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Genetic differentiation in the New Zealand sea urchin *Evechinus chloroticus* (Echinodermata: Echinoidea)

P. V. MLADENOV
Department of Marine Science
University of Otago
P. O. Box 56, Dunedin
New Zealand

R. M. ALLIBONE[1]*
G. P. WALLIS[1,2]
[1]Department of Zoology
[2]Centre for Gene Research
University of Otago
Dunedin, New Zealand

*Present address: Natiuonal Institute of Water and Atmospheric Research Ltd, P. O. Box 11 115, Hamilton, New Zealand.

Abstract Genetic differentiation in the New Zealand sea urchin *Evechinus chloroticus* (Valenciennes) was studied by examining individuals collected from six widely separated (250–2200 km apart) sites from around New Zealand for genetic variation at five polymorphic enzyme loci. Despite the large geographic separations, values of Nei's unbiased genetic distance, D (0–0.019) and standardised genetic variation among populations, F_{ST} (0.01–0.02) were small. This indicates high levels of gene flow among populations. However, one population sampled in a fiord in south-western New Zealand was genetically differentiated from the others, although the scale of differentiation was not large ($D = 0.011$–0.019). These findings indicate: (1) that the long-lived planktotrophic larva of *E. chloroticus* provides this species with considerable dispersal ability throughout its range; and (2) that this is little affected by oceanographic features peculiar to its range, such as the Subtropical Convergence or the southward flowing East Cape Current. The slight differentiation of the fiord population probably results from restricted larval dispersal into and out of the fiord. In terms of management of the *E. chloroticus* fishery, the results provide no evidence for discrete stocks, with the possible exception of Fiordland. It is prudent to manage the fiord populations conservatively until they are better studied.

Keywords sea urchin; isozymes; genetic variation; gene flow; larval dispersal; fishery management

INTRODUCTION

Evechinus chloroticus (Valenciennes) is an exclusively New Zealand species of sea urchin, commonly known as kina or sea egg. It is widely distributed on hard substrata in shallow (< 50 m) waters around both the North and the South Island of New Zealand, as well as Stewart Island, the Snares, Chatham Islands, and Three Kings Islands (McRae 1959; Fell 1960; Pawson 1965; Dix 1970a). The range of the population thus extends over 14° of latitude and straddles a major oceanographic feature, the Subtropical Convergence, that defines the boundary between the two major surface water masses that surround New Zealand (Fig. 1): the Subantarctic and Subtropical waters (Heath 1985). The Convergence is characterised by rapid spatial changes in water properties (Heath 1985).

The pioneering studies of Dix (1970a, 1970b, 1970c, 1972) revealed much about the basic biology and ecology of *Evechinus chloroticus* at sites from northern South Island (Kaikoura and Kaiteriteri). Dix (1970c) determined that there was an annual reproductive cycle, with spawning occurring in summer and early autumn, although there was considerable variation in reproductive effort and timing of spawning between his sites. Walker (1982) studied *E. chloroticus* in the Hauraki Gulf and found

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that most spawning occurred in mid to late summer. Keogh & Mladenov (1994) found considerable between-site variability in population size structure, timing of the reproductive cycle, and gonad size of *E. chloroticus* in the Marlborough Sounds at a scale of tens of kilometres. Such variations are likely related, at least in part, to patchiness of macroalgal food supply. On the basis of analysis of growth bands on test plates, Dix (1972) suggested that *E. chloroticus* was 3 or 4 years old at first maturity and could live for up to 10 or even 15 years. A large body of literature (summarised by Andrew 1988) shows that *E. chloroticus* has a direct effect on the distribution and abundance of large brown algae in northern New Zealand waters, there being a strong inverse correlation between the abundance of this sea urchin and that of large brown algae.

Dix (1969) and Walker (1984) have shown that *Evechinus chloroticus* possesses a typical planktotrophic echinopluteus larval stage with a pelagic existence of 1–2 months. The species thus has the potential for long-distance dispersal over a scale of hundreds of kilometres. Dix (1969) suggested that this accounted for the wide distribution of the species around New Zealand. He also pointed out that variable larval survival likely would result in an irregular larval supply along with unpredictable recruitment rates.

In New Zealand, *Evechinus chloroticus* has long been a traditional food item among Maori and other Polynesian peoples; large numbers are regularly taken by hand-picking (scooping up urchins by hand while snorkelling) for customary (Maori traditional) purposes. There is also a new but expanding commercial fishery for *E. chloroticus* to supply the Japanese market with high-quality roe. The commercial fisheries are centred presently in the Gisborne, Marlborough Sounds, and southern Fiordland regions. Commercial harvesting is based almost exclusively on hand-picking, although there is some limited dredging. Commercial landings in New Zealand were in the order of 500 metric tonnes live weight in 1992 (Keogh & Mladenov 1994). The size of the recreational and customary catch is unknown, but is likely to be at least half the size of the commercial catch.

Overfishing of sea urchins is a common occurrence in many parts of the world (e.g., Le Gall 1987; Scheibling & Mladenov 1987) and there are now some examples of overfishing of *Evechinus chloroticus* along certain coastal areas of New Zealand (Keogh & Mladenov 1994). Recreational, customary, and commercial fishing of *E. chloroticus* in New Zealand must therefore be underpinned by research that will provide a sound biological basis for the future management of the fishery.

An important question, from both evolutionary and fishery management perspectives, is the extent of gene flow and associated genetic differentiation among *Evechinus chloroticus* populations at a macrogeographic (greater than 100s of km) scale. Does the species consist of a single genetically homogeneous stock throughout its range, or a number of stocks with differing attributes with regard, for example, to growth rate, longevity, or reproductive effort? Knowledge of this kind would help determine whether a single management regime for the fishery is suitable for the whole of New Zealand, or whether management options must be tailored on a stock-by-stock basis. Furthermore, such information would help test present concepts regarding the relationships between larval life span, dispersal, gene flow, geographic range, genetic differentiation, and genetic variation in marine taxa (Burton & Feldman 1982; Scheltema & Williams 1983; Hedgecock 1986; Strathmann 1986; Palumbi 1995). Marine species with longer larval phases are generally thought to disperse further and have more gene flow, larger geographic ranges, lower levels of genetic differentiation among populations, and higher levels of genetic variation within populations (e.g., Scheltema 1971; Scheltema & Williams 1983; Waples 1987; McMillan et al. 1992; Williams & Benzie 1993; Palumbi 1995). There are, however, unexpected exceptions to these patterns that cast doubt on the generality of such conclusions (Hines 1986; Palumbi 1995).

Evechinus chloroticus, with its large geographic range and planktotrophic larval phase, is a useful model for further investigation of the genetic consequences of long larval life. The prolonged larval phase of *E. chloroticus* would, *a priori*, be expected to facilitate high levels of gene exchange among widely separated populations around New Zealand, leading to low levels of differentiation among them. However, expected patterns of gene flow and population connectivity in *E. chloroticus* could be altered by oceanographic features peculiar to its range, such as the presence of the Subtropical Convergence, which bisects its range, and the generally eastward flow of currents past New Zealand (Fig. 1).

In this paper we examine the genetic structure of *Evechinus chloroticus* collected from six widely separated (up to 2200 km) sites around New Zealand, using isozyme electrophoresis to establish

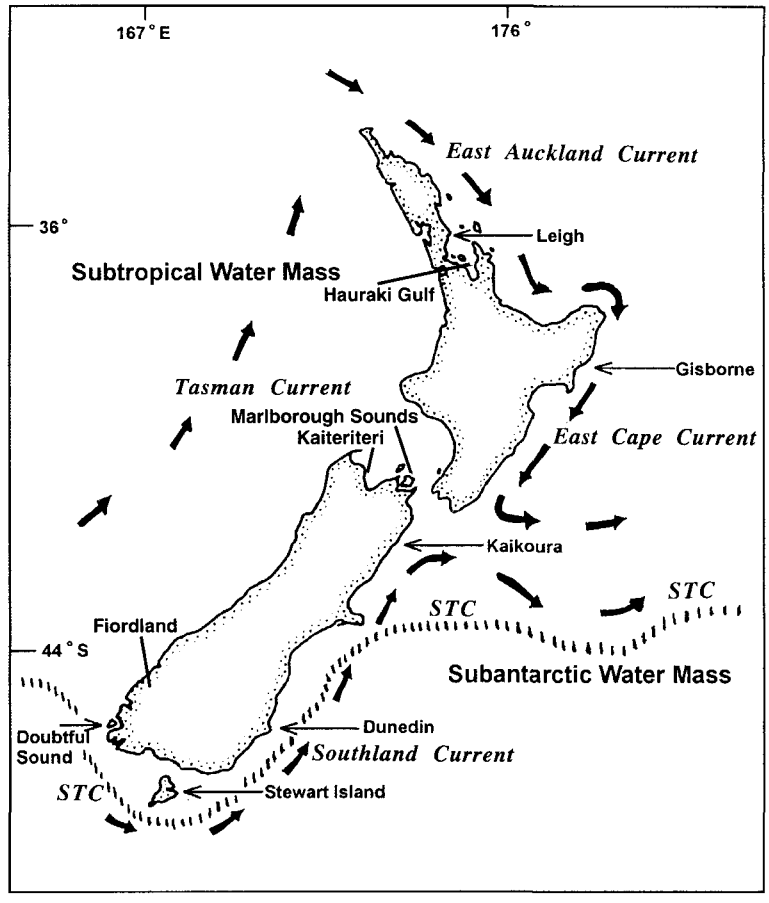

Fig. 1 Map of New Zealand with major oceanographic features showing the six sites (arrowed) where *Evechinus chloroticus* was collected; STC, Subtropical Convergence.

the extent of gene flow and levels of genetic differentiation.

METHODS

Individuals of *Evechinus chloroticus* were collected by diving from six widely separated sites from around New Zealand (Fig. 1): Cape Rodney (36°17′S, 174°47′E) near Leigh (N = 42 individuals); Aerial Reef (38°45′S, 178°5′E) near Gisborne (N = 18); Kaikoura (43°60′S, 173°50′E) (N = 25); Seacliff (45°40′S, 170°36′E) near Dunedin (N = 39); Thule Bay, Stewart Island (46°53′S, 168°9′E) (N = 65); and Doubtful Sound, Fiordland (45°17′S, 167°5′E) (N = 68). The sea urchins were either transported to Dunedin alive, or the Aristotle's lantern from each individual was dissected in the field and frozen on dry ice before being shipped to Dunedin and stored in a –80°C freezer. Live sea urchins were dissected in the laboratory immediately upon arrival and the lanterns stored at –80°C.

Muscle tissue was scraped from the lanterns and placed in 1.5 ml Eppendorf tubes with 4–6 drops of homogenising buffer (Watts et al. 1990). The tissue was then ground for about 10 s with a stirring rod and returned to a –80°C freezer pending electrophoresis.

Horizontal starch gel electrophoresis was conducted using two buffer systems to resolve four polymorphic enzyme systems encoded by five presumptive loci. A modified continuous tris-citrate buffer (Ward & Beardmore 1977) was used to score 6-phosphogluconate dehydrogenase (EC 1.1.1.44: *6Pgd*), malate dehydrogenase (EC 1.1.1.37: *Mdh–1*, *Mdh–2*), mannose phosphate isomerase (EC 5.3.1.8: *Mpi*), and a continuous tris-EDTA-borate buffer (Selander et al. 1971) was used for

phosphoglucomutase (EC 5.4.2.2: *Pgm*). Staining techniques were based on those of Shaw & Prasad (1970) and Harris & Hopkinson (1976). Loci were numbered according to increasing mobility and alleles at each locus were labelled according to their relative mobility to the most common allele at that locus.

Data were analysed using the computer program BIOSYS–1 (Swofford & Selander 1989). The program was used to test for Hardy-Weinberg equilibrium, to provide *F*-statistics and Nei's (1978) unbiased genetic distances (*D*) and identities (*I*). A UPGMA cluster analysis (Sneath & Sokal 1973) was also performed using I values. Coastal distances separating the sites sampled were estimated from a New Zealand map (1 : 5 000 000).

RESULTS

Of the five loci studied, *Pgm* was the most variable in all six populations of *Evechinus chloroticus*, followed by *Mpi* (Table 1). The same common allele at the *Mpi* locus was the most frequent in all populations, with up to five other alleles occurring at lower frequencies. One main allele was present for *Pgd* in all populations, with one or two alleles present at lower frequencies. Two alleles were present for *Mdh–2*, with one allele predominant in all populations. *Mdh–1* was invariable in all populations except for Leigh, where a single heterozygote for a rare allele was found.

Mean number of alleles per locus ranged from 2.8 to 3.4 among the six populations of *Evechinus chloroticus* (Table 2). Mean heterozygosities for the populations ranged from 35 to 42% (Table 2). After pooling a total of five rare alleles (< 0.08), no significant deviations from Hardy-Weinberg expectations for genotype frequencies were detected across a total of 25 tests. The observed heterozygosities agreed well with those expected under Hardy-Weinberg equilibrium conditions (Table 2 and 3). Although there was a slight, but consistent,

Table 1 Allele frequencies for the five polymorphic loci screened in six populations of *Evechinus chloroticus* from New Zealand. *n*, number of individuals scored.

Locus, allele	Leigh	Gisborne	Kaikoura	Dunedin	Stewart Island	Doubtful Sound
Mdh-1						
n	42	18	25	39	64	68
A	0.988	1.000	1.000	1.000	1.000	1.000
B	0.012	0.000	0.000	0.000	0.000	0.000
Mdh-2						
n	42	18	25	39	63	68
A	0.655	0.778	0.720	0.654	0.619	0.610
B	0.345	0.222	0.280	0.364	0.381	0.390
Pgd						
n	42	18	23	37	57	68
A	0.286	0.333	0.239	0.338	0.202	0.228
B	0.607	0.667	0.761	0.662	0.798	0.735
C	0.107	0.000	0.000	0.000	0.000	0.037
Mpi						
n	42	18	25	38	63	68
A	0.143	0.056	0.180	0.079	0.151	0.037
B	0.679	0.694	0.680	0.684	0.651	0.853
C	0.155	0.194	0.140	0.224	0.183	0.096
D	0.024	0.056	0.000	0.000	0.000	0.000
E	0.000	0.000	0.000	0.013	0.016	0.015
Pgm						
n	42	18	25	37	63	68
A	0.012	0.028	0.040	0.000	0.024	0.051
B	0.060	0.083	0.080	0.162	0.119	0.184
C	0.131	0.139	0.180	0.230	0.214	0.235
D	0.250	0.306	0.240	0.270	0.302	0.074
E	0.452	0.361	0.420	0.297	0.270	0.382
F	0.095	0.083	0.040	0.041	0.063	0.074
G	0.000	0.000	0.000	0.000	0.008	0.000

heterozygote deficit at many loci across all populations (Table 3), the only significant deviation from expected was at the *Pgm* locus in the Leigh population.

Genetic distances, D, among the six populations of *Evechinus chloroticus* from New Zealand were on the whole small, ranging from 0 to 0.019 (Table 4). A Mantel (1967) test using 50 000 randomisations (Manly 1996) showed some evidence (one-tailed) for a correlation between genetic and geographic (coastal) distance. Maximum coastal distance gave a correlation of marginal significance ($P = 0.028$); the minimum distance correlation was not significant ($P = 0.131$). However, all five comparisons involving the Doubtful Sound population were associated with a value of D that was greater than 0.01 (Table 4). This comparatively high value of D was independent of the geographic distance separating any one population from Doubtful Sound (Table 4). For example, the value of D for Doubtful Sound and Stewart Island (geographic distance = 250 km) was 0.017, and the

Table 2 Genetic variability measures for six populations of *Evechinus chloroticus* from New Zealand. A locus was considered polymorphic if the frequency of the most common allelle was < 0.95; HDYWBG expected: heterozygosity expected under conditions of Hardy-Weinberg equilibrium (Nei's unbiased estimates: Nei 1978).

Population	Mean sample size/locus ± SD	Mean number of alleles/locus ± SD	% of loci polymorphic	Mean heterozygosity	
				Observed ± SD	HDYWBG expected ± SD
Leigh	42.0 ± 0.0	3.4 ± 1.7	100	0.42 ± 0.24	0.44 ± 0.25
Gisborne	18.0 ± 0.0	3.0 ± 2.0	80	0.40 ± 0.15	0.40 ± 0.17
Kaikoura	24.6 ± 0.9	2.8 ± 1.9	80	0.35 ± 0.18	0.37 ± 0.16
Dunedin	38.0 ± 1.0	2.8 ± 1.6	80	0.41 ± 0.16	0.43 ± 0.15
Stewart Island	62.0 ± 2.8	3.2 ± 2.4	80	0.38 ± 0.17	0.42 ± 0.19
Doubtful Sound	68.0 ± 0.0	3.2 ± 1.9	80	0.37 ± 0.22	0.37 ± 0.21

Table 3 Genetic variability measures for six populations of *Evechinus chloroticus* from New Zealand. H_o, observed heterozygosity (direct count); H_e, expected heterozygosity; H_d, degree of departure of genotypic frequencies from Hardy-Weinberg expectations where $H_d = (H_o - H_e)/H_e$ (Selander 1970).

	Leigh			Gisborne			Kaikoura		
Locus	H_o	H_e	H_d	H_o	H_e	H_d	H_o	H_e	H_d
Mdh-1	0.02	0.02	0.01[a]	–	–	–	–	–	–
Mdh-2	0.40	0.45	–0.11[a]	0.33	0.34	–0.04[a]	0.40	0.40	–0.01[a]
Pgd	0.60	0.54	0.11[ns]	0.56	0.44	0.25[a]	0.22	0.36	–0.40[a]
Mpi	0.52	0.49	0.06[ns]	0.44	0.47	–0.06[ns]	0.48	0.49	–0.01[ns]
Pgm	0.57	0.70	–0.19*	0.67	0.74	–0.10[ns]	0.64	0.72	–0.12[ns]
Means	0.42	0.44	–0.02	0.40	0.40	0.01	0.35	0.39	–0.14

	Dunedin			Stewart Island			Doubtful Sound		
Locus	H_o	H_e	H_d	H_o	H_e	H_d	H_o	H_e	H_d
Mdh-1	–	–	–	–	–	–	–	–	–
Mdh-2	0.59	0.45	0.30[a]	0.48	0.47	0.10[a]	0.46	0.48	–0.04[ns]
Pgd	0.35	0.45	–0.22[a]	0.26	0.32	–0.18[a]	0.43	0.41	0.05[a]
Mpi	0.42	0.48	–0.11[ns]	0.48	0.52	–0.08[ns]	0.22	0.26	–0.16[ns]
Pgm	0.70	0.76	–0.07[ns]	0.68	0.77	–0.12[ns]	0.76	0.75	0.02[ns]
Means	0.41	0.43	–0.03	0.38	0.42	–0.07	0.37	0.38	–0.03

*significant deviation from expected at $P < 0.05$
[ns]non-significant
[a] no test possible because fewer than five sea urchins expected for one genotypic class

value of D for Doubtful Sound and Leigh (geographic distance at least 1650 km) was 0.015. The genetic distance between the Stewart Island and Leigh and the Stewart Island and Gisborne populations was also comparatively high (0.011 and 0.007, respectively). All other values of D were less than 0.003.

Values of F_{IT} were effectively zero or very slightly positive for each locus (Table 5). This is largely explained by the slight but consistent deficit of heterozygotes observed at many loci across all populations (Table 3 and F_{IS} in Table 5). Population subdivision, as assessed by F_{ST} statistics, was slight (Table 5), and largely attributable to the Doubtful Sound sample. By Eq. 2 of Dobzhansky & Wright (1941), this equates to an estimate for N_em of 12.9 migrants per generation, more than sufficient to prevent accumulation of genetic differentiation through genetic drift.

A cluster analysis based on the unweighted pair group method and Nei's (1978) co-efficient of unbiased genetic identity showed that all populations were genetically quite similar, with the Fiordland population most distinct (Fig. 2).

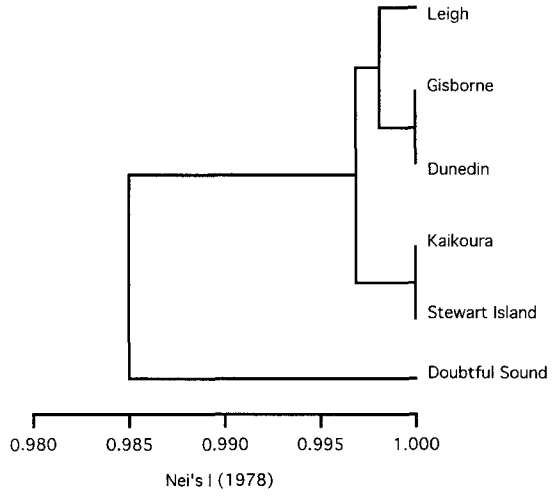

Fig. 2 A phenetic dendrogram showing the relationships of six populations of the sea urchin, *Evechinus chloroticus*, based on five polymorphic loci. Cophenetic correlation = 0.878.

DISCUSSION

Very little genetic differentiation was found among five of six populations of *Evechinus chloroticus* sampled over distances greater than 2000 km along the New Zealand coastline (D = 0–0.019, F_{ST} = 0.01–0.02). This indicates high levels of gene flow and suggests that these populations act as a single interbreeding population. However, one population sampled in Doubtful Sound, Fiordland, was genetically distinct from the others, although the scale of differentiation was not large (D = 0.011–0.019).

A slight but consistent heterozygote deficit was observed at several loci across all populations. Heterozygote deficiencies are a general finding in marine invertebrates, and possible explanations (mis-scoring, inbreeding, null alleles, aneuploidy, molecular imprinting, selection, Wahlund effect) have been discussed extensively elsewhere (Fujio et al. 1983; Gaffney et al. 1990). No one of these seems either sufficient or plausible alone for *Evechinus chloroticus*, and the overall deficit probably results from several small effects, all tending to reduce heterozygosity, which add to a significant overall deficit.

Our findings suggest that the long-lived (1–2 months) larvae of *Evechinus chloroticus* provide the species with considerable dispersal ability throughout its range, and that this dispersal is little affected by oceanographic features such as the Subtropical Convergence, which bisects the range of the species, or the generally eastward flow of currents past New Zealand (Fig. 1). Indeed, the

Table 4 Relationship between geographic distances in km and Nei's unbiased genetic distances D (in parentheses) separating six New Zealand populations of *Evechinus chloroticus*.

Population	Leigh	Gisborne	Kaikoura	Dunedin	Stewart Island
Leigh	–				
Gisborne	550 (0.000)	–			
Kaikoura	1100 (0.000)	550 (0.000)	–		
Dunedin	1550 (0.003)	1000 (0.000)	450 (0.000)	–	
Stewart Island	1500 (0.011)	1250 (0.007)	700 (0.000)	250 (0.001)	–
Doubtful Sound	1650–2050 (0.015)	1500–2200 (0.019)	950 (0.011)	500 (0.012)	250 (0.017)

almost complete lack of genetic differentiation between such populations as Dunedin and Gisborne suggests that larval transport along the east coasts of the South and North Islands does take place, perhaps in stepping-stone fashion, with each generation of larvae dispersing short distances close to the coast (where the influences of the Southland and East Cape Currents would be smaller). The slight differentiation of the Doubtful Sound population relative to the other populations is likely due to its location within the Doubtful-Thompson-Bradshaw Sounds fiord system which has two narrow openings to the open ocean with comparatively shallow (100 and 150 m) sills at the entrance to each opening. These features would tend to restrict larval dispersal, and hence gene flow, into and out of the fiord system.

These findings match the results of isozymal analyses of asteroids on the Great Barrier Reef, Australia, with high dispersal capability. In the Crown-of-Thorns sea star (*Acanthaster planci*), which has a 14-day larval period, Nash et al. (1988) and Benzie & Stoddart (1992) found low genetic differentiation among populations separated by as much as a 1000 km (F_{ST} = 0.019–0.038). Williams & Benzie (1993) found even less differentiation among equally separated populations of the sea star, *Linckia laevigata*, which has a larval period of 28 days (D = 0–0.003, mean F_{ST} = 0.0011). These findings also agree with studies based on mtDNA comparisons, which reported little genetic differentiation and high gene flow in echinoids with planktotrophic larvae, including *Strongylocentrotus purpuratus* which was studied along a 2500 km stretch of the west coast of North America that spanned several biogeographic boundaries (Palumbi & Kessing 1991; Palumbi 1995). However, similar studies on sea urchin species in the tropical Pacific genus *Echinometra*, which also possess planktotrophic larvae, have revealed population genetic heterogeneity (Palumbi 1995). This may be because larval dispersal in these species must occur across long stretches of water between islands or island archipelagoes, whereas step-wise dispersal over several generations could occur in species inhabiting a long stretch of coastline (Palumbi 1995).

Isozyme analyses of other New Zealand marine species have so far revealed differing levels of interpopulational differentiation. For example, the tuatua clam (Smith et al. 1989) and green-shelled mussel (Smith 1988) display geographic structuring of populations. By contrast, spiny rock lobster (Smith et al. 1980) and several commercial fish species—orange roughy (Smith 1986), groper (Smith & Johnston 1985), hoki (Smith et al. 1981), and whitebait (Barker & Lambert 1988, Allibone & Wallis 1993)—fail to show significant genetic differentiation.

In terms of management of the *Evechinus chloroticus* fishery of New Zealand, our results provide no evidence for discrete stocks with the possible exception of the Fiordland region. Management practices for much of New Zealand can thus be independent of macrogeography. Instead, it is more likely that management practices developed for this species will have to focus on the harvesting problems associated with a much smaller scale (tens of km) of differentiation of populations caused by localised environmental differences (e.g., food supply), and which is unrelated to genetics. Discrete management procedures might, however, be appropriate for the fiord populations of *E. chloroticus* which appear to be more isolated and genetically differentiated from other populations. In those populations inhabiting fiords, rate of larval supply from sources external to the fiord is likely to be a limiting factor to stock recovery following any overfishing event within a fiord. It is thus prudent to treat the fiord populations as a separate stock, or a series of separate stocks, to be managed conservatively, at least until more is known about their genetics and about recruitment processes within and between fiords.

Table 5 Summary of F-statistics for six populations of *Evechinus chloroticus* from New Zealand. F_{ST}, standard genetic variance between populations; F_{IT}, total genetic variance; F_{IS}, standardised genetic variance within populations

Locus	F_{IS}	F_{IT}	F_{ST}
Mdh-1	–0.012	–0.002	0.010
Mdh-2	–0.023	–0.007	0.016
Pgd	0.045	0.064	0.020
Mpi	0.054	0.073	0.020
Pgm	0.095	0.112	0.019
Mean	0.050	0.068	0.019

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