



# Incipient speciation of *Catostylus mosaicus* (Scyphozoa, Rhizostomeae, Catostylidae), comparative phylogeography and biogeography in south-east Australia

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## ABSTRACT

**Aim** Phylogeography provides a framework to explain and integrate patterns of marine biodiversity at infra- and supra-specific levels. As originally expounded, the phylogeographic hypotheses are generalities that have limited discriminatory power; the goal of this study is to generate and test specific instances of the hypotheses, thereby better elucidating both local patterns of evolution and the conditions under which the generalities do or do not apply.

**Location** Coastal south-east Australia (New South Wales, Tasmania and Victoria), and south-west North America (California and Baja California).

**Methods** Phylogeographic hypotheses specific to coastal south-east Australia were generated *a priori*, principally from existing detailed distributional analyses of echinoderms and decapods. The hypotheses are tested using mitochondrial cytochrome c oxidase subunit I (COI) and nuclear internal transcribed spacer 1 (ITS1) DNA sequence data describing population variation in the jellyfish *Catostylus mosaicus*, integrated with comparable data from the literature.

**Results** Mitochondrial COI distinguished two reciprocally monophyletic clades of *C. mosaicus* (mean  $\pm$  SD:  $3.61 \pm 0.40\%$  pairwise sequence divergence) that were also differentiated by ITS1 haplotype frequency differences; the boundary between the clades was geographically proximate to a provincial zoogeographic boundary in the vicinity of Bass Strait. There was also limited evidence of another genetic inhomogeneity, of considerably smaller magnitude, in close proximity to a second hypothesized zoogeographic discontinuity near Sydney. Other coastal marine species also show genetic divergences in the vicinity of Bass Strait, although they are not closely concordant with each other or with reported biogeographic discontinuities in the region, being up to several hundreds of kilometres apart. None of the species studied to date show a strong phylogeographic discontinuity across the biogeographic transition zone near Sydney.

**Main conclusions** Patterns of evolution in the Bass Strait and coastal New South Wales regions differ fundamentally because of long-term differences in extrinsic factors. Since the late Pliocene, periods of cold climate and low sea-level segregated warm temperate organisms east or west of an emergent Bassian Isthmus resulting in population divergence and speciation; during subsequent periods of warmer and higher seas, sister taxa expanded into the Bass Strait region leading to weakly correlated phylogeographic and biogeographic patterns. The Sydney region, by contrast, has been more consistently favourable to shifts in species' ranges and long-distance movement, resulting in a lack of intra-specific and species-level diversification. Comparisons between the Sydney and Bass Strait

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regions and prior studies in North America suggest that vicariance plays a key role in generating coastal biodiversity and that dispersal explains many of the deviations from the phylogeographic hypotheses.

### Keywords

Australia biodiversity, climate change, dispersal, jellyfish, marine, mitochondrial DNA, nuclear ribosomal DNA, three-times rule, vicariance.

## INTRODUCTION

The complex processes influencing modern patterns of biodiversity in coastal marine taxa are not well understood (Colin, 2003; Taylor & Hellberg, 2003; Warner & Palumbi, 2003). Phylogeography explicitly integrates micro-evolution and macro-evolution, relating ecology to evolution, current distributions to historical events, the physical environment to genetic structure, and patterns of variation within species to patterns of variation across species (Avice, 2000), thereby establishing a framework for investigating the many evolutionary entities and processes comprising multiple levels of biodiversity (see CBD, 1992). The framework is based on three phylogeographic hypotheses and several corollaries, with parallels in other areas of evolutionary biology, intended to explain generally observed trends in geographic variation (Avice *et al.*, 1987; Walker & Avice, 1998; Avice, 2000; Table 1). In a synopsis of the exponentially growing discipline of phylogeography, Avice (2000, p. 211) concluded that these 'phylogeographic hypotheses ... have been supported abundantly by ... molecular genetic research.'

However, phylogeographic patterns, which often appear in studies of single species, generally have been explained *a posteriori* with reference to possible causal factors rather than tested using specific *a priori* hypotheses. Exceptions to the hypotheses are often de-emphasized (e.g. Avice, 2000, pp. 136, 208) although they may be relatively common (Avice, 2000, p. 262). Knowlton & Keller (1986), for example, discuss larvae that disperse less far than expected, i.e. potential anomalies to  $H_2$  (Table 1). Figures 5.4 and 5.10 of Avice (2000) indicate that deep phylogenetic gaps are concordant with a zoogeographic boundary in eastern Florida but not in western Florida, contrary to  $H_{3iii}$ , and even in eastern Florida the concordance may not be geographically very precise. In one of the most explicit comparisons in the marine realm, Burton (1998) reported multiple lines of evidence, showing discordant biogeographic and phylogeographic discontinuities in southern California, contrary to the phylogeographic hypotheses. He suggested the hypotheses were situation specific – being relevant to areas in which sibling species pairs are common – and not generally applicable (Burton, 1998). Although the apparent lack of concordance reported by Burton (1998) may now have been resolved – the major genetic and biogeographic discontinuities both seem to be in the Los Angeles region (Dawson, 2001) – it is still true to say that the suite of

phylogeographic hypotheses proposed by Avice *et al.* (1987) have rarely been tested, if at all, in a rigorous way using marine taxa. For example, Avice (2000, pp. 10, 220) referred to over 300 phylogeographic publications, but reported only two that explicitly searched for phylogeographic concordance between mitochondrial and nuclear gene trees ( $H_{3i}$ ). Regional comparisons draw predominantly on original studies of single species and single markers ( $H_3$ ; Avice, 2000, pp. 9, 224–262) which, while meta-analyses of such eclectic data sets can be informative (e.g. Avice, 1992, 2000; Dawson, 2001) and a diversity of approaches has merit, may be difficult and at worst inappropriate to compare when the original studies had such variable intentions and methods. This is a concern given the popularity of the approach and its fundamental implications, which pertain to geographic patterns of speciation and biodiversity management (e.g. Montz *et al.*, 2001). Moreover, while 'statistical phylogeography' has made dramatic advances in quantifying theoretical expectations under different demographic scenarios, thereby aiding interpretation of observed patterns of intra-specific genetic variation (Knowles, 2004), the conceptual and quantitative integration of intra-specific and inter-specific patterns is still generally lacking (but see e.g. Burton, 1998; Walker & Avice, 1998; Dawson, 2001). More rigorous, *a priori*, tests of situation specific hypotheses derived from the generalized phylogeographic hypotheses are required, preferably in new geographic regions with different taxa (Avice *et al.*, 1987; Burton, 1998; Dawson, 2001).

South-eastern Australia provides an opportunity to test new situation-specific phylogeographic hypotheses and to learn more about a particularly interesting fauna. South-eastern Australia has been tectonically more stable than some areas studied previously in this context (e.g. California), yet has important coastal and oceanographic features similar to those linked to genetic structuring in marine taxa in other regions (e.g. California, Florida), including points and capes, temperature variation, distinct water masses, eddies, and topographical alteration with sea-level change (Fig. 1). Southern Australian endemism in some shallow-water marine taxa is as high as 85–95% (Wilson & Allen, 1987), yet little is known about synoptic patterns of distribution in the majority of the fauna (O'Hara & Poore, 2000). The region's history is complex, but palaeontological details are lacking (Poore, 1994; O'Hara & Poore, 2000). Cryptic biodiversity may be high, and thousands of kilometres of multifarious coastline offer much potential for isolation, but many 'general southern'

**Table 1** Two of the phylogeographic hypotheses of Avise *et al.* (1987), the corollaries to hypothesis three (H<sub>3</sub>; e.g. Avise, 2000), their mode of operation, and some related concepts

Phylogeographic hypotheses and corollaries	Mode*	Related concepts
H <sub>2</sub> Species with limited phylogeographic population structure have life histories conducive to dispersal and have occupied ranges free of firm impediments to gene flow	Intrinsic (and extrinsic)	Gene flow in marine animals is a function of planktonic larval duration (e.g. Waples, 1987)
H <sub>3</sub> Monophyletic groups distinguished by large phylogenetic gaps usually arise from long-term extrinsic (zoogeographic) barriers to gene flow	Extrinsic	Allopatric speciation predominates (e.g. Mayr, 1942, p. 215)
(i) As time since isolation increases, the degree of phylogeographic concordance across separate gene genealogies increases	Intrinsic	The three-times rule (Palumbi <i>et al.</i> , 2001)
(ii) The geographic placements of phylogenetic gaps are concordant across species	Extrinsic	Vicariance (cladistic) biogeography (e.g. as summarized by Briggs, 1995, pp.13–14)
(iii) Phylogenetic gaps within species are geographically concordant with boundaries between traditionally recognized zoogeographic provinces	Extrinsic	Evolutionary uniformitarianism (gradualism): 'variability within the smallest taxonomic units has the same ... basis as the differences between the subspecies, species, and higher categories' (Mayr, 1942, p. 70, also see p. 298)

\*Referred to by Mayr (1942) as the 'biology of speciation', which was either 'internal' or 'external'. He emphasized that intrinsic factors are always involved even when the primary factor is extrinsic.

species are thought to span its range while other species are disjunct and the limits and ranges of 'provincial' faunas have been the source of considerable debate (Wilson & Allen, 1987). Molecular studies of some taxa have reported population structure that reflects physical heterogeneity (e.g. Jerry, 1997; Hoskin, 2000; Ward & Elliot, 2001), but have not provided the much needed historical perspective available in species' phylogenies (but see Waters & Roy, 2003a). Published studies exploring all levels of coastal biodiversity have recognized the need for more intensive sampling of additional species and the application of new markers and quantitative approaches better suited to the task (e.g. Hoskin, 2000; O'Hara & Poore, 2000).

Here, I describe the phylogeography of *Catostylus mosaicus*, a scyphozoan jellyfish endemic to south-eastern Australia (Quoy & Gaimard, 1824; type locality Port Jackson, Sydney), integrate new phylogenetic analyses of two other sympatric scyphozoan genera – *Aurelia* and *Cyanea* (M. N Dawson, unpubl. data) – and review 10 prior genetic studies with similar geographic range. I test phylogeographic hypotheses for south-eastern Australia and compare the results with studies in south-western North America (Dawson, 2001).

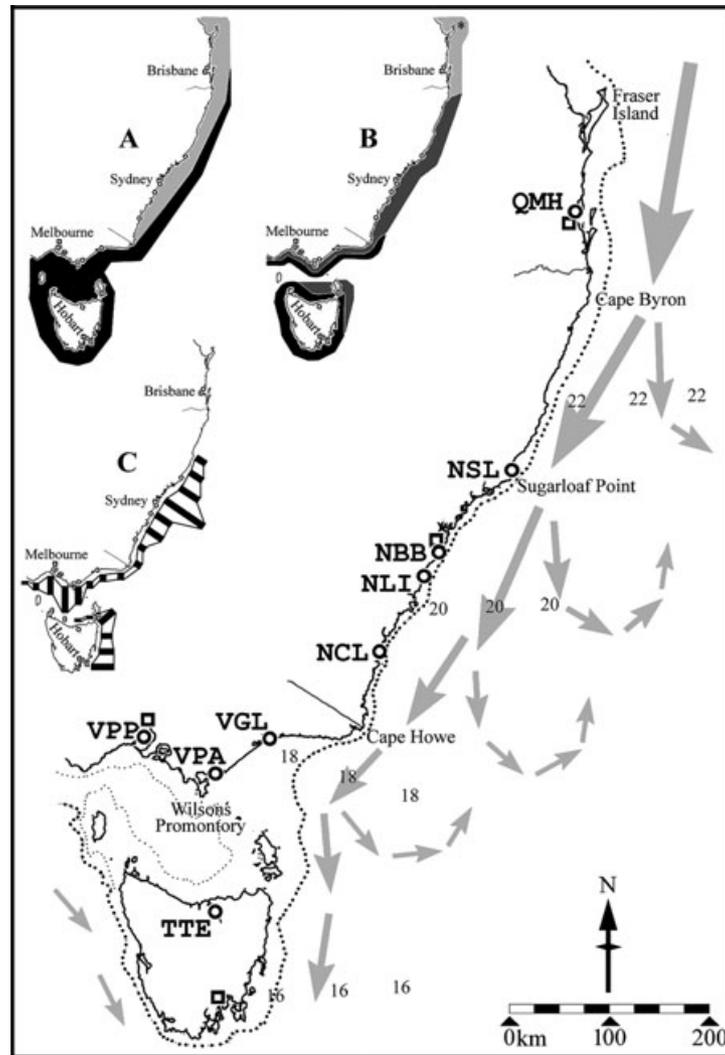
## MATERIALS AND METHODS

### Geological-geographic setting and hypothesis generation

Based on the predominantly tropical distribution of other species of *Catostylus* and the current distribution of *C. mosaicus*, this species has predominantly warm water affinities. The ancestral range of *C. mosaicus* most likely approximated its current range, spanning warm temperate waters around

south-eastern Australia, possibly extending farther south during warmer climates in the late Pliocene (Frakes *et al.*, 1987).

The Pleistocene 'icehouse' climate [Ocean Drilling Program (ODP), 2000] was associated with considerable fluctuations in climate and sea-level (Harland *et al.*, 1989). At sea-levels of c. –50 m or lower, flow across Bass Strait was prevented by an emergent Bassian Isthmus that connected modern-day Victoria and Tasmania; any gene flow between marine populations of macrozooplankton on opposite sides of the land-bridge would have to have circumscribed the southern tip of Tasmania. However, dispersal of warm-temperate species around southern Tasmania during glacial periods seems unlikely because temperatures were considerably depressed, possibly by 5–10 °C relative to even today's unfavourable temperatures (Wilson & Allen, 1987). Warm-temperate species, such as *C. mosaicus*, therefore were almost certainly isolated in lower latitudes (Poore, 1994) on either side of the Bassman Peninsula (Fig. 1). During exit from the last glacial maximum, the Bassian Isthmus was flooded primarily from the west, with early formation of a very large semi-enclosed bay, probably at first a brackish coastal lagoon as sea water inundated an extant fresh-water lake (Unmack, 2001). Continued sea-level rise subsequently eradicated the embayment and divided the contiguous coastline into separate proto-Victoria and proto-Tasmania coastlines as Bass Strait reformed. Sea-level stabilized ± 5 m of its current level about 5000 yr BP (Harland *et al.*, 1989; Dawson, 1992). Thus, during the last glacial maximum, no Bass Strait populations could have existed within tens to hundreds of kilometres of most modern coastal locations and modern biogeographic and phylogeographic patterns in the Bass Strait region therefore result from recent redistribution of species (Wilson & Allen, 1987).



**Figure 1** (Main) Map of south-eastern Australia showing sample locations (round symbols, three-letter acronyms), prevailing current patterns [grey arrows, based on Autumn schematic ([www.marine.csiro.au/](http://www.marine.csiro.au/))] and annual mean surface velocity vectors from the ACOM 3 model [([www.pmel.noaa.gov/~kessler/sverdrup/csirowebfiles/sverdrup/mean-currents-aust-coast-subdomain\\_new.gif](http://www.pmel.noaa.gov/~kessler/sverdrup/csirowebfiles/sverdrup/mean-currents-aust-coast-subdomain_new.gif))], January sea-surface isotherms [numbered rows; redrawn from O'Hara & Poore (2000)] with which echinoderm and decapod species richness is correlated [ $r = 0.70$ ,  $P < 0.05$ ; August temperatures are  $c. 4\text{ }^{\circ}\text{C}$  lower and shifted slightly latitudinally, an  $18\text{ }^{\circ}\text{C}$  isotherm occurring just south of Sugarloaf Point and  $14\text{ }^{\circ}\text{C}$  isotherm at Cape Howe (O'Hara & Poore, 2000)], and 100 m bathymetric contour (dotted line, redrawn from Unmack, 2001). The 70 m bathymetric contour, shown for Bass Strait (fine dotted line, redrawn from Evans & Middleton, 1998), delimits a depression that probably holds a freshwater lake at lower sea-level (Unmack, 2001) and which opens to the north-east when sea-level rises above  $c. -50\text{ m}$  (Gibbs, 1992). Therefore Port Philip, Tamar Estuary, and Port Albert drainages lay west of the emerging Bassian Isthmus (which, with Tasmania, is herein referred to as the Bassmania Peninsula). Annually, there is a small net eastward flow through Bass Strait, a seaway in which flow may vary considerably with, for example, season, atmospheric fronts, and the tidal cycle (e.g. Baines *et al.*, 1991; Gibbs, 1992). Queensland: QMH Mooloolaba Harbour. New South Wales: NSL Smiths Lake, NBB Botany Bay, NLI Lake Illawarra, NCL Coila Lake. Victoria: VGL Gippsland Lakes, VPA Port Albert, VPP Port Philip. Tasmania: TTE Tamar Estuary. State capitals are included as landmarks (squares, see inset maps). Map redrawn from graphical index to scanned 1 : 250,000 geology map sheets at Geoscience Australia (<http://www.agso.gov.au/map/>). *Inset A*, biogeographic hypothesis of Wilson & Gillet (1971) showing tropical (light grey) and temperate (black) regions and a zone of overlap. *Inset B*, biogeographic hypothesis of Bennett & Pope (1953) showing tropical ('Solanderian', light grey), warm temperate ('Peronian', dark grey), and cool temperate ('Maugean', black) regions, and a zone of overlap in Victoria and north-eastern Tasmania; the hypothesis is modified from Whitley (1932) in which the principal differences are (1) a more northerly boundary (see \*) between tropical and warm temperate provinces and (2) a boundary across Bass Strait rather than a region of overlap at Wilson's Promontory. *Inset C*, the number (bars; min. = 1, max. = 12, '0' = none) of 'endemic' species (i.e. range  $c. \leq 5\text{ }^{\circ}$ ) per degree latitude/longitude of echinoderms and decapods in south-eastern Australia (O'Hara & Poore, 2000; data were not collected in south-west Tasmania nor north of  $30^{\circ}\text{ S}$ ). The greatest species-diversity and greatest species turnover also occur in the Sydney cell. The biogeographic boundary in Bass Strait is located most precisely at Wilson's Promontory (O'Hara & Poore, 2000).

A feature analogous to the Bassmania Peninsula is notably absent from the NSW coast, where the most obvious structures are several major drowned river valleys around Sydney (Port Hacking to Broken Bay) and, c. 100 km to the north, Sugarloaf Point. There are no large submarine promontories, and the coastline runs essentially north–south (Fig. 1). Consequently, Pleistocene glaciation had relatively small effects on coastal New South Wales. The large-scale coastal topology changed little, even since the Miocene (Poore, 1994). The hydrography of the region has been dominated by the East Australian Current since at least the Eocene, although its strength has been variable and possibly included a late-Miocene hiatus (ODP, 2000). The East Australian Current generally departs the coast at Sugarloaf Point, potentially causing a discontinuity (Hoskin, 2000), but also occasionally extends as far south as Sydney and casts off warm-core rings leading to occasional appearance of subtropical fauna as far south as Tasmania (Wilson & Allen, 1987). Descriptions of the region include a broad biogeographic transition zone characterized by overlap and replacement of subtropical and temperate organisms (Wilson & Allen, 1987). Biogeographic descriptions of south-eastern Australia and key features mentioned in the text are summarized with sources in Fig. 1.

Extant biogeographic data implicitly constitute *a priori* hypotheses of phylogenetic patterns for subsequent studies (Avisé *et al.*, 1987; Dawson, 2001). Here, I use the phylogeographic hypotheses (Avisé *et al.*, 1987; Avisé, 2000) and a quantitative biogeographic analysis of echinoderms and decapods (O'Hara & Poore, 2000) to generate *a priori* expectations specific to south-eastern Australia. After establishing COI and ITS1 are variable (H<sub>1</sub> Avisé *et al.*, 1987), I test the hypotheses: (1) that patterns in COI and ITS1 are concordant in *C. mosaicus*; (2) that, considering *C. mosaicus*, *Aurelia*, and *Cyanea*, concordance between COI and ITS1 genealogies increases with time since isolation; (3) that phylogenetic gaps are concordant across species; and (4) that genetic discontinuities occur (a) at the same latitude as Sydney in New South Wales and (b) in Bass Strait around Wilson's Promontory or (c) at Cape Howe (Fig. 1).

## Collection

*Catostylus mosaicus* medusae were collected with a dip net from a small boat, the waters-edge, or docks at eight of the nine locations (Table 2) between December 2002 and April 2003. Oral arm tissue was clipped and preserved in 90% ethanol prior to preservation of medusa in 4% formalin in seawater. Additional *C. mosaicus* tissue samples were preserved in 80% ethanol from the remaining location (Mooloolaba) in 2000. Reference specimens were deposited at the Australian Museum, Sydney.

## Molecular analyses

DNA was extracted from the ethanol-preserved tissues using a CTAB-phenol/chloroform based protocol (Dawson *et al.*, 1998; Dawson & Jacobs, 2001). Cytochrome oxidase c subunit I (COI) was amplified using LCOjf (5'-gggtcaacaaatcataagatattggaac-3') and HCOcato (5'-cctccagcaggatcaaagaag-3'). Internal transcribed spacer 1 (ITS1) was amplified using primers jfITS1-5f (5'-ggtttccgttagtgtaacctgcggaagatc-3') and jfITS1-3r (5'-cgcagagccgagtgatccacctagaag-3'; Dawson & Jacobs, 2001). All polymerase chain reactions (PCRs) consisted of six steps of 94 °C for 8 min, 49 °C for 2 min, 72 °C for 2 min, 94 °C for 4 min, 50 °C for 2 min, 72 °C for 2 min, then 33 cycles of 94 °C/45 s, 51 °C/45 s, and 72 °C/60 s, followed by an extension step at 72 °C for 10 min; the reaction was terminated by cooling to 4 °C. Amplified COI fragments were then purified using Qiagen (Valencia, CA, USA) PCR clean-up columns, whereas ITS1 fragments were cloned using TOPO TA technology (Invitrogen, Carlsbad, CA, USA) and purified using Pharmacia's (Piscataway, NJ, USA) Flexiprep kit. Purified PCR products were labelled with BigDye and sequenced on ABI 377 automated sequencers according to the maker's protocols (Applied Biosystems, Foster City, CA, USA). Electropherograms were checked visually, misreads corrected, and poorly resolved terminal portions of sequences discarded. The identities of sequences were confirmed by BLAST searching sequences in GenBank (Altschul *et al.*, 1997) and verifying the existence of open reading

**Table 2** List of sample locations, type, surface area, geographic position, and sample sizes (*n*) for COI and ITS1 data sets

State	Location	Type	Area (km <sup>2</sup> )	Lat (S)	Long (E)	<i>n</i> <sub>COI</sub>	<i>n</i> <sub>ITS1</sub>
Queensland	Mooloolaba	Harbour	–	26 °41'	153 °08'	2	2
New South Wales	Smiths Lake	Lagoon	10.5	32 °22'	152 °30'	3	2
	Botany Bay	Bay	38.3	33 °58'	151 °11'	9	6
	Lake Illawarra	Lagoon	35.8	34 °31'	150 °50'	9	7
	Coila Lake	Lagoon	6.9	36 °01'	150 °07'	6	5
Victoria	Gippsland Lakes	Lagoon	485.6	37 °52'	147 °59'	10	7
	Port Albert	Entrance/ channel		38 °40'	146 °41'	10	5
	Port Philip	Bay	1897.4	38 °06'	144 °53'	6	7
Tasmania	Tamar Estuary	Estuary	91.7	41 °13'	146 °56'	10	6

Latitude, longitude, and type from the Gazetteer of Australia 2002 (<http://www.agso.gov.au/map/names/>); Gippsland Lakes = Lakes Entrance, Tamar Estuary = Deviot Pier and Gravelly Beach. Areas taken from the National Land and Water Resources Audit Estuary Assessment 2000 'OzEstuaries' Database (<http://www.ozestuaries.org/>).

frames in all COI sequences translated into amino acid data using the *Drosophila* mitochondrial code in DNA Strider 1.2 (Marck, 1988). COI sequences were aligned on the basis of the amino acid translations whereas ITS1 sequences were aligned in Clustal X (Jeanmougin *et al.*, 1998) and then corrected by eye. All positions with missing data were excluded from subsequent analyses.

Pairwise sequence difference (PSD), base composition, gene and nucleotide diversity, minimum spanning trees (MSTs), and mismatch distributions (using PSD) were calculated in Arlequin 2.0 (Schneider *et al.*, 2000) and the mean  $\pm$  SD PSD between populations was calculated in PAUP\* 4.0b10 (Swofford, 2002) for Macintosh Powerbook G3. The partitioning of genetic variance among populations and biogeographic regions (Fig. 1) was explored using analysis of molecular variance (AMOVA, 1000 permutations; Excoffier *et al.*, 1992). If Mantel tests (10,000 permutations, R Package 4.0; Casgrain & Legendre, 1999) indicated significant correlation between geographic and genetic distances, these measures were also related to each other using ordinary-least-squares regression (Hellberg, 1994) in SPSS 10.0 for Macintosh. Any relationship between genetic diversity and habitat area was explored using Spearman's rank correlation; the relationship between genetic diversity and habitat type could not be explored because there were too few sites to satisfy the assumption of expected frequencies  $\geq 5$  in contingency chi-square analyses.

Phylogenetic reconstruction of the COI gene tree used maximum parsimony (MP) and maximum likelihood (ML) optimality criteria in PAUP\* 4.0b10. The MP analyses employed the branch-and-bound search algorithm on unweighted (all changes have equal weight) and weighted (changes weighted as the inverse of the relative frequencies of transitions and transversions, and of variable first, second, and third positions) data sets including only variable positions. Bootstrap analyses (10,000 replicates) of unweighted data employed an heuristic search using the tree-bisection-reconnection (TBR) algorithm and random sequence addition (10 replicates, saving  $\leq 5000$  trees of  $\leq 53$  steps). The ML analyses, via quartet puzzling (10,000 steps; Strimmer & von Haeseler, 1996), assumed among-site rate variation (Gamma distribution shape parameter = 0.02, proportion of invariable sites = 0), unequal base frequencies, and a transition : transversion ratio of 15.5, equivalent to the HKY + G model chosen using MODELTEST (Posada & Crandall, 1998).

Sequence similarity among ITS1 haplotypes, which contained microsatellites, was assessed primarily by unweighted MP. ML analyses were not undertaken because different models of molecular evolution apply to microsatellites and non-repetitive DNA sequence (e.g. Nishizawa & Nishizawa, 2002; cf. Posada & Crandall, 1998) and because some sequences may have been amplified from different repeat-units of rDNA. The MP analyses used four data sets. The first included all positions. The second excluded gapped positions (indels), which effectively removed all microsatellites, because the utility of indels may vary between data sets (e.g. Swofford *et al.*, 1996; van Dijk *et al.*, 1999). Then, repeat units within

the two microsatellite regions were recoded as single characters (i.e. each  $n$ -nucleotides-long repeat was given unit weight, equivalent to a single indel or other nucleotide substitution) and analyses repeated, third, including and, fourth, excluding indels. Bootstrap analyses (1500 replicates) employed an heuristic search using TBR and random sequence addition (10 replicates, saving  $\leq 5000$  trees of  $\leq 118$  steps).

## RESULTS

The COI datamatrix comprised 65 medusae and 487 nucleotide positions. Base composition was 19.3% C, 34.6% T, 26.0% A, and 20.1% G. Thirty-nine positions were variable, with 37 transitions, three transversions, and no indels; 25 positions were phylogenetically informative, of which two resulted in non-synonymous amino acid substitutions. The numbers of variable first, second, and third positions were 9, 0, and 30, respectively. There were 28 distinct haplotypes, giving gene diversity ( $h$ ,  $\pm$  SD)  $0.9418 \pm 0.0134$  and nucleotide diversity ( $\pi$ ,  $\pm$  SD)  $0.0207 \pm 0.0106$ . Gene diversity within populations was high ( $h \geq 0.69$ ) and nucleotide diversity low ( $\pi \leq 0.40$ ), excepting Coila Lake ( $h = 0.00$ ) and the poorly sampled Smiths Lake ( $\pi = 0.0068$ ; Table 3). Inter-individual uncorrected PSDs ranged from 0 to 25, i.e. maximum 5.13% (K2P genetic distances ranged from 0.0000 to 0.0539) and were distributed bimodally, with mean 3.61% (SD 0.40) sequence divergence separating 'central' (Queensland, New South Wales) from 'southern' (Tasmania, Victoria) haplotypes, reflecting the dumb-bell structure of the haplotype network and reciprocally monophyletic clades recovered by MP and ML analyses (Fig. 2). Over 80% of variation in COI occurred between regions (Table 4). Within groups, mismatch distributions were unimodal and more similar to the expected distribution for a rapidly expanded population than the expected distribution for a long-term stable population, although both were statistically differentiable from all tested hypothetical distributions (chi-square test,  $P < 0.025$ ; Fig. 3). Harpending's raggedness index (HRI), however, did not differ significantly from the expectation for a rapidly expanded population for either the central (HRI = 0.059,  $P = 0.367$ ) or southern (HRI = 0.020,  $P = 0.806$ ) clades. The central clade ( $h = 0.8276 \pm 0.0488$ ,  $\pi = 0.0041 \pm 0.0026$ ) was genetically less diverse than the southern clade ( $h = 0.9190 \pm 0.0268$ ,  $\pi = 0.0061 \pm 0.0036$ ).

The ITS1, ranging in length from 296 to 430 nucleotides (aligned length 464 positions), was sequenced from 47 medusae (one sequence per medusa). The ITS1 datamatrix comprised 419 nucleotide positions and 46 medusae after exclusion of ambiguous positions and the shortest sequence, which had a unique 57 nucleotide deletion. Base composition was 28.4% C, 28.5% T, 14.9% A, and 28.2% G. There were two hypervariable regions: one up to 144 nucleotides long (aligned length) comprised of tetramer repeats (ttgc, ttgc, ctgc), the other up to 14 nucleotides long comprised of dimers (gt). Overall, 153 positions were variable, with 25 transitions, 12 transversions, and 122 gaps; 95 positions were phylogenetically informative. Thirty-four of the 46 haplotypes

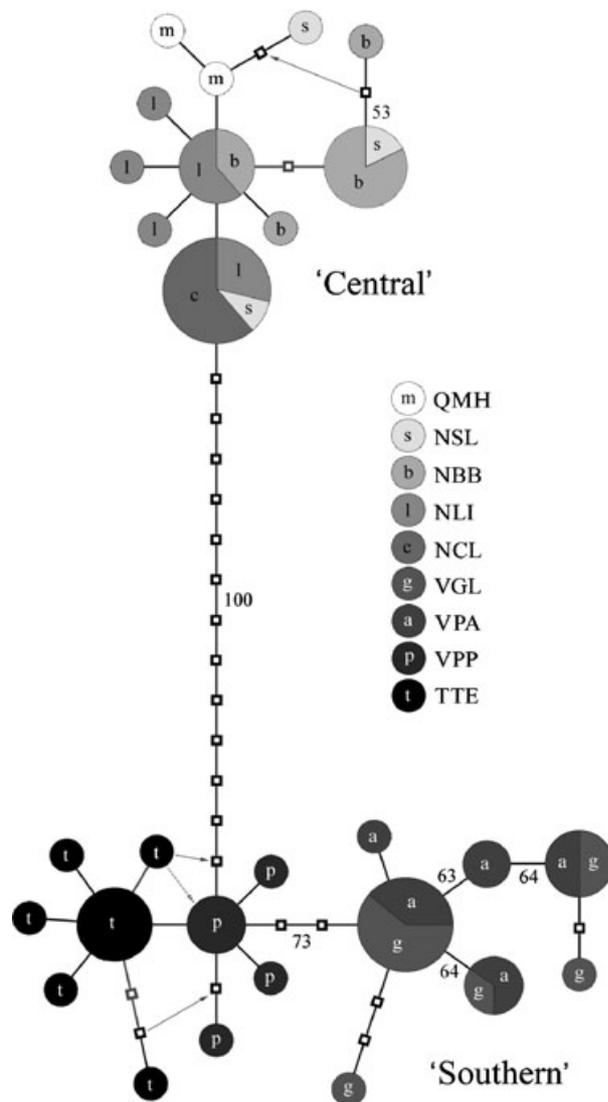
**Table 3** (a) Diversity in COI (haplotype diversity  $h$ , nucleotide diversity  $\pi$ ). (b) Diversity in ITS1 ( $h$ ,  $\pi$ , calculated including and excluding microsatellite-like regions)

State	Location	COI			
		$h$ ( $\pm$ SD)	$\pi$ ( $\pm$ SD)		
(a)					
Queensland	Mooloolaba	1.000 $\pm$ 0.500	0.0021 $\pm$ 0.0029		
New South Wales	Smiths Lake	1.000 $\pm$ 0.272	0.0068 $\pm$ 0.0060		
	Botany Bay	0.694 $\pm$ 0.147	0.0034 $\pm$ 0.0025		
	Lake Illawarra	0.833 $\pm$ 0.098	0.0024 $\pm$ 0.0019		
	Coila Lake	0.000 $\pm$ 0.000	0.0000 $\pm$ 0.0000		
Victoria	Gippsland Lakes	0.756 $\pm$ 0.130	0.0040 $\pm$ 0.0028		
	Port Albert	0.867 $\pm$ 0.071	0.0030 $\pm$ 0.0022		
	Port Philip	0.800 $\pm$ 0.172	0.0027 $\pm$ 0.0022		
Tasmania	Tamar Estuary	0.778 $\pm$ 0.137	0.0029 $\pm$ 0.0022		
State	Location	ITS1 (including microsatellites)		ITS1 (excluding microsatellites)	
		$h$	$\pi$	$h$	$\pi$
(b)					
Queensland	Mooloolaba	1.000 $\pm$ 0.500	0.0368 $\pm$ 0.0382	1.000 $\pm$ 0.500	0.0034 $\pm$ 0.0048
New South Wales	Smiths Lake	1.000 $\pm$ 0.500	0.0432 $\pm$ 0.0446	1.000 $\pm$ 0.500	0.0168 $\pm$ 0.0184
	Botany Bay	1.000 $\pm$ 0.127	0.0518 $\pm$ 0.0325	0.700 $\pm$ 0.218	0.0094 $\pm$ 0.0070
	Lake Illawarra	0.857 $\pm$ 0.137	0.0472 $\pm$ 0.0275	0.810 $\pm$ 0.130	0.0067 $\pm$ 0.0049
	Coila Lake	1.000 $\pm$ 0.127	0.1305 $\pm$ 0.0800	1.000 $\pm$ 0.127	0.0155 $\pm$ 0.0107
Victoria	Gippsland Lakes	0.857 $\pm$ 0.137	0.0320 $\pm$ 0.0190	0.857 $\pm$ 0.137	0.0087 $\pm$ 0.0060
	Port Albert	0.900 $\pm$ 0.161	0.0384 $\pm$ 0.0243	0.700 $\pm$ 0.218	0.0027 $\pm$ 0.0027
	Port Philip	1.000 $\pm$ 0.076	0.0244 $\pm$ 0.0148	0.714 $\pm$ 0.181	0.0029 $\pm$ 0.0026
Tasmania	Tamar Estuary	1.000 $\pm$ 0.096	0.0256 $\pm$ 0.0159	0.800 $\pm$ 0.172	0.0034 $\pm$ 0.0030

were unique giving gene diversity ( $h$ ,  $\pm$  SD)  $0.9739 \pm 0.0150$  and nucleotide diversity ( $\pi$ ,  $\pm$  SD)  $0.0562 \pm 0.0280$ . Minimum and maximum PSDs were 0 and 90 (out of 419), respectively. After recoding microsatellite repeats as single characters, 70 positions were variable, of which 35 were phylogenetically informative; minimum and maximum pairwise differences were 0 and 25 (out of 319), respectively. If microsatellite regions were excluded, 25 positions were variable of which nine were phylogenetically informative; minimum and maximum PSDs were 0 and 10 (out of 261), respectively. All data sets indicated the same broad pattern. Central and southern populations were not reciprocally monophyletic for ITS1 haplotypes although southern haplotypes clustered within one part of the generally weakly resolved tree (Fig. 4). AMOVA indicated significant variation in ITS1 between regions although most variation occurred within populations (Table 4).

Across the range sampled, mean inter-population PSD, corrected for within-population variation, in COI was not correlated with geographic distance (Mantel's  $r = 0.217$ ,  $P = 0.1878$ ). The region between Coila Lake and Gippsland Lakes was characterized by a high rate of genetic change per unit geographic distance leading to bimodal distribution of genetic distances (Table 5; Fig. 5). Mean corrected PSD in COI was correlated with geographic distance in the southern group (Mantel's  $r = 0.699$ ,  $P = 0.0423$ ) but not the central

group (Mantel's  $r = 0.570$ ,  $P = 0.0560$ ), and neither relationship was significant after sequential Bonferroni correction for three tests. Linear regression of genetic distance on geographic distance was non-significant for all comparisons using five subsets of data that corresponded to the five regions that would result from one or two hypothesized biogeographic boundaries (Fig. 1;  $P > 0.05$ ). Across the range sampled, mean inter-population corrected PSD in ITS1 was positively correlated with geographic distance between populations (Mantel's  $r = 0.440$ ,  $P = 0.0190$ ); linear regression of genetic distance ( $y$ ) on geographic distance ( $x$ ) yielded the relationship  $y = 0.00001149x + 0.01063$ ,  $R^2 = 0.193$ ,  $P = 0.007$  (Fig. 5). The highest rates of genetic change in ITS1 occurred in the Botany Bay–Lake Illawarra–Coila Lake region but comparisons across this region, which was also a region of a relatively high rate of change in COI (Table 5), did not obviously deviate from the fitted regression. AMOVA analyses that considered a second regional boundary between NBB–NCL did not greatly increase the percentage of variation attributed to inter-regional comparisons (COI, 81% if boundary between NLI and NCL, 82% if between NBB and NLI; ITS1, 42.39% for NLI–NCL boundary, 32% for NBB–NLI boundary). Considering only the central clade, defining regional boundaries between NBB–NLI and between NLI–NCL resulted in 26% ( $P = 0.10$ ) and 11% ( $P = 0.40$ ) of variation in COI being attributed to regional level compari-



**Figure 2** Network of COI haplotypes. The minimum spanning tree (MST) calculated in Arlequin, also showing alternatives to the grey MST connections indicated by unweighted maximum parsimony (MP; length = 48 steps, CI = 0.8333; solid grey arrows) and maximum likelihood (ML;  $-\ln L = 869.46$ ; broken grey arrows) analyses in PAUP\*4.0 b10. All other relationships were the same in MST, MP, and ML analyses. MP bootstrap values > 50% are shown adjacent to branches. Key to sample acronyms is given in legend to Fig. 1. Small squares represent unsampled, inferred, haplotypes. GenBank accession numbers AY319476, AY737184–AY737247.

sons compared with 52% and 54% ( $P < 0.001$ ) attributed to within population variation, respectively. The corresponding figures for ITS1 were inter-regional 4% ( $P = 0.81$ ) and intra-population 97% ( $P = 0.22$ ) for an NBB–NLI boundary, and inter-regional 21% ( $P < 0.001$ ) and intra-population 85% ( $P = 0.22$ ) for an NLI–NCL boundary. The greatest mean inter-population genetic distances in ITS1 involved comparisons between Coila Lake and the four southern populations (Fig. 5).

**Table 4** Partitioning of molecular variation among populations and between the central (QMH, NSL, NBB, NLI, NCL) and southern (VGL, VPP, VPA, TTE) regions calculated using AMOVA

	COI	ITS1†
Source and percentage of variation		
Among regions	83.66	41.30
Among populations within regions	8.21	4.45
Within populations	8.12	54.25
Fixation indices‡		
$\Phi_{CT}$	0.8367**	0.4130*
$\Phi_{SC}$	0.5027***	0.0758
$\Phi_{ST}$	0.9188***	0.4575***

The AMOVA distance matrix comprised pairwise sequence differences. †Calculated using ITS1 sequence data excluding gapped positions. Calculations using ITS1 data including gapped positions gave similar results: among regions 38.78%, among populations 3.08%, within populations 58.13%,  $\Phi_{CT}$  0.3879\*,  $\Phi_{SC}$  0.0503<sup>ns</sup>,  $\Phi_{ST}$  0.4187\*\*\*.

‡Correlation of random haplotypes:  $\Phi_{CT}$  within groups cf. whole species,  $\Phi_{SC}$  within populations cf. regions,  $\Phi_{ST}$  within populations cf. whole species.

Probability of an equal or more extreme  $\Phi$ -statistic and associated variance component ( $\sigma$ ) by chance alone: \* $P < 0.05$ , \*\* $P < 0.01$ , \*\*\* $P < 0.001$ . Probabilities were calculated using 1023 permutations of the datamatrix.

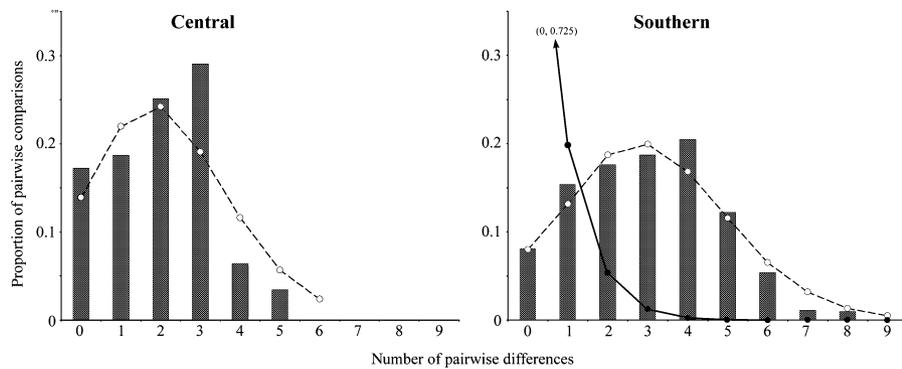
Lowest genetic diversity in COI was observed in Coila Lake, the smallest and most isolated location, although the NCL population had high diversity in ITS1. Neither measure of genetic diversity in either marker was significantly correlated with habitat area ( $-0.389 \leq \text{Pearson's } r \leq 0.18$ ,  $0.39 \leq P \leq 0.90$ ).

## DISCUSSION

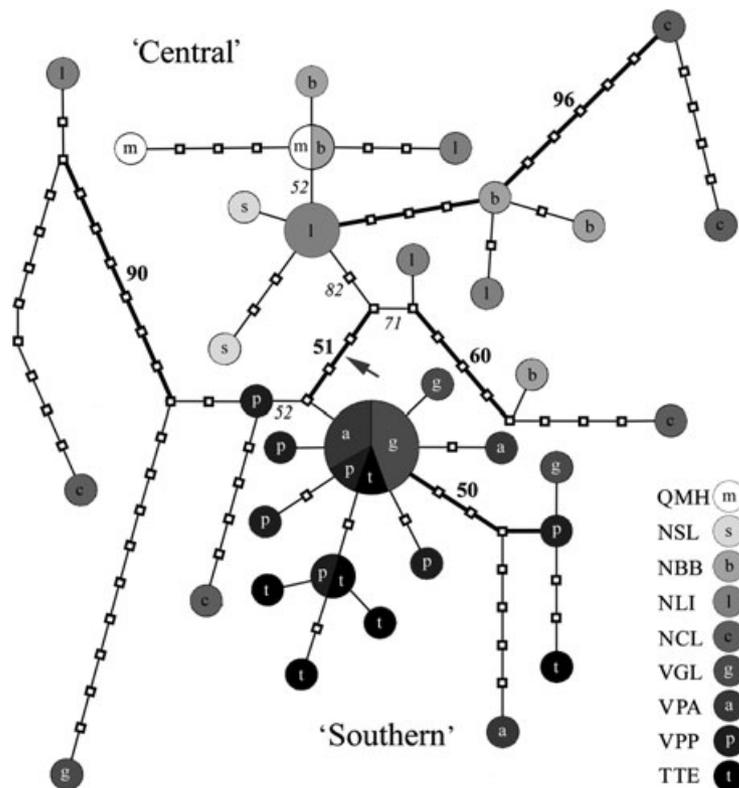
### Evolution in south-east Australia *Catostylus*

Two reciprocally monophyletic clades of *C. mosaicus* are delineated by deeply divergent mitochondrial COI and different complements of ITS1 haplotypes. One clade (central) occurs north of Cape Howe, the other (southern) west of Cape Howe. The southern clade is further subdivided; ancestral haplotypes lie to the south or west of Wilson's Promontory, and derived haplotypes to the east. Thus, although their limits are not established precisely, boundaries between major clades and subclades are geographically proximate to a hypothesized provincial zoogeographic boundary in the vicinity of Bass Strait. There is limited evidence of a phylogeographic discontinuity, of considerably smaller magnitude, in close proximity to a second hypothesized zoogeographic discontinuity in the vicinity of Sydney.

The estimated divergence time of central and southern clades c. 1.4 Myr BP (Table 6) corresponds well with the period 1.6–1.2 Myr BP during which sea-level was generally much lower (Haq *et al.*, 1987) and average global climate much cooler – similar to that at the Pleistocene–Holocene boundary as indicated by  $\delta^{18}\text{O}$  (Billups, 2004) when sea-level was c. –40 m



**Figure 3** Cytochrome oxidase c subunit I (COI) mismatch distributions. *Central populations* (Queensland and New South Wales): the observed mismatch distribution (bars; mean  $m = 1.99$ , variance  $v = 1.74$ ) differed significantly from the distribution expected for a population that recently expanded rapidly (white circles dashed line:  $\chi^2 = 39.66$ , 5 d.f.,  $P < 0.005$ ). *Southern populations* (Tasmania and Victoria): the observed mismatch distribution (bars;  $m = 2.98$ ,  $v = 3.12$ ) differed statistically from that expected for rapid expansion (white circles dashed line:  $\chi^2 = 19.02$ , 8 d.f.,  $P < 0.025$ ) and from that expected for long-term stable population size (black circles solid line:  $\chi^2 = 25,022$ , 8 d.f.,  $P < 0.005$ ). The expectation for stable population size was calculated using the equation  $F_i \approx \vartheta^i / (\vartheta + 1)^{i+1}$  and  $\vartheta_0$  was estimated as  $\sqrt{(v-m)}$ , where  $F_i$  is the probability that two random alleles differ at exactly  $i$  nucleotides and  $\vartheta$  is the expected pairwise difference ( $\vartheta_0$  at time zero) (Rogers & Harpending, 1992; Rogers, 1995).  $\vartheta_0$  could not be estimated for the central group because  $v < m$ .



**Figure 4** One of 56 most parsimonious ITS1 haplotype networks based on unweighted maximum parsimony analysis (UMP) of the data set including microsatellites recoded as single characters (length = 113 steps, CI = 0.6814). Internal branches present in the majority rule consensus tree are annotated with their majority rule indices (i.e. the percentage of shortest trees in which the branch occurred, in italics); thickened branches were present in the strict consensus (majority rule index of 100%). Bootstrap values  $> 50\%$  are shown (in bold) adjacent to branches. The branch indicated by an arrow, among others, was also present in the strict consensus trees yielded by UMP of the original ITS1 data set excluding missing/ambiguous positions with gaps coded as a fifth character (46 shortest trees, length = 339 steps, CI = 0.7109; bootstrap support = 75%). Symbols and abbreviations as in Fig. 2. GenBank accession numbers AY737137–AY737183.

**Table 5** Ratios of genetic distance (percentage pairwise sequence difference; %PSD) to geographic distance separating populations of *Catostylus mosaicus*. Magnitude is calculated as %PSD km<sup>-1</sup> × 10<sup>4</sup>

	QMH to NSL	NSL to NBB	NBB to NLI	NLI to NCL	NCL to VGL	VGL to VPA	VPA to VPP	VPP to TTE
<b>COI</b>								
Mean genetic difference (%PSD ± SD)	0.58 ± 0.15	0.46 ± 0.28	0.48 ± 0.26	0.21 ± 0.17	3.52 ± 0.27	0.33 ± 0.26	0.73 ± 0.21	0.29 ± 0.25
Mean geographic distance (km)	636	215	68	179	343	144	217	395
Magnitude (± SD)	9.2 ± 2.4	21.5 ± 12.8	70.4 ± 37.9†	11.5 ± 9.5	102.3 ± 7.9‡	22.9 ± 18.3	33.9 ± 9.8	12.2 ± 5.7
<b>ITS1</b>								
Mean genetic difference (%PSD ± SD)	1.57 ± 0.81	1.88 ± 0.81	2.25 ± 1.70	4.59 ± 1.68	4.86 ± 1.52	1.47 ± 1.67	1.11 ± 0.96	1.29 ± 0.70
Mean geographic distance (km)	636	215	68	179	343	144	217	395
Magnitude (± SD)	7.7 ± 4.0	27.3 ± 11.75	103.3 ± 78.1†	80.4 ± 29.5†	44.3 ± 13.9	43.1 ± 36.2	17.6 ± 13.6	10.8 ± 5.2

†Magnitude > mean magnitude + 1 SD.

‡Magnitude > mean magnitude + 2 SD.

Approximate coastal distances calculated using the Geoscience Australia website distance calculator (<http://www.agso.gov.au/map/names/distance.jsp>). Distances are straight-line distances except NCL to VGL (via Cape Howe) and VPA to VPP (via Wilson's Promontory). COI, mean magnitude 35.5, SD 33.5. ITS1, mean magnitude 41.8, SD 34.2.

(Shackleton, 1987) – for the first time since at least the Miocene. Other candidate cool-climate-low-sea periods existed as early as *c.* 2.6–2.4 Myr BP, but the combinations were not so strong (Haq *et al.*, 1987 *cf.* Billups, 2004). Divergence during this period is consistent with a pulse of marine speciation in Australia and central and northern America *c.* 2 Myr BP (Jackson, 1995; O'Hara & Poore, 2000) and, as in many other coastal marine taxa (e.g. Avise, 1992; Dawson *et al.*, in press), the mtDNA genealogy of *C. mosaicus* likely records the influences of late-Pliocene and, particularly, Pleistocene climate and sea-level change. During glacial low-stands, *C. mosaicus* ancestral to contemporary Victoria and Tasmania populations were isolated west of the Bassmania Peninsula (Figs 1 and 2). The lineage then underwent at least two range expansions, one eastward to VPA and VGL and another latitudinally onto the north and south coasts of Bass Strait, consistent with the geographical evolution of the area during deglaciation and sea-level rise. Subsequent isolation of a VGL/VPA-like group on the eastern side of the peninsula or in a distinct embayment on the west of the isthmus during late-Pleistocene low-stands would be consistent with drainage patterns of paleorivers (Unmack, 2001). The more recent separation of VPP and TTE populations is consistent with expansion of the most westerly group into northern and southern drainages during late-Pleistocene (perhaps the post-80 Ka BP) low-stand followed by restriction of gene flow across the Bass Strait when it reopened.

Central *C. mosaicus* have a shallower evolutionary history than southern *C. mosaicus*, as indicated by lower genetic variation and a mismatch distribution which has a smaller  $\tau$  (estimated from the position of the crest of the distribution) and steeper leading face consistent with a more recent expansion (Rogers & Harpending, 1992). Recent range expansion may in part be responsible for the greater genetic homogeneity of the region, although the estimated times of population separations,

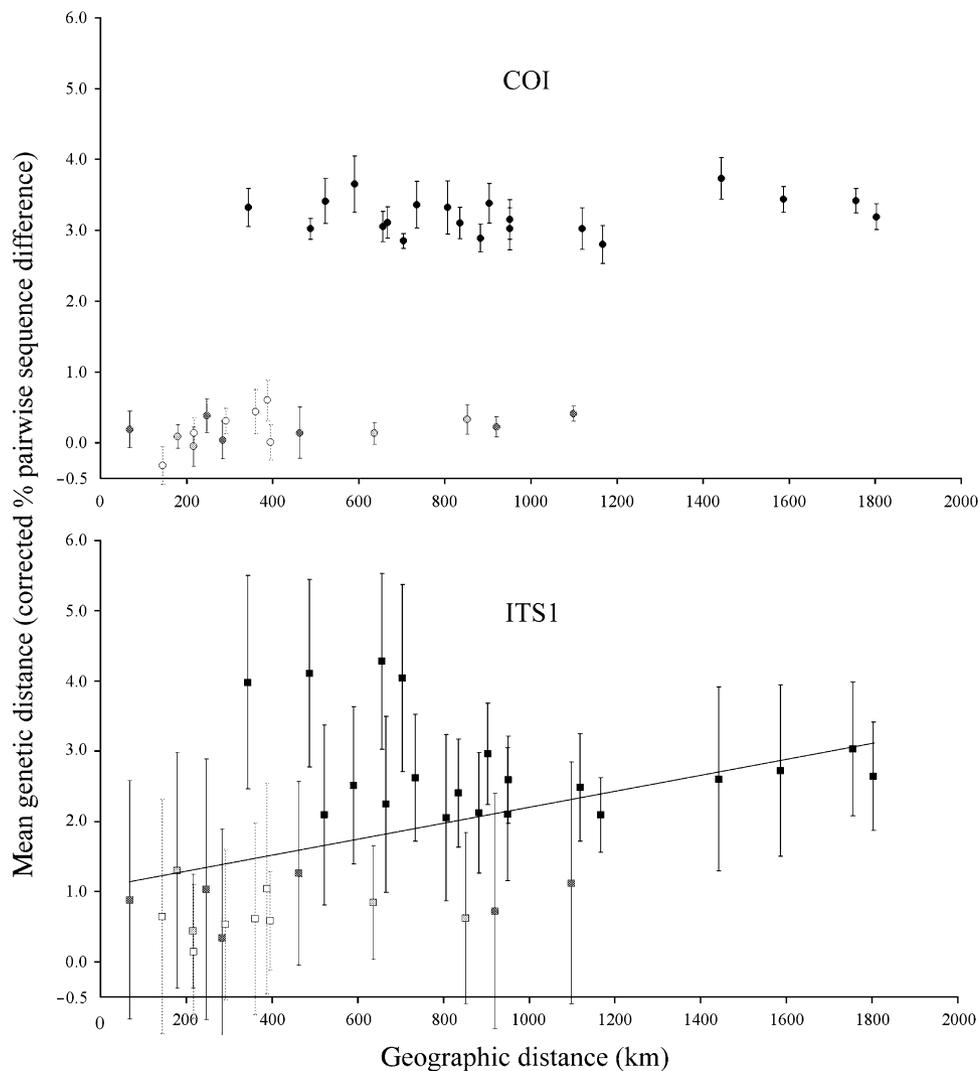
which are comparable to some in the southern clade, suggest this alone is an insufficient explanation. Dispersal in the East Australia Current throughout the time period in question and the absence of strong disruptive geographical features in the region seem likely to have also played a role in preventing strong segregation within the central clade.

Central and southern *C. mosaicus* appear to be in an intermediate stage of speciation. The possibility of a zone of secondary contact around Cape Howe represents probably the best opportunity yet identified to study the dynamics of speciation in scyphozoan jellyfishes.

### Testing phylogeographic hypotheses in south-east Australia

[1] *That patterns in COI and ITS1 are concordant in C. mosaicus (H<sub>3i</sub>).*

Although the central and southern clades of *C. mosaicus* distinguished by COI also have different complements of ITS1, concordance of COI and ITS1 is equivocal. The ITS1 tree is not well resolved but, as it stands, is polyphyletic with respect to the COI tree, and the ITS1 data set also would show significant variation if segregated into other regions. The ratio of inter-clade/intra-clade mean PSD in COI was between 4.4 and 6.6, so congruence would have been expected on the basis of the three-times rule (Palumbi *et al.*, 2001). However, the three times rule is refuted, and the phylogeographic hypothesis (H<sub>3i</sub>) only conditionally supported (or conditionally refuted) because, among other things, COI and ITS1 have differing and variable rates of molecular evolution (see [2] below) and PCR may have amplified various copies of rDNA that had not been homogenized by concerted evolution in the time period of interest (see also Hudson & Turelli, 2003; Waters & Roy, 2003a).



**Figure 5** Relationships between geographic and genetic distances (mean percent PSD, corrected for within population variation) among populations of *Catostylus mosaicus*. Error bars show  $\pm 1$  SD. Black symbols indicate comparisons between central (QMH, NSL, NBB, NLI, NCL) and southern (VGL, VPA, VPP, TTE) groups. Lighter symbols indicate comparisons within central and within southern groups: grey, between QMH-NBB and NLI-NCL subgroups; pale grey, within QMH-NBB and NLI-NCL subgroups; white, within the southern group. COI, five linear regressions of genetic distance on geographic distance were completed using (1–4) each of the four groups mentioned above and (5) all within groups data combined (i.e. lighter symbols only); none differed statistically from a line with no slope at  $\alpha = 0.05$  after sequential Bonferroni correction for five tests (minimum observed  $P = 0.03$ ). ITS1, considering all points, genetic distances (% PSD) are significantly related to geographic distances ( $y = 0.001149x + 1.063$ ,  $R^2 = 0.193$ ,  $P = 0.007$ ); the five comparisons tested using COI also all yielded non-significant relationships when tested with ITS1 data (minimum observed  $P = 0.25$ ).

[2] That, considering *C. mosaicus*, *Cyanea*, and *Aurelia*, concordance between COI and ITS1 genealogies increases with time since isolation ( $H_{3i}$ ).

Concordance among genealogies is found in two other scyphozoan jellyfishes in south-east Australia, both of which show greater sequence differences than *C. mosaicus*, supporting the hypothesis. The 'snottie', *Cyanea*, shows PSDs (mean  $\pm$  SD) of  $15.2 \pm 0.10\%$  in COI and  $10.84 \pm 0.22\%$  in ITS1 between southern New South Wales and Tasmania populations (M. N Dawson, unpubl. data; Table 7). The moon

jellyfish, *Aurelia*, shows PSDs of  $17.56 \pm 0.11\%$  in COI and  $19.71 \pm 0.99\%$  in ITS1 in the vicinity of Bass Strait (M. N. Dawson, unpubl. data; Table 7).

[3] That phylogenetic gaps are concordant across species ( $H_{3ii}$ ).

The scyphomedusae *C. mosaicus*, *Cyanea*, and *Aurelia* all show phylogenetic breaks in the vicinity of Bass Strait (Fig 6). Neither *C. mosaicus* nor *Aurelia* (the two medusae sampled

**Table 6** Some population divergence times estimated as  $T = d/2\lambda$ , where  $d$  is the mean nucleotide distance between populations corrected for intra-population variation and the mutation rate  $\lambda = 4.87 \times 10^{-6}$  [calculated as a function of COI divergence rate of 1% per million years (see Knowlton & Weigt, 1998; Marko, 2002)]. BP, before present

	Estimated divergence time (years BP)		
	Mean	-1 SD	+1 SD
Central			
QMH vs. NCL	205,750	152,221	259,279
NBB vs. NCL	188,556	68,699	308,412
NLI vs. NCL	42,917	<0	127,805
Central vs. southern			
VPP vs. NCL	1,423,117	1,371,140	1,475,094
Southern			
VPP vs. TTE	3417	<0	128,241
VPP vs. VPA	71,958	<0	178,051
VPP vs. VGL	219,433	63,992	374,875

sufficiently) showed strong differentiation across Sydney. Of 10 prior studies, five reported genetic differentiation in the Bass Strait-Cape Howe region (Brown, 1991; Billingham & Ayre, 1996; Colgan & Paxton, 1997; Kassahn *et al.*, 2003; Waters & Roy, 2003a), one reported a latitudinal cline north of Sydney (Hoskin, 2000), and one a second discontinuity in northern New South Wales (Kassahn *et al.*, 2003); four showed no significant genetic differentiation across New South Wales (Nurthen *et al.*, 1992; Jerry, 1997; Murray-Jones & Ayre, 1997; Wong *et al.*, 2004; Table 7). Thus, at least seven of eight taxa sampled across Bass Strait-Cape Howe showed a genetic discontinuity of some kind in that region, the eighth isolation by distance (Brown, 1991). At least seven, and as many as nine, of nine taxa sampled across Sydney showed no significant break in central New South Wales. Concordance among species therefore appears well supported, at least at a regional level. On smaller scales, within the Bass Strait-Cape Howe region, close concordance of phylogenetic gaps is difficult to assess because the geographic sampling of taxa is so varied (Table 7) but several examples of discordance are implied (e.g. Billingham & Ayre [1996]; cf. Colgan & Paxton [1997]).

[4] *That genetic discontinuities occur (a) at the same latitude as Sydney in New South Wales, (b) in Bass Strait around Wilson's Promontory, and/or (c) at Cape Howe ( $H_{3iii}$ ).*

It is clear from the prior paragraph that hypothesis 4a is rejected. There is only weak evidence for only two very small genetic inhomogeneities in the two latitudinal cells adjacent to Sydney (Hoskin, 2000; this study). In contrast, hypotheses 4b and 4c appear to gain partial support, at the regional level, albeit imprecisely. But phylogenetic analyses and the topographical evolution of Bass Strait on glacial time-scales indicate this support is only superficial corroboration of phylogeographic expectations ( $H_{3iii}$ ; Table 1). Cape Howe, the current

limit of 'northern' and 'southern' *Coscinasterias muricata*, for example, is not considered to be the original region of divergence in any of the evolutionary hypotheses proposed by Waters & Roy (2003a). The same is true with respect to *C. mosaicus*, the southern clade of which diverged when isolated west of the Bassmania Peninsula and then expanded east towards Cape Howe as rising sea-level flooded the Bassian Isthmus (this study). Comparable patterns – i.e. modern allopatry or parapatry across approximately Bass Strait, including four boundaries at Cape Howe, but overall no strong biogeographic concordance – in sister species originating from vicariance by the Bassian Isthmus are evident in at least four pairs of fishes, four pairs of crabs, seven pairs of molluscs, two pairs of ascideans, and two pairs of seastars (see Dartnall, 1974; Wilson & Allen, 1987; Poore, 1994; Waters & Roy, 2003a). Thus, Cape Howe is only a modern proxy – highlighted by Holocene influences such as habitat distribution, oceanography (e.g. M. N Dawson, A. Sen Gupta, and M. H. England, unpubl. data), dispersal, and ecological interactions – for the actual long-term barrier to gene flow: the geographically expansive Bassmania Peninsula. Similarly, the geographically and temporally diminutive Wilson's Promontory cannot have had a long-term effect on phylogenetic structure in coastal marine taxa because it is a significant coastal feature during only relatively short periods of high sea-level, when it is not subsumed within the Bassian Isthmus. Thus the patterns that currently exist in Bass Strait, while drawing on millions of years of evolution, are heavily influenced by processes operating within the last few thousands of years and, relatively speaking, current geographic limits do not relate directly to 'long-term extrinsic (zoogeographic) barriers'. That the moon jellyfish, *Aurelia*, is common and undifferentiated throughout New South Wales, where it is probably introduced, but rare in Tasmania (M. N. Dawson *et al.*, unpubl. data), indicates that modern ecological processes may now be responsible for maintaining these proxy patterns in other taxa.

## Clarifying the expectations of $H_2$

The phylogeographic hypothesis that 'species with limited phylogeographic population structure have life histories conducive to dispersal and have occupied ranges free of firm impediments to gene flow' ( $H_2$ ; Avise *et al.*, 1987) raises two questions. First, what constitutes a 'life-history conducive to dispersal'? *Catostylus mosaicus* has a long-lived medusa and historically has been considered a highly dispersive zooplankton, yet it has a marked phylogeographic discontinuity. The apparent contradiction can be solved by recognizing the historical de-emphasis of the sometimes strong locomotory and sensory abilities of medusae (see Hamner & Hauri, 1981; Hamner *et al.*, 1994) and the site-specific genetic reservoir that probably exists in the asexually reproducing benthic polyp stage (Ayre, 1990). Secondly, of what is a 'firm impediment to gene flow' comprised? Species with different dispersal abilities may be influenced differently by the same 'impediment' (e.g. Mayr, 1942, p. 243; Dawson *et al.*, 2002). As such,

**Table 7** Habitat, life-history, range sampled, and phylogeographic characteristics of some coastal south-eastern Australia animals

Species	Habitat†	Life history†	Range sampled‡	Markers§	Genetic discontinuity? (geographic precision)¶	Reference
<i>Anthothoe albocincta</i> (Hutton, 1878) anemone	Subtidal to 25 m on hard substrate	Benthic adult, fissiparous and sexual reproduction, planktonic larvae	Sydney to Melbourne	Six allozymes	'The very south-east corner' (1. north of Cape Howe, 200 km) (2. west of Cape Howe, 410 km)	Billingham & Ayre (1996)
<i>Catostylus mosaicus</i> (Quoy & Gaimard, 1824) jellyfish	Estuaries, bays	Benthic polyp, short-lived larva/ephyra, months-long planktonic medusae	Brisbane to Melbourne, nTas	COI, ITS1	1° Bass Strait (east-west 250 km; north-south 100 km); 2° Cape Howe (140 km); Sydney?	This study,
<i>Aurelia 'aurita'</i> (cryptic species, no authority) jellyfish	Estuaries, bays	As above	Brisbane to sNSW, Tas	COI	Bass Strait (north-south 400 km)	M. N Dawson <i>et al.</i> (unpubl. data)
<i>Cyanea annaskala</i> von Lendenfeld, 1882 jellyfish	Estuaries, bays	As above	sNSW, Tas	COI, ITS1	Bass Strait (north-south 400 km)	M. N Dawson (unpubl. data)
<i>Bedevia hanleyi</i> (Angas, 1867) gastropod	Sheltered rocky (estuary) shores	Benthic, direct development	sQld to sNSW	Six allozymes	East Australian Current: cline, Sugarloaf Pt – Sydney (100 km)	Hoskin (2000)
<i>Haliotis rubra</i> Leach, 1814 gastropod	Subtidal to 40 m on rock substrates	Broadcast spawner, short-lived planktonic larva, benthic adult	sNSW to SA, Tas	15 allozymes	Bass Strait (north-south 200 km) (isolation by distance)	Brown (1991)
<i>Donax deltoideus</i> Lamarck, 1818 bivalve	Surf-zone, exposed sand beaches	6–8 week planktonic larva, infaunal adult	sQld to approx. NCL	Six allozymes	None	Murray-Jones & Ayre (1997)
<i>Sepia apama</i> Gray 1849 cuttlefish	Shallow coastal waters	Benthic egg, no dispersive larva, neritic adult	nNSW to Perth	COIII, 8 microsatellites	nNSW (320 km) Cape Howe (450 km)	Kassahn <i>et al.</i> (2003)*
<i>Coccinasterias muricata</i> Verrill, 1867 seastar	Shallow coastal waters	Benthic adult, fissiparous/sexual reproduction, larva several weeks in plankton	cNSW to Perth, Tas	COI, mtCR, ITS2	1° Bass Strait (east-west 1300 km); 2° Cape Howe (0 km)	Waters & Roy (2003a)**
<i>Pseudomugil signifer</i> Kner, 1866 teleost	Streams, estuaries, coastal islands	Eggs scattered in open water or substratum, most stages in streams/estuaries	NSW	ATP synthase 6	None	Wong <i>et al.</i> (2004)***
<i>Rexia solandri</i> (Cuvier, 1832) teleost	Coastal and offshore waters 100–700 m	Planktonic larva, pelagic juvenile, demersal adult	nNSW to Perth, Tas	36 allozymes mtDNA (RFLP)	Bass Strait (at western end)	Colgan & Paxton (1997)

Table 7 continued

Species	Habitat†	Life history‡	Range sampled‡	Marker§	Genetic discontinuity? (geographic precision)¶	Reference
<i>Pomatomus saltatrix</i> (Linnaeus, 1766) teleost	Brackish-to-marine waters, usually off coast 2 to 200 m	Planktonic larvae, pelagic adult	sQld, Sydney, and sNSW	24 allozymes	None	Nurthen <i>et al.</i> (1992)****
<i>Macquaria novemaculeata</i> (Steindachner, 1866) teleost	Coastal drainages <12.5‰	Adults in freshwater but spawn in estuaries, larvae and juveniles in <12.5‰	sQld to eVic	24 allozymes	None (isolation by distance)	Jerry (1997)

†Additional information taken from Norman *et al.* (1999), FishBase ([www.fishbase.org](http://www.fishbase.org)), seashellsofnsw.org.au/Haliotidae/Pages/haliotis\_rubra.htm, Waters & Roy (2003b).

‡State acronyms: Qld, Queensland; NSW, New South Wales; SA, South Australia; Tas, Tasmania; Vic, Victoria. Regional prefixes: n, northern; c, central; s, southern; e, eastern.

§COI, cytochrome c oxidase subunit I; COIII, cytochrome c oxidase subunit III; ITS1, first internal transcribed spacer region; ITS2, second internal transcribed spacer region; mtCR, mitochondrial control region; mtDNA (RFLP), mitochondrial DNA restriction fragment length polymorphisms.

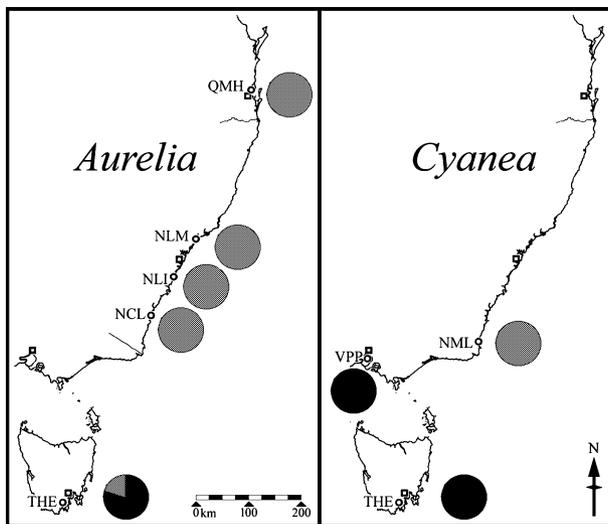
¶Geographic precision was calculated when possible as the approximate distance between the nearest sample locations either side of the stated feature. 1°, a feature considered by the authors to be involved in generating divergence. 2°, a feature considered by the authors to be the modern-day placement of genetic discontinuity albeit one that was not directly involved in the origin of the discontinuity.

\*Analyses of allozymes and morphology were consistent with microsatellites but at lower resolution because of missing samples.

\*\*New Zealand animals also sampled but not reported here.

\*\*\*Queensland animals also sampled but not reported here.

\*\*\*\*Perth animals also sampled but not reported here.



**Figure 6** Occurrence of species of the moon jellyfish, *Aurelia* [sp. 1 (grey) and sp. 7 (black)] and the lions mane jellyfish, *Cyanea*, in south-eastern Australia (M. N Dawson, unpubl. data). The fraction of each circle in a particular colour indicates the proportion of COI genotypes of each species found at that location. *Aurelia*: QMH  $n = 3$ ; NLM  $n = 6$ ; NLI  $n = 3$ ; NCL  $n = 5$ ; THE  $n = 6$ . *Cyanea*: NML  $n = 5$ ; THE  $n = 6$ ; VPP  $n = 1$ . The same result occurs for *Cyanea* when ITS1 is analysed. ITS1 was not analysed for *Aurelia*. Location acronyms as in Fig. 1, except, NLM Lake Macquarie, NML Merimbula Lake, THE Huon Estuary.

impediments, barriers, and boundaries may better be viewed as 'filters' (e.g. Carlquist, 1965) that can have multiple components of varying kinds and strengths, including, for example, changes in temperature, substrate, or wave action (Wilson & Allen, 1987; Poore, 1994; see also Diaz *et al.*, 2001), and may range from absolute barriers, such as the Isthmus of Panama in its current conformation, through very strong filters that are incomplete in time or space, such as the Baja California peninsula (Brusca, 1973; Bernardi *et al.*, 2003), to free movement of all species. This terminology emphasizes a more appropriate dynamic framework (Chew & Laubichler, 2003) in which both organisms (intrinsic) and filters (extrinsic) are considered iteratively and one that should better explain, for example, apparent exceptions (e.g. Knowlton & Keller, 1986; Shulman & Bermingham, 1995; Taylor & Hellberg, 2003) to the predicted relationships between phylogeographic structure and fecundity, habitat, or planktonic larval duration (e.g. Waples, 1987; Doherty *et al.*, 1995; Dawson, 2001).

### Comparison of Bass Strait and Sydney regions

Detailed analyses of echinoderms and decapods (O'Hara & Poore, 2000) suggest that the Sydney area is at least as significant biogeographically as Bass Strait: species diversity is higher (per 1° cell: max. 366 cf. 286), short-range endemics are more common [maximum 12 cf. 7 (i.e. 3.3% cf. 2.4%)] and species-turnover is similar [107 cf. 68 (i.e. 8.9% cf. 9.7%)]. Maxima in range terminations, short-range endemics, and

species turnover occur in the same latitudinal cell at Sydney but are geographically disparate across Bass Strait, indicating a coherent extrinsic influence at Sydney but not Bass Strait. So why do phylogeographic data sets from Bass Strait and Sydney contrast so starkly?

The biogeography of fishes provides an important clue. More congeneric fishes are closely allopatric or parapatric across the Bass Strait region (c. 11 pairs) than across Sydney (c. three pairs; see Kuiter, 2000). Allopatry or parapatry of sibling-species across a zootic filter is a logical evolutionary link between, and therefore should be a good predictor of congruence in, intra-specific phylogeographic and inter-specific biogeographic patterns (Burton, 1998), a conclusion supported by this study.

Thus, a physical barrier to movement or other strong zootic filter arguably never formed in the vicinity of Sydney, in stark contrast to the Bassian Isthmus. Thus, species' ranges were more-or-less free to contract northward and expand southward with glacial cycles rather than being trapped and divided (e.g. Addicott, 1966; Fields *et al.*, 1993; Poore, 1994). Biogeographic and phylogeographic influences in the Sydney region – in contrast to those in Bass Strait which are characterized by long-term vicariance and recent dispersal – therefore are dominated by a long history of range fluctuations, unpredictable dispersal within and between years, and environmental heterogeneity on subregional scales, resulting in a broad transition zone characterized by overlap and replacement of subtropical and temperate organisms (Wilson & Allen, 1987) and only weak, if any, genetic inhomogeneities.

### Comparisons with south-west North America

The precision with which phylogeographic and biogeographic patterns show concordance in southern California is currently c. 100–150 km, compared with 250 km or more across Bass Strait. This is in part because of the frequency of sampling, but comparing biogeographic patterns also indicates a fundamental difference between the regions. Correlation among the frequencies of short-range endemics and species' end-ranges (i.e. turnover) is low in south-eastern Australia (Pearson's  $r = 0.63$ ,  $P = 0.001$ ,  $n = 24$ ; calculated from data of O'Hara & Poore, 2000) but high in southern California ( $r = 0.97$ ; Valentine, 1966). The discrepancy is attributable largely to a lack of concordance in Bass Strait ( $r = 0.35$ ,  $P = 0.27$ ,  $n = 12$ ) and in part to an only moderately strong correlation in New South Wales and eastern Tasmania ( $r = 0.766$ ,  $P = 0.004$ ,  $n = 12$ ). Thus, the recent redistribution of organisms across the Bass Strait following inundation of the Bassian Isthmus may explain much of the difference in the level of concordance between biogeographic and phylogeographic patterns in south-east Australia vs. in south-west North America. Comparing just the New South Wales region with California provides further insight. The coastlines of both run approximately linearly north–south for hundreds of kilometres, have a 'Point' at which the prevailing current (one an eastern, the other a western boundary current) departs from the coast, span major biogeographic transitions, have modern

Mediterranean climates and cooler wetter climates in recent evolutionary times, and are punctuated by large open and smaller semi-enclosed or intermittently closed estuaries (e.g. Dawson, 2001 cf. Fig. 1). Yet, despite the similarities, phylogeographic divisions are rare and weak in the vicinity of Sydney in contrast to the relatively common and strong signals in the Los Angeles region of southern California (Dawson, 2001). This may be attributable to differences between the two regions analogous to the difference between Sydney and Bass Strait (assuming differences in techniques and taxa are of secondary importance): the NSW coast lacks obvious physical barriers, such as the California Channel Islands and Palos Verdes peninsula, that are geographically proximate to other potential long-term zootic filters (Dawson, 2001). This comparison therefore emphasizes that both structure and stability are required to generate close concordance.

Comparison of the Tasman and the Baja California peninsulas and of trans- or circum-peninsular routes of dispersal can clarify the role of strong physical barriers to movement and their interaction with other zootic filters. In both regions, closing of trans-peninsular seaways has been a key influence in the origination of disjunct taxa (Poore, 1994; Bernardi *et al.*, 2003). An interesting contrast, however, is that, because the peninsulas have the same orientation at different latitudes, glacial periods should promote dispersal of cold-water organisms around the tip of the Baja California peninsula but restrict gene flow in warm-water populations separated by the Bassman Peninsula; interglacials should restrict movement around the tip of Baja California but promote movement through Bass Strait (e.g. Brusca, 1973; Poore, 1994). Thus, conceptually, the two regions are currently in different stages of the same cycle, allowing the potential for erosion of ancient divergences by modern gene flow to be studied from two perspectives. Traditionally, subtropical waters bathing the tip of Baja California have been thought to prevent circum-peninsular gene flow between Pacific and Sea of Cortez populations of cold water species (e.g. Brusca, 1973). Ancient divergences, however, can also be maintained when no such barrier exists (Dartnall, 1974; this study), increasing support for the contention that disjunct populations across the Baja California peninsula are maintained by a more complex suite of factors (Bernardi *et al.*, 2003; Dawson *et al.*, in press).

### Studying other regions

The Florida peninsula is clearly a case for reconsideration. The peninsula lies approximately north-south at a similar latitude to Baja California, is oriented in the same direction with respect to the shift of isotherms with climate change, but in the opposite direction with respect to the prevailing current (Gulf Stream). Issues of trans- vs. circum-peninsular dispersal are also pertinent, as are matters relating to the influence of topographical changes and adjacent island chains. Testing specific *a priori* hypotheses based on a detailed quantitative review of existing biogeographic data – including the distributions of edge effect species (e.g. Dawson, 2001)

and sibling species pairs (e.g. Burton, 1998) – may offer the best chance of resolving the phylogeographic paradox in which apparently equivalent zootic filters have very different phylogeographic effects on the eastern and western coasts of Florida (see Avise, 1992, 2000). The approach may also be applied profitably elsewhere around the globe.

These analyses that integrate across biotic levels, from molecules to ecosystems, are central to the multifaceted concept of biodiversity that is currently favoured (CBD, 1992). It is promising, therefore, that such analyses demonstrate, in some cases, coincident intra-specific, species, and higher-level patterns of organization; in other cases they clarify our understanding of specific local processes. Concordance in particular should simplify efforts to protect important coastal resources (Moritz *et al.*, 2001), including areas of process (Smith *et al.*, 2001) at a time when extinctions, including those of species as yet undescribed – but species that likely have common patterns of evolution – are proceeding at an unprecedented rate (Pimm *et al.*, 1995; Jackson *et al.*, 2001).

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## BIOSKETCH

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