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A historical perspective of the genus *Mytilus* (Bivalvia: Mollusca) in New Zealand: multivariate morphometric analyses of fossil, midden and contemporary blue mussels

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The taxonomic status of smooth shelled blue mussels of the genus *Mytilus* has received considerable attention in the last 25 years. Despite this, the situation in the southern hemisphere remains uncertain and is in need of clarification. Recent work suggests that contemporary New Zealand mussels from two cool/cold temperate locations are *M. galloprovincialis*. However, the distribution of *Mytilus* in New Zealand ranges from 35 ° to 52 ° south (~ 1800 km), meaning that large areas of the subtropical/warm temperate north and the subantarctic south remain unsampled, an important consideration when species of this genus exhibit pronounced macrogeographical differences in their distributions which are associated with environmental variables such as water temperature, salinity, wave action and ice cover. This study employed multivariate morphometric analyses of one fossil, 83 valves from middens, and 92 contemporary valves from sites spanning the distributional range of blue mussels to determine a historical and contemporary perspective of the taxonomic status of *Mytilus* in New Zealand. The findings indicated that all fossil and midden mussels are best regarded as *M. galloprovincialis* and confirmed that contemporary mussels, with one possible regional exception, are also best regarded as *M. galloprovincialis*. Contemporary mussels from the Bay of Islands (warm temperate/subtropical) exhibited much greater affinity to *M. edulis* than they did to *M. galloprovincialis*, indicating that mussels from this area require detailed genetic examination to determine their taxonomic status. The analyses revealed a significant difference between the fossil/midden mussels and the contemporary mussels, consistent with levels of present day differentiation among intraspecific populations and not thought to reflect any substantive temporal change between mussels of the two groups. The continuous distribution of *M. galloprovincialis* in New Zealand from the warm north to the subantarctic south indicates that the physiology of this species is adapted to a wide range of water temperature conditions. Therefore, the distribution of this species on a worldwide scale is unlikely to be restricted by its adaptation to warm water alone, as has previously been widely assumed.

ADDITIONAL KEYWORDS: distribution – *Mytilus galloprovincialis* – shell trait variation – southern hemisphere.

INTRODUCTION

The taxonomy of marine mussels of the genus *Mytilus* has for a long time been complex and confused, with many different species and/or subspecies being recognized (reviewed by Soot-Ryen, 1955; Koehn, 1991; McDonald, Seed & Koehn, 1991). Much of the apparently speciose nature of the genus can be attributed to the phenotypic plasticity exhibited by mussels, such that gross morphological differences among populations often reflect the shell's response to environmental variability rather than genuine morphometric differences between taxa (i.e. species-specific genetic differences). The genus *Mytilus* is presently thought to include three species of smooth shelled blue mussel (*Mytilus edulis* Linnaeus, 1758; *M. galloprovincialis* Lamarck, 1819; *M. trossulus* Gould, 1850), and one species of blue mussel with radiating ribs on its shell, the sea mussel *M. californianus* Conrad, 1835, which is restricted in its distribution to the Pacific coast of the United States, extending from Baja California to

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Alaska (Seed, 1992; Coan, Valentich Scott & Bernard, 2000). The systematic status of *M. coruscus* Gould, 1861, a thick shelled, ribbed mussel with minute crenulations along the ventral margin close to the apex, is presently unclear (Seed, 1992), but given its distinctness from the smooth shelled mussels it is not considered here. The three extant smooth shelled species are now recognized on the basis of internal shell morphology, which has moderate discriminating power among the taxa (McDonald *et al*., 1991; Seed, 1992; Gardner, 1996), but more importantly through allozyme frequency differences, species-specific nuclear DNA markers, and the analysis of mitochondrial DNA restriction fragment length polymorphisms and the mitochondrial 16S rRNA gene (e.g. Seed, 1971; Skibinski, Cross & Ahmad, 1980; Skibinski, Beardmore & Cross 1983; Varvio, Koehn & Väinölä, 1988; McDonald *et al*., 1991; Heath, Rawson & Hilbish, 1995; Inoue *et al*., 1995; Beynon & Skibinski, 1996; Rawson *et al*., 1996; Martel *et al*., 1999; Apte *et al*., 2000; Hilbish *et al*., 2000).

Recently, the worldwide distributions of the three smooth shelled taxa have received considerable attention (McDonald & Koehn, 1988; Varvio *et al*., 1988; McDonald *et al*., 1991; Gosling, 1992; Hilbish *et al*., 2000). *M. trossulus* is confined to the northern hemisphere, and is found in the north Pacific, the northwest Atlantic, and the Baltic Sea. In the northern hemisphere, *M. edulis* is found in the north Atlantic, while *M. galloprovincialis* is found in the Mediterranean Sea, in the eastern north Atlantic, and in the north Pacific. However, the taxonomy of blue mussels in the southern hemisphere is still unclear and warrants further attention. Based on allozyme and shell morphometric differences, McDonald *et al*. (1991) suggested that *M. edulis*-like mussels occur in southern South America, the Falkland Islands, and the Kerguelen Islands (many mussels were intermediate between northern hemisphere *M. edulis, M. galloprovincialis* and *M. trossulus*, but on balance were considered to be more similar to *M. edulis*). McDonald *et al*. (1991) also suggested that *M. galloprovincialis* occurs in western and southern Australia, and throughout New Zealand (NZ), and a more recent analysis of the mitochondrial 16S rRNA gene has tended to confirm this interpretation (Hilbish *et al*., 2000).

The fossil record for *Mytilus* in NZ dates back a little over 1.0 Mya, to the early Castlecliffian (Sutherland, Nathan & Turnbull, 1995 with an appendix by A. G. Beu), and supports a Pleistocene (1.5–2.5 Mya) origin of *Mytilus* spp. in the southern hemisphere (Hilbish *et al*., 2000). While there are fossil deposits of *Mytilus* in NZ, the extraction of intact valves from these is usually impossible, the material crumbling as soon as it is freed from the surrounding matrix (J. P. A. Gardner, pers. observ. and A. Beu, pers. comm.) with the result that only one complete fossil valve of *Mytilus* is known from NZ (A. Beu, pers. comm.). *Mytilus* valves occur in abundance in Maori middens throughout NZ (B. F. Leach, pers. comm.). The fossil, midden and contemporary material was traditionally accepted as being *M. edulis* or *M. edulis aoteanus*, depending on the taxonomic thinking of the time (e.g. Soot-Ryen, 1955; Powell, 1958; Fleming, 1959; Morton & Miller, 1968). This was revised following a comparison between northern and southern hemisphere material which indicated that Australasian mussels (samples from Wellington Harbour (NZ), and western Australia and Tasmania) were very similar in allozyme allele frequencies and shell morphology to *M. galloprovincialis* from the northern hemisphere (McDonald *et al*., 1991). Most recently, an evaluation of the antitropical distribution of *Mytilus* indicated that samples of NZ mussels from Wellington Harbour (North Island) and Otago Harbour (South Island) were most closely related to North Atlantic *M. galloprovincialis*, were likely to be native, and were unlikely to have been recently introduced (Hilbish *et al*., 2000).

The present day distribution of *Mytilus* in NZ (Fig. 1) is from the Bay of Islands in the north (~ 35° south), as far south as Campbell Island (approx. 52° south), and includes remote offshore locations such as the Chatham Islands which are ~ 800 km to the east (Powell, 1955; Morton & Miller, 1968). This distribution spans 17 degrees of latitude (~ 1800 km), and encompasses subtropical/warm temperate, cold temperate and subantarctic waters. Typically, blue mussels are more common in the cooler south and are rare in the warmer, northern half of North Island (Powell, 1955; Morton & Miller, 1968; J. P. A. Gardner, pers. observ.). The most recent morphometric, allozyme, and molecular data (McDonald *et al*., 1991; Hilbish *et al*., 2000) suggest that blue mussels in NZ are *M. galloprovincialis*, but collecting for these studies was from only two locations (Wellington and Otago Harbours), which are located in cool and cold temperate regions, respectively. If the NZ blue mussel is indeed *M. galloprovincialis*, then this gives rise to a number of interesting questions, the answers to which may require a re-evaluation of some aspects of the environmental tolerance of the species.

This study employed multivariate analyses of fossil, midden and contemporary valves to provide a historical perspective on the taxonomic status of the genus *Mytilus* in NZ. The strength of this approach is that multivariate morphometric analyses can differentiate among taxa with reasonable accuracy (McDonald *et al*., 1991; Gardner, 1995, 1996), the approach is relatively quick and cheap, and, perhaps most impor-

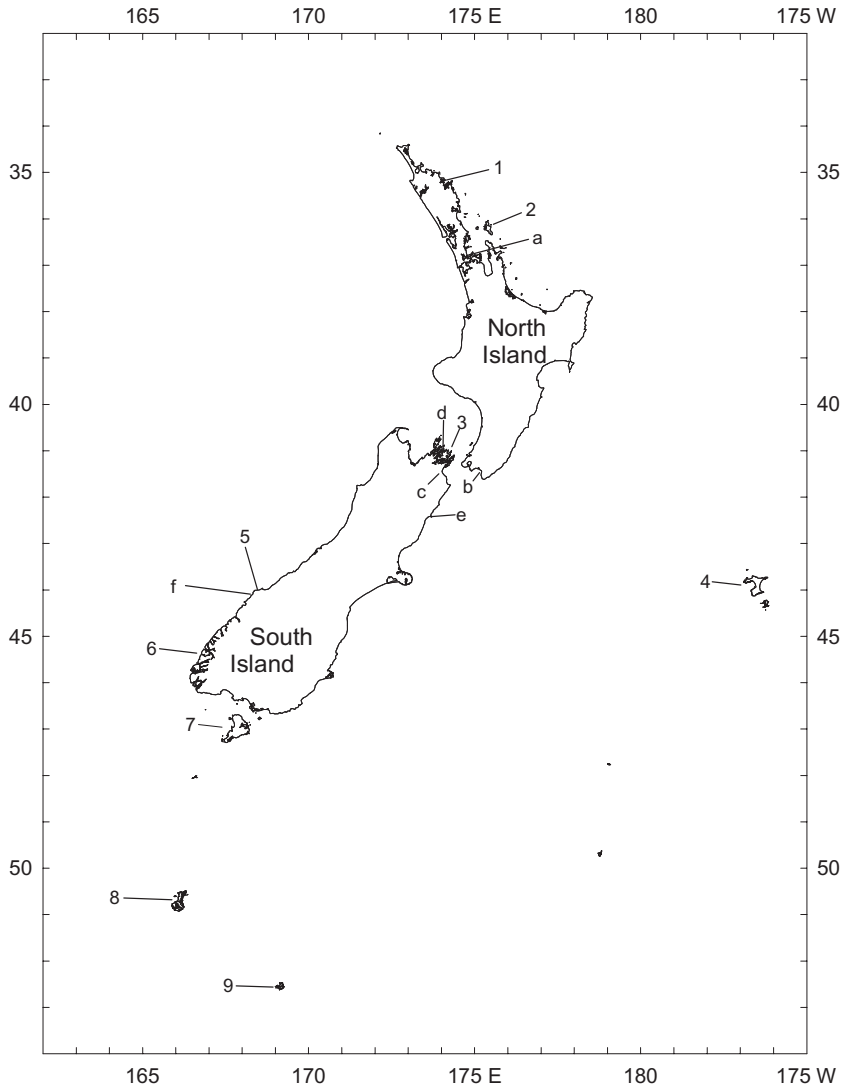

Figure 1. New Zealand sampling locations for mussel valves used in this study (a–f, midden and fossil material; 1–9, contemporary material). a, Motutapu Island; b, Washpool; c, Wairau Bar; d, Titirangi Island; e, Clarence River; f, Cascade Valley; 1, Bay of Islands (including Kerikeri Inlet and Poroporo Island); 2, Great Barrier Island; 3, Marlborough Sounds (including Anakiwa, Maud Island and Stephens Island); 4, Chatham Islands; 5, Jackson Bay; 6, Fiordland (including Caswell Sound, South Port – Chalky Inlet, Revolver Bay Head – Preservation Inlet, and Thompson Sound); 7, Stewart Island; 8, Auckland Islands; 9, Campbell Island.

tantly, it permits assessment of the status of material (fossil and midden) that predates the arrival of European sailing vessels, which were often vectors for the introduction of non-native taxa (Carlton & Hodder, 1995). Unfortunately, the morphometric approach cannot discriminate among taxa with as much power as can genetic techniques, with the result that findings are not unequivocal, and this may result in interpretation being, at times, speculative. However, because of the absence of tissue from ancient material in NZ, the discriminatory power of the genetic approach cannot be employed. Thus a historical perspective is solely dependent on a multivariate morphometric approach.

MATERIAL AND METHODS

Reference material

Samples of *M. edulis* (Lowestoft, eastern England; Caswell Bay, south Wales), *M. galloprovincialis* (Bude, south-west England; Grau d'Age, southern France), and *M. trossulus* (Tvärminne, Baltic Sea, Finland) from contemporary populations were measured to be

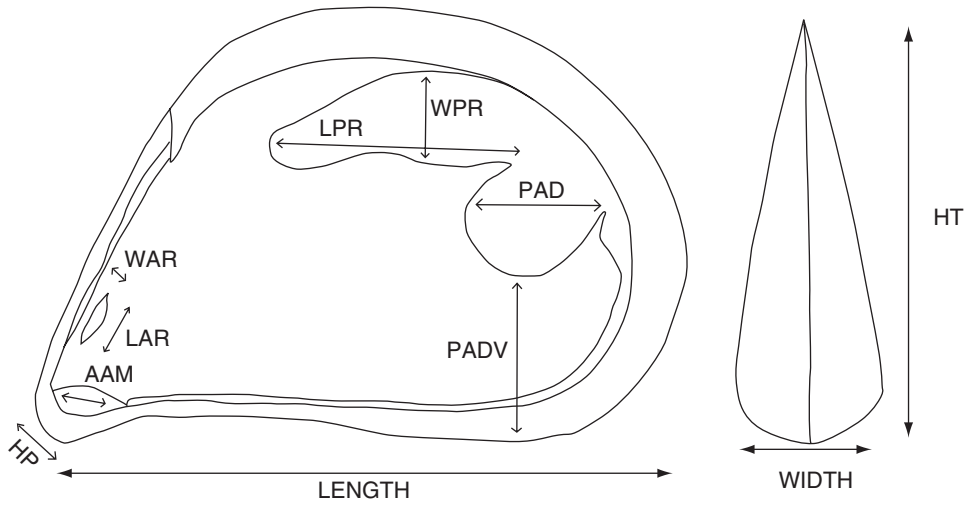

Figure 2. The ten shell traits which were measured (taken from Gardner, 1995). 1, AAM, length of anterior adductor muscle scar; 2, HP, length of hinge plate; 3, LAR, length of anterior retractor muscle scar; 4, WAR, width of anterior adductor muscle scar; 5, WPR, width of posterior retractor muscle scar; 6, LPR, length of posterior retractor muscle scar; 7, PAD, length of posterior adductor muscle scar; 8, PADV, distance between ventral edge of posterior adductor muscle scar and ventral shell margin; 9, HT, height of shell; 10, WID, width of shell.

used as reference material, against which the NZ material could be compared. The *M. edulis* and *M. galloprovincialis* populations are the same valves as those used by Gardner (1995), but all were remeasured for this work. A total of 147 reference valves were measured (see next section and Fig. 2).

New Zealand material

Valves from fossil, midden and contemporary populations were obtained from a number of different sources (Table 1; Fig. 1).

Fossil material

Only one fossil *Mytilus* valve is recorded from NZ (A. Beu, pers. comm.). It is dated to the Castlecliffian formation, 1.0–1.5 Mya. Because of its age, this valve is considered to be native to NZ.

Midden material

Valves were measured from five midden deposits, most of which predate the earliest arrival of European shipping in NZ (e.g. Abel Tasman in 1642 and James Cook in 1769). The five midden sites cover much of the North Island and part of the South Island, from Motutapu Island in the Hauraki Gulf, to Clarence River on the Kaikoura Peninsula (Fig. 1). The dates for this material refer to the specific layer within each site, and are conventional radiocarbon ages (CRA) expressed in ybp, where 'present' for ^{14}C dates is 1950. To convert a CRA to calendrical years requires correction for secular effects in the case of floral carbon from the land and a stated value of delta R for marine samples (B. F. Leach, pers. comm.). The important point to remember is that most of the material predates the arrival of European shipping; these valves are assumed to represent native NZ mussels. A total of 83 left valves from middens were measured.

Contemporary material

Valves from 19 locations which are either geographically isolated (e.g. the Auckland Islands, the Chatham Islands) or on islands which are removed from modern ports were measured. The collection sites covered the range of the genus in NZ, from the Bay of Islands to Campbell Island (Fig. 1). Because this material is contemporary (< 100 years old) there exists the possibility that it is not native, but has been recently and accidentally introduced to NZ. However, this seems unlikely given the isolated locations from which the material was collected. A total of 92 valves was measured.

Valve measurements

The left valve of each mussel was measured for shell length and ten morphometric traits (Fig. 2) that have been used extensively in studies of morphometric variation among the taxa (e.g. Skibinski, 1983; Beaumont, Seed & Garcia-Martinez, 1989; McDonald *et al*., 1991; Gardner, 1995, 1996). Characters were measured using vernier calipers accurate to 0.01 mm or using a stereomicroscope fitted with a calibrated eyepiece. Each of the ten traits is partially diagnostic for differences among the taxa on a worldwide scale (McDonald

Table 1. Details of the sites of collection, age of material, and present location of material

Location	Number of valves	Approx. date of material	Comments & source of material
Reference material			
Caswell Bay, south Wales	30	1988	*Mytilus edulis* (JPAG)
Lowestoft, eastern England	28	1990	*Mytilus edulis* (JPAG)
Bude, south-west England	30	1988	*Mytilus galloprovincialis* (JPAG)
Grau d'Age, southern France	30	1990	*Mytilus galloprovincialis* (JPAG)
Tvärminne, Baltic Sea, Finland	29	1989	*Mytilus trossulus* (JPAG)
NZ fossil material			
Cascade Valley, south Westland	1	1–1.5 Mybp	Early to mid Castlecliffian (IGNS)†
NZ midden material*			
Clarence River, Kaikoura	3	500–1000 ybp	(NMNZ)
Motutapu Island, Hauraki Gulf	52	200–350 ybp	Station Bay Pa (NMNZ)
Titirangi, Marlborough Sounds	25	700 ybp	Titi Mound (NMNZ)
Wairau Bar, Cloudy Bay	1	200–650 ybp	(NMNZ)
Washpool, Wairarapa	2	770 ybp	Makotukutuku river mouth (NMNZ)
NZ contemporary material			
Anakiwa, Marlborough Sounds	3	No date‡	(IGNS)
Auckland Islands	4	1942	Musgrove Peninsula, Auckland Islands (IGNS)
Auckland Islands	4	1927	Port Ross (NMNZ)
Campbell Island	6	1947	Cast ashore, Shoal Point (NMNZ)
Campbell Island	1	1975	Intertidal, Meteorological Stn and Lookout Point (NMNZ)
Chatham Islands	5	1983	Rangiriri Beach, Kaingaroa (NMNZ)
Chatham Islands	5	2000	Cast ashore, Blind Jim's Creek (JPAG)
Chatham Islands	1	2000	Port Hutt, Whangaroa Harbour (JPAG)
Fiordland	2	1995	Caswell Sound (NMNZ)
Fiordland	3	1996	South Port, Chalky Inlet (NMNZ)
Fiordland	8	1996	Revolver Bay Head, Preservation Inlet (NMNZ)
Fiordland	1	1995	Thompson Sound (NMNZ)
Great Barrier Island, Hauraki Gulf	7	1938	Port Fitzroy, Gt Barrier Island (NMNZ)
Jackson Bay, Westland	1	1964	(IGNS)
Kerikeri Inlet, Bay of Islands	2	1982	(NMNZ)
Maud Island, Marlborough Sounds	20	2000	(JPAG)
Poroporo Island, Bay of Islands	1	1980	(IGNS)
Stephens Island	8	1995	(JPAG)
Stewart Island	10	1972	Disappointment Cove, Port Pegasus (NMNZ)

*These dates are conventional radiocarbon ages expressed in years before present and relate to the specific layer from which the valves were collected, not the age of the site itself. †GS 12290, National Fossil Record No. E38/f15, collected by A. G. Beu, S. Nathan and I. M. Turnbull from the large boulders of Teer Formation in Whiskey Creek, north coast of Cascade Point, south Westland, between Teer Creek and the 'giant slip', grid ref. E38/448788 (Sutherland *et al*., 1995). ‡Material from collection of Sir Charles Fleming now held at IGNS NZ (A. Beu, pers. comm.) (IGNS) = material held in the collection of The Institute of Geological and Nuclear Sciences, Gracefield, Lower Hutt, NZ; (JPAG) = material held in the personal collection of Jonathan P. A. Gardner, Victoria University, Wellington, NZ; (NMNZ) = material held in the collection of The National Museum of NZ Te Papa Tongarewa, Wellington, NZ. NZ = New Zealand.

et al., 1991) and reflects the underlying genetic differentiation among the taxa.

Measurement error

Of the 323 valves that were measured, 24 were selected at random (via a random number table) and were re-measured for all ten traits and shell length without reference to the original measurements. For each of the 11 traits, an individual's first measurement was subtracted from its second measurement (the re-measure) and the mean of the difference for each trait was calculated. A *t*-test comparison was employed to test the hypothesis that the mean was

equal to zero. Bonferroni adjustment was employed to correct for multiple testing (adjusted $\alpha = 0.05/11 = 0.0045$), and in the event that the mean of the measures minus the re-measures was not equal to zero, then that trait was dropped from subsequent analyses.

Statistical analyses

Data analysis was carried out using Statistica (v. 6.0) software (StatSoft, 1994). Each trait value was divided by shell length to standardize for size (e.g. McDonald *et al*., 1991; Gardner, 1995). Principal component analysis (PCA), which can be thought of as a data reduction method, was employed to examine the relationships between individuals' multivariate morphometric variation and their population of origin. PCA summarizes multivariate information (in this case the ten shell traits) and permits the detection of structure in the relationships among variables. That is, PCA is a classification technique. When principal component Factor 2 (Factor 2) is plotted as a function of Factor 1, individual points in 2D space summarize multitrait variation, and when these points are close together they are more similar morphometrically to one another than are points which are far apart. In such a case, two separate clusters of points can therefore be thought of as two populations, each displaying low within-population variation, but high between-population variation.

A number of separate analyses were employed to test the various null hypotheses. The approach taken was to use PCA to determine the extent of multivariate separation among reference taxa and among the NZ populations. Where appropriate, one-way analysis of variance (ANOVA) was used to test for differences in group mean factor scores, and when a significant result was observed, Tukey's HSD posthoc test for unequal sample size was used to find the location of this difference. Discriminant function analysis (DFA) was used to calculate the Mahalanobis distance between pairs of populations or groups, and to determine what per cent of each population could be correctly assigned to their population of origin (= observed classification). For the purposes of the DFA, the single fossil individual had to be reclassified as belonging to the midden group.

Six analyses were carried out to permit the testing of the following null hypotheses:

Analysis No. 1: H_0 = Multi-trait variability cannot discriminate among the three taxa. Although the alternate hypothesis is clearly supported (e.g. McDonald *et al*., 1991; Gardner, 1995, 1996), this hypothesis was tested here to demonstrate that the reference material used in this study could discriminate among the three taxa, and therefore that comparisons of NZ material with the reference material were meaningful. This and subsequent analyses involving the inclusion of NZ mussel populations with all five reference populations indicated that the *M. trossulus* population always clustered in a separate group away from all other reference and NZ populations. Because of this, and to permit the PCA to focus more specifically on the taxa of interest (*M. edulis* and *M. galloprovincialis*), the *M. trossulus* population was dropped from all subsequent analyses.

Analysis No. 2: H_0 = NZ fossil and midden material is not similar to either *M. edulis* or *M. galloprovincialis*.

Analysis No. 3: H_0 = NZ contemporary material is not similar to either *M. edulis* or *M. galloprovincialis*.

Analysis No. 4: H_0 = NZ contemporary material from the Bay of Islands is not similar to either *M. edulis* or *M. galloprovincialis*. As part of Analysis 3 each separate NZ contemporary population was tested in turn with the reference *M. edulis* and *M. galloprovincialis* populations to clarify the NZ population's relationship to these taxa (data not shown). Arising from this, a more detailed examination of material from the far north of NZ was required, so a PCA and a DFA were conducted to examine multitrait variability among the reference populations and among contemporary material from the Bay of Islands.

Analysis No. 5: H_0 = NZ fossil, midden and contemporary material is not similar to either *M. edulis* or *M. galloprovincialis*.

Analysis No. 6: H_0 = NZ fossil, midden and contemporary material is not similar. Following analysis 5, a more detailed examination of contemporary, midden, and fossil material was required, so a PCA was conducted to examine multitrait variability among these three NZ groupings.

RESULTS

Measurement error

After correction for multiple testing all means were not significantly different from zero, and therefore all traits were retained in subsequent analyses.

Statistical analysis: testing the null hypotheses

Analysis No. 1a: H_0 = Multi-trait variability cannot discriminate among the three taxa. Multi-trait morphometric variation among individuals of the five reference populations was sufficient to permit identification of taxon-specific clusters (Fig. 3A). The *M. trossulus* cluster was distinct, whereas there was some degree of overlap between the *M. edulis* and

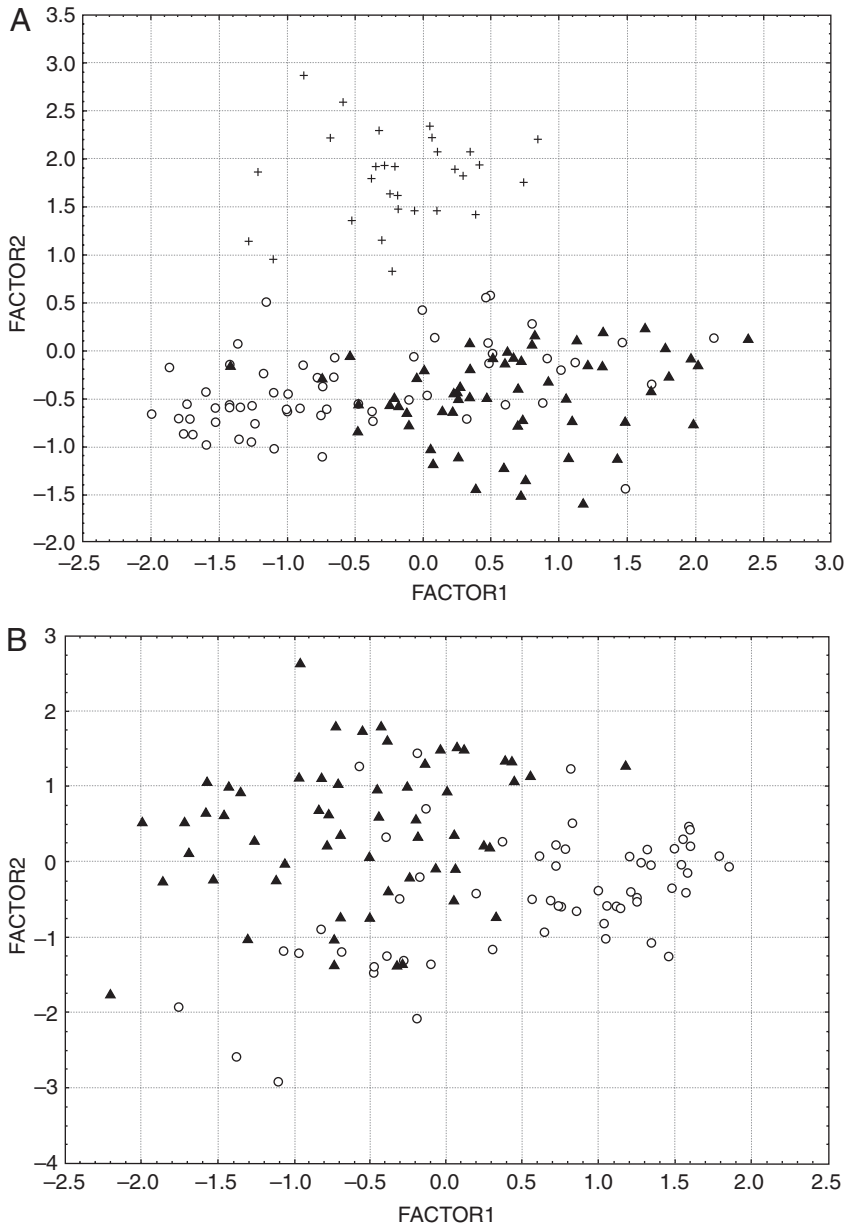

Figure 3. Principal component analysis: Factor 2 as a function of Factor 1, with the per cent value of the total variation that the plot represents. A, *Mytilus edulis* (▲), *M. galloprovincialis* (○), *M. trossulus* (+) (92.1%); B, *M. edulis* (▲), *M. galloprovincialis* (○) (49.9%); C, *M. edulis* (▲), *M. galloprovincialis* (○), NZ fossil (■), NZ middens (+) (45.0%); D, *M. edulis* (▲), *M. galloprovincialis* (○), NZ contemporary mussels (+) (54.5%); E, *M. edulis* (▲), *M. galloprovincialis* (○), NZ Bay of Islands mussels (+) (49.4%); F, *M. edulis* (▲), *M. galloprovincialis* (○), NZ fossil (■), NZ middens (∗), NZ contemporary mussels (+) (50.5%); G, NZ middens (○), NZ fossil (■), NZ contemporary mussels (+) (46.8%).

M. galloprovincialis clusters. Eight of ten pairwise comparisons of mean Factor 1 scores, and six of ten comparisons of mean Factor 2 scores were statistically significant (Table 2). DFA revealed that 91.8% of the mussels could be classified correctly according to population of origin (Table 3). Highly significant differences ($P < 0.001$ in all cases) were observed among populations as determined by Mahalanobis distance estimates (Table 4). The results of the PCA and the DFA indicated that these techniques can separate and identify with accuracy mussels of the different taxa, despite the existence of some overlap between the *M. edulis* and *M. galloprovincialis* clusters (Fig. 3A).

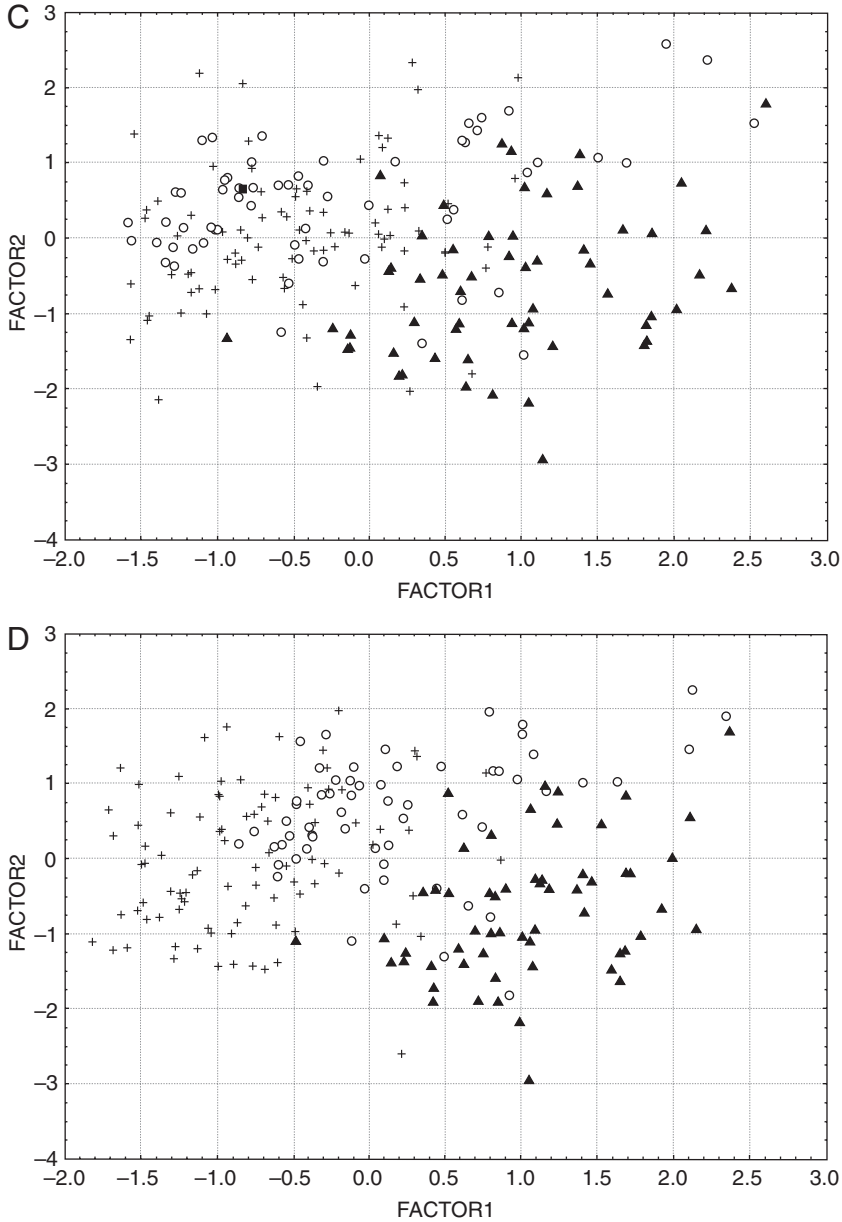

Figure 3. *Continued*

Analysis No. 1b: H_0 = There is no difference in multi-trait variability among the *M. edulis* and *M. galloprovincialis* populations. Multi-trait variation among the two *M. edulis* and two *M. galloprovincialis* reference populations revealed taxon-specific clusters with some degree of overlap (Fig. 3B). Five of six pair-wise comparisons of mean Factor 1 scores, and three of six comparisons of mean Factor 2 scores were significant ($P < 0.05$) (Table 2). DFA revealed that a total of 91.5% of the mussels could be classified correctly according to population of origin (Table 3). Highly significant differences ($P < 0.001$ in all cases) were observed among populations as determined by Mahalanobis distance estimates (Table 4). The results of the PCA and the DFA indicated that these techniques can separate and accurately identify mussels of the two taxa, despite the existence of some overlap between them.

Analysis No. 2: H_0 = NZ fossil and midden material is not similar to either *M. edulis* or *M. galloprovincialis*. PCA indicated that the fossil and midden material formed a cluster which showed considerable similarity to the *M. galloprovincialis* cluster, and was reasonably

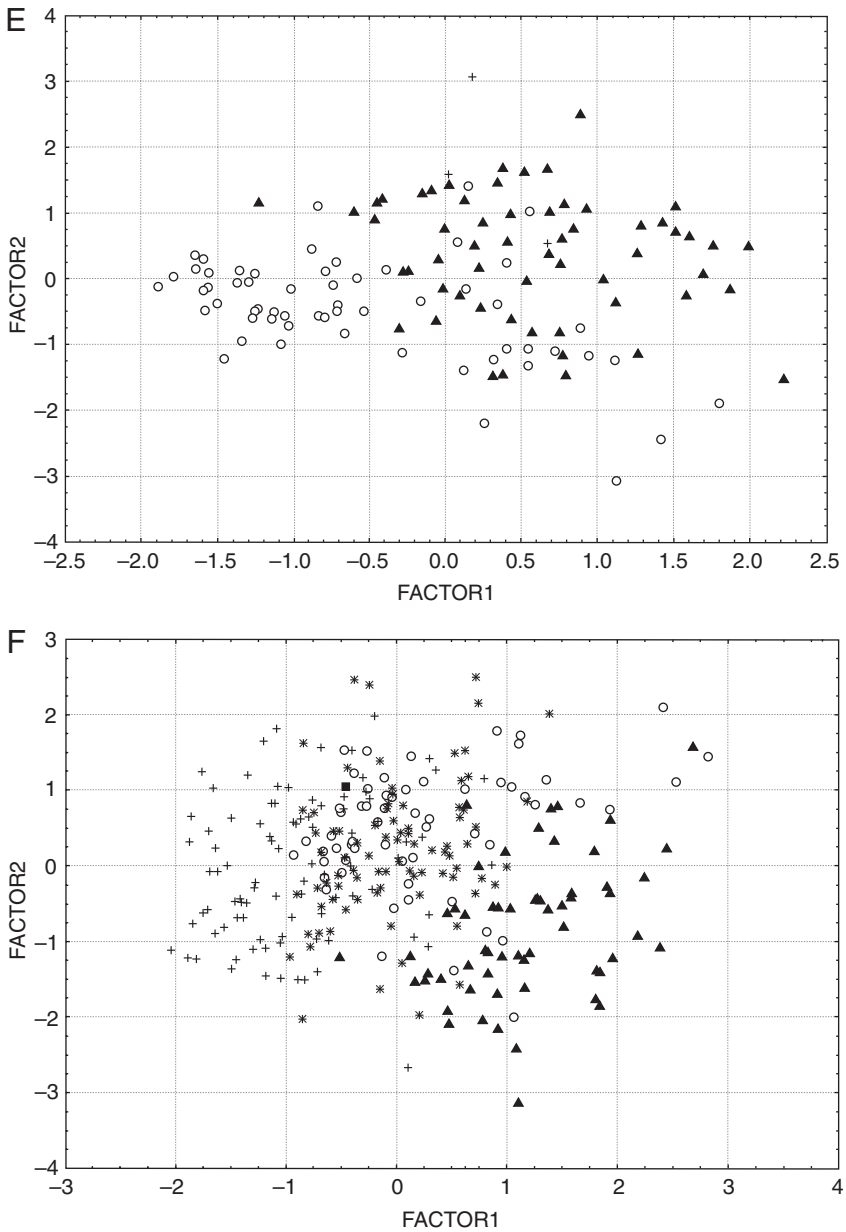

Figure 3. *Continued*

distinct from the *M. edulis* cluster (Fig. 3C). Testing of among-group variability revealed two significant differences in mean Factor 1 (*M. edulis* vs. *M. galloprovincialis*, $P < 0.0001$; *M. edulis* vs. NZ Middens, $P < 0.0001$) and in mean Factor 2 (*M. edulis* vs. *M. galloprovincialis*, $P < 0.0001$; *M. edulis* vs. NZ Middens, $P < 0.0007$) scores. The single NZ fossil valve was non-significantly different for mean Factor 1 and 2 scores from all other groups in this analysis. DFA indicated that a total of 86.1% of mussels could be classified correctly according to population or group of origin (Table 3) with the majority of 'misclassifications' involving the *M. galloprovincialis* and the NZ midden mussels being incorrectly assigned to each others' group. Mahalanobis distance estimates were all highly significant, but emphasized the similarity between the *M. galloprovincialis* and the NZ midden mussels, and the difference between these two groups and the reference *M. edulis* mussels (Table 4).

Analysis No. 3: H_0 = NZ contemporary material is not similar to either *M. edulis* or *M. galloprovincialis*. PCA revealed three overlapping clusters of points, with the *M. edulis* group exhibiting the highest and

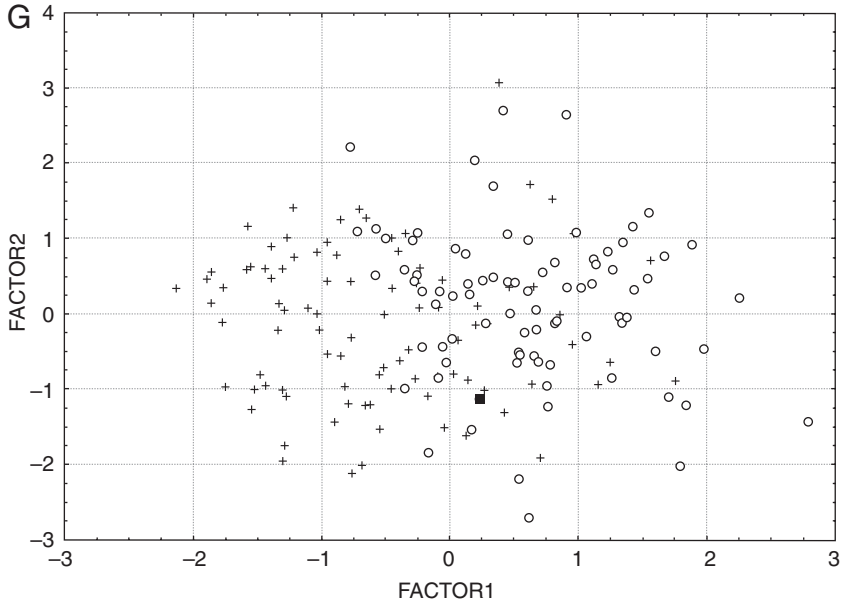

Figure 3. *Continued*

the NZ contemporary group exhibiting the lowest mean Factor 1 scores (Fig. 3D). All pairwise comparisons were significantly different for mean Factor 1 and mean Factor 2 scores ($P < 0.0001$ in all cases) (Table 3). DFA was able to classify correctly a total of 93.3% of all mussels (Table 3), and Mahalanobis distance estimates revealed that the reference *M. galloprovincialis* and *M. edulis* groups were more similar to one another than either was to the NZ contemporary group. The PCA and DFA results indicated that the NZ contemporary material is much more similar to *M. galloprovincialis* than it is to *M. edulis*.

Analysis No. 4: H_0 = NZ contemporary material from the Bay of Islands is not similar to either *M. edulis* or *M. galloprovincialis*. PCA revealed that most of the triangular grouping of the three Bay of Islands mussels fell within the *M. edulis* grouping and outside the *M. galloprovincialis* grouping (Fig. 3E). The reference *M. galloprovincialis* and *M. edulis* mussels were significantly different in mean Factor 1 and Factor 2 scores ($P < 0.0002$ in both cases). The Bay of Islands mussels were non-significantly different from the *M. galloprovincialis* ($P = 0.421$) and the *M. edulis* ($P = 0.902$) samples in terms of mean Factor 1 scores, and were non-significantly different from the *M. edulis* ($P = 0.145$) but significantly different from the *M. galloprovincialis* ($P < 0.008$) in terms of mean Factor 2 scores (Table 2). DFA was able to classify correctly a total of 93.4% of all mussels, including 100% of the mussels from the Bay of Islands (Table 3). Mahalanobis distance estimates were lowest for the *M. edulis* vs. *M. galloprovincialis* comparison, and highest for the Bay of Islands vs. *M. galloprovincialis* comparison (Table 4).

Analysis No. 5: H_0 = NZ fossil, midden and contemporary material is not similar to either *M. edulis* or *M. galloprovincialis*. PCA revealed considerable overlap among the clusters, with the single fossil valve falling within three of the four clusters (Fig. 3F). Post-hoc tests revealed five of ten pairwise comparisons to be non-significantly different for mean Factor 1 scores, and six of ten pairwise comparisons to be non-significantly different for mean Factor 2 scores (Table 2). The single NZ fossil valve accounted for four of the five (for Factor 1) and four of the six (for Factor 2) non-significant results. DFA revealed that a total of 83.7% of all mussels could be classified correctly according to population or group of origin (Table 3). Misclassification rates were greatest among the *M. galloprovincialis*, NZ contemporary and NZ midden groupings, reflecting their considerable similarity. Mahalanobis distance estimates revealed greatest similarity between the NZ contemporary and NZ midden groups, and greatest dissimilarity between the reference *M. edulis* group and all other material (Table 4). These analyses confirmed the outcomes of Analyses 2 and 3, namely that NZ material is much more similar to *M. galloprovincialis* than it is to *M. edulis*, but also revealed a degree of dissimilarity between the NZ contemporary and the NZ midden mussels.

Analysis No. 6: H_0 = NZ fossil, midden and contemporary material is not similar. PCA revealed a cluster of points with higher Factor 1 scores (NZ midden mus-

Table 2. Mean (SD) scores for Factors 1 and 2 derived from principal component analysis, and results of posthoc Tukey's HSD for unequal sample sizes which was used to identify the location of significant differences among mean scores

Analysis	Groups or populations in analysis	*N*	Mean (SD) Factor 1	Mean (SD) Factor 2
1a	Bude (*M. galloprovincialis*)	30	0.31 (0.81)^{A}	–0.27 (0.46)^{AD}
	Caswell (*M. edulis*)	30	0.19 (0.60)^{AB}	–0.66 (0.44)^{B}
	Grau d'Age (*M. galloprovincialis*)	30	–1.36 (0.34)	–0.55 (0.33)^{ABC}
	Lowestoft (*M. edulis*)	28	1.11 (0.63)	–0.28 (0.39)^{CD}
	Tvärminne (*M. trossulus*)	29	–0.18 (0.53)^{B}	1.80 (0.47)
1b	Bude (*M. galloprovincialis*)	30	–0.16 (0.71)^{A}	–0.64 (1.08)^{A}
	Caswell (*M. edulis*)	30	–0.08 (0.46)^{A}	0.27 (0.95)^{BC}
	Grau d'Age (*M. galloprovincialis*)	30	1.29 (0.31)	–0.25 (0.48)^{AB}
	Lowestoft (*M. edulis*)	28	–1.12 (0.54)	0.66 (0.89)^{C}
2	*M. edulis*	58	0.93 (0.74)^{B}	–0.60 (0.97)^{A}
	M. galloprovincialis	60	–0.23 (1.02)^{AC}	0.50 (0.83)^{B}
	NZ fossil	1	–0.84 (–)^{BCD}	0.66 (–)^{ABC}
	NZ middens	83	–0.47 (0.66)^{AD}	0.05 (0.92)^{C}
3	*M. edulis*	58	1.04 (0.58)	–0.65 (0.90)
	M. galloprovincialis	60	0.21 (0.75)	0.63 (0.81)
	NZ contemporary	92	–0.80 (0.59)	0.00 (0.91)
4	*M. edulis*	58	0.58 (0.72)^{A}	0.38 (0.92)^{A}
	M. galloprovincialis	60	–0.57 (0.93)^{B}	–0.46 (0.81)
	NZ Bay of Islands	3	0.28 (0.34)^{AB}	1.73 (1.27)^{A}
5	*M. edulis*	58	1.18 (0.65)^{E}	–0.82 (0.91)^{F}
	M. galloprovincialis	60	0.28 (0.86)^{AD}	0.52 (0.81)^{BE}
	NZ fossil	1	–0.45 (–)^{BCDE}	1.05 (–)^{CDEF}
	NZ middens	83	–0.01 (0.55)^{AC}	0.21 (0.93)^{ABD}
	NZ contemporary	92	–0.91 (0.65)^{B}	–0.02 (0.93)^{AC}
6	NZ fossil	1	0.23 (–)	–0.13 (0.99)^{BC}
	NZ middens	83	0.62 (0.74)	0.16 (1.00)^{AB}
	NZ contemporary	92	–0.57 (0.87)	–0.13 (0.99)^{AC}

Analysis No. 1: H_0 = Multi-trait variability cannot discriminate among the three taxa. Analysis No. 2: H_0 = NZ fossil and midden material is not similar to either *M. edulis* or *M. galloprovincialis*. Analysis No. 3: H_0 = NZ contemporary material is not similar to either *M. edulis* or *M. galloprovincialis*. Analysis No. 4: H_0 = NZ contemporary material from the Bay of Islands is not similar to either *M. edulis* or *M. galloprovincialis*. Analysis No. 5: H_0 = NZ fossil, midden and contemporary material is not similar to either *M. edulis* or *M. galloprovincialis*. ANOVA posthoc comparisons of means were carried out using Tukey's HSD test for unequal sample sizes. Means which were NOT significantly different ($P > 0.05$) are marked by superscript alphanumeric codes. For example, in Analysis No. 1a, comparison of mean Factor 2 scores, ^{A} indicates that Bude is not significantly different from Grau d'Age, ^{B} indicates that Caswell is not significantly different from Grau d'Age, ^{C} indicates that Grau d'Age is not significantly different from Lowestoft, and ^{D} indicates that Bude is not significantly different from Lowestoft. All other pairwise comparisons are significantly different. NZ = New Zealand.

sels) that overlapped with a cluster of points with lower Factor 1 scores (NZ contemporary mussels). The single fossil mussel fell more or less equally between the clusters (Fig. 3G). The NZ contemporary and NZ midden mussels were highly significantly different in terms of their respective mean Factor 1 scores, but were not significantly different in their mean Factor 2 scores (Table 2). DFA indicated that 90.9% of all mussels were classified correctly according to their group (Table 3), and the Mahalanobis distance estimate of 7.44 was highly significant (Table 4). These results indicate that significant morphometric differences exist between NZ contemporary and NZ midden and fossil mussels of the genus *Mytilus*.

DISCUSSION

The material used in this study represents a haphazard subset of NZ blue mussel valves. The material was collected from sites spanning nearly 2000 km along a north–south axis, and from different time periods spanning hundreds (midden populations) to tens (contemporary populations) of years. The collections were made by different people, sometimes from the same

Table 3. Percentage of mussels of each population or grouping identified correctly by discriminant function analysis

Analysis	Groups or populations in analysis	*N*	% classified correctly
1a	Bude (*M. galloprovincialis*)	30	76.7
	Caswell (*M. edulis*)	30	93.3
	Grau d'Age (*M. galloprovincialis*)	30	100.0
	Lowestoft (*M. edulis*)	28	89.3
	Tvärminne (*M. trossulus*)	29	100.0
	Total	147	91.8
1b	Bude (*M. galloprovincialis*)	30	76.7
	Caswell (*M. edulis*)	30	96.7
	Grau d'Age (*M. galloprovincialis*)	30	100.0
	Lowestoft (*M. edulis*)	28	92.9
	Total	118	91.5
2	*M. edulis*	58	96.6
	M. galloprovincialis	60	68.3
	NZ middens	84	91.2
	Total	202	86.1
3	*M. edulis*	58	94.8
	M. galloprovincialis	60	83.3
	NZ contemporary	92	98.9
	Total	210	93.3
4	*M. edulis*	58	96.7
	M. galloprovincialis	60	90.0
	NZ Bay of Islands	3	100.0
	Total	121	93.4
5	*M. edulis*	58	93.1
	M. galloprovincialis	60	61.7
	NZ middens	84	83.3
	NZ contemporary	92	92.4
	Total	294	83.7
6	NZ middens	84	88.1
	NZ contemporary	92	93.5
	Total	176	90.9

Analysis No. 1: H_0 = Multi-trait variability cannot discriminate among the three taxa. Analysis No. 2: H_0 = NZ fossil and midden material is not similar to either *M. edulis* or *M. galloprovincialis*. Analysis No. 3: H_0 = NZ contemporary material is not similar to either *M. edulis* or *M. galloprovincialis*. Analysis No. 4: H_0 = NZ contemporary material from the Bay of Islands is not similar to either *M. edulis* or *M. galloprovincialis*. Analysis No. 5: H_0 = NZ fossil, midden and contemporary material is not similar to either *M. edulis* or *M. galloprovincialis*. For the discriminant function analysis the fossil valve was included with the midden material.

general locations, but at different times. The material examined was therefore, in effect, an unbiased sample covering the full distributional range of this genus in NZ.

The NZ midden material was significantly different from contemporary northern hemisphere *M. galloprovincialis* and *M. edulis*, but the midden material was far more similar to *M. galloprovincialis* than it was to *M. edulis* (*M. edulis* was significantly different from *M. galloprovincialis* and NZ middens with respect to PCA Factor 1 and 2 scores, and this was supported by the DFA Mahalanobis distance estimates). The majority of the DFA 'misclassifications' involved *M. galloprovincialis* and NZ midden material, which emphasizes their similarity. Because of the sample size of one, it is not possible to conclude with any degree of certainty about the taxonomic status of the fossil, other than to say that it exhibited much greater similarity to *M. galloprovincialis* and the midden material than it did to *M. edulis*. The null hypothesis of analysis 2 was rejected, and it is concluded that NZ midden (and most likely the fossil) material is consistent with *M. galloprovincialis* and inconsistent with *M. edulis*.

Contemporary NZ *Mytilus* valves were more similar to *M. galloprovincialis* than they were to *M. edulis*, although all three groupings were significantly different as judged by the PCA and DFA. However, the sim-

Table 4. Mahalanobis distance and associated significance level (*P*) for pairwise comparisons of populations or groupings analysed by discriminant function analysis

Analysis	Pairwise comparison	Mahalanobis distance	*P*
1a	Tvärminne (*M. t*) vs. Lowestoft (*M. e*)	83.17	<0.001
	Tvärminne (*M. t*) vs. Caswell (*M. e*)	64.09	<0.001
	Lowestoft (*M. e*) vs. Grau d'Age (*M. g*)	64.08	<0.001
	Tvärminne (*M. t*) vs. Grau d'Age (*M. g*)	55.78	<0.001
	Tvärminne (*M. t*) vs. Bude (*M. g*)	46.20	<0.001
	Grau d'Age (*M. g*) vs. Caswell (*M. e*)	30.52	<0.001
	Bude (*M. g*) vs. Lowestoft (*M. e*)	22.00	<0.001
	Grau d'Age (*M. g*) vs. Bude (*M. g*)	17.55	<0.001
	Lowestoft (*M. e*) vs. Caswell (*M. e*)	17.28	<0.001
	Bude (*M. g*) vs. Caswell (*M. e*)	7.99	<0.001
1b	Lowestoft (*M. e*) vs. Grau d'Age (*M. g*)	52.76	<0.001
	Grau d'Age (*M. g*) vs. Caswell (*M. e*)	24.50	<0.001
	Bude (*M. g*) vs. Lowestoft (*M. e*)	19.95	<0.001
	Lowestoft (*M. e*) vs. Caswell (*M. e*)	14.04	<0.001
	Grau d'Age (*M. g*) vs. Bude (*M. g*)	12.25	<0.001
	Bude (*M. g*) vs. Caswell (*M. e*)	6.76	<0.001
2	NZ middens vs. *M. edulis*	11.83	<0.001
	M. edulis vs. *M. galloprovincialis*	11.22	<0.001
	NZ middens vs. *M. galloprovincialis*	3.24	<0.001
3	NZ contemporary vs. *M. edulis*	20.10	<0.001
	NZ contemporary vs. *M. galloprovincialis*	9.05	<0.001
	M. galloprovincialis vs. *M. edulis*	8.94	<0.001
4	NZ Bay of Islands vs. *M. galloprovincialis*	26.41	<0.001
	NZ Bay of Islands vs. *M. edulis*	22.57	<0.001
	M. galloprovincialis vs. *M. edulis*	9.96	<0.001
5	NZ contemporary vs. *M. edulis*	22.81	<0.001
	NZ middens vs. *M. edulis*	12.65	<0.001
	M. galloprovincialis vs. *M. edulis*	10.51	<0.001
	NZ contemporary vs. *M. galloprovincialis*	10.42	<0.001
	NZ contemporary vs. NZ middens	5.30	<0.001
6	NZ contemporary vs. NZ middens	7.44	<0.001

For the DFA the fossil valve was included with the middens material. Analysis 1a & 1b: (*M. e*) = *Mytilus edulis*; (*M. g*) = *Mytilus galloprovincialis*; (*M. t*) = *Mytilus trossulus*. NZ = New Zealand.

ilarity to *M. galloprovincialis*, and in particular the dissimilarity to *M. edulis*, are sufficient to permit rejection of the null hypothesis of analysis 3, and to conclude that contemporary blue mussels are consistent with *M. galloprovincialis* and inconsistent with *M. edulis* with only one exception (see next section). This finding, based on samples from 19 island and/or remote sites across the full distributional range of the genus, confirms previous studies which identified contemporary NZ mussels as *M. galloprovincialis*, as judged by allozymes (Wellington Harbour only: McDonald *et al*., 1991) and mtDNA sequencing (Wellington and Otago Harbours: Hilbish *et al*., 2000). This taxonomic identification means that the distributional range of this species in NZ is the largest natural range recorded for this species anywhere in the world. Ecologically, taxa of the genus *Mytilus* are partially separated according to their environmental preferences and tolerances (Koehn, 1991; Seed, 1992; Gardner, 1994, 1996, 1997; Suchanek *et al*., 1997; Bierne *et al*., 2002). *M. edulis* is a cold-water taxon usually found at sheltered or open-water sites under some degree of fresh-water influence, whereas *M. galloprovincialis* is a warm-water mussel found at wave exposed sites and can tolerate much higher thermal maxima than can *M. edulis*, but it is less tolerant of low-salinity water (Koehn, 1991; Seed, 1992; Gardner, 1994, 1997; Bierne *et al*., 2002). The presence of NZ contemporary *M. galloprovincialis* as far south as Campbell Island (52° south) indicates that this species is, under certain circumstances, physiologically adapted to tolerate subpolar conditions. That is, it is not necessarily

restricted in its distribution by its inability to tolerate cold temperate to subpolar conditions as previously thought (Koehn, 1991; Seed, 1992; Gardner, 1994, 1997; Hilbish, Bayne & Day, 1994). Why this adaptation has occurred in NZ and not elsewhere is unknown, but warrants further investigation. The *M. galloprovincialis* collected from subantarctic regions of NZ are typically large and robust, and do not exhibit the sort of low-quality shell characteristics that one might expect for a species at the very limit of its environmental tolerance (seven of the eight Auckland Islands mussels were >105 mm in length, the largest being 138 mm; all seven of the Campbell Island mussels were >50 mm in length, the largest being 84 mm). These mussels thrive under these conditions, in contrast to the anticipated situation based on the environmental distributions of this species everywhere else in the world.

Examination of NZ contemporary mussels on a population-by-population basis when compared with the reference taxa indicated that the three valves from the Bay of Islands (35° south) differed to some degree from all other contemporary valves. PCA revealed non-significant differences of Bay of Islands mussels from *M. edulis*, but a significant difference compared with *M. galloprovincialis*. The DFA confirmed these findings, with the greatest Mahalanobis distances being recorded between the Bay of Islands mussels and *M. galloprovincialis* mussels (although it should be noted that according to the Mahalanobis distance estimates, the Bay of Islands were more dissimilar to either *M. edulis* or *M. galloprovincialis* than these two species were to one another). The greater similarity of the Bay of Islands mussels to *M. edulis* than to *M. galloprovincialis* raises the possibility of a second species (i.e. *M. edulis*) in NZ. The Bay of Islands region is interesting for several different reasons. First, it is the northern-most limit of the distribution of *Mytilus* in NZ. Second, the atypical presence of blue mussels this far north represents '. . . one of its most interesting and isolated northern records' (Morton & Miller, 1968: 395) and third, the Bay of Islands is a warm temperate to subtropical environment, and is therefore much more suited to *M. galloprovincialis* (the warm-adapted species of the genus) rather than it is to *M. edulis* (a cold-adapted species). While only three valves from the Bay of Islands were examined, and the analyses could not confirm unequivocally the specific status of these mussels, it is nonetheless interesting to speculate briefly on a couple of points. First, regardless of the taxonomic status of these mussels, their presence in the region is atypical of the intertidal community structure usually encountered in the far north (Morton & Miller, 1968), and is disjunct from other blue mussels, the nearest of which occur hundreds of km further south. This unusual mussel 'hot spot' is consistent with an introduction of mussels (either from overseas or from more southerly regions of NZ) into the Bay of Islands, a region which has a long history of visits from vessels from all over the world [James Cook visited and named the area in late 1769 (Hough, 1995)]. Such speculation requires, however, detailed examination. Second, wherever two species of the smooth shelled blue mussels co-occur, there is hybridization between them (Gardner, 1997). The possibility of interspecific hybridization between two NZ taxa of the genus *Mytilus* will require detailed genetic examination if it is demonstrated that two taxa do indeed co-occur.

Both the PCA and the DFA revealed significant morphometric differences between NZ contemporary and midden material. The fact that the fossil/midden mussels formed one and the contemporary mussels formed a second discrete cluster is unexpected, given the often small sample sizes per site, and the spatial and temporal extent of sampling which would be expected to obscure differences between the groups. The extent of the differentiation between the two groups was low, consistent with intraspecific differentiation between and among present day populations (e.g. Table 4), and it is therefore unlikely that this reflects a substantive change such as a natural invasion (range expansion), or human-mediated invasion (e.g. hull fouling), or a genetic modification that may have occurred in the fossil/midden mussels to give rise to the contemporary mussels (e.g. genetic drift or a change in environmental conditions giving rise to a change in gene frequencies).

The application of multivariate morphometric analyses of *Mytilus* valves has demonstrated that fossil, midden and contemporary blue mussels from throughout the range of the genus in NZ are most similar to *M. galloprovincialis*, and that this species is best viewed as being native to NZ. The application of molecular techniques will resolve the possibility of *M. edulis* occurring in the Bay of Islands, and clarify whether interspecific hybridization occurs in this general region. Finally, it is suggested that physiological adaptations to cold temperate and subantarctic environments displayed by NZ *M. galloprovincialis* require detailed examination as a means to improve understanding of the interaction of this species with conspecifics in transitional environments such as south-west England, the Pacific coast of North America and Japan, where fine-scale distributional differences are thought to be moderated by the environment.

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