventós & Macpherson 2005; clupeid, Meekan et al. 2006; snapper, D’Alessandro et al. 2013; sardine, Garrido et al. 2015; reviewed by Miller et al. 1988, Anderson 1988, Houde 1997, Sogard 1997, and Johnson et al. 2014). Survival during the larval stage may be enhanced by large body sizes due to its effect on greater energy reserves (e.g., Gagliano et al. 2007), predator evasion (e.g. Cowan et al. 1996), and/or ability to catch food (e.g. Dower at al. 2009). Thus, the plasticity of body size might be adaptive for survival, and any consequences for dispersal might simply be byproducts.

*Non-significant effect of treatment on critical swimming speed*

We did not find an effect of parental food ration on swimming speed (Ucrit). However, we are cautious with this conclusion because it is difficult to measure a behavioral trait such as Ucrit; it has greater phenotypic variability and thus is harder to detect an effect of one predictor variable, such as parental diet. In support of this, it is worth noting that our manipulation influenced both mean larval body size and mean larval Ucrit by 3%, but the standard errors for Ucrit were much greater. This variability may come from our inability to standardize the individual experience of every sampled larva, such as the number of rotifers it ate prior to the swimming flume trial for example. Additionally, while standard length is a trait that can be measured with high repeatability, performance in a swimming flume could be different every time we measured if we repeated trials for an individual. Unfortunately, we cannot measure Ucrit multiple times because the trial is designed to measure the moment a larva is spent and can no longer maintain its position against the current. Any possible subsequent trials would be inaccurate, measuring an already exhausted individual. Additionally, a nonsignificant result from determining a predictor of Ucrit of Day 0 larvae is consistent with similar studies. Schlatter et al. (2022) found no effect of genetic variance on Ucrit, despite finding a significant effect on larval body size. Also, Fuiman & Cowan (2003) showed no repeatability in behavioral assays of larval swimming, highlighting the difficulty in determining predictors of the variation.

Given the significance of Ucrit in predicting larval dispersal distance (Burgess et al. 2021), it is worth considering our result of a significant effect of parental environment on larval body size and prior evidence that body size predicts Ucrit. Through ontogeny of the larval stage, larger body sizes are correlated with faster swimming speeds (Fisher 2005; Majoris et al. 2019). Importantly, body size is positively related to swimming speed even at early developmental stages in *Amphiprion* larvae (Bellwood & Fisher 2001) and other fishes (e.g., Fisher & Hogan 2007; Downie et al. 2021). Previous studies have shown that larvae with larger body size-at-hatch have faster growth (Vigliola & Meekan 2002; D’Alessandro et al. 2013), suggesting larger larvae at-hatch may maintain their relatively larger body sizes through ontogeny because of faster growth compared to larvae with smaller body size-at-hatch. In sum, larger offspring at-hatch may also then maintain greater swimming speeds through the larval dispersal stage than smaller offspring, and therefore may have greater propensities to disperse greater distances.

*Future indirect test of the dispersal plasticity hypothesis using otoliths*

Otolith analyses provide a convenient history of a fish’s age, growth, and importantly, body size at hatch from back calculations (e.g. Meekan et al. 1998; D’Alessandro et al. 2013; Garrido et al. 2015). We found a significant effect of parental food ration on otolith core size. However, we found that otolith core major diameter is smaller in offspring from parents during the ‘low ration’ treatment, even though those offspring were larger than offspring from parents in the ‘high ration’ treatment. Although unexpected, this effect of poor parental environments resulting in smaller otolith core size (sometimes referred to as ‘hatch-check’) is seen elsewhere (e.g. cod, Grønkjær & Schytte 1999). Taken together, our contradictory result of larger offspring body size and smaller otolith core sizes may reveal that parents do not just produce bigger larvae in response to poor environments, rather they produce larvae with a specific suite of dispersal-related traits (i.e., dispersal syndrome) that may be matched to environmental conditions (Sih et al. 2012, Cote et al 2022). Importantly, one could use otoliths collected from specimens in the field to perform an indirect test of the dispersal plasticity hypothesis. For example, one could test whether settled larvae, or ‘recruits’, with small, medium, or large otolith cores have different dispersal distance distributions estimated from parentage analysis (Almany et al. 2017). We predict that larvae with long dispersal distances would have small otolith cores, resulting from being born in a poor environment.

*Future direct tests of the dispersal plasticity hypothesis*

In this study, we found plasticity of a dispersal-related trait in response to variation in the parental environment. However, to demonstrate dispersal plasticity in *A. percula*, we still need to conduct a direct test of plasticity of larval dispersal distance. Given that there is positive spatial autocorrelation of habitat quality in the wild (anemone size, female size, clutch size; Francis et al. 2024), selection might favor parents in poor environments that produce larvae that disperse out of those environments and parents from good environment that produce larvae that remain in those environments. To test this hypothesis observationally, one would need to test whether parents in good habitat (large females living in large anemones and producing large egg clutches) have a greater fraction of their offspring dispersing short distances and a smaller fraction of their offspring dispersing long distances, relative to parents in poor habitats (small females living in small anemones producing small egg clutches). This requires measuring both reproduction of breeding pairs (e.g., Barbasch et al. 2020) and the dispersal of larvae using parentage analysis (e.g., Almany et al. 2017) at the same time and place. To test this hypothesis experimentally, one could manipulate the parental habitat quality, either by supplementing food availability (e.g., Barbasch et al. 2020), or by moving breeding pairs between high-quality and low-quality habitats (e.g., Branconi et al. 2020), and measuring the response in offspring’ dispersal distance.

*Broader implications for marine fish population dynamics*

While parental diet explains 16% of variation in larval size, Schlatter et al. (2022) found 20% of the variation is explained by heritability. Together, we explain a large portion of the variation in this important dispersal-related trait, suggesting body size may be described by genetic and environmental interactions. In terms of marine fish dispersal patterns as a result of variation in larval body sizes, this trait-based approach has the potential to provide a more predictive framework for metapopulation ecology (De Bie et al. 2012). Incorporating plasticity of body size, and other dispersal-related traits, in our investigations of marine fish dispersal patterns may enhance fishery management (Kritzer & Sale 2004; Harrison et al. 2012; Almany 2013) and reserve design (Botsford et al. 2009; Moffitt et al. 2011; A Di Franco 2012; Anadon 2013; Green et al. 2015; Abesamis 2017). Variation in dispersal distances in response to parental habitat quality may help to explain why certain reef fish populations collapse. Fishing and other pressures may be adjusting the dispersal strategies of the remaining fish, exacerbating the effect on population levels if offspring disperse elsewhere rather than recruit to the local population. If habitat quality is improved, then dispersal plasticity may drive larvae to remain within the population, re-establishing healthy population levels. In sum, dispersal plasticity may be a currently overlooked process that could explain fisheries collapse and reserve recovery by influencing the variation we observe in marine fish larval dispersal distances.

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**AUTHOR CONTRIBUTIONS**

RKF, KGC, PMB designed this experiment. RKF and KGC collected these data. JEM, ST, and PMB designed a preliminary experiment. ST and JEM collected preliminary data. RKF, KGC and PMB were involved with analyses. RKF wrote the first draft of the manuscript. All authors were involved in subsequent drafts. All authors gave their final approval for publication and agreed to be held accountable for the work.

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**CONFLICT OF INTEREST**

The authors declare no conflict of interest.

**DATA AVAILABILITY STATEMENT**

Data and *R* scripts are publicly available at <https://github.com/robinkellyfrancis/AperculaDispPlast>.

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