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Phylogeography of New Zealand's coastal benthos

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Abstract During the past 30 years, 42 molecular studies have been undertaken in New Zealand to examine the phylogeography of coastal benthic invertebrates and plants. Here, we identify generalities and/or patterns that have emerged from this research and consider the processes implicated in generating genetic structure within populations. Studies have used various molecular markers and examined taxonomic groups with a range of life histories and dispersal strategies. Genetic disjunctions have been identified at multiple locations, with the most frequently observed division occurring between northern and southern populations at the top of the South Island. Although upwelling has been implicated as a cause of this disjunction, oceanographic evidence is lacking and alternative hypotheses exist. A significant negative correlation between larval duration and genetic differentiation ($r^2 = 0.39$, $P < 0.001$, $n = 29$) across all studies suggests that larval duration might be used as a proxy for dispersal potential. However, among taxa with short larval durations (<10 days) there was greater variability in genetic differentiation than among taxa with longer pelagic periods. This variability implies that when larval duration is short, other factors may determine dispersal and connectivity among populations. Although there has been little congruence between the phylogeographic data and recognised biogeographic regions, recent research has resolved population subdivision at finer spatial scales corresponding more closely with existing biogeographic classifications. The use of fast-evolving and ecologically significant molecular markers in hypothesis-driven research could further improve our ability to detect population subdivision and identify the processes structuring marine ecosystems.

Keywords genetic differentiation; genetic subdivision; gene flow; larval transport; population connectivity; biogeography

INTRODUCTION

Determining the sources of new recruits to a population is fundamental to ecological research in marine benthic systems. However, determining recruitment pathways has been difficult for many taxa as adults are largely sedentary and dispersal is achieved during a pelagic larval stage (Grantham et al. 2003). Although it is widely acknowledged that pre-settlement pelagic processes play an important role in structuring benthic communities (e.g., Underwood 1981; Menge 1991; Gaines & Bertness 1993), the pelagic component of larval life histories remains largely unknown. Numerous synergistic factors including ocean currents and larval duration, behaviour and mortality can determine patterns of larval dispersal (Roughgarden et al. 1985, 1988; Menge 1991; Cowen & Sponaugle 2009). These patterns govern exchange between populations, influencing local and metapopulation dynamics, community structure, genetic diversity and the resilience of populations to human exploitation (Hastings & Harrison 1994; Botsford et al. 2001;

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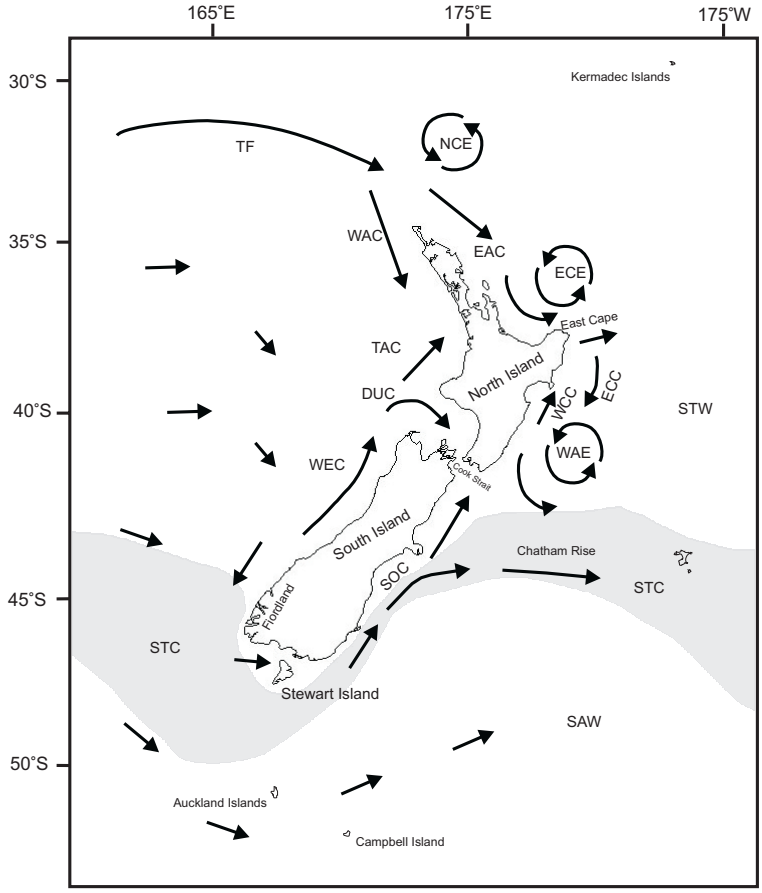

Fig. 1 New Zealand's major coastal current systems and boundaries between water masses. DUC, D'Urville Current; EAC, East Auckland Current; ECC, East Cape Current; ECE, East Cape Eddy; NCE, North Cape Eddy; SOC, Southland Current; SAW, Subantarctic water; STC, Subtropical Convergence; STW, Subtropical water; TAC, Tasman Current; TF, Tasman Front; WAC, West Auckland Current; WAE, Wairarapa Eddy; WCC, Wairarapa Coastal Current; WEC, Westland Current (redrawn after Heath (1982) and Carter et al. (1998)).

Cowen et al. 2007). Understanding population connectivity is therefore essential for the effective management of species and ecosystem resources (Botsford et al. 2001; Palumbi 2003; Levin 2006). Previously, it was considered that few barriers to dispersal existed in the marine environment (Mayr 1954; Scheltema 1986). This paradigm was retained for many years, in part because of the difficulties associated with tracking larval dispersal (Levin 1990; Palumbi et al. 2003). With the advent and subsequent development of molecular techniques it is now possible to estimate rates of larval migration between populations, as a population's genetic structure is likely to reflect patterns of dispersal (Wright 1951; Neigel 1997). Molecular studies have produced conflicting evidence as to whether wide-ranging dispersal and high connectivity are pervasive among marine populations. For example, some studies have shown high levels of connectivity over thousands of kilometres (Takabayashi et al. 2003; Cassista & Hart 2007) whereas in others, boundaries have been identified between genetically distinct populations allowing the location of dispersal barriers to be inferred (e.g., Bird et al. 2007; Gruenthal & Burton 2008). These results suggest that larval duration on its own may not be a suitable proxy for predicting dispersal potential (Bay et al. 2006).

In New Zealand, marine phylogeographic studies have been used to examine meta-population dynamics, larval transport and the processes that determine connectivity among populations. Stretching 2700 km from the subtropical Kermadec islands (29°S) to the subantarctic Auckland and Campbell islands (50°S and 52°S; respectively), New Zealand is an archipelago of over 700 islands (Fig. 1; Laing & Chiswell 2003). The oceanography of this region is complex as the archipelago straddles the subtropical convergence, the division between subtropical water approaching from the north and subantarctic water in the south (Heath 1982; de Lange et al. 2003; Laing & Chiswell 2003). Major current systems divide as they reach the continental shelf creating

numerous smaller currents and eddies. Coastal currents are further modified through interactions with topography (e.g., headlands, islands, and canyons) and temporally variable wind, waves, and tide. This complexity makes it difficult to predict how oceanographic and physical features might influence connectivity among coastal populations of benthic marine organisms.

Here we review peer-reviewed journal articles, graduate theses, and government reports in which the relationship between genetic structure of New Zealand's coastal flora and fauna and geographic locations has been examined. Specifically, we focused on benthic invertebrates and plants and excluded studies of recently introduced species (e.g., Smith et al. 1986) as their genetic structure is likely to have been influenced by their method of introduction (Provan et al. 2005; Rius et al. 2008). We identified generalities and/or patterns in population structure and the processes implicated in generating subdivision, examine the relationship between larval duration and population differentiation and contrast current knowledge of population subdivision with biogeographic classification schemes.

New Zealand literature

Forty-two phylogeographic studies, published between 1980 and 2008 were included in the review (Table 1). Where more than one species was included in a single publication, each was considered separately. During this period, there has been an increase in the number of studies using molecular techniques as well as in the types and number of molecular markers used (Fig. 2, Table 1). Early studies used allozyme electrophoresis, and later used sequencing and fragment analysis of mitochondrial and nuclear DNA as these techniques became increasingly available (for descriptions of markers and their uses in molecular ecology see Wan et al. 2004; DeYoung & Honeycutt 2005; Anne 2006). As methods have developed, concerns about the comparability of genetic data have arisen where analyses of different markers in a single species (e.g., green-lipped mussel *Perna canaliculus*) produced conflicting results (Smith 1988; Gardner et al. 1996; Apte & Gardner 2001, 2002). However, recent studies have produced more consistent results (Apte & Gardner 2002; Apte et al. 2003; Star et al. 2003). It is possible that chance effects associated with the low numbers of populations and individuals typically sampled in early population genetic studies (Table 1) may have contributed to the initial variability in phylogeographic patterns detected.

Twenty-nine species were covered in these studies, the majority of which were crustaceans, echinoderms, or molluscs. The taxa studied have a range of dispersal strategies and include brooding species that lack a dispersive larval stage (e.g., the anemone *Actinia tenebrosa*), species with pelagic larval durations (PLDs) ranging from as little as a few days (e.g., the limpet *Cellana ornata*) to greater than 12 months (e.g., the rock lobster *Jasus edwardsii*), and one plant (the seagrass *Zostera muelleri*) able to undergo dispersal in its adult form (Table 1).

Panmictic taxa

Eight studies of seven taxa found no significant genetic subdivision (Table 1) suggesting that for these species, gene flow is high, barriers to dispersal are absent, and that populations can be considered as part of a single interbreeding unit. For the rock lobsters *J. edwardsii* and *J. verreauxi* with PLDs of 8–15 months and the gastropod *Nerita atramentosa* with a PLD of 5–6 months, this lack of genetic structure was expected (Smith et al. 1980; Brasher et al. 1992; Ovenden et al. 1992; Waters et al. 2005). For species with extended PLDs, larval transport across great distances is expected to connect distant populations (Mayr 1954; Scheltema 1986) despite temporal variability in coastal oceanography or the occurrence of short-lived hydrological dispersal barriers (e.g., Roberts & Paul 1978). Conversely, for the bivalve *Austrovenus stutchburyi* and the echinoderm *Coscinasterias muricata*, both with shorter PLDs (2–5 weeks), the lack of population subdivision was unexpected (Lidgard 2001; Waters & Roy 2003).

North-south population differentiation

The most prominent pattern in the reviewed studies was that of genetically distinct northern and southern populations. This pattern was detected in 16 of the 26 studies in which populations were sampled at a New Zealand-wide scale (5–12° latitude; Table 1). On the west coast of New Zealand, the location of this divergence has been consistently reported at the top of the South Island or in the vicinity of Cook Strait (e.g., Apte et al. 2003; Stevens & Hogg 2004; Ayers & Waters 2005; Goldstien et al. 2006; Veale 2007; Jones et al. 2008), whereas on the east coast the location of divergence has been more variable. A division was detected in the East Cape region (Fig. 1) for two species of estuarine amphipod (*Paracorophium lucasi* and *P. excavatum*) (Stevens & Hogg 2004), whereas for other taxa the demarcation between northern and southern

Table 1 Summary of phylogeographic studies of coastal benthic invertebrates and plants undertaken in New Zealand. PLD, pelagic larval duration; *n*, number of populations sampled; NZ, New Zealand; mtDNA, mitochondrial DNA; RFLP, restriction fragment length polymorphism; AFLP, amplified fragment length polymorphism; nDNA, nuclear DNA; ITS, internal transcribed spacer; COI, cytochrome c oxidase subunit I; D–loop, displacement loop; NADH IV, NADH dehydrogenase subunit IV; RAPD, random amplification of polymorphic DNA. Unless specified, reproductive strategy and PLD were given in the cited study or references therein. *Number in parentheses indicates sampling spread when North and South island outgroups are included. (a) Stevens 1991; (b) Perrin et al. 2004; (c) Lamare 1997; (d) Tond et al. 1992; (e) Buchanan 1994.

Species	Subphylum or class	Reproductive strategy	PLD	Reference	Distribution of sampling	Sampling scale (°latitude)	*n*	Results	Genetic marker
Arthropoda									
Jasus edwardsii	Crustacea	Pelagic larvae	possibly >1yr	Smith & McKoy1980	NZ wide	8	3	No structure	Allozymes
Jasus edwardsii	Crustacea	Pelagic larvae	possibly >1yr	Ovenden et al. 1992	NZ east coast	7	2	No structure	mtDNA RFLP
Jasus verreauxi	Crustacea	Pelagic larvae	>8 months	Brasher et al. 1992	NZ northeast coast	3	2	No structure	mtDNA RFLP
Paracorophium excavatum	Crustacea	Brooded young	No pelagic larval phase	Schnabel 1998; Schnabel et al. 2000	NZ east coast	8	4	North-south differentiation	Allozymes
Paracorophium excavatum	Crustacea	Brooded young	No pelagic larval phase	Stevens & Hogg 2004	NZ wide	9	21	North-south differentiation	Allozymes
Paracorophium lucasi	Crustacea	Brooded young	No pelagic larval phase	Schnabel 1998; Schnabel et al. 2000	Central New Zealand	3	11	East-west & north-south differentiation	Allozymes
Paracorophium lucasi	Crustacea	Brooded young	No pelagic larval phase	Stevens & Hogg 2004	NZ wide	6	18	North-south & east-west differentiation	Allozymes
Pinnotheres novaezelandiae	Crustacea	Pelagic larvae	Unknown—Genera mean = 23 days [(a)]	Stevens 1990	NZ North Island	6	5	Differentiation within and among locations	Allozymes
Pinnotheres atrinicola	Crustacea	Pelagic larvae	Unknown—Genera mean = 23 days	Stevens 1991	NZ North Island	6	7	Latitudinal clinal pattern	Allozymes
Brachiopoda									
Liothyrella neozelanica	Articulate	Brooded young	No pelagic larval phase	Ostrow 2004	Fiordland	<1	6	Differentiation within and among fjords	AFLP
Terebratella sanguinea	Articulata	Pelagic larvae	Unknown	Ostrow 2004	Fiordland and Stewart Island	3	23	Some differentiation among fjords	Allozymes & AFLP
Cnidaria									
Actinia tenebrosa	Anthozoa	Brooded young	No pelagic larval phase	Veale 2007	NZ wide	11	27	Isolation by distance	Microsatellites
Antipathes fiordensis	Anthozoa	Marginally pelagic larvae	~10 days	Miller 1997	Fiordland and Stewart Island	3	28	Divergence within and among fjords	Allozymes
Antipathes fiordensis	Anthozoa	Marginally pelagic larvae	~10 days	Miller 1998	Doubtful Sound (Fiordland)	<1	3	Data suggest limited dispersal within fjords	Allozymes

Errina novaezealandia	Anthozoa	Brooded young	No pelagic larval phase	Miller et al. 2004	Fiordland	<1	9	Differentiation within and among fjords	Allozymes
Echinodermata									
Amphipholis squamata	Ophiuroidea	Brooded young	No pelagic larval phase	Sponer 2002; Sponer & Roy 2002	NZ wide	12	16	North-south differentiation	mtDNA 16s (nDNA ITS)
Astrobrachion constrictum	Articulata	Pelagic Larvae	4–8 days	Steele 1999	Fiordland	1	7	No Structure	Allozymes and mtDNA COI
Coscinasterias muricata	Asteroidea	Pelagic larvae	~30 days [b]	Waters & Roy 2003	NZ wide	10	4	No Structure	mtDNA COI (and nDNA ITS2)
Coscinasterias muricata	Asteroidea	Pelagic larvae	~30 days	Perrin 2002; Perrin et al. 2004	Fiordland (+ 2 South Island and 1 North Island sites)	2 (10)*	17	Isolation-by-distance amongst northern fjords. Restricted gene flow between southern fjords	mtDNA D–loop
Coscinasterias muricata	Asteroidea	Pelagic larvae	~30 days [b]	Skold et al. 2003	Fiordland (+ 2 South Island and 1 North Island sites)	2 (10)*	16	Differentiation among fjords	Allozymes
Evechinus chloroticus	Echinoidia	Pelagic larvae	3–6 weeks [b]	Mladenov et al. 1997	NZ wide	11	6	Doubtful Sound distinct from other NZ populations	Allozymes
Evechinus chloroticus	Echinoidia	Pelagic larvae	3–6 weeks [c]	Perrin 2002	Fiordland (+ 2 South Island and 2 North Island sites)	2 (12)*	20	Differentiation within and among fjords	Microsatellites
Ophiomyxa brevirima	Ophiuroidea	Brooded young	No pelagic larval phase	Garrett 1995	South and Stewart islands	5	4	Differentiation between populations	Allozymes
Patiriella regularis	Asteroidea	Pelagic larvae	9–10 weeks	Waters & Roy 2004	NZ wide	12	19	North-south differentiation	mtDNA control region
Patiriella regularis	Asteroidea	Pelagic larvae	9–10 weeks	Ayers & Waters 2005	NZ wide	12	22	North-south differentiation	mtDNA control region
Mollusca									
Austrovenus stutchburyi	Bivalvia	Pelagic larvae	2–3 weeks	Lidgard 2001	NZ wide	10	10	No structure	Allozymes
Cellana flava	Gastropoda	Pelagic larvae	3–11 days	Goldstien 2005; Goldstien et al. 2006	NZ wide	5	8	North-south differentiation	mtDNA cytochrome b
Cellana ornata	Gastropoda	Pelagic larvae	3–11 days	Goldstien 2005; Goldstien et al. 2006	NZ wide	12	31	North-south differentiation	mtDNA cytochrome b
Cellana radians	Gastropoda	Pelagic larvae	3–11 days	Goldstien 2005; Goldstien et al. 2006	NZ wide	12	31	North-south differentiation	mtDNA cytochrome b
Haliotis iris	Gastropoda	Pelagic larvae	5–9 days[d]	Smith & McVeagh 2006	NZ wide	11	4	Differentiation between locations	mtDNA COI and microsatellites
Nerita atramentosa	Gastropoda	Pelagic larvae	5–6 months	Waters et al. 2005	Northern NZ and Three Kings	4	10	No structure	mtDNA COI

Table 1 (*continued*)

Species	Subphylum or class	Reproductive strategy	PLD	Reference	Distribution of sampling	Sampling scale (°latitude)	*n*	Results	Genetic marker
Paphies subtriangulata	Bivalvia	Pelagic larvae	~3 weeks	Smith et al. 1989	NZ wide	11	13	Distinct north, central and Chatham islands populations	Allozymes
Perna canaliculus	Bivalvia	Pelagic larvae	>4 weeks [e]	Smith 1988	NZ wide	11	6	North-south differentiation	Allozymes
Perna canaliculus	Bivalvia	Pelagic larvae	>4 weeks [e]	Gardner et al. 1996	NZ wide	11	10	Isolation by distance	Allozymes
Perna canaliculus	Bivalvia	Pelagic larvae	>4 weeks [e]	Apte & Gardner 2001	NZ wide	12	35	No structure	Allozymes
Perna canaliculus	Bivalvia	Pelagic larvae	>4 weeks [e]	Apte & Gardner 2002	NZ wide	12	22	North-south differentiation	mtDNA NADH IV
Perna canaliculus	Bivalvia	Pelagic larvae	>4 weeks [e]	Star et al. 2003	NZ wide	12	19	North-south differentiation	RAPD
Perna canaliculus	Bivalvia	Pelagic larvae	>4 weeks [e]	Apte et al. 2003	NZ wide	12	36	North-south differentiation	Allozymes, mtDNA & RAPD
Scutellastra kermadecensis	Gastropoda	Pelagic larvae	unknown—possibly 4–10 days	Wood & Gardner 2007	Kermadecs: northern and central islands	1	11	Differentiation within and among regions: isolation-by-distance at small scales	RAPD
Siphonaria raoulensis	Gastropoda	Pelagic larvae	unknown—possibly 9 days – 10 weeks	Wood & Gardner 2007	Kermadecs: northern islands	<1	6	Differentiation within and among regions	RAPD
Sypharochiton pelliserpentis	Gastropoda	Pelagic larvae	unknown—possibly <4 days	Veale 2007	NZ wide	12	28	North-south differentiation and east-west in northern NZ	mtDNA COI
Plantae									
Zostera muelleri	Magnoliophyta	Mainly vegetative	No pelagic larval phase—dispersal as adult	Jones 2004; Jones et al. 2008	NZ wide	11	8	North-south and east-west differentiation	RAPD

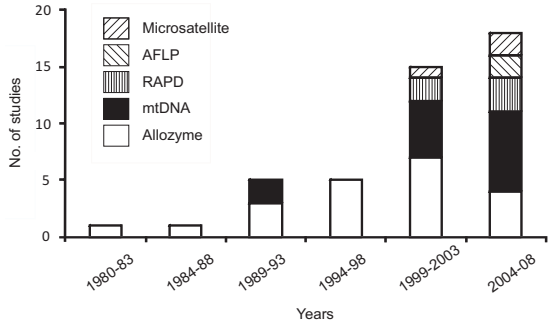

Fig. 2 Number of phylogeographic studies of the New Zealand coastal benthos conducted between 1980 and 2008 and molecular techniques used. AFLP, amplified fragment length polymorphisms; RAPD, random amplification of polymorphic DNA; mtDNA, mitochondrial DNA.

populations has been located in the vicinity of Cape Campbell (Fig. 3) on the east coast of the South Island (e.g., limpet (*C. ornata*, Goldstien et al. 2006), green-lipped mussel (*P. canaliculus*, Apte & Gardner 2002; Apte et al. 2003), cushion star (*Patiriella regularis*, Waters & Roy 2004; Ayers & Waters 2005), brittle star (*Amphipholis squamata*, Sponer & Roy 2002) and snakeskin chiton (*Sypharochiton pelliserpentis*, Veale 2007)). Divergence between northern and southern populations was also detected in some Fiordland-focused studies that included North Island outgroups (e.g., Perrin 2002; Skold et al. 2003; Perrin et al. 2004). However, owing to the small number of northern populations included in these studies, no conclusions could be made about the location of genetic breaks occurring between northern and southern populations.

Where a genetic division between northern and southern populations occurs in the upper South Island, upwelling has often been implicated as a barrier to larval dispersal (Apte & Gardner 2002; Star et al. 2003; Waters & Roy 2004; Ayers & Waters 2005; Veale 2007). It has been hypothesised that upwelling on the northern east and west coasts of the South Island could cause larvae passing into these regions to be advected from coastal habitats into offshore waters where they will perish. Upwelling as a barrier to population connectivity and larval dispersal has been studied in a number of systems, particularly in areas with well characterised oceanography such as Chile (Poulin et al. 2002; Narvaez et al. 2006), the west coast of the United States (Roughgarden et al. 1988; Hohenlohe 2004), the Iberian Peninsula, Portugal (Santos et al. 2007), and the west coast of Africa (Lett et al. 2007). In these areas, which are dominated by major current systems (i.e., Humbolt, California, Canary, and Benguela currents), upwelling occurs seasonally and once established may persist for months (Largier et al. 1993). Even in these systems, there is limited evidence to suggest that upwelling isolates coastal populations (Hohenlohe 2004; Shanks & Brink 2005; Narvaez et al. 2006; Lett et al. 2007; Johansson et al. 2008). There is, however, evidence to suggest that the effects of upwelling on larval transport are strongly modified by larval behaviour (Poulin et al. 2002; Shanks & Brink 2005). Shanks & Brink (2005) demonstrated that vertical positioning could determine the cross-shelf transport of larvae under upwelling conditions. They observed that the larvae of some species were transported offshore during upwelling as predicted, whereas others were moved shoreward or maintained position relative to the coast despite experiencing the same cross-shelf currents (Shanks & Brink 2005). Consequently, in the absence of detailed sampling, upwelling should not be invoked as a cause of variation in larval settlement patterns.

In New Zealand, weather patterns are highly variable and wind-driven oceanographic features such as upwellings also vary at equivalent time scales (Heath 1972; de Lange et al. 2003; Laing & Chiswell 2003). Throughout any given breeding season, particularly where spawning duration is protracted, it is likely that larvae will experience both upwelling and downwelling conditions. Accordingly, upwelling alone is unlikely to be responsible for the genetic divergence observed across this region. Detailed small spatial scale studies of oceanography and phylogeography and a more complete understanding of the consequences of larval behaviour are required if this hypothesis is to be adequately tested.

An alternative to upwelling as the cause of north-south subdivision on the east coast is the East Cape Current (ECC) and Wairarapa Eddy. The ECC flows from East Cape down the east coast of the North Island to approximately 42°S—the same latitude as the upwelling at the top of the South Island (cf. Fig. 1 and 3). At the southern limit of its flow, the ECC splits with some of its flow proceeding to the north-east while the remainder flows into and along the subtropical convergence (de Lange 2003; Laing & Chiswell 2003; Chiswell 2005). The transport of larvae from northern to southern populations on the east coast could be prevented if larvae carried south by the ECC are advected either back to the north or out across the Chatham Rise. Chiswell & Roemmich

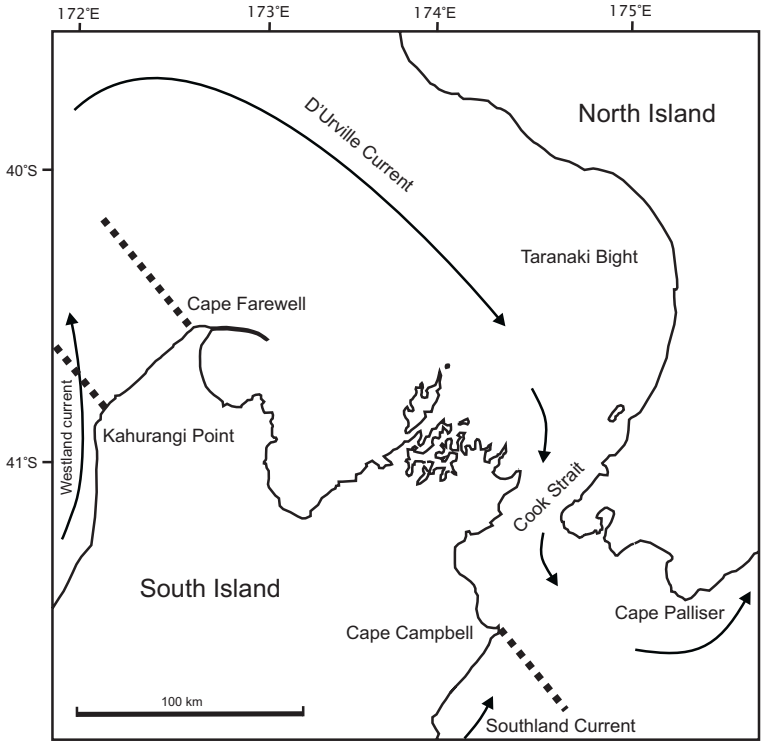

Fig. 3 The Cook Strait region (New Zealand) with major currents and locations of interest indicated (redrawn after Heath (1982) and Carter et al. (1998)). Dotted lines south of Cook Strait indicate the location of upwelling zones implicated in preventing larval transport between northern and southern populations (Apte & Gardner 2002).

(1998) simulated larval trajectories around the East Cape region and suggested that if larvae were passively drifting they could potentially be retained in the Wairarapa and East Cape eddies for up to 2–3 years. For taxa with short pelagic larval durations (e.g., *Cellana* spp., PLD 3–11 days; Goldstien et al. 2006), retention within an eddy even for a short time would probably be terminal as larvae reaching settlement maturity would not reach the required habitat within their larval life stage. Conversely, for *J. edwardsii* larvae which have a pelagic duration of over 12 months (Booth 1994), and for other species with long-lived pelagic larvae, retention in eddies or gyres could act to promote local recruitment.

On the west coast of the South Island there is little data to support the hypothesis that upwelling is a barrier to gene flow and a cause of divergence between northern and southern populations. The Westland Current generally flows in a northerly direction along the west coast of the South Island before merging with the D'Urville Current and moving into the South Taranaki Bight (Fig. 3; Heath 1982; de Lange et al. 2003; Laing & Chiswell 2003). The D'Urville Current sweeps into Cook Strait from the northwest, mixing with water from the Southland and East Cape currents before moving eastwards across Cook Strait and around Cape Palliser (Heath 1982). Upwelling does occur on the northwest coast between Kahurangi Point and Cape Farewell (Fig. 3), but is temporally variable in intensity and occurrence (Shirtcliffe et al. 1990). During upwelling, water is advected offshore with much of it moving northeast and into the D'Urville Current then Cook Strait (Bradford-Grieve et al. 1993). Rather than preventing the transport of larvae between southwestern populations and populations north of Cape Farewell, this hydrology may promote the mixing of larvae from the greater Cook Strait region, although the degree of larval transport likely varies with larval behaviour and PLD (Bradford-Grieve et al. 1993; Shanks & Brinks 2005). Indications of this mixing can be found in the genetic makeup of some Cook Strait populations where both northern and southern haplotypes are present (e.g., Veale 2007) or where differentiation among central New Zealand populations is small (e.g., Waters & Roy 2004).

East-west population differentiation

Of the 15 studies in which multiple populations were sampled on both east and west coasts of the North and South islands, divergent east and west coast populations were detected in four studies of

three species. These include the amphipod *P. lucasi* (Schnabel et al. 2000; Stevens & Hogg 2004) and the snakeskin chiton *S. pelliserpentis* (Veale 2007), in which North Island populations were distinct between coasts, and the seagrass *Z. muelleri* (Jones et al. 2008), in which distinct east and west coast populations were detected in both the North and South islands.

Upwelling at the top of the North Island (Roberts & Paul 1978) was suggested as a possible impediment for gene flow between coasts (Veale 2007). However, without detailed knowledge of local oceanography and larval characteristics, this kind of hypothesis should be treated with caution (Shanks & Brink 2005). It has also been hypothesised that east-west differentiation in the North Island is a consequence of the significant geological changes that New Zealand has undergone over the last 65 million years (Stevens & Hogg 2004). Marine intrusions during the upper Miocene and Pliocene may have turned what is now the North Island into an archipelago of smaller ephemeral islands (Fleming 1979; Stevens et al. 1995). East-west migration among populations would have been possible until sea level dropped, creating a barrier that physically separated populations. The few examples of east-west differentiation may relate to the timing with which species arrived in New Zealand and whether their population structure has been influenced by geological processes (Lamb & Avise 1992; Knowlton et al. 1993; Stevens & Hogg 2004). Alternatively, differences in population subdivision may relate to species-specific differences in ability to disperse across hydrodynamic features such as the north coast upwelling as suggested by Veale (2007) and/or the requirement for specific settlement habitats (e.g., estuaries; Stevens & Hogg 2004; Jones et al. 2008).

Small-scale population genetic structure

Few studies have detected population structure either within a region or along stretches of continuous coast. Where reported, it has largely been in studies designed specifically to test hypotheses at small spatial scales, with the majority being conducted in Fiordland. An exception is Veale's (2007) New Zealand-wide study in which microsatellite loci were used to examine the population genetics of the Waratah anemone *A. tenebrosa*. Seven regional *A. tenebrosa* subpopulations were described and an isolation-by-distance relationship among populations was attributed to the reproductive characteristics of the species (Veale 2007). As most comparable studies have used mtDNA, it is not possible to determine whether the finer-scale resolution attained in this study resulted from differences in the molecular marker used or life history characteristics of *A. tenebrosa*. Smith & McVeagh (2006) also used microsatellite markers and found significant geographic differentiation among populations of the abalone *Haliotis iris*. However, as only four locations were sampled, it was not possible to determine the spatial scale at which differentiation occurred.

Fiordland in the southwestern corner of the South Island is an ideal system for examining population connectivity as each fjord constitutes a discrete habitat isolated by geography and hydrology (Stanton & Pickard 1981, Lamare 1998, Gibbs 2001). As a consequence of extremely high rainfall in the region (up to 7 m per year), the fjords have a low salinity surface layer and two layer estuarine circulation (Stanton & Pickard 1981; Gibbs 2001). This circulation determines the degree to which larvae are physically transported within and among fjords (Lamare 1998; Metaxas 2001; Bilton et al. 2002; Wing et al. 2003). Depending on the life history characteristics of larvae, such as vertical positioning in the water column and tolerance to the low salinity outflowing surface waters, it is possible that larvae will be retained within the fjords, limiting connectivity among fjord populations (Lamare 1998).

Nine studies have examined phylogeography within Fiordland, detecting genetic differentiation at very small spatial scales (<50 m) for some species (e.g., the coral *Antipathes fiordensis*; Miller 1998), whereas other species such as the snake star (*Astrobrachion constrictum*; Steele 1999) with similar dispersal potential (i.e., PLD) showed little evidence of restricted larval exchange. Although all but one of these studies detected population subdivision either within or among the fjords, interpretation of phylogeographic patterns is complicated. For example, Skold et al. (2003) detected significant variation among fjord populations of *Coscinasterias muricata* using allozyme electrophoresis, but found no correlation between genetic structure and geographic distribution. In contrast, Perrin et al. (2004) analysed mtDNA of the same species at the same sites and detected an isolation-by-distance relationship among populations in the northern fjords and restricted gene flow between southern fjords particularly Long Sound.

In another study, populations of the urchin, *Evechinus chloroticus* clustered into two groups corresponding to inner and outer fjord environments (Perrin 2002). Inner fjord populations among fjords

were more similar to each other than were inner and outer populations within the same fjord. The same was so for outer fjord populations among fjords. Although often thought to be neutral (Schlotterer 2000), microsatellite loci may be under selection themselves or linked to DNA that is under selection (*sensu* Wright & Andolfatto 2008). If the loci used in the Perrin (2002) study were under selection, the observed genetic structure could reflect adaptation to and/or differential settlement/survival in sub-habitats within the fjords rather than patterns of connectivity among populations.

In the only study conducted on offshore islands, Wood & Gardner (2007) examined the genetic structure of two limpets (*Siphonaria raoulensis* and *Scutellastra kermadecensis*) endemic to the isolated Kermadec Islands. The assumption of self-recruitment was used to test hypotheses on connectivity among islands and to examine the scale over which self-recruitment occurs. Limited connectivity was observed among populations separated by less than 1 km, suggesting that larvae did not disperse or alternatively settle far from their population of origin (Wood & Gardner 2007).

Larval duration and phylogeographic structure

Some common patterns of geographical subdivision have emerged from New Zealand phylogeographic studies, yet patterns have not been consistent across taxa, suggesting that species-specific traits are likely to influence population genetic structure. Although it is known that larval behaviour interacts with hydrology to determine physical transport (e.g., Shanks & Brink 2005), the complexities of coastal oceanography have made it difficult to predict dispersal pathways and explain the observed differences in genetic structure. In many instances, estimates of PLD are available (e.g., Sponaugle et al. 2006), but there is no consensus as to how variation in the length of larval duration might determine the scale at which propagules disperse or the genetic structure of populations (Mayr 1954; Ehrlich & Raven 1969; Burton 1983; Scheltema 1986; Bohonak 1999; Bay et al. 2006; Bradbury et al. 2008; Miller & Ayre 2008).

For species with limited dispersal ability, it is expected that migration among subpopulations will be rare and subpopulations may diverge owing to genetic drift (Wright 1951). Conversely, for taxa with extended dispersal stages, gene flow among populations is expected to be high and populations genetically homogeneous (Wright 1951, Mayr 1954; Scheltema 1986). However, the relationship between early life history characteristics and genetic structure varies significantly among taxa (Bohonak 1999; Bay et al. 2006; Bradbury et al. 2006). Bohonak (1999) and Bradbury et al. (2008) compared estimates of genetic differentiation among species and reported inverse relationships between larval duration and genetic differentiation, suggesting that increased larval duration is associated with decreases in genetic structure. Moreover, Bradbury et al. (2008) in their analysis of 246 species that included echinoderms, molluscs, crustaceans and sea grasses, reported that genetic differentiation was more variable for species with limited larval duration.

To examine the relationship between larval duration and genetic differentiation in New Zealand, we considered the two most commonly used measures of population differentiation, F_{ST} (and PHI_{ST}) and Nei's genetic distance (D) (Nei 1972). F_{ST} and PHI_{ST} are measures of population differentiation with a maximum value of one indicating complete fixation of different alleles in each population (i.e., no gene flow), and a value of zero indicating an absence of subdivision, (i.e., high gene flow; Wright 1951). Despite controversy over the use of F-statistics as a measure of relative differentiation (Hedrick 1999, 2005; Neigel 2002; Palumbi 2003; Bradbury & Betzen 2007; Jost 2008), F_{ST} and its analogues are the measures of genetic differentiation most frequently used in population genetics and therefore the most readily incorporated into a multi-study analysis (e.g., Bohonak 1999; Bradbury et al. 2008).

Estimates of population differentiation (F_{ST} or PHI_{ST}) were available for 29 of the 42 New Zealand studies, with several studies presenting multiple values where a number of markers were analysed. Estimates based on mitochondrial DNA were corrected following the methods of Kinlan & Gaines (2003) to allow comparison with markers possessing biparental inheritance and diploid gene flow. Research has been conducted at a variety of spatial scales. Twenty-three studies included populations from across the entire length of New Zealand, whereas in the remaining 19 studies sampling was conducted regionally or restricted to specific locations. To test whether the geographical scale of sampling influenced genetic differentiation, we regressed F_{ST} against the latitudinal range of sampling in each study, and there was no significant effect of sampling scale on differentiation ($r^2 = 0.0042$, $P > 0.10$, $n = 29$).

In most studies, PLDs are provided (Table 1), although these estimates are generally based on laboratory rather than field studies, and in some instances are based on congeners or similar invertebrate

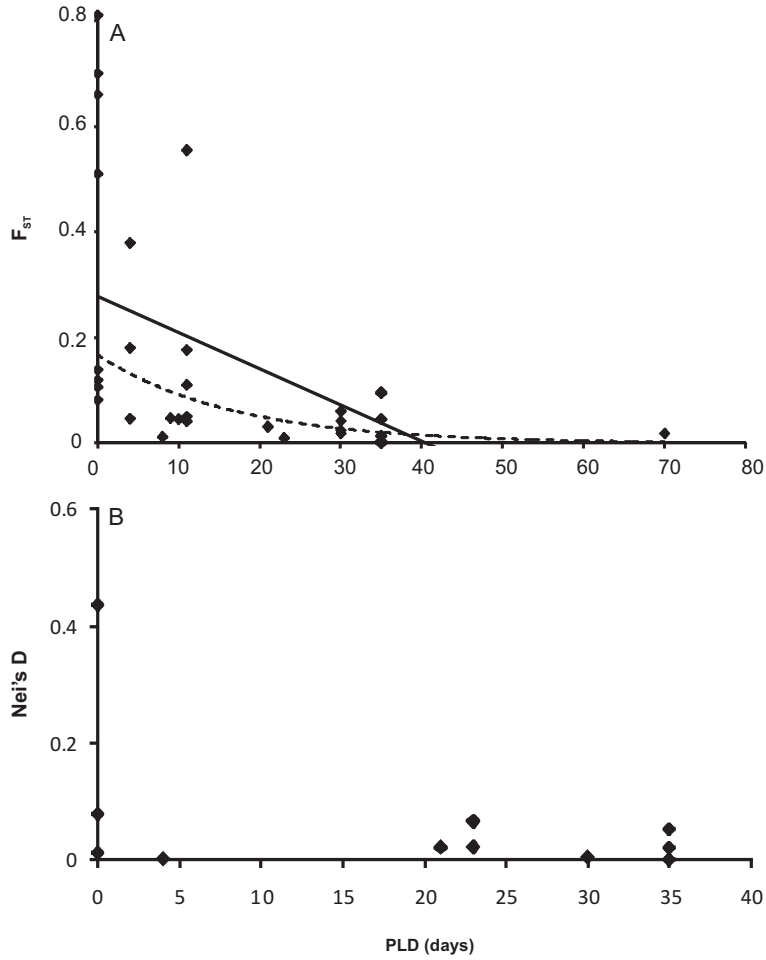

Fig. 4 Relationship between pelagic larval duration, PLD and: **A**, genetic differentiation (F_{ST} or PHI_{ST}; continuous line, $F_{ST} = -0.0068 \times PLD + 0.028$, $r^2 = 0.27$, $P < 0.01$, $n = 29$) and natural log transformed genetic differentiation (dashed line, $\ln(F_{ST}) = -0.0595 \times PLD - 1.785$, $r^2 = 0.39$, $P < 0.001$, $n = 29$); **B**, Nei's measure of genetic distance (D). Data from phylogeographic studies of New Zealand coastal benthos.

families (e.g., Wood & Gardner 2007). Where PLD is presented as a range (e.g., 20–30 days), the longest estimate (i.e., 30 days) was used in our analysis. A significant linear relationship between F_{ST} and PLD was observed ($r^2 = 0.27$, $P < 0.01$, $n = 29$; Fig. 4A) and a natural log transformation of F_{ST} values improved the fit ($r^2 = 0.39$ $P < 0.001$, $n = 29$; Fig. 4A).

Nei's measure of genetic distance was only available in 12 of the 42 reviewed studies. Although frequently used to construct phylogenetic trees, raw values are published infrequently. There was no significant relationship between Nei's D and PLD ($r^2 = 0.19$, $P > 0.10$, $n = 12$; Fig. 4B), although similar to F_{ST}, Nei's D was more variable for taxa with reduced PLDs, with the greatest genetic distances among populations recorded for taxa with limited larval durations.

Taxa with extended PLDs appear to be good dispersers with low levels of differentiation recorded among populations; for taxa with shorter PLDs, differentiation among populations is generally greater but highly variable. This result suggests that when PLD is short, other biological (e.g., larval behaviour and post-settlement dispersal) and physical (e.g., oceanographic) factors become more important in determining the scale of dispersal and population genetic structure. That similar relationships are found in more extensive analyses of the global literature (Bohonak 1999; Bradbury et al. 2008) suggests that the observed patterns are not biased by the small number of phylogeographic studies conducted in New Zealand, but represent a more general trend.

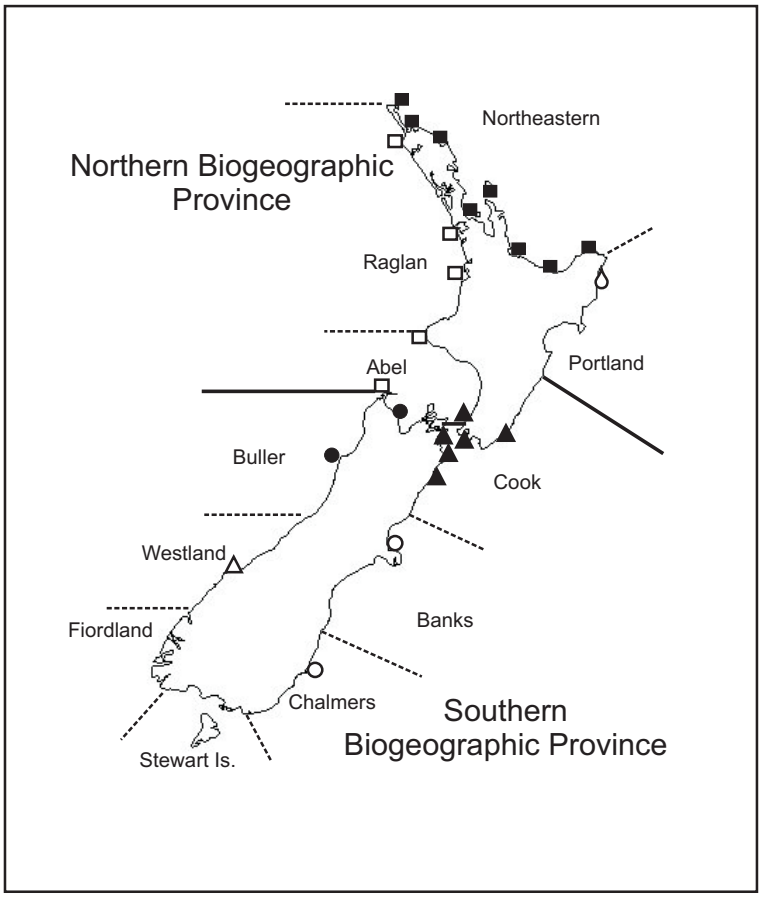

Fig. 5 *Actinia tenebrosa* population clusters (as defined by Veale (2007) based on data at four microsatellite loci) and biogeographic regions (as defined by Shears et al. (2008)). Dashed lines denote boundaries between bioregions; solid lines denote boundaries between bioprovinces (redrawn after Veale (2007) and Shears et al. (2008)).

Phylogeography versus biogeography

It is expected that the processes influencing the distribution of species (e.g., larval supply and environmental gradients) would also influence the genetic structure of populations through the regulation of gene flow or natural selection. Consequently it has been suggested that phylogeographic breaks may frequently coincide with biogeographic boundaries (Avise 1992, 1994). This hypothesis has been tested across a number of biogeographic boundaries, providing conflicting evidence for a close association between phylogeographic (divisions based on the geographical distribution of genetic variation) and biogeographic (divisions based on the geographical distribution of biodiversity) boundaries (e.g., Burton 1998; Lamb & Avise 1992; Knowlton et al. 1993). Consequently, it has been suggested that the different processes responsible for causing biogeographic breaks have varying impacts on the phylogeography of wide-ranging species and that the occurrence of phylogeographic breaks may be governed by the geological history of a region (Burton 1998).

Generally, the phylogeographic breaks evident in New Zealand species do not coincide with biogeographic boundaries (Moore 1949; Knox 1975; Nelson 1994; Walls 1995; Francis 1996; Shears et al. 2008). Differences in community composition have been consistently detected either at finer spatial scales or at different locations from the genetic breaks observed in populations of wide-ranging species (e.g., *P. canaliculus*). Biogeographic classification schemes based on the distribution of macroalgae, benthic invertebrates and reef fish have divided the New Zealand coast into between 2 and 11 biogeographic regions with the most recent scheme describing 11 bioregions falling within two bioprovinces (Shears et al. 2008). Seven of 28 New Zealand-wide phylogeographic studies found no population subdivision, 12 studies detected two genetically distinct subpopulations, 3 studies detected

three subpopulations, and a single study detected four distinct subpopulations. The almost ubiquitous disparity between phylogeographic structure and biogeographic classification schemes may relate to the molecular markers used, their differing rates of evolution, and suitability for detecting fine scale genetic structure (Wan et al. 2004; DeYoung & Honeycutt 2005; Anne 2006). Alternatively, the discrepancy may relate to differences in the processes responsible for structuring the species and population boundaries measured in phylo- and biogeography. Two phylogeographic studies did report genetic subdivision that more closely resembles the biogeographic classification scheme of Shears et al. (2008). Veale's (2007) examination of *A. tenebrosa* revealed seven regional subpopulations using microsatellite data. When the biogeographic divisions proposed by Shears et al. (2008) are overlayed on Veale's (2007) phylogeographic groupings, parallels between the two schemes are apparent with Veale's subpopulations falling within single or adjacent bioregions (Fig. 5). Jones et al. (2008) using random amplification of polymorphic DNA (RAPD) analysis of the seagrass *Z. muelleri* also found a similar agreement between phylogeography and biogeography albeit with fewer sampling locations.

CONCLUSIONS

Genetic divergences were identified across large spatial scales for several marine benthic taxa in New Zealand and may indicate regions across which dispersal is limited. Two areas of particular interest are the East Cape and the Cook Strait regions. Upwellings south of Cook Strait have been widely proposed as a barrier to larval transport. However, there are limited oceanographic data to support this hypothesis and few phylogeographic studies have had sufficient sampling resolution to adequately test it. Genetic divergences have also been detected between the east and west coasts on both the North and South islands and among offshore islands. The mechanisms responsible for generating and maintaining these divergences remain largely unknown. In contrast, the hydrology of Fiordland is well characterised which has aided in the interpretation of genetic patterns observed there.

The New Zealand taxa studied to date have predominantly been rocky reef dwellers. In many parts of New Zealand inter- and sub-tidal reefs occur either continuously along stretches of coast or in close proximity separated by stretches of sandy beach. Because of the small distances between suitable habitats, larvae may be able to move incrementally around the coast over successive generations and genetic divergences that could infer dispersal barriers may be masked by successive dispersal events. For organisms with specific habitat requirements (e.g., estuarine or island restricted species) occurring as discrete populations separated by greater distances, gene flow among populations is likely to be lower. These species are also more likely to exhibit the genetic effects of dispersal barriers and may be a useful target for future studies.

Different molecular markers can provide information at different temporal and spatial scales (Anne 2006). For example, fast evolving neutral markers are likely to provide information on breeding systems and/or gene flow among populations, whereas slower evolving markers may provide information about evolutionary relationships with other taxa. The selection of suitable molecular markers is therefore crucial for testing hypotheses at specific spatial or temporal scales and is likely to have influenced the phylogeographic patterns observed in New Zealand to date. The use of different markers has also hampered comparisons among studies, especially where there is uncertainty over the spatial and temporal scale of information provided by the specific markers (Anne 2006).

Studies of dispersal and/or population connectivity have generally used selectively neutral markers rather than genes that might reflect environmental gradients or transitions that drive shifts in community structure (e.g., Gardner & Kathiravetpillai 1997). However, the study of ecologically significant genes may further improve our understanding of population connectivity. Specifically, the capacity of individuals to disperse great distances is irrelevant if new recruits lack the ability to survive and reproduce in a new environment. Dispersal potential is therefore likely to be a function of both physical transport and biological suitability with the relative importance of each varying between locations. The identification and inclusion of ecologically significant genes (*sensu* Schmidt et al. 2008) in population genetic studies would help determine the role of genetic variation in adaptation to environmental heterogeneity and is also likely to provide insight into the relationship between biogeographic and phylogeographic boundaries.

Phylogeographic research can contribute to the management of the marine environment (Hauser & Carvalho 2008). Many marine ecosystems are threatened by human activities such as fishing,

coastal development and pollution, and resource managers are increasingly required to identify areas or habitats requiring protection (Himes 2007; Wood & Dragicevic 2007). Understanding population connectivity and subdivision would better allow for characterisation of population units for exploitation and/or conservation purposes. With few exceptions (e.g., *A. tenebrosa*), current knowledge of population connectivity and subdivision is inadequate to aid in management level decision making.

New Zealand with its variable and extensive coastal landscape is ideal for studying the processes that drive larval dispersal patterns and population genetic structure. However, much of the research to date has been characterised by haphazard sampling and *post hoc* speculation rather than driven by *a priori* hypotheses. Consequently, patterns of genetic subdivision have been identified while the processes responsible for generating them remain elusive. Future studies would benefit greatly from a more structured sampling regime and a multidisciplinary approach designed to test hypotheses driven by physical and biological oceanography. This approach would result in a better understanding of the processes generating population subdivision as well as factors responsible for recruitment, dispersal and population connectivity.

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