Title: First genealogy for a wild marine fish population reveals multi-generational philopatry

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Abstract

Natal philopatry — the return of individuals to their natal area for reproduction — has advantages and disadvantages for animal populations. Natal philopatry may generate local genetic adaptation but may also increase the probability of inbreeding that can compromise persistence. While natal philopatry is well documented in anadromous fishes, marine fish may also return to their birth site to spawn. How philopatry shapes wild fish populations is, however, unclear because it requires constructing multi-generational pedigrees that are currently lacking for marine fishes. Here we present the first multi-generational pedigree for a marine fish population by repeatedly genotyping all individuals in a population of the orange clownfish (*Amphiprion percula*) at Kimbe Island (Papua New Guinea) over a 10-year period. Based on 2927 individuals, our pedigree analysis revealed that longitudinal philopatry was recurrent over five generations. Progeny tended to settle close to their parents, with related individuals often sharing the same colony. However, successful inbreeding was rare and genetic diversity remained high, suggesting occasional inbreeding does not impair local population persistence. Local reproductive success was dependent on the habitat larvae settled into, rather than the habitat they came from. Our study suggests that longitudinal philopatry can influence both population replenishment and local adaptation of marine fishes. Resolving multi-generational pedigrees over a relatively short time period, as we present here, provides a framework for assessing the ability of marine populations to persist and adapt to accelerating climate change.

Significance Statement

Evidence for natal philopatry — the return of individuals to their natal location for reproduction — is scarce in marine fish populations despite being common in anadromous fishes. The proportion of individuals returning to natal sites is an important metric for estimating the effects of inbreeding and the potential for local adaptation to generate resilience to climate change. Here, we present the first multi-generational pedigree for a wild marine fish. We resolved the genealogical tree of families of orange clownfish *Amphiprion percula* spanning up to five generations using data from a 10-year genetic survey of a population at Kimbe Island, Papua New Guinea. We found that
longitudinal philopatry plays a significant role in driving population renewal of the orange
clownfish.

Introduction

The dispersal of immature individuals away from their natal area in search of breeding sites can
negatively impact population replenishment and, when not offset by immigration, put small
populations at risk of extinction (1). Long-distance dispersal may also reduce the potential for local
adaptation to environmental change, as individuals may be poorly adapted to distant habitats and
suffer higher rates of mortality prior to reproduction (2). Natal philopatry— the return of
individuals to their natal area (3) — provides a mechanism to avoid at least some of the negative
consequences of dispersal, because genetically adapted individuals contribute to the renewal of their
population of origin. Yet philopatry is a double-edged sword, because although it can contribute to
population replenishment, it may also increase inbreeding (3) that often has a deleterious effect on
fertility and poses an extinction risk for small populations (4). Inbreeding may also reduce genetic
diversity (5) that can reduce the potential of populations to adapt to changing conditions through
natural selection (6). Therefore, understanding the balance between dispersal and philopatry is
critical in animal populations because of the implications for genetic diversity (7), adaptation (8)
and conservation (9).

The vast majority of benthic marine species, including most coral reef fishes, have a dispersive
larval stage in their early life history before settlement into adult habitat (10). Historically, larval
offspring were considered as essentially passive particles carried by ocean currents to locations far
from their natal population (11). More recently, it has been demonstrated that, like many
anadromous species, marine fish may also return to their birth area (11-15). It has proved more
difficult to verify that those individuals returning to their natal location later successfully reproduce
as part of the adult population. Philopatric behavior has been widely documented in terrestrial
vertebrate species, including birds and large mammals (16), using multi-generational pedigrees of local populations. Multi-generational pedigrees have yet to be constructed for a wild marine fish population, perhaps because of the presumed dissociation between parents, offspring and their relatives (17). However, natal philopatry may be more prevalent in marine species than previously thought. Evidence for self-recruitment in coral reef fishes is accumulating (11-14, 18) and these findings raise questions about the role of philopatry in determining the structure and persistence of local populations. For example, do long-term family lineages contribute to generational turnover in local populations? Are the benefits of natal philopatry offset by the negative effects of inbreeding?

Here, we resolve the first multi-family genealogical trees for a wild marine fish population using a 10-year genetic survey and evaluate the extent and effects of philopatry on inbreeding.

Results

Pedigree reconstruction. We found that self-recruitment (i.e., the ratio of locally produced settlers to settlers from all origins arriving at a given settlement site (19)) occurs over multiple generations in a wild population of the orange clownfish, *Amphiprion percula*, on coral reefs around Kimbe Island, Papua New Guinea. Self-recruitment averaged 56% over a 10-year period (20). We followed the fate of every fish (2927 individuals) and their philopatric progeny over 10 years using genotypic profiling and parentage analysis (see methods, Fig. 1A). The multi-generational pedigree we reconstructed contained 502 informative founders, 987 parent-progeny links, 1809 full-siblings, 412 maternal half-siblings and 248 paternal half-siblings, 278 paternal grand-mothers and grand-fathers, and 135 maternal grand-mothers and grand-fathers (Table 1). The pedigree included up to five generations of individuals within the same family over the 10-year period (Fig. 1B; see examples of families in Fig. S1). We found examples of families that spread throughout the Kimbe Island population and others that grouped in small geographic areas around the island (Fig. 2). On the smallest spatial scale, we found 57 instances of family members recruiting to the same anemone (2% of individuals from the local population), including cohabitation of parents and offspring, full-siblings and half-siblings (Table 1). The pedigree reconstruction revealed that 37% of adults (649
individuals) contributed nearly 56% to the renewal of the local orange clownfish population every two years (20). Clearly, some individuals contributed more than others to future generations, as is shown in the variety of family tree sizes reconstructed (Fig. S1). Our findings imply that inter-generational continuity in this insular population is dependent on a small proportion of the breeders contributing most of the local replenishment.

**Inbreeding and extra-pair mating.** The potential downside of philopatry over multiple generations in marine fish populations is inbreeding; *i.e.* that mating partners are genetically related. Our pedigree reconstruction generally showed that most juveniles from the same family settled in different anemones from parents and siblings. Only two cases of successful inbreeding were observed, one between a brother and sister and one between a grandson and grandmother (Table 1). Whatever the mechanism, inbreeding in the orange clownfish population was rare ($F_{IS} = 0.018$) and average genetic diversity remained high ($H_S = 0.714$, Table S1 for detailed results).

Family trees were almost entirely based on adult pairs that co-habit the same anemone. We previously documented the presence of two cases of adults moving from their anemones to another anemone to reproduce (extra-pair mating, (20)). The distance between the anemones of the two parents for these 2 cases were 13 and 133 meters, respectively. Our data indicate extra-pair mating was uncommon, presumably because individual *A. percula* are strongly site-attached and rarely stray more than a few meters beyond the periphery of their anemone (21, 22).

**Parental and environmental effects.** We tested the role that parental habitat and environment played in offspring survival and reproduction on Kimbe Island reefs. At the study location *A. percula* occupied two anemone species, *Stichodactyla gigantea* and *Heteractis magnifica*. We compared local reproductive success for individuals breeding on the two different host species. We found that offspring spawned by adults residing in *H. magnifica* and those from *S. gigantea* recruited in similar proportions in the two species of anemone ($\chi^2=1.32$, $P=0.250$, Fig. 3A). There was no tendency for individuals to recruit to their natal anemone species. However, local
reproductive success \textit{(i.e., the likelihood of an individual to produce a self-recruiting offspring)} was always higher for individuals living in \textit{S. gigantea} than for those living in \textit{H. magnifica} (\textit{T}= -2.41, \textit{P}=0.016, Fig. 3B). Hence, local reproductive success was dependent on which anemone species larvae settled into, rather than which host anemone they came from. The largest extended families at Kimbe Island were those in which offspring, perhaps by chance, settled on \textit{S. gigantea} in each generation. The geographic location of the anemone species \textit{(i.e.} in shallow water and close to the land for \textit{S. gigantea} and in the lagoon for \textit{H. magnifica}) may explain the difference observed between the two anemones in contributions to self-recruitment. \textit{Heteractis magnifica} is generally more abundant further from shore than \textit{S. gigantea} so may produce more dispersive larvae while \textit{S. gigantea} produces more self-recruiters.

\textbf{Discussion}

Our study revealed that consistently high levels of self-recruitment in the focal Kimbe Island orange clownfish population resulted in longitudinal philopatry over five generations in a 10-year period. The high self-recruitment rate observed is likely linked to biological characteristics of the orange clownfish that include benthic spawning and relatively short pelagic larval duration \textit{(i.e.} \textit{~}10 days, (25)). Other factors, including local current patterns, may also influence the larval dispersal kernel to some degree. Kimbe Island sits in a dynamic oceanic regime that is influenced by mesoscale eddies, likely originating from instabilities in the South Equatorial Current and the New Guinea Coastal Current (26), that may favor local retention (Fig. S2). Whatever the ultimate cause of the high self-recruitment to Kimbe Island, we have demonstrated that it is possible to construct genealogies in a clownfish population and test for effects of anemone species on local reproductive success.

In most coral reef fish populations, dispersal acts to reduce the probability for inbreeding. When self-recruitment is negligible, then the probability for inbreeding is also low. In the presence of significant self-recruitment, we would expect a proportional frequency of inbreeding. While we
identified incidents of inbreeding in \textit{A. percula}, it occurred at a very low frequency (>0.01%).

When dispersal is limited or natal philopatry is frequent, inbreeding may be avoided by mate choice that excludes kin. Previous results from experiments conducted in aquaria on \textit{A. percula} showed that larvae do not discriminate between parents and unrelated individuals when choosing settlement sites (27). The level of inbreeding in \textit{A. percula} was much lower than in small, closed populations of terrestrial animals where inbreeding depression results in a severe decline in genetic diversity (23, 24). Although we found high levels of self-recruitment (~56%), the number of juveniles arriving from other reefs appears to be sufficient to maintain high genetic diversity in the study clownfish population. The two incidences of inbreeding that we observed may be due to the limited number of anemones available for settlement at any given time (28) that suggests it will be advantageous for settlers to remain at the first anemone they encounter (29). A dispersive larval phase and a hierarchical breeding system likely compensates for the potential inability of individuals to accurately identify and actively avoid mating with relatives. The hierarchical breeding system is a size-based queue for the two breeding positions in an anemone that means it can take up to 10 years to become a breeder (30); \textit{i.e.} newly settled relatives that could engage in inbreeding may never get the chance.

High levels of self-recruitment do not preclude long distance dispersal events in \textit{A. percula}. Our observation of 56% self-recruitment means that 44% of the population arrived as larvae from reefs beyond Kimbe Island. Larvae that dispersed to the study population from other locations likely represented a significant influx of genetic diversity. Therefore while the larval dispersal kernel may be weighted towards self-recruitment, immigration nonetheless has a significant impact on the genetic structure of the study clownfish population. It remains unknown whether local adaptation can occur in this \textit{A. percula} population. Locally adapted genes may be swamped by gene flow from immigrants. However, evolutionary adaptive divergence and therefore local adaptation may occur despite gene flow if selection is strong (31). The high levels of self-recruitment suggest local
adaptation is at least possible in *A. percula*. Identifying the possible extent, nature, and implications of local adaptations represents an important area for future research.

Our findings have consequences for the management of spatially-structured marine fish populations and the ability of future generations to adapt to environmental change. While it is well known that exploited populations can be protected in marine reserves such as Kimbe Island, our study has demonstrated that this benefit can ensure the protection of multiple generations. It is conceivable that such long-term protection may prove futile if coral reef fish species are unable to cope with rapid global climate change. Climate change may act to reduce the potential dispersal distance and functional connectivity between populations of many species in oceans (27, 32). Philopatric behavior may become the major source of local replenishment in the future. While inbreeding is currently very low, the population may be at risk in the long term if immigration and hence genetic diversity decrease. However, our discovery of five-generation family trees in the space of 10 years suggests that the potential for local adaptation may be higher than previously thought in marine fish populations. The presence of local adaptation would, in turn, provide a mechanism for population resilience to climate-induced changes in environmental conditions.

**Materials and Methods**

**Study species and data collection.** Exhaustive sampling was carried out every two years from 2003 to 2013 on the entire orange clownfish (*Amphiprion percula*) population at Kimbe Island (5°12’22.56” S, 150°22’35.58” E), West New Britain Province, Papua New Guinea. Here, *A. percula* live in a mutualistic association with one of two host sea anemone species, *Stichodactyla gigantea* and *Heteractis magnifica*. Within each clownfish group (i.e. clownfish within one anemone) of typically 3-5 individuals, there is a size-based dominance hierarchy: the female is largest, the male is second largest and the non-breeders rank progressively lower in the hierarchy as they decrease in size. Bigger is the group, longer a settler has to wait to achieve reproductive status, so the lower the
likelihood of surviving to maturity (33). If the single female adult of a group dies, then the male
changes sex to female and the largest juvenile from the anemone becomes sexually mature as male.

At Kimbe Island, reproduction occurs year round, with females laying several hundred eggs in a
clutch near the pedal disk of the host anemone each lunar month. The eggs hatch after ~7 days of
paternal care into larvae that spend ~10 days (34) in the pelagic environment before settling on an
anemone that may or may not be on the natal reef (35).

The Kimbe Island population of *A. percula* consists of 310 different anemones (176 *H. magnifica*
and 134 *S. gigantea*). Anemone positions were recorded with a GPS and depth was measured using
a dive computer. Anemones were surveyed during each bi-annual sampling period and all fish
within the anemones were counted, captured using hand nets, measured using calipers (total length
TL), fin-clipped underwater for genetic analysis. Each fish was processed on SCUBA *in situ*, with
each individual caught, processed next to the anemone and then released back on the same
anemone. The biggest fish in each anemone was identified as the female, the second largest
individual was assumed to be the male, and all other individuals were classified as subadult
(TL>35mm) or new-recruits (TL<35mm). The small pieces of fin tissue were preserved in 95%
ethanol in 2mL vials. The new-recruits were collected whole, and preserved in vials with 95%
ethanol.

We extracted DNA from a total of 4829 fin-clips (including 1192 new-recruits) following a
modified HotSHOT method (36) and subsequently stored the DNA at -20°C. We then screened the
DNA at 22 polymorphic microsatellite loci (20). We controlled for human errors and sample
contamination by using negative controls during PCR and electrophoresis. We also controlled for
genotype errors by re-amplifying and re-analyzing a sample of 789 individuals with the same typing
software (GeneMapper v3.7). The error rate was approximately 2%. Genetic diversity metrics such
as allelic richness, average expected and observed heterozygosities (*H*<sub>S</sub> and *H*<sub>O</sub>, respectively) and
the departure from Hardy-Weinberg equilibrium fixation index or inbreeding coefficient (*F*<sub>IS</sub>) were
estimated by using the R package HIERFSTAT (37).
Pedigree and family reconstructions. Pedigree reconstruction was carried out by using the genotype data from the parentage analysis. We first identified the individuals sampled multiple times over the years by using the Excel macro GenAlex v6.5 (38) to compare multilocus genotypes from the 2003, 2005, 2007, 2009, 2011 and 2013 samples. Juvenile fish were assigned to parental pairs using software FaMoz (39). This software is based on the calculation of Log of the odds ratio of putative parent-offspring pairs being true and determines critical thresholds to accept or reject assignments by simulating true and false parent-offspring pairs. FaMoz does not require a priori information of the proportion of candidate parents in the sample in order to determine critical LOD thresholds (40). Overlapping generations were assumed for the pedigree construction to accommodate the biology of the clownfish species (i.e., reproduction frequency and lifetime), such that two individuals within a cohort were defined as a potential parent for any individual sampled the same year or the following years (Fig. 1A). We only retained offspring-parent-pair assignments when genotypes were matched to fish living in the same anemone or in an anemone in close proximity within the same year period (for more details see (20)). Because of the presence of overlapping generations in this system, we rejected all assignments to single parents to avoid possible false assignments to other related individuals that were not true parents. We accepted offspring-parent-pair couples with LOD scores > 30.

We tested all the possible parent couple-offspring links between the different year-periods (Fig. 1A). First, we compared individuals sampled in the same year and we hypothesized that (i) two adults from same or nearby anemone can be potential parents of subadults and new-recruits, (ii) two adults from same or nearby anemone can be potential parents of other adults (i.e., the data set of offspring to test in FaMoz is exactly the same as the data set of parents). Second, we compared individuals sampled in two different years and we hypothesized that (iii) two individuals from adult or subadult categories living in same or nearby anemone and sampled at a specific year period can be the parents of adults, subadults and new-recruits sampled at the following years, (iv) two individuals from adult or subadult categories sampled in two consecutives sampling years can be
the parents of adults, subadults and new-recruits sampled the year periods following. We measured
the local reproductive success for each individual as the sum of self-recruiting offspring produced
from 2003 to 2013.

**Pedigree and dispersal analyses.** Pedigree summary statistics estimating pairwise relatedness
between all individuals and maximal depth pedigree were obtained by using the R package
pedantics (41). We constructed the pedigree containing only those individuals that were informative
(i.e., a member of a family from Kimbe Island). Then, we analyzed separately the structure and
depth of each family that was present in the pedigree. The families were plotted as family trees
using the R package KINSHIP2 (42). Mothers are represented with a circle, males and subadults
with a square and new-recruits with a diamond. The same individual can be both a father and a
mother because of the sex changes through the life of the clownfish. This hermaphroditism has no
effect on the pedigree reconstruction. We used as representative symbol a circle within a square for
the individuals for which we detected sex change during the studied period.

Parentage analyses combined to sampling site information allowed us to identify offspring dispersal
from the natal anemone to the anemone of settlement. We evaluated if descendants preferentially
returned to the same anemone species (*H. magnifica* or *S. gigantea*) as their founder ancestors or
not. Chi-square test ($\chi^2$) was used to evaluate if the anemone species of offspring was independent
of the anemone species occupied by parents. Then, we tested if the local reproductive success of
offspring was linked by the parental anemone species to evaluate a potential effect of parental
environment by using Student's test (T). Statistical analyses were performed using R version 3.0.2
(43) and their significance was interpreted with $P=0.05$.

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Author contributions

S.P., G.P.J., and S.R.T. conceived the study; O.C.S., P.S.A., G.R.A., G.P.J., M.S., M.L.B., S.R.T., and S.P. collected field data; O.C.S. and P.S.A. carried out the molecular laboratory work and parentage analysis; O.C.S. and B.P. carried out the analyses; O.C.S., J.A.M., B.P. and S.P. wrote the first draft and all authors contributed substantially to revisions.

References


**Figures**

**Fig. 1.** Philopatric events found in the wild marine orange clownfish population of Kimbe Island spanning over five generations. (A) Generational links among the six sampling periods (i.e., 2003 - '05,'07, '09, '11,'13) revealed by DNA parentage analysis. Orientation of the arrows gives the generation direction (i.e., from parent to offspring). (B) Pedigree representation - each line connects a parent with one of its offspring (blue and red lines represent respectively paternal and maternal links, an individual can be both mother and father). The generation of individuals is indicated on the left from first generation (F0) to fifth generation (F4).
**Fig. 2.** Philopatric events in the wild marine orange clownfish population of Kimbe Island within and between microhabitats. Five representative families were selected to present the variation in size and depth of family trees (see Fig. S1). (A) Families spanning from 2 to 5 generations and (B) a family of 4 generations. Arrows represent links between parents and offspring. The direction of the arrow indicates the geographical origin and settlement of dispersal events. Dots refer to anemone locations (black and white dots correspond respectively to *Heteractis magnifica* and *Stichodactyla gigantea*). Numbers from 0 to 4 identify the corresponding generation in the pedigree. A dot with two numbers indicates the presence of related fish from different generations in the same anemone. White corresponds to the lands and shades of gray refer to the water, shallow water 0–2 m (light gray) and lagoons 2–15 m (dark gray).
Fig. 3. Effect of parental anemone species on the local reproductive success of their offspring in orange clownfish from Kimbe Island. (A) Settlement choice distribution of offspring (N=987 individuals) on the two species of anemones, *Heteractis magnifica* or *Stichodactyla gigantea*, according to the anemone species of their parents. Offspring native from *H. magnifica* and those native from *S. gigantea* recruited in similar proportion in the two species of anemone ($\chi^2=1.32$, $P=0.250$). (B) Effect of anemone species transmission from parent to offspring on the local reproductive success of offspring. Whatever the anemone species from which the clownfish progeny originated, the local reproductive success was always higher for individuals living in *S. gigantea* than for those living in *H. magnifica* ($T=-2.41$, $P=0.016$). NS and * mean Student's statistical test was not significant and significant, respectively.
Table 1. Pedigree statistics and inbreeding in the Kimbe Island Amphiprion percula wild population. The number of individuals, families, founders and family links are listed in the central column. Total number of pairs of related individuals found within the same anemone are listed in the last column. Among these links, the number of cases of inbreeding are presented in brackets.

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