

# CHAPTER 1

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## General Introduction

### 1. 1 Marine environments and species diversity

Marine environments host a huge diversity of organisms, presenting special challenges to evolutionary biologists. Given the opportunities for gene flow through dispersive larvae across vast oceanic barriers (Lessios et al. 2001) and the sheer scale of tropical marine environments it is difficult to conceptualise the evolutionary processes that have generated high diversities in marine organisms. The well documented examples of high diversity in tropical marine organisms in general and marine fish in particular presents a paradox. Marine environments do not have “hard” barriers, which tend to promote speciation among terrestrial vertebrates (Palumbi 1994; Palumbi 1997). Most marine organisms have external fertilisation, high fecundities, a dispersive larval phase and migratory capacities (Palumbi 1994; Palumbi 1997; Lessios et al. 2001; Feral 2002). This would explain why marine organisms in general, and marine fish species in particular, display a different pattern of diversity than terrestrial species (Feral 2002).

Tropical reef systems support a highly diverse and abundant range of organisms, such as coral reef fish species. Many co-occurring, and ecologically similar, species of fish are closely related and have broad distributions. It is unclear what modes of speciation have

lead to such patterns in marine environments where present day barriers to gene flow are not apparent.

Models of speciation in the marine environment have been studied since the early 1950s (Palumbi 1994). Mayr (1954) proposed that the mode of speciation for most marine organisms is allopatric (he also refers to it as “geographic speciation”). If allopatric speciation is the case, it still presents a difficulty, because the lack of known extrinsic barriers and the bipartite life history traits of most marine organisms would/should operate against patterns and processes of allopatric speciation (Palumbi 1994).

Furthermore, large population sizes of many marine species also tend to slow genetic divergence between populations (Palumbi 1994).

Therefore, as Palumbi (1994) proposed, “allopatric speciation events may be infrequent and slow” in marine organisms.

Later in this thesis, I will revisit this issue and present evidence that allopatric speciation can indeed occur in reef fish species (chapter 7).

Additional questions regarding coral reef fish divergence relate to patterns of diversification.

- How quickly did reef fish diversify and are they representatives of ancient taxa with long evolutionary histories?
- What are the ecological consequences of such diversifications? Do common patterns of morphology and structure underlie the evolutionary relationships of reef fishes?

- If allopatric speciation is important in reef fishes, what were the vicariant events, more specifically, were crucial tectonic and palaeoenvironmental events associated with major episodes of divergence?
- What does analysis of the genetic structure of widespread populations tell us about past episodes of divergence, and are these divergences in genetic structures of populations deep or shallow?

To resolve these issues, several aspects must be examined:

- Have a comprehensive understanding of the taxonomy, ecology and distribution patterns of the reef fish group to be examined.
- Use a methodological (phylogenetic) approach to establish relationships and patterns of descent among reef fish species.
- Provide a time frame to establish species diversification, if possible by fossil records or by using important tectonic events.
- Understand major changes in the environment of reef fishes over their history.
- Use a methodology (phylogeography) that allows the analysis of genetic structure of reef fish populations.

## **1.2 Tropical reef fish systems**

Coral reef fish species are represented overwhelmingly by perciform species (Bellwood 1997; Bellwood 1998). The fossil record strongly suggests that their origin was associated with episodes of rapid diversification in shallow tropical systems at the commencement of the Tertiary (Blot and Tyler 1991; Bellwood 1996; Bellwood 1997).

The taxon selected for this study is a genus of acanthurid fishes, *Naso*, a strongly reef-associated group of perciform fishes with 19 extant species (Randall 2002). There is a substantial literature on the taxonomy (Smith 1966; Tyler et al. 1989; Randall 1994; Randall 2001; Johnson 2002; Randall 2002) and ecology (Jones 1968; Clements and Choat 1995; Choat and Clements 1998; Wilson and McCormick 1999; Leis and Carson-Ewart 2000; Choat et al. 2002; Choat and Robertson 2002; Leis and McCormick 2002) of acanthurid fishes and their evolutionary relationships in terms of fossil records (Tyler 2000) and morphology-based phylogenetic analyses (Winterbottom and McLennan 1993; Borden 1998; Borden 1999).

Although, the acanthurid fishes are a diverse family (80 species) (Randall 2002) there are no fossil records of extant species or genera (Tyler 2000; Bellwood and Wainwright 2002). Accordingly, the primary approach used in this study was to develop a molecular phylogenetic hypothesis of the genus *Naso* and use this to establish patterns of relationship and descent amongst the 19 extant species. Fossil records (Bannikov and Tyler 1992; Bannikov and Tyler 1995; Sorbini and Tyler 1998b; Tyler and Sorbini 1998; Tyler 1999a; Tyler 1999b; Tyler 2000; Tyler and Bannikov 2000) of related acanthurid fishes allowed estimation of ages for the most recent common ancestors (MRCA) with local rates designed to establish dates at which major divergences occurred within the genus. Because fossil dates are essentially more recent than the origin of the fossilized lineage, the timing of divergences estimated by fossil-calibrated age estimate, were examined in relation to major vicariant and palaeoclimatic events in the tertiary history of coral reefs (Haq et al. 1987; Pickering 2000; Kiessling 2001b; Stanley 2001; Zachos et al. 2001a). An appropriately fossil-calibrated molecular phylogeny provides an opportunity

to examine the ecological pattern of diversification within the genus and test specific hypotheses with respect to relationships amongst different ecological traits (foraging modes). The molecular phylogeny with estimated local rates of divergence also provides age estimates of the timing of divergence between sister species, which can be used in conjunction with distribution ranges and phylogeographic studies to determine modes of speciation.

For this purpose, a hierarchical approach was used to examine the processes that may have been responsible for divergence and cladogenesis in the genus *Naso* (Figure 1.1).

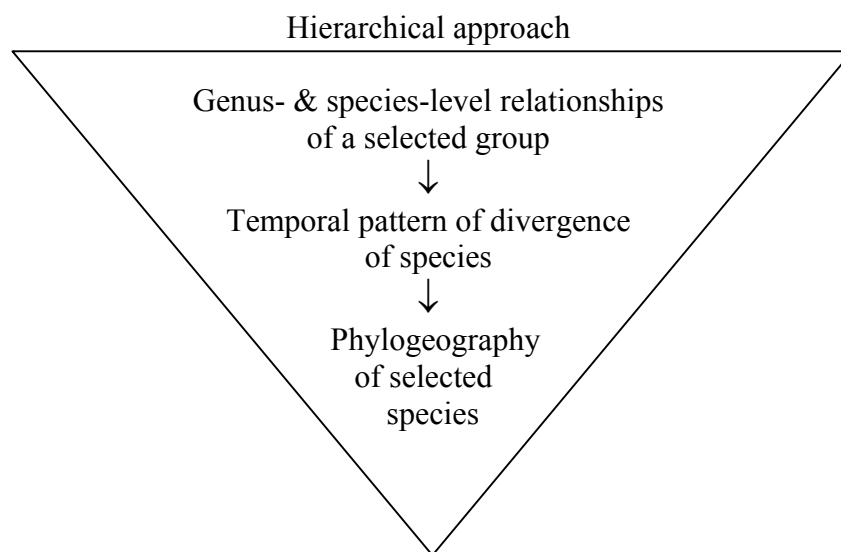


Figure 1.1: Illustration of the approach used in this study to explain the evolutionary patterns in a group of fish relative to history, biogeography and species characteristics.

More specifically the major aim of this thesis is:

- To use a phylogenetic approach to examine the relationships and descent amongst all species of the genus *Naso*.
- To test existing hypotheses based on morphological data.

- To examine the temporal pattern of divergence in the genus, using related fossil records.
- To relate the diversification in the group to palaeoclimatic and palaeoecological events to better understand the evolutionary history of the genus.
- To examine the phylogeography of several species to ascertain the population genetic structure and probable mechanisms that may have been responsible for speciation (see bridging introduction, chapter 5).

### **1.3 Thesis chapter outline**

This thesis is divided into two major sections. Section A examines the phylogenetic relationships within the genus *Naso* and establishes temporal patterns of divergences. Section B examines possible modes of speciation using phylogeographic studies of several diverse *Naso* species, given the evolutionary relationships and ages of species (obtained in section A).

The **second chapter** outlines the molecular methods used in this study. In particular, a technique that allowed the extraction of DNA from museum specimens which were fixed in formalin prior to preservation in alcohol is presented. This method allowed me to generate the first complete species-level phylogeny of the genus *Naso*.

#### ***1.3.1 Section A: Evolutionary history of Naso.***

In the **third chapter**, I present the inferred genus-level relationships of the family Acanthuridae and the species-level phylogeny of the genus *Naso*, based on 3 genetic

markers. Several hypotheses that are relevant to the evolution/cladogenesis of this genus (morphology and ecological traits), which were proposed in previous studies, are tested here.

In the **fourth chapter**, a curve displaying the accumulation of extant lineages over time is generated by nonparametric rate smoothing from the species-level phylogeny of chapter 3. This curve describes the diversification of lineages over evolutionary time, and age estimates for the most common recent ancestor (MCRA) are generated using dates of fossil records. I also relate the diversification events to palaeoclimatic and palaeoecological events.

### ***1.3.2 Section B: Phylogeography of several *Naso* species.***

The **fifth chapter** is an introduction to Section B. This chapter gives an overview of phylogeographic studies, which have used mtDNA sequence data and explains in detail how diversity indices can be used to infer evolutionary histories of species.

The last two data chapters (**chapter 6 & 7**) examine the phylogeography of a widely distributed species, *N. vlamingii* (**chapter 6**), and two pairs of sister species (*N. lituratus* – *N. elegans*, and *N. tuberosus* – *N. tonganus*) (**chapter 7**).

The evolutionary histories of these species are discussed in terms of distribution ranges, the ages of each lineage, important environmental changes at the time of cladogenesis and diversity indices.

In the general conclusion (**chapter 8**), the findings of this study are synthesised and placed into a broader context of reef fish evolutionary history with suggestions of possible future research directions.