

Mothers matter: contribution to local replenishment is linked to female size, mate replacement and fecundity in a fish metapopulation

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Abstract A major assumption of marine population ecology and marine fisheries management is that female size is related to the number of eggs they produced, and therefore, to the number of recruits they produce. Yet, this assumption has seldom been tested. In the past, the difficulties associated with following the fate of individual larvae through the pelagic phase have precluded such analyses. Here, we used field estimates of reproduction combined with DNA profiling of all members of a wild population of the panda anemonefish (*Amphiprion polymnus*) over two consecutive years to investigate (1) the predictors of egg production and (2) the predictors of the number of recruits produced. We found that across one and two life history transitions, female size was a significant predictor of egg production, and egg production was a significant predictor of the number of recruits produced (when controlling for fairness) respectively. When looking across three

life history transitions, we found that large females and couples where no male replacement occurred were more likely to produce at least one recruit that settled within the local population than small females or females where the original male died and was replaced. However, we found no evidence supporting the hypothesis that larger females contributed numerically more recruits than smaller ones to local replenishment. These findings provide the first support for the common assumption that egg production is correlated with recruit production. They also suggest that the duration of partnership in anemonefishes couples might be an important factor in their population dynamics.

Introduction

Understanding the mechanisms generating variability in larval replenishment to local populations remains a critical question in marine ecology (Caley et al. 1996; Roughgarden et al. 1988; Underwood and Fairweather 1989) and fisheries (Rickman et al. 2000). In both fields, it is often assumed that high and highly variable mortality rates of larval fish lead to a decoupling of egg production and year-class strength at the scale of individual stocks (e.g. Rickman et al. 2000; Doherty and Williams 1988). Hence, parental factors are usually not considered in explanations of spatial and temporal patterns in recruitment (Caley et al. 1996). More recently, there has also been a growing realization that processes acting immediately before and during spawning significantly impact larval survival and subsequent recruitment success (Vallin and Nissling 2000; Begg and Marteinsdottir 2000). Understanding the key links between larval production and population replenishment is critical in order to understand the dynamics of marine populations and how best to implement effective management

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and conservation strategies (Jones et al. 2009; Mora et al. 2006; Sale et al. 2005). New techniques have emerged that allow the tracking of individual recruits to their population of origin (Thorrold et al. 2002; Almany et al. 2007), and even to their parents (Almany et al. 2013; Berumen et al. 2012; Christie et al. 2011; D'Aloia et al. 2013; Harrison et al. 2012; Planes et al. 2009; Saenz-Agudelo et al. 2011), making it possible to study the links between larval production and recruitment at the individual level.

Parental effects play an important role in the early stages of larval development with carry-over effects that influence performance later in life (Green and McCormick 2005; Green 2008; Gagliano and McCormick 2007). These effects represent interactions between parental genotype, phenotype and parental environment and their influence on offspring characteristics and performance (Beckerman et al. 2006). There are many lines of evidence to suggest that parental genotypes and environment can have a major influence on larval quality, which in turn may influence survival (Green 2008). Perhaps the most pervasive hypothesis relating to parental effects is that large females produce more and better quality eggs than small females, which results in large females producing more and larger larvae that have a higher probability of survival (Green 2008; Roberts and Polunin 1991; Berkeley et al. 2004a, b; Birkeland and Dayton 2005; Palumbi 2004; Russ 2002). There have, however, been few empirical tests of this hypothesis despite the observation that fishing pressure almost invariably results in a differential impact on larger individuals (Birkeland and Dayton 2005).

There are four key transition stages in a generalized fish life cycle: from (1) mother to egg, (2) egg to larvae, (3) larvae to juvenile and (4) juvenile to adult. Maternal effects must carry over across the first three of these transitions to have an impact on juvenile recruitment. Most studies to date have, however, focussed on the different stage transitions independently. For instance, it is well known that female size is positively related to egg production. Also, there is support for older females producing larger and higher quality larvae than smaller females (Berkeley et al. 2004a; Venturelli et al. 2010). In anemonefishes, egg production and larval production have been related to different parental attributes, including female size, male and female growth and breeding experience (Buston and Elith 2011; Mitchell 2003). For some fish, larger juveniles have also been shown to have lower pre- and postsettlement mortality than smaller ones (Bergenius et al. 2002; Gagliano et al. 2007; Macpherson and Raventos 2005; Meekan et al. 2006; Raventos and Macpherson 2005; Vigliola et al. 2007; Vigliola and Meekan 2002). Finally, a handful of studies have found a positive relationship between variations in female age class structure and the number of recruits for temperate water gadids (Vallin and Nissling 2000; Wright and Gibb 2005). However, the relationship between variation in

individual parental qualities and the production of juveniles or the number of juveniles surviving to breed has yet to be established in the field.

The presence of a pelagic larval phase and assumed long-distance dispersal (Shanks et al. 2003) has represented a significant barrier to examine the link between the quality of individual parents and their subsequent reproductive success in coral reef fishes. However, recent studies have shown that offspring from local parents can be identified with DNA parentage analysis (Beldade et al. 2012; Berumen et al. 2012; Christie et al. 2010; Jones et al. 2005; Planes et al. 2009; Saenz-Agudelo et al. 2011). One of the most interesting advantages of this approach is that it allows the linking of parental phenotypes to recruitment success. To date, only one study has used this approach to show that in a coral reef fish population, females that produce larvae that return to the natal population (self-recruitment) can be significantly larger than those that do not (Beldade et al. 2012). This study is the first qualitative evidence of a link between maternal phenotype and local replenishment in a natural population. However, no study has yet attempted to quantify this relationship in the wild or has evaluated the effect of parental environment and its possible interaction with parental phenotype.

In this study, we applied a combination of DNA fingerprinting to track individuals through time, parentage analysis to assign offspring to their parents, and field observations on egg production to assess the relative contribution of different factors in two of the four key transition stages in a population of anemone fish (*Amphiprion polymnus*) in Bootless Bay, Papua New Guinea. This combined approach allowed us to test the following specific hypotheses that look across one, two and three life history transitions, respectively: (1) larger females produce more eggs than do smaller females (after controlling for other variables). (2) More eggs produce more recruits (controlling for other variables). Finally, given support for the previous hypotheses, we tested if these could be verified across three life history transitions: (3a) larger females have higher probabilities of producing at least one recruit, and (3b) among females producing at least one recruit, larger females produce more recruits than smaller females (controlling for other variables). Together, these data represent the first empirical test of the effect of parental influences across three key transitions in the life cycle of marine fishes.

Methods

Study population and observational methods

Our study was conducted at Bootless Bay (09°31'S, 147°17'E) near Port Moresby, Papua New Guinea (Fig. 1).

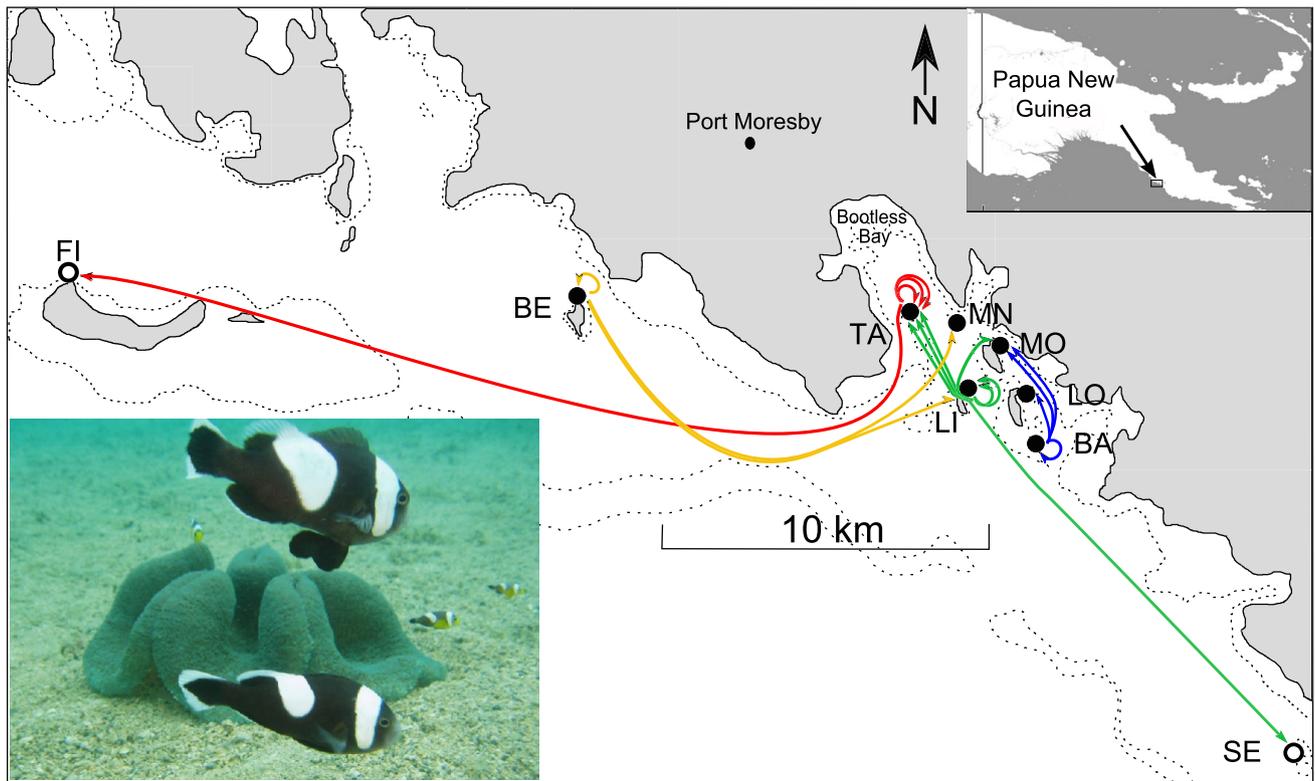


Fig. 1 Map of the study area showing 9 sites of anemone aggregations hosting *Amphiprion polymnus*. Dotted lines correspond to the limit of shallow reefs. Solid circles correspond to the seven sites where complete surveys were carried out in both 2008 and 2009. Open circles correspond to two sites that were partially sampled and for which females were not included in the analyses. Arrows represent individual trajectories of fish larvae produced by four different females (each colour represents one female) that were chosen to illustrate how different juveniles from the same mother recruited both

within and outside their natal site (only a few trajectories were plotted because the full set would have saturated the image making it unreadable). Site abbreviations are as follows: Manubada Island (BE), Lion Island (LI), Taurama (TA), Motupore North Patch Reef (MN), Motupore Island (MO), Loloata Island (LO), Loloata South Bank (BA), Fishermen Island (FI), South East Bank (SE). Inset Location of Bootless Bay in Papua New Guinea. Image: *Amphiprion polymnus* colony in a *Stichodactyla hadonni* anemone, courtesy of S. Planes

It focused on seven discrete aggregations of the anemones *Stichodactyla hadonni* and *Heteractis crispa*, each of which occupied a ~1 ha patch of shallow sand and sea grass (hereafter termed *sites*). In January 2008, all anemones colonized by *A. polymnus* ($N = 155$) were individually tagged using small underwater buoys and numbered plastic tags attached to metal pins that were buried in the sand next to each anemone. Anemone depth was measured to the nearest 0.1 m using a dive computer (Suunto, Vyper). All fish at each anemone were counted, captured on SCUBA using hand nets, measured underwater to the nearest 1 mm using calipers (total length TL), fin-clipped for genetic analysis and then released back on the same anemone. We collected all juveniles that were too small to be fin-clipped (<30 mm TL). Resident anemonefish may prevent recruitment of new individuals at high densities (Buston 2003a, b). Therefore, removal of the small individuals homogenized conditions for larval settlement among all anemones. Samples were preserved in 95 % ethanol and returned to the laboratory

for subsequent genetic analyses. The same procedure was repeated 1 year later in February 2009.

Genetic data and parentage analysis

We defined three arbitrary size/maturity categories for all subsequent analyses as follows: (1) Breeders: the two largest individuals in each anemone, each of which measured at least 50 mm TL (Moyer and Steene 1979). (2) Non-breeders: individuals smaller than the two breeders that were present in the first survey in 2008. (3) Juveniles: all remaining individuals that settled between 2008 and 2009 surveys (see determinants of the number of recruits below for details).

A total of 942 individuals in 2008 and 927 individuals in 2009 were screened for 18 microsatellite DNA loci (Beldade et al. 2009; Quenouille et al. 2004) that satisfied Hardy–Weinberg equilibrium and linkage disequilibrium assumptions. We used the package Genalex v6 (Peakall and

Smouse 2006) to compare each of the individual genotypes from fish sampled in 2008 and 2009 to identify all pairs of individuals between years that had the same multilocus genotype. Given the number of loci, sample size and allele frequencies, the probability that two individuals drawn at random from a population will have the same genotype at the 18 loci (probability of identity) was small (6.19×10^{-7}) even using the conservative estimate of probability of identity between siblings proposed by Waits et al. (2001). Therefore, if two fin clips from different years (2008 and 2009) had the same genotype, they were assumed to be from the same individual. To account for possible genotyping errors, mismatches of up to two loci between genotypes were allowed in pair-wise genotype comparisons. Probability of identity and probability of identity between siblings were still small when removing the two loci with the highest exclusion probabilities (9.10×10^{-13} and 2.20×10^{-5} , respectively), and individual matches that fell in this category were accepted if other available data such as size, site and anemone corresponded to expectations between years (same size or increment, same anemone or movement to an anemone from the same site).

We used the FAMOZ platform (Gerber et al. 2003) to assign juveniles that settled between April 2008 and April 2009 to sampled breeders among the seven sites. These assignments included all potential parents sampled in 2008 plus all new parents sampled in 2009 that had replaced fish that disappeared between both surveys. We used an introduced error rate (to account for genotyping errors) of 0.0001 to simulate the distribution of LOD scores for true and false parents. Based on these simulations, LOD score threshold values to accept parents as true were set at 4.5 (individual parent) and 11 (parent pairs). Under these conditions, 30 assignment tests were run using simulated data to estimate Type I error (probability of excluding a true parent when this individual was among the candidate parents) and Type II error (probability of assigning a false parent when the true parent was not sampled), which were acceptably low (~1 and 5 %, respectively). Because the presence of full/half-sibs is a potential source of Type II error, as a conservative measure, we excluded all single-parent assignments with two mismatches between parental offspring genotypes from the resulting parent–offspring assignments in the real data set (after testing for genotyping errors in the original data set).

Determinants of egg production

In 2008, after the general fish census and tissue sampling, each anemone was surveyed twice a week for 2 months (February–April) to record the presence of egg clutches and new recruits. To estimate egg production for each breeding pair, a 49-cm² (7 × 7 cm) ceramic tile was placed next to

each anemone 2 weeks before the beginning of each survey to standardize access to spawning surfaces among anemones. Egg clutches were photographed using an underwater digital camera (Panasonic, Lumix DMC ZS-19), and clutch area (cm²) was estimated using ImageJ software (Abramoff et al. 2004). The mean density of eggs per clutch was estimated from egg counts along two transects across the clutch (transects were 5 mm wide, perpendicular to one another, and their length was equal to the diameter of each clutch). For 30 clutches, we counted the number of eggs and compared it to the number of eggs estimated by multiplying the clutch area and egg density. The number of eggs estimated from clutch area and egg density was highly correlated to the real number of eggs ($y = 1.03x$, $R^2 = 0.987$, $P < 0.001$, $n = 30$) and was used as a proxy of the number of eggs in each clutch. In total, 79 breeding pairs had complete observations (all clutches laid in 2 months were on tiles and photographed) and were used for subsequent analysis. We used the sum of the number of eggs produced by each female during the 2 months as a measure of individual potential fecundity (Lambert 2008). Time from laying of eggs to hatching of larvae for this species is ~5–6 days in captivity (Rattanayuvakorn et al. 2005). We were able to photograph 95 clutches (40.2 %) from 58 breeding pairs on two occasions (with an interval of 3 or 4 days between photographs). Egg loss was estimated as the difference in number of eggs between the first and second observations (number of eggs that disappeared in 3 days). We evaluated whether egg production, egg density (as a proxy for egg size) and egg loss (to test if egg production differs from the actual number of released larvae in a predictable way) were associated with particular parental phenotypes (size) and environmental characteristics (depth and fish colony size).

Determinants of the number of recruits produced per female in a year

Breeding in *A. polymnus* in this location is likely to occur throughout the year, as is the case for other anemonefish species in tropical waters of Papua New Guinea (Buston 2004). To study the relationships between the number of successful offspring produced in 1 year and parental characteristics (phenotype and environment), the main challenge was in identifying all females that reproduced and survived for the period from 2008 to 2009 and the juveniles that they produced and successfully settled in that time. In both cases, multilocus genotype comparisons were used as described previously to identify these individuals.

In 2008, we identified 97 anemones that hosted at least a pair of *A. polymnus* and where both fish were large enough to be considered potential active breeders. The minimum size of potential active breeders for this analysis was the smallest female and male couple that was observed laying

at least one egg clutch over the entire study period (68 mm TL and 63 mm TL, respectively). Of the 97 *A. polymnus* breeding pairs observed in 2008, 58 females survived to be observed in 2009 and were used in a posteriori analyses. Among these females, 35 had the same male mate in both surveys and the remaining 23 had had their original male mate replaced by a large nonbreeder from the same anemone ($n = 14$) or an anemone nearby ($n = 9$).

Data analysis

One life history transition

Large females produce more eggs We constructed three independent linear models (LM) to evaluate the relationship between female TL each of the three measured egg variables (egg production, mean egg density and egg loss), respectively, controlling for other parental variables. Egg production and egg loss values were square-root-transformed to fit normality assumptions. Each full model included (1) female TL, (2) difference in size between female and male (Δ_{F-M}), (3) anemone depth and (4) nonbreeders' total length (NBTL) as a measure of fish colony density. We used Δ_{F-M} as a function of male size because male size is strongly correlated to female size ($R^2 = 0.81$, $F_{1,56} = 257.6$, $P < 0.001$). Model simplification from the full model followed the analysis of deviance procedure described by (Crawley 2007). Previous studies have shown that breeding experience and male growth can be important determinants of reproductive success (measured as fecundity) in other anemonefish species (Buston 2004; Buston and Elith 2011). We did not include these two variables as potential determinants of egg production because we could not determine if or in which anemone mate replacement happened during the 2 months where egg production was measured. However, these variables were included as potential determinants of the number of recruits produced (see below).

Two life history transitions

More eggs produce more recruits Since this data set included several zero recruit observations, a two-step approach was used to test for correlations between the number of recruits produced per female and the number of eggs they produced controlling for other parental variables. Such approach is recommended when dealing with zero-inflated data sets (Martin et al. 2005; Buston and Elith 2011). First, we used a logistic model to test for factors that predicted whether at least one recruit was produced or not (0–1 response). The model included (1) egg production, (2) difference in size between female and male (Δ_{F-M}), (3) anemone depth, (4) nonbreeders' total length (NBTL) as a cumulative measure of the TL of each nonbreeder in the

anemone, and (5) farness. Farness is a measure that reflects how isolated a given anemone is in the metapopulation. We included this metric because the probability to produce successful recruits in a metapopulation could depend on the position of the anemone in the network as the probability of successful dispersal varies with distance (Saenz-Agudelo et al. 2011; Buston et al. 2012). For each anemone, farness was calculated as the sum of the distances to all other anemones in the network.

Second, we used a generalized linear model (GLM) with a Poisson error distribution to test if the number of eggs predicted the number of recruits produced after controlling for the other variables. In this step, only nonzero observations in the number of recruits were included in the model.

Three life history transitions

Large females produce more recruits As in the previous section, we used a two-step approach. First, we constructed two logistic models to test for factors that predicted whether recruits were produced or not (0–1 response). The first model included (1) female TL, (2) difference in size between female and male (Δ_{F-M}), (3) anemone depth, (4) nonbreeders' total length (NBTL) as a cumulative measure of the TL of each nonbreeder in the anemone, and (5) farness. In the second, female TL was replaced by male replacement (whether a male had been replaced during the period 2008–2009 or not) as a proxy for breeding experience. We built separate models because female TL is correlated with male replacement (females that did not lose their mate were significantly larger than females that did; mean \pm SE: female TL_{no replacement} = 110.1 \pm 1.7 mm; female TL_{male replaced} = 103.7 \pm 2.7 mm. Model simplification was performed via analysis of deviance as described above, and the two resulting models were compared using the Akaike Information Criterion (AIC).

Second, we used a generalized linear model (GLM) with a Poisson error distribution to test if female TL predicted the number of recruits produced after controlling for other variables. In this step, only females that produced at least one recruit were included. Here, we also included male replacement as a proxy for breeding experience. As in the previous step, we constructed two independent models to evaluate the effects of female TL and breeding experience separately. We compared the results of the models using the AIC.

Finally, we investigated if male growth was a primary determinant in reproductive success (number of recruits). Male growth is also known to be a primary determinant of reproductive success (fecundity) in another anemonefish species (Buston and Elith 2011). For this, we used a GLM with the number of recruits produced as a response variable excluding all zero observations and a Poisson error

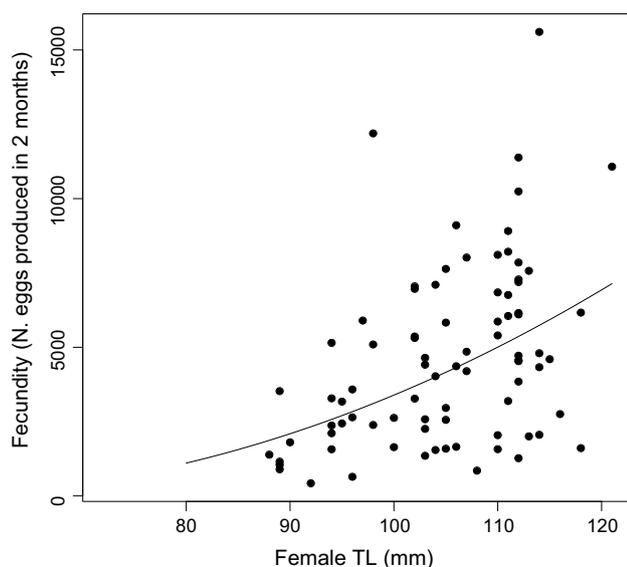


Fig. 2 Relationship between female size (mm total length) and egg production (sum of the number of eggs laid in 2 months) measured in 2008. Resulting regression line from the reduced linear model is shown ($\sqrt{y} = 1.25x - 66.81$, $R^2 = 0.23$, $P < 0.001$, $n = 79$). Note that the smallest female that was observed laying eggs was 68 mm (TL) but was one of the females for which we collected only incomplete observations. Only values for females with complete observations were plotted

distribution using data from the 35 pairs that were stable throughout the study period. Male growth was measured as the difference in male TL between 2008 and 2009 censuses.

All statistical analyses were performed using R version 3.0.2 (R Development Core Team 2007).

Results

We sampled 554 juveniles that settled among the 7 sites within the metapopulation between April 2008 and April 2009 and obtained an individual genetic profile of each juvenile. Of these individuals, 83 were assigned to 58 females older than 1 year and 14 were assigned to individuals that became females between the 2008 and 2009 surveys.

Table 1 Female to egg life history transition for *A. polymnus*

Effect	Number of eggs		Egg density (eggs cm^{-2})		N eggs lost	
	$F_{(1,77 \text{ df})}$	<i>P</i> value	$F_{(1,77 \text{ df})}$	<i>P</i> value	$F_{(1,52 \text{ df})}$	<i>P</i> value
Female TL	21.72	<0.001	3.02	0.089	1.08	0.303
Depth	0.12	0.728	0.25	0.613	3.73	0.058
NBTL	1.01	0.316	0.18	0.670	1.03	0.314
Δ_{F-M} TL	0.14	0.700	0.06	0.802	0.28	0.596

Results of three generalized linear models testing for determinants of number of eggs, egg density and egg loss in *A. polymnus*. Explanatory variables (rows) were removed one at a time, starting from the bottom of the table to the top if $P > 0.05$

One life history transition

Determinants of egg production

A linear model reduced to the number of significant correlates with egg production included female size only (analysis of deviance: female TL, $F_{1,78} = 22.29$, $R^2 = 0.23$, $P \leq 0.001$). Egg production over 2 months increased with female length (Fig. 2). None of the explanatory variables (female TL, male TL, anemone depth and nonbreeders' total length) had an effect on either egg density or egg loss. Both linear models were reduced to the null model without significant changes in the analysis of deviance (Table 1).

Two life history transitions

Relationship between egg production and number of recruits

Egg production on its own was a marginally significant predictor of the presence or absence of recruits (Table 2) (egg production: log-odds = 0.0002, SE = 0.0001, Z value = 1.77, $P = 0.076$). Similarly, it was marginally significant in predicting the number of recruits produced per female (analysis of deviance: number of eggs, $F_{1,33} = 3.64$, $P = 0.056$. Dispersion parameter = 1).

We explored the effect of egg production on both the probability of producing at least one recruit and the number of recruits produced per female. To do this, we tested if egg production controlled by the relative farness of the respective anemone in the network would produce a better model fit. This was done following the rationale that isolated females are less likely to produce successful recruits than females that have a central position in the network. Egg production controlled by relative farness was a slightly better predictor of the probability of producing at least one recruit than egg production alone (egg production: log-odds = 0.0003, SE = 0.0001, Z value = 1.90, $P = 0.054$). In other words, for every increase in 1,000 eggs produced, there is a predicted increase of 30 % in the odds of the presence of at least one recruit (Fig. 3a). Similarly, the prediction

Table 2 Test across two life history transitions for *A. polymnus*

Effect	$F_{(df)}$	P value
A		
N eggs	3.70 _(1,47)	0.054
Depth	1.25 _(1,46)	0.262
Δ_{F-M} TL	1.36 _(1,45)	0.243
Farness	2.53 _(1,44)	0.111
NBTL	2.02 _(1,43)	0.150
B		
N eggs	3.64 _(1,33)	0.056
Depth	0.01 _(1,32)	0.944
Δ_{F-M} TL	1.36 _(1,31)	0.243
Farness	2.04 _(1,30)	0.153
NBTL	0.03 _(1,29)	0.863

(A) Results of a logistic model testing for factors predicting the probability of producing at least one recruit. (B) Results of a general linear model testing for factors predicting the number of recruits produced. Explanatory variables (rows) were removed one at a time, starting from the bottom of the table to the top if $P > 0.05$

power of egg production as determinant of the number of recruits produced, when controlled by farness, was better than egg production alone (analysis of deviance: number of eggs, $F_{1,32} = 5.32$, $P = 0.021$. Dispersion parameter = 1, $R^2 = 0.061$). Based on this model, for every increase in 1,000 eggs produced (controlled for farness), there was an increase of 9.8 % in the number of recruits produced (Fig. 3b). We repeated this analysis after excluding one data point (number of recruits = 7, Fig. 3a, b), to test whether this point drove the results of the model. The removal of this point did reduce considerably the variance explained by the model, but the relationship remained marginally significant (analysis of deviance: number of eggs/farness, $F_{1,32} = 3.52$, $P = 0.060$. Dispersion parameter = 1, $R^2 = 0.038$). Based on this model, for every increase in 1,000 eggs produced (controlled for farness), there was an increase of 8.3 % in the number of recruits produced.

Three life history transitions

Determinants of probability of producing a recruit

A logistic model revealed that female size was the only factor predicting the presence or absence of recruits within our data set (Table 3a) (female TL: log-odds = 0.1, SE = 0.04, Z value = 2.74, $P = 0.002$). In other words, for one unit increase in female TL, there is a predicted increase of around 10 % in the odds of the presence of recruits (Fig. 4a). We repeated the analysis after excluding one data point (the smallest female) to test whether or not this point drove the results of the previous model. The removal of this point did not alter the significance of the previous model (analysis of

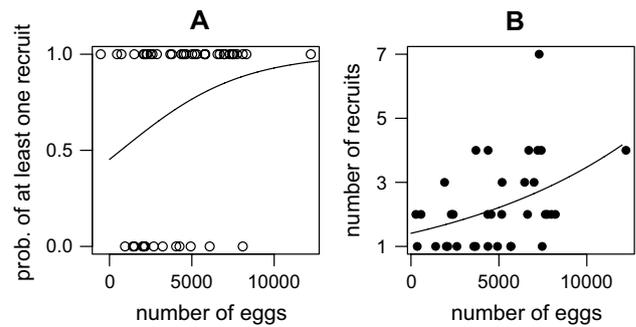


Fig. 3 Relationship between egg production (corrected by farness) and (a) probability of producing at least one recruit and (b) the number of recruits produced among females that produced at least one recruit. Resulting regression lines from logistic model and general linear models are shown [a odds of producing at least one recruit = $e^{0.0003x}$, $n = 49$, deviance: $F_{1,48} = 3.70$, $P = 0.054$; b log (number of recruits) = $0.685 + 0.000098x$, deviance: $F_{1,32} = 5.32$, $P = 0.021$, $R^2 = 0.061$, $n = 35$]

deviance: female TL, $F_{1,55} = 7.09$, $P = 0.007$. Dispersion parameter = 1, log-odds = 0.1, SE = 0.04, Z value = 2.51).

Similarly, when female size was replaced by mate replacement, this was the only factor predicting the presence or absence of recruitment in the metapopulation (Table 3a) (mate replacement: log-odds = 3.19, SE = 0.75, Z value = 4.23, $P < 0.001$). In this case, the model predicted that the odds of producing a recruit were 24 times higher for females in stable couples than for females where the male was replaced between both censuses (Fig. 4b). Mate replacement was a relatively better predictor of recruitment probability than female size (mate replacement AIC = 52.74, log-likelihood_(df = 2) = -24.37; female size AIC = 68.23, log-likelihood_(df = 2) = -32.11).

Determinants of the number of recruits

A general linear model found that the number of recruits produced per female (excluding observations with zero recruits) could not be explained by any of the variables we measured. The model was reduced to the null model without significant changes in deviance. Similar results were obtained when female size was replaced by mate replacement or egg production (Table 3b). Controlling for relative farness did not improve any of the correlations.

A general linear model found no relationship between the numbers of recruits produced by the 35 couples that were stable throughout the study period and any of the variables examined, including male growth (Table 4).

Discussion

Our field application of DNA parentage analysis showed for the first time that individual variation in reproductive

Table 3 Test across three life history transitions in *A. polynus*

Effect	$F_{(df)}$	P value	Effect	$F_{(1,52 df)}$	P value
A					
Female TL	9.13 _(1,56)	0.002	Mate replac.	24.6 _(1,56)	<0.001
Depth	3.60 _(1,55)	0.058	Depth	0.75 _(1,55)	0.387
Δ_{F-M} TL	0.58 _(1,54)	0.443	Δ_{F-M} TL	2.23 _(1,54)	0.134
Farness	0.51 _(1,53)	0.474	Farness	0.51 _(1,53)	0.473
NBTL	2.21 _(1,52)	0.137	NBTL	1.64 _(1,52)	0.200
B					
Female TL	0.50 _(1,33)	0.476	Mate replac.	1.43 _(1,33)	0.231
Depth	0.03 _(1,32)	0.858	Depth	0.04 _(1,32)	0.828
Δ_{F-M} TL	3.51 _(1,31)	0.061	Δ_{F-M} TL	1.96 _(1,31)	0.161
Farness	1.18 _(1,29)	0.277	Farness	0.67 _(1,30)	0.412
NBTL	0.58 _(1,28)	0.444	NBTL	0.51 _(1,29)	0.476

(A) Results of two logistic models testing for factors predicting the probability of producing at least one recruit. (B) Results of two general linear models testing for factors predicting the number of recruits produced. Explanatory variables (rows) were removed one at a time, starting from the bottom of the table to the top if $P > 0.05$

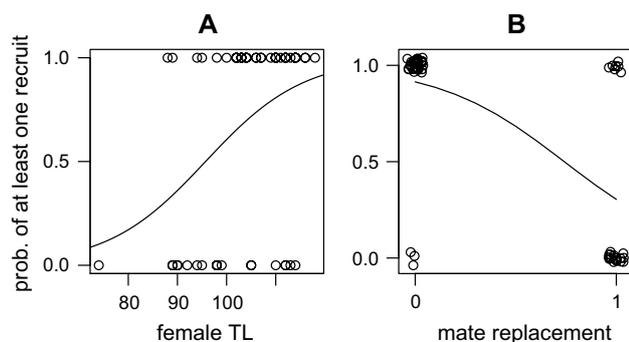


Fig. 4 Relationship between (a) female TL and (b) mate replacement (0 = no replacement, 1 = male replaced) and the probability of producing at least one recruit. Resulting regression lines from logistic models are shown (a odds of producing at least one recruit = $e^{-9.61 + 0.1x}$, $n = 58$, deviance: $F_{1,56} = 9.13$, $P = 0.002$; b odds of producing at least one recruit = $e^{2.37 - 3.19x}$, $n = 58$, deviance: $F_{1,56} = 24.6$, $P < 0.001$)

success, measured post-recruitment, as the actual number of juveniles recruiting to a metapopulation, can be quantified in marine organisms with a dispersive larval stage. In doing so, we tested the common assumption that large females have a higher reproductive success than small females, measured across one life history stage. That is, larger females produce more eggs. More important, we were able to investigate for the first time in a marine fish, the determinants of reproductive success across two and three life history transitions. We tested the common hypothesis that more eggs produce more recruits. However, we found that this relationship is weak. In addition, we confirmed, at least at the scale of a small metapopulation,

Table 4 Determinants of the number of recruits in pairs of *A. polynus* that were stable during the study period (2008–2009)

Effect	$F_{(df)}$	P value
Model 1		
Female TL	0.02 _(1,31)	0.476
Male growth	0.53 _(1,30)	0.462
Depth	0.11 _(1,29)	0.734
Δ_{F-M} TL	1.14 _(1,28)	0.284
Farness	1.64 _(1,27)	0.438
NBTL	0.58 _(1,26)	0.434
Model 2		
N eggs	2.77 _(1,31)	0.095
Male growth	0.84 _(1,30)	0.359
Depth	0.06 _(1,29)	0.802
Δ_{F-M} TL	0.01 _(1,28)	0.899
Farness	2.16 _(1,27)	0.141
NBTL	0.01 _(1,26)	0.898

Explanatory variables (rows) were removed one at a time, starting from the bottom of the table to the top if $P > 0.05$

that the probability of producing at least one recruit by individual females is directly influenced by their size and whether or not a mate replacement took place within the resident anemone. However, we found no evidence supporting the hypothesis that larger females contribute more to the metapopulation numerically than do smaller females or females that changed mate during the study period.

Our results compliment the only previous study providing evidence that bigger and/or older females contribute disproportionately to local population replenishment in the field (Beldade et al. 2012). These authors showed that in an anemonefish (*A. chrysopterus*) population at Moorea, French Polynesia, females that produced larvae that settled at Moorea were significantly larger than females that were not observed to produce any locally settling larvae. In this study, we were able to confirm that for *A. polynus*, larger females are more likely to produce at least one juvenile that recruit to the metapopulation than smaller females. In addition, our results indicate that females that had only one mate during the study period were more likely to produce recruits than females whose original mate died and was replaced. In other anemonefish, it has been shown that newly formed pairs tend to perform worse than experienced pairs in terms of the number of eggs that are produced and hatched (Buston 2004; Buston and Elith 2011). Here, we show that the effect of breeding experience might be continued through the larval phase and recruitment. However, in our study, females with a stable partner were, on average, larger than females where mate replacement occurred. As a consequence, it is difficult in this case, to tease apart the relative effect of female size and breeding experience

on reproductive success measured post-recruitment. This correlation between female size and mate stability might be the result of differences in microhabitat quality among anemones. Larger females and their mates may have better survival, grow larger and have higher reproductive success in places where microhabitat conditions are more favourable (Buston and Elith 2011). An experiment where female size and breeding experience can be controlled would be required to disentangle the relative contribution of each one of these factors to local replenishment.

Although this study and the one carried out by Beldade et al. (2012) support the positive relationship between female size and contribution to local replenishment, they differ in whether fecundity alone could be responsible for the higher contribution of larger females to local replenishment. Beldade et al. (2012) found that the relationship between female size and fecundity could not explain the higher contribution of larger females to self-recruitment; thus, other maternal effects were implicated. In this study, we found that female size was a significant predictor of egg production and that egg production was a significant predictor of the number of recruits produced when corrected by fecundity. Furthermore, we found that female size was a good predictor of the probability of successful recruit production but was not a good predictor of the number of recruits produced. Overall, these results suggest that the number of eggs produced is indeed an important predictor of the number of recruits produced that contribute to local replenishment. Yet, these results do not imply a causal relationship between female size and local replenishment. As suggested by Buston and Elith (2011), in anemonefishes, large females are often found in large anemones, are associated with large groups and produce large numbers of offspring. In turn, these occurrences could be driven by external factors that affect microhabitat quality such as small-scale differences in productivity. A field experiment controlling for small-scale environmental differences would be required to demonstrate the causal effect of female size on egg production and recruit production.

Previous studies on other anemonefish species have documented a strong correlation between female size and the number of eggs in a clutch (Green and McCormick 2005; Beldade et al. 2012). However, anemonefish have a particular reproductive strategy that includes demersal eggs, parental care and egg production all year long. Because of these features, even if the number of eggs laid per clutch for a particular female size class is fairly constant, the number of clutches that are laid by a female over a given period of time (long-term fecundity) can vary significantly because of differences in environmental conditions (Clarke 1992). For *A. polymnus*, fecundity was measured as the number of eggs produced over two months, comprising between one and five egg clutches per female. As a consequence, the size–fecundity relationship was weaker, and data were

more dispersed, than in other anemonefish studies where fecundity was measured as the number of eggs in a single clutch (Beldade et al. 2012; Green and McCormick 2005). This extra variation was not explained in the present study by male size, fish density or colony depth. Additional environmental factors that we did not measure, such as microhabitat quality, could underlie variability in clutch size with time (Clarke 1992) and overall reproductive success (Buston and Elith 2011), but further studies are required to determine whether this is the case.

Our findings do not rule out the possibility of maternal size effects on larval quality accounting also for some of the difference in contribution to local replenishment of larger females. However, our results do show that it is more challenging to predict the determinants of reproductive success across two or three life history transitions than it is across one, especially when there are multiple factors that can influence every transition. Independent studies have shown that besides female phenotype, environmental factors can affect fecundity (Clarke 1992) and larval quality (Donelson et al. 2008; McCormick 2006), with effects on this last factor sometimes leading to contrasting results in terms of selective mortality of fish larvae (Gagliano et al. 2007). The fact that in *A. polymnus* the amount of variation in reproductive success explained by female size was much higher when examined across one life history transition (female to egg) than when examined across three transitions (female to suggest that there might be antagonistic interactions between maternal size effects and environmental effects on larval quality across different transitions. However, our data are not sufficient to definitively conclude that larval quality associated with female size was less important than fecundity associated with female size in terms of contribution to local replenishment. Maternal size effects on phenotypic traits of offspring might be more likely to be detected in species reproducing only once a year/season (Berkeley et al. 2004a) as its within individual variance associated to environmental effects will be minimal. Nevertheless, further studies will likely be necessary to accurately partition variance in offspring phenotypic traits and survival rates and quantify individual contributions of fecundity and maternal size effects on phenotypic larval traits of offspring to the replenishment of marine populations.

The fact that female size and mate replacement are positively linked with recruitment success in anemone fish has important implications in terms of reef fish conservation and management. First, the effects of female age/size and mate replacement on local replenishment might be similar for other species with similar reproductive modes (demersal egg layers with parental care), which represents a significant fraction of coral reef fish. Also, large females of this small coral reef fish species

with high population turnover rates are much more likely to contribute to local replenishment than smaller females. We expect that this effect would be more pronounced in long-lived species, as bigger females would likely have higher egg contributions for longer periods of time. Similarly, we expect that this effect will be in synergy with maternal size effects on offspring phenotypic traits for many commercial species that reproduce once per year/season (Birkeland and Dayton 2005). Second, our focal metapopulation was characterized by low self-recruitment (Saenz-Agudelo et al. 2011) relative to some other studies (Berumen et al. 2012; Almany et al. 2007; Hogan et al. 2012; Jones et al. 1999; Planes et al. 2009), and yet, we still were able to document a significant effect of female size in the contribution to local replenishment. There is little reason to think that the female size effect on local replenishment would not also be maintained in terms of export outside the metapopulation. However, the degree to which these results can be extrapolated to other scales, species and places obviously requires further investigation. Certainly, the observation that maternal size effects can be maintained through the two stages of the life cycle of these small marine fishes warrants further testing of this phenomenon. If indeed maternal size effects turn out to be of general importance in marine fishes, there will be strong support for management strategies that not only regulate total mortality, but also for no-take reserves that can help restore natural age/size structure and protect large adults (Kritzer and Sale 2004; Palumbi 2004; Sale et al. 2005; Venturelli et al. 2009). These results also suggest that the anemonefish might not be an ideal model for testing maternal effects in isolation, as paternal influence (breeding experience) seems to be also important.

In conclusion, our study demonstrates that assessing the reproductive success (measured post-recruitment) of individuals in wild marine fish populations is no longer an intractable problem. Rather, combining DNA parentage assignments and long-term monitoring of adults within metapopulations can be used to address these questions. In addition, we have tested one of the fundamental assumptions in coral reef fish behavioural ecology, which is that the number of eggs produced (perhaps the most common metric of reproductive success) correlates with the number of offspring produced (which is never measured). Although applied here to an anemonefish with a relatively short pelagic larval duration and a particular reproductive strategy, recent data suggests that species with different life history traits may also exhibit significant and similar levels of local retention (Almany et al. 2007, 2013; Harrison et al. 2012; Berumen et al. 2012; Jones et al. 2009). These species may therefore be similarly accessible to the approach that we outlined here.

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