Chapter 7: General Discussion

General summary

This thesis demonstrates the complex nature of the factors that determine the population genetic structure of coral reef fishes on the GBR. By examining a low dispersal species in detail I demonstrated that population genetic structure may be scale dependent and vary between local and regional spatial scales. I also revealed the capacity of a low dispersal species to display metapopulation dynamics at local scales. The frequency of local extinctions varied geographically among regions and increased towards the margin of this species' range. Using the length of the pelagic larval duration as a proxy for dispersal potential, I could only predict population genetic structure in eight pomacentrid species, that varied little in their biological and ecological attributes, when a directly developing species was included in the analysis. Population genetic structure, therefore, did not appear to be related to this life-history trait among species from this reef-fish family. Position in the species range did not appear to influence the level of genetic structure and levels of genetic differentiation were similar among species sampled towards the periphery of their ranges compared to those sampled in the centre of their ranges. Genetic diversities were not reduced in peripheral populations compared to central populations, however, genetic diversities were much greater in peripheral species overall compared to central species. In all, these results suggest that the population genetic structure of coral reef fishes may be affected by the spatial scale at which it is examined, it may vary geographically within the species range and be greatly influenced by historical factors that may act in a species-specific manner.

Summary of key findings

The application of population genetic models to the genetic structure of *A. polyacanthus* on the GBR varied among spatial scales, with evidence of isolation-by-distance at the largest spatial scale (among regions) and metapopulation dynamics within regions (Chapter 2). Consequently, these results demonstrate that isolation-by-distance and metapopulation models are not mutually exclusive, but instead can operate within the same species at different spatial scales. Genetic structures conforming to the isolation-by-distance model have been commonly identified across large spatial scales in many species (e.g., Palumbi et al. 1997; Planes and Fauvelot 2002; Bay et al. 2004). It is unclear, however, whether such species display significant genetic structure at local scales, because the sampling regimes of most population genetic studies of coral reef fishes have not included any local-scale sampling (but see Doherty et al. 1995). The effect of scale was also evident in the demographic history analyses of *A. polyacanthus* (Chapter 3). In the southern region of the GBR, half the sampled populations contained a genetic signal of a recent demographic bottleneck and this was evident at the regional level, with the southern region displaying lower genetic diversities, a more recent demographic expansion, and a higher growth rate. Consequently, an accurate appraisal of the population genetic structure of coral reef fishes require an understanding of both local and regional scale patterns.

I identified an extensive capacity of a coral reef fish with low dispersal to display complex genetic structure that conformed to predictions based on metapopulation theory largely developed and tested in terrestrial systems (Chapter 2 and 3). Populations of *A. polyacanthus* displayed a genetic structure consistent with low migration (Chapter 2), propagule-pool colonisation (Chapter 2), and periodic local extinctions (Chapter 3). This represents the first comprehensive example of metapopulation dynamics in a coral reef fish and is one of only a handful of investigations examining the genetic consequences of migration, extinction and re-colonisation in a single study (reviewed by Giles and Goudet 1997). It is at present unclear whether other coral reef species, in particular those with pelagic larvae, also display metapopulation dynamics. Investigations of the population genetic structure of coral reef fishes have either not sampled populations at local scales, or when local scale genetic structure has been examined, metapopulation theory has not used to interpret the patterns, even when strong genetic structure was found (e.g., Nelson et al. 2000; Planes et al. 2001; but see Planes et al. 1996).

The length of the pelagic larval phase has commonly been used to predict population genetic structure of coral reef fishes (e.g., Waples 1989; Doherty et al. 1995; Riginos and Victor 2001), however, most previous relationships have included a range of distantly related species and consequently, we have a limited understanding of how this relationship applies within the taxonomic level of families. Estimates of PLD typically show little variation at a particular time and place, but may vary greatly among sampling times, locations with regions, and regions (Chapter 4). It is likely that such variation in PLDs may affect the population genetic structure of species, however, this has not previously been incorporated into examinations of the relationship between PLD and genetic structure. I identified a relationship between PLD and population genetic structure based on mtDNA and nucDNA markers, however, this relationship was dependent on the inclusion of a directly developing and highly genetically structured species (Chapter 4). The relationship between PLD and population genetic structure varied depending on the estimate of PLD and molecular marker used. Genetic structure based on the mtDNA could be predicted from mean, minimum and maximum PLD, whereas the genetic structure based on nucDNA (both the ISSRs and allozymes from Doherty et al. 1995) could only be predicted from my estimate (Chapter 4) of minimum PLD. These results suggest that the relationship between PLD and population genetic structure may depend on the molecular markers used, the estimate of PLD and its variation, and the species included in analyses.

Theory suggests that species borders may evolve in response to a decline in demographic processes from the centre to the periphery of geographic ranges or through changing metapopulation dynamics towards the species' range margin (Lennon et al. 1997; Holt and Keitt 2000). Empirical support for this theory, however, remains equivocal. The population genetic structure of *A. polyacanthus* appeared to support the predictions of this theory (Chapter 3). Population expansions were more recent, population growth rates were higher and genetic diversities were lower in half of the populations in the southern region located close to the species' margin of this species. This indicates that extinction rates in local populations may increase towards the margin of the species' range. Although this design did not allow a separation of the population genetic species' border effects from any potential geographical effects, these results indicate that metapopulation effects may play an important role in determining the geographical border in this low dispersal species (Chapter 3). The predicted species border effects were not evident in species with greater dispersal potential (Chapter 6). All species included in this analysis displayed a population genetic structure consistent with moderate gene flow between sampling locations and genetic diversities were not reduced in peripheral populations. It is likely that moderate levels of gene flow may have prevented the predicted decay of genetic diversity in the peripheral populations (Vucetich and Waite 2003). Genetic diversities were much greater in the peripheral species, and higher than most comparable estimates from other reef fishes (e.g., Grant and Bowen 1998; Fauvelot et al. 2003). This result indicates that processes are operating on the periphery of these species' ranges are complex and are not easily explained within the existing theoretical framework.

The distribution of genetic variation within and among populations can be greatly affected by historical processes (Benzie 1999; Avise 2000). All the species examined in this thesis appear to have been substantially affected by historical effects, however, these effects differed greatly among species. Most species contained a signal of demographic bottleneck, most likely associated with the initial colonisation of the GBR (Chapter 3, 5 and 6). This result supports the suggestion that species in habitats affected by Pleistocene sea level fluctuations may contain a signal of demographic expansion (Fauvelot et al. 2003). I identified extensive intraspecific variation in the timing of demographic bottlenecks and population growth rates in *A. polyacanthus* among regions and reefs within regions of the GBR (Chapter 3). Reductions in size and/or local extinctions appeared to be frequent in this species and one fifth of sampled populations contained a genetic signal of recent expansion, a high population growth rate and reduced genetic diversities (Chapter 3). This suggests that coral reef fish metapopulations may be more greatly affected by local extinctions than previously thought (e.g., Planes et al. 1996; Planes 2002). Species sampled towards the periphery of their ranges also appeared to be affected by historical processes, however, in these species such processes increased rather than reduced genetic diversity (Chapter 6). The distribution of genetic variation in at least two of the peripheral species indicated secondary contact among historically differentiated lineages, suggesting either hybridisation between different species, or that historical gene flow on the species periphery was restricted compared to gene flow among population in species that were sampled in the centre of their ranges.

Overall conclusions and future directions

Studies of the population genetic structure of coral reef fishes are accumulating at a rapid rate and, concomitantly, so is our understanding of the processes that determine the population genetic structure in such systems. By examining one species in detail in this thesis I demonstrated an extensive capacity of a low dispersal species to display complex spatial genetic structure that conformed to predictions from metapopulation theory. There is, however, a poor understanding of how this theory may apply to other coral reef species with greater dispersal potential. A good understanding of the spatial genetic structure of coral reef fishes is critically important to their effective management and conservation (Palumbi et al. 2003; Palumbi 2004). The use of highly sensitive molecular markers, such as microsatellites or ISSRs, coupled with nested sampling designs incorporating local and regional spatial scales may facilitate the resolution of this issue.

The application of a comparative framework has revealed many insights into the processes that determine the population genetic structure of coral reef fishes (e.g., Doherty et al. 1995; Riginos and Victor 2001; Fauvelot et al. 2003; Rocha et al. 2005; Chapter 5 and 6). Further insights into the evolution of population genetic structure of coral reef fishes are likely to be gained from studies that not only compare patterns among species, but also apply phylogenetically controlled analyses to such data. The application of comparative designs will allow relationships between, for example, PLD and population genetic structure, to be compared among species with different biological and ecological attributes such as spawning strategy, level of ecological specialisation, and geographical range size among others, while controlling for the role of phylogeny. Such analyses have the potential to increase our understanding of this important relationship further.

This study used ISSRs, a genetic fingerprinting technique, for the first time to examine the population genetic structure of coral reef fishes. The application of this technique increased the resolution of this study and allowed a comparison between mtDNA and nucDNA markers rarely undertaken in population level analyses. While mtDNA genes suitable for population level analyses can be readily amplified from universal primers, nuclear population level markers (such as microsatellites and SNPs) generally require prior sequence information that may not be easily obtained for a large number of species. ISSRs may be useful in comparative investigations because they allow highly variable and repeatable nuclear genetic fingerprints to be obtained from a range of distantly related species using universal primers. Despite of analytical restrictions because of their dominant nature, ISSRs may therefore provide an alternative nuclear marker in studies where the number of species or the lack of sequence information make the development of co-dominant markers impracticable.

Lastly, this thesis reports of substantial differences in the population genetic structure in a single species and generally among species sampled towards the periphery of their ranges. In the species with pelagic larvae, however, the population genetic structure associated with range edges were contrary to theoretical expectations with genetic diversities being much greater in these species compared to most other coral reef fishes for which comparable diversity estimates exist. The use of more sensitive molecular markers, such as microsatellites, and a sampling strategy that includes multiple populations sampled towards the species margin, may reveal any potential border effects that were not evident from the analyses presented in Chapter 6. Such an approach would allow a more comprehensive evaluation of the application of species border theory to species with moderate dispersal levels. Furthermore, it would be interesting to examine if the patterns reported here apply more generally among species, among borders (latitudinal and longitudinal) and among reef systems. Such investigations will facilitate a better understanding of the processes that determine the extent of species' ranges in coral reef fishes, in particular, and evolutionary dynamics in tropical marine systems in general.