

REPORT

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Genetic evidence of closed life-cycles for some coral reef fishes within Taiaro Lagoon (Tuamotu Archipelago, French Polynesia)

Accepted: 28 August 1997

Abstract Taiaro Lagoon has no permanent or regular connection with the ocean (ingress is restricted to episodes of high sea-level and/or strong wave action) raising the question of how fish populations with normally dispersive larvae are maintained inside this lagoon. We compared the genetic population structures of two coral reef fishes, *Acanthurus triostegus* and *Chaetodon ulietensis*, present on both sides of the atoll rim to determine whether there is evidence of reproductive isolation. Genetic surveys showed that the lagoonal and oceanic populations were statistically different at five loci (*AAT**-3, *GDA**, *HPD**, *MDH** and *SDH**) in *A. triostegus* and three loci (*PGI*-2*, *IDH** and *PGD**) in *C. ulietensis*, producing high F_{st} values of 0.055 and 0.021, respectively. Our genetic and demographic data on these species suggest that both may be completing their life-cycles inside the lagoon, which leads us to question the common assumption that coral reef fishes require oceanic conditions for larval development.

Key words Population genetics · Allozymes · Larval dispersal · Genetic drift

Introduction

Most coral reef fishes have a pelagic larval stage, resulting in a life history with two distinct phases. Pelagic and benthic stages differ in many characteristics, in-

cluding morphology, size, habitat utilisation, diet and behaviour. Although a few types of fish larvae complete their pelagic stage in the immediate vicinity of their natal reef, the majority apparently do not (Leis 1991).

Many hypotheses have been proposed over the last twenty years to explain the significance of larval development in the ocean. Johannes (1978) suggested that the low abundance of fish larvae near reefs is caused by intense predation in shallow water. Bourret et al. (1979) suggested that oceanic development is energetically efficient. Barlow (1981) suggested that oceanic dispersal is advantageous because coral reefs are patchy and unstable habitats over evolutionary time. Doherty et al. (1985) suggested that dispersal is a risk-spreading strategy that is advantageous in a patchy oceanic environment. Bakun (1986) suggested that larvae avoid water near reefs to reduce potential pulverisation in the surf zone. While most of these hypotheses assume that the observed distributions, behaviour and patterns are adaptive (Shapiro et al. 1988), Leis (1991) noted that direct observation of larvae is difficult and warned that all should be regarded with caution. Few authors have questioned the necessity for development in oceanic nurseries; yet the successful aquaculture of some marine fishes in enclosed environments shows that an oceanic stage is not obligatory.

Taiaro Atoll (15°45'S, 144°38'W), located on the northern edge of the Tuamotu Archipelago (French Polynesia), provides a natural testing ground for these assumptions. This lagoon has no permanent or regular connection with the ocean (ingress is restricted to episodes of high sea level and/or strong wave action) raising the question of how healthy fish populations are maintained inside this lagoon (Galzin et al., this volume). To answer this question, we compared the genetic population structures of two common reef fishes found on both sides of the atoll rim, to determine whether (1) lagoonal stocks must be replenished from oceanic sources during episodic inflow, or (2) lagoonal stocks can be self-sustaining.

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Methods

Sampling

In 1994, we collected samples of 50 individuals from Taiaro Lagoon and the adjacent reef slopes of two abundant reef fishes assumed to have larvae specialised for oceanic dispersal: the surgeonfish, *Acanthurus triostegus*, and the butterflyfish, *Chaetodon ulietensis*. The former has been the subject of previous genetic surveys throughout French Polynesia (Planes 1993). Fish were speared and kept on ice until we could remove their liver, eyes, and 2 ml of dorsal muscle. Dissected tissues were stored in liquid nitrogen in the field and thereafter at -80°C . Ten fish of each species from each location were selected randomly for removal and storage of their otoliths for subsequent demographic analysis.

Enzyme analysis

Each tissue sample was thawed and homogenised at 4°C in an equal volume of Tris/EDTA/NAPD buffer (pH 6.8). Homogenates were centrifuged at 15 000 G for 30 min at 4°C . Supernatants were stored at -80°C and then used for routine electrophoresis, which followed Pasteur et al. (1987) and Planes (1993). Enzyme nomenclature followed Shaklee et al. (1990). Eleven polymorphic loci (where the frequency of the most common allele was < 0.95 in at least one population) were surveyed in *A. triostegus* following Planes (1993). Thirty-five loci were tested in *C. ulietensis* of which nine representing eight enzymes were found to be polymorphic.

Gene frequencies, measures of genetic variability (Hardy-Weinberg equilibrium, heterozygosity, polymorphism), genetic distance and cluster analysis were performed using programs in the "Genetix package (Bonhomme et al. 1993). Genetic differences between populations were tested using G-tests, after adjusting the significance levels for multiple comparisons using the sequential Bonferroni technique (Rice 1989). Nei's (1978) genetic distances were calculated between the lagoon and ocean samples. Allelic frequencies of *A. triostegus* were compared with similar data from 11 other sites in French Polynesia sampled in 1991 (Planes 1993) to provide a yardstick for the differences detected in this study. *F*-statistics were calculated for single-locus values and multiple loci using procedures in Weir and Cockerham (1984) but variances could only be estimated from the latter given that only two samples were taken from each habitat. Unbiased estimates of these variances were performed using the jack-knife procedure over loci (Reynolds et al. 1983) and significance levels were calculated at alpha of 5%. F_{st} estimates were used to calculate the average number of migrants per generation ($N_{em} = (1 - F_{st})/4F_{st}$) according to the island model of Wright (1951).

Otolith analysis

Otoliths were used to estimate three variables: duration of the larval stage (based on putative daily increments), individual fish age (based on putative annuli) and back-calculations of growth rates. Sagittal otoliths were weighed to the nearest 0.1 mg, embedded in epoxy resin, ground (convex side) by hand on wet abrasive paper (grit 1000–1500) and etched with EDTA (5% in solution, pH 7.4) for a few minutes. Annuli were counted after staining with toluidine blue. Daily increments were counted with a scanning electron microscope (Hitachi S520) after coating the ground surface of the otolith with gold. No validation of either daily increments or annuli (Panella 1980) was possible, but we have relied upon the results of comparable studies: Acanthuridae (Lou and Moltshaniwskyj 1992; Choat and Axe 1996) and Chaetodontidae (Fowler 1989).

All estimates of age (daily and annual) were compared between samples using Student t-tests. Growth rates were back-calculated following Worthington et al. (1995) and also compared with Student t-tests.

Results

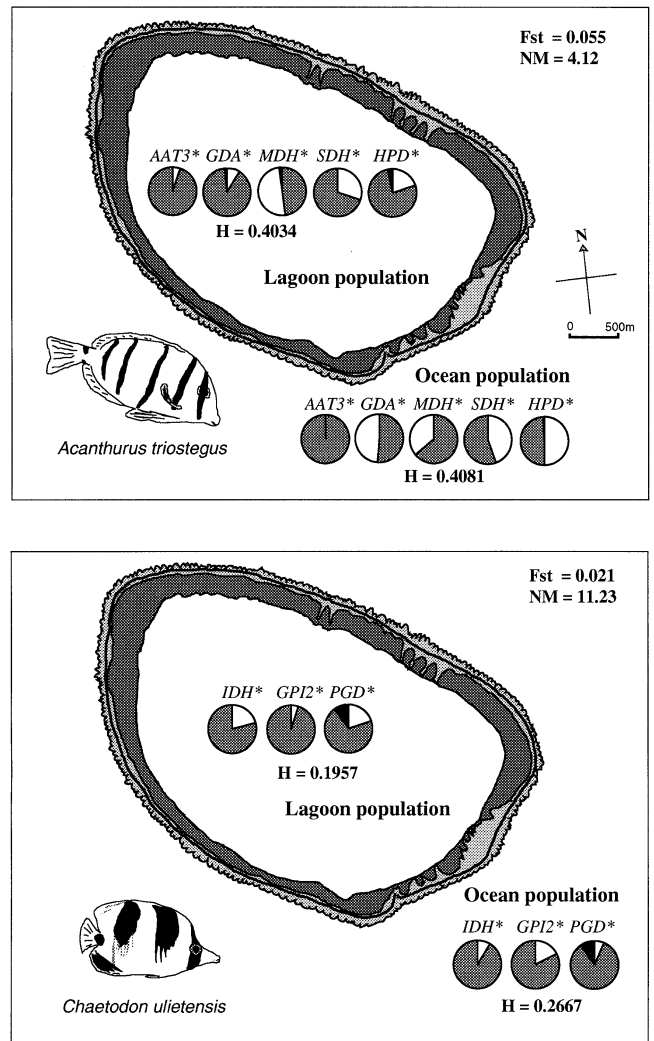
Allele frequencies and G-test results are given in Tables 1 and 2. For both species, no significant deviations of genotype frequencies from Hardy-Weinberg equilibrium were observed in either population. Five loci (*AAT**-3, *GDA**, *HPD**, *MDH** and *SDH**) in *A. triostegus* and three loci (*PGI*-2*, *IDH** and *PGD**) in *C. ulietensis* exhibited significant differences between samples collected inside and outside the lagoon (Fig. 1). Heterozygosity in the oceanic sample was greater for *C. ulietensis* (0.27 versus 0.19) and similar

Table 1 Allele frequencies of lagoon and ocean populations of *Acanthurus triostegus*. Sample sizes in parentheses. Statistical details are provided only for loci found to be significantly different ($p < 5\%$)

| Loci | Alleles | Lagoon (48) | Ocean (47) | G-test |
|----------------|---------|-------------|------------|-------------------------------|
| <i>AAT</i> -2* | 140 | 0.385 | 0.362 | |
| | 100 | 0.615 | 0.638 | |
| <i>AAT</i> -3* | 100 | 0.945 | 1.000 | G = 5.03 ($P = 0.0249$) |
| | 20 | 0.055 | 0.000 | |
| <i>ADA</i> * | 100 | 0.542 | 0.585 | |
| | 90 | 0.437 | 0.372 | |
| | 60 | 0.021 | 0.043 | |
| <i>ADH</i> * | 100 | 0.510 | 0.521 | |
| | 50 | 0.490 | 0.479 | |
| <i>GDA</i> * | 140 | 0.083 | 0.489 | G = 38.99 ($P = 0.0001$) |
| | 100 | 0.906 | 0.511 | |
| | 70 | 0.011 | 0.000 | |
| <i>HPD</i> * | 110 | 0.031 | 0.011 | G = 19.39 ($P = 0.0001$) |
| | 100 | 0.771 | 0.489 | |
| | 50 | 0.198 | 0.500 | |
| <i>MDH</i> * | 150 | 0.021 | 0.000 | G = 6.22 ($P = 0.0446$) |
| | 100 | 0.500 | 0.362 | |
| | 50 | 0.479 | 0.638 | |
| <i>PGI</i> -1* | 100 | 0.698 | 0.808 | |
| | 70 | 0.302 | 0.192 | |
| <i>PGI</i> -2* | 150 | 0.531 | 0.532 | |
| | 100 | 0.469 | 0.468 | |
| <i>PGM</i> * | 120 | 0.000 | 0.020 | |
| | 100 | 0.875 | 0.893 | |
| | 90 | 0.021 | 0.010 | |
| | 70 | 0.104 | 0.047 | |
| <i>SDH</i> * | 100 | 0.698 | 0.553 | G = 4.25 ($P = 0.0039$) |
| | 20 | 0.302 | 0.447 | |

Table 2 Allele frequencies of lagoon and ocean populations of *Chaetodon ulietensis*. Details as in Table 1

| Loci | Alleles | Lagoon (48) | Ocean (47) | G-test | |
|----------------|---------|-------------|------------|--------------------------------|----------------------------------|
| <i>AAT-2</i> * | 110 | 0.120 | 0.087 | $G = 5.66$ ($P = 0.0174$) | |
| | 100 | 0.820 | 0.826 | | |
| | 90 | 0.060 | 0.087 | | |
| <i>EST</i> * | 120 | 0.110 | 0.120 | | |
| | 100 | 0.520 | 0.380 | | |
| | 80 | 0.370 | 0.500 | | |
| <i>IDH</i> * | 130 | 0.210 | 0.087 | | |
| | 100 | 0.790 | 0.913 | | |
| <i>MPI</i> * | 100 | 0.870 | 0.239 | | $G = 7.6$ ($P = 0.0233$) |
| | 80 | 0.130 | 0.761 | | |
| <i>PGD</i> * | 110 | 0.200 | 0.065 | | |
| | 100 | 0.700 | 0.837 | | |
| | 70 | 0.100 | 0.098 | | |
| <i>PGI-1</i> * | 120 | 0.050 | 0.011 | $G = 2.42$ ($P = 0.0060$) | |
| | 100 | 0.950 | 0.989 | | |
| <i>PGI-2</i> * | 150 | 0.050 | 0.174 | | |
| | 100 | 0.950 | 0.826 | | |
| <i>PGM</i> * | 110 | 0.090 | 0.065 | | |
| | 100 | 0.900 | 0.924 | | |
| | 80 | 0.010 | 0.011 | | |
| <i>SDH</i> * | 130 | 0.030 | 0.054 | | $F_{st} = 0.055$ $N_m = 4.12$ |
| | 100 | 0.970 | 0.946 | | |



for *A. triostegus* (0.41 versus 0.40). Nei's genetic distances across the atoll rim were 0.041 for *A. triostegus* and 0.007 for *C. ulietensis*.

Both species showed significant F_{is} and F_{st} multi-locus values (Fig. 1) with estimated values for $N_e m$ of 4.12 (*A. triostegus*) and 11.13 (*C. ulietensis*). When compared with data from 11 other sites in French Polynesia, both samples of *A. triostegus* from Taiaro were closely related (Fig. 2). However, clustering analysis showed that differences between the lagoon and ocean populations at Taiaro were as great as those taken from reefs widely-spaced within the Tuamotu and Gambier archipelagoes (Planes 1993).

Otoliths from both species showed a clear settlement ring (Victor, 1991). Electron microscopy of daily increments preceding the settlement mark showed no difference in the pelagic larval duration of either species between fish collected from the lagoon and the ocean (Table 3). Only two parameters appeared significantly different: otolith weights and estimated ages of *C. ulietensis* were higher in the lagoon sample than in the ocean sample (11 versus 4 mg; 6.8 versus 4 years).

Fig. 1 Map of Taiaro Atoll showing genetic data for *Acanthurus triostegus* (upper) and *Chaetodon ulietensis* (lower). Only polymorphic loci showing significant divergence between oceanic and lagoonal populations are shown. Pie diagrams identify the frequencies of alleles for these loci. Heterozygosity (H) was calculated for each sample. F_{st} and gene flow ($N_e m$) were calculated between oceanic and lagoonal populations

Although only 10 individuals were analysed for each species, the lagoon samples contained a wide range of ages: (3, 4, 5, 7, 8, 9, 11 years for *C. ulietensis* and 3, 4, 5, 6 for *A. triostegus*).

Discussion

Genetic analyses of two common reef fishes (*C. ulietensis* and *A. triostegus*) showed significant differentiation across the rim of Taiaro Atoll. These collection sites were separated by < 1 km and yet Nei's genetic distances (0.041 and 0.007) and F_{st} values (0.055 and 0.021)

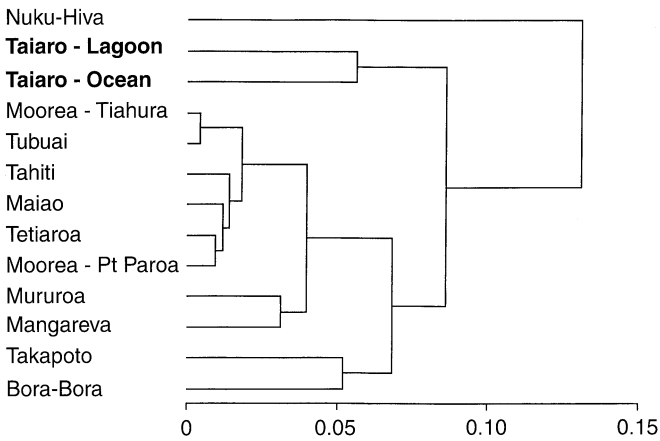


Fig. 2 UPGMA dendrogram of Nei's genetic distances for *Acanthurus triostegus* from 13 locations within French Polynesia formed by reanalysing Planes (1993) with the inclusion of samples from Taiaro Atoll

Table 3 Demographic parameters for both fishes estimated from otoliths. Growth rate was calculated as the slope of the length at age relationship in each sample

| | Lagoon | Ocean | Students-t | Probability |
|------------------------------|--------|-------|------------|-------------|
| <i>Acanthurus triostegus</i> | | | | |
| Number of larval increments | 27.0 | 26.6 | 0.64 | ns |
| Number of annuli | 4.1 | 4.3 | 0.76 | ns |
| Growth rate | 0.107 | 0.095 | 0.53 | ns |
| <i>Chaetodon ulietensis</i> | | | | |
| Number of larval increments | 52.4 | 53.0 | 0.62 | ns |
| Number of annuli | 6.8 | 4.0 | 0.02 | < 0.05 |
| Growth rate | 0.091 | 0.107 | 0.61 | ns |

were comparable to values found between populations separated by > 1000 km in French Polynesia (Planes 1993). G-tests on individual polymorphic loci showed that these differences were expressed at multiple loci: five for *A. triostegus* and three for *C. ulietensis*.

Three hypotheses may explain the genetic differentiation between lagoonal and oceanic populations. First, elevated temperatures or the hypersalinity of the lagoon (Dufour et al., this volume) might cause selective extinction of particular alleles with age and so maintain a genetic gradient. Examples of such selection are known from both invertebrates and fish (Koehn 1978; Koehn and Williams 1978; Burton and Feldman 1983; Krause 1989) due to both salinity (Hilbish 1985) and temperature (Smith and Francis 1983). Second, the differences might derive from a special form of the Wahlund Effect where there is pooling of individuals from different demes (Hedgecock 1978). The impossibility of regular recruitment from oceanic populations

to Taiaro Lagoon, due to its closure, lends weight to this hypothesis but it is an area that has not been well researched in marine populations. In most cases where such effects have been claimed, they have been attributed to the dominance of a few cohorts (Johnson and Black 1984; Macleod et al. 1985) whereas our samples contained multiple year-classes. Third, reef fishes may reproduce as closed populations in Taiaro Lagoon but experience distortions from founder effects and/or subsequent genetic drift in the absence of regular gene flow from the ocean.

Taiaro lagoon is about 3.8 km in length and 2.4 km in width with a mean depth of 18–20 m. While it has a small internal volume, the fish fauna in this lagoon is diverse with 123 species identified in the most recent survey (Galzin et al. This volume). Carbon dating of dead corals in old passages (hoa) permitting access of oceanic water into Taiaro Lagoon suggest that active exchange was possible 860 y BP. Since that time, ingress of ocean water has been restricted, occurring mainly during storms (Chevalier and Salvat 1976). The modern lagoon is hypersaline (42.5‰) and is deficient in many elements of a normal reef community including reef-building corals. Consequently, it is impossible to separate the potential effects of environmental selection from that of limited gene flow. On the one hand, the limited amount of habitat space seems likely to impose a severe constraint on population size, which increases the chance of genetic drift in the absence of regular gene flow. On the other hand, the unusual environmental conditions could result in strong selection in lagoonal populations.

Allele frequencies in the lagoonal samples did not reveal any significant deviation from Hardy-Weinberg equilibrium for either fish species which is consistent with random mating within local populations. In addition, the general levels of both polymorphism and heterozygosity did not differ between the lagoonal and oceanic populations, which argues against extreme selection. In contrast, we found significant differences in allele frequencies (ranging between 5 and 41%) across the atoll rim and these differences were spread across eight different loci: *AAT-3**, *GDA**, *HPD**, *MDH** and *SDH** in *A. triostegus*, and *PGI-2**, *IDH** and *PGD** in *C. ulietensis*. Although intense selection theoretically could produce such major shifts in allele frequencies, it is very unlikely that selection operating on a common pool of recruits could produce the observed differences within a single generation. While admitting the possibility of episodic gene flow, we propose that both species of fish may complete their life-cycles within Taiaro Lagoon.

Our conclusions from the genetic analyses are supported by the demographic data from the two species and meteorological records over the last decade (Galzin et al., this volume). Back-calculated ages of 10 *C. ulietensis* collected from inside the lagoon revealed seven year classes (3–11 y) suggesting that the lagoonal

population received some replenishment in most years, which is unlikely to be attributable to fish entering the lagoon only during occasional storms. The weather records from French Polynesia, although incomplete, record few such events during the last decade (Galzin et al., this volume). Thus, we believe that historical connections between the ocean and the lagoon have been too infrequent to explain the number of year-classes found in the lagoonal populations of either species

The literature on pelagic spawning of coral reef fishes is replete with the idea that individuals spawn at times and places that ensure immediate and rapid dispersal into offshore waters (Shapiro et al. 1988). The unspoken corollary of this behaviour is that coral reef fishes benefit from (or require) an oceanic phase, whereas our results suggest that it may not be necessary. If reef fish can reproduce in an enclosed space such as that offered by Taiaro Lagoon, why do more species not show this pattern under normal circumstances? Is it because few planktonic propagules can remain near their sources due to active hydrodynamics, or is it because the risk of predation is too high as suggested by Johannes (1978)? It may be relevant that the community of fishes inside the enclosed lagoon of Taiaro Atoll is deficient in planktivorous taxa (Galzin et al., this volume), presumably as a result of the depauperate zooplankton (Carleton and Doherty, this volume), and that this could relax predation. Although the low plankton diversity should also restrict the choice of foods for larval fish, detection of ichthyoplankton in the lagoon shows that local development is possible in some damselfishes (Leis et al., this volume). Our genetic evidence suggests that local development may also be possible for taxa with more specialised larvae (Leis 1991).

Acknowledgements We gratefully acknowledge funding and/or logistic support from the Commandement Supérieur des Forces Armées de la Polynésie Française, the Direction des Centres d'Expérimentation Nucleaires, the Service Mixte de Contrôle Biologique, the Service Mixte de Sécurité Radiologique, the French Man And Biosphere Committee, the Ministère de l'Environnement, Naturalia and Biologia, and the crew of the BCB Marara who assisted with transport and sample collection. We thank also P. Doherty, J. Leis, M. Pichon, R. Galzin and two anonymous reviewers for improving the manuscript.

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