

Exchange between populations of *Adamussium colbecki* (Mollusca: Bivalvia) in the Ross Sea

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Abstract: The endemic Antarctic scallop *Adamussium colbecki* (Mollusca: Bivalvia) represents a key species in the Ross Sea littoral benthic ecosystem, locally reaching very high densities. This species has an annual gametogenic cycle, with a summer spawning event, and a pelagic larval behaviour. This paper aims at describing population structure and genetic polymorphism (using AFLP) of the large populations inhabiting the Ross Sea (Terra Nova Bay and McMurdo Sound) in order to investigate possible genetic exchange between *A. colbecki* in these areas. In Terra Nova Bay, size-frequency distributions show, generally, the dominance of large individuals, although site related differences are found in the abundance of smaller size classes (less than 40 mm), suggesting that recruitment is not a regular event. All McMurdo sites are characterized by large individuals and, at least during this sampling period, recruitment is completely absent. Nuclear DNA analyses show that the largest differences are found at the largest scale (between McMurdo Sound and Terra Nova Bay), but all populations sampled, even at a smaller spatial scale, have a well-settled genetic structure, notwithstanding the pelagic larval strategy. The *panmixia* hypothesis has therefore to be rejected for this species.

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Introduction

Adamussium colbecki (Smith) is the most conspicuous and widely distributed bivalve along Antarctic shores (Nicol 1966). It is considered a circumpolar species, although patchily distributed. Fischer & Hureau (1985) reports that it is found from 53°E in the Ross Sea, in the Bellingshausen Sea, around the Antarctic Peninsula, and in the South Shetland, South Orkney and Sandwich Islands. Specimens were also recently found in the Weddell Sea and in the Marguerite Bay area of the Antarctic Peninsula (Hain & Melles 1994, Tyler *et al.* 2003). The largest populations live close to Syowa Station (Nakajima *et al.* 1982), at Stonington Island (Ralph & Maxwell 1977), in west McMurdo Sound (Stockton 1984, Berkman 1990) and in Terra Nova Bay (Amato 1990, Berkman & Nigro 1992, Di Geronimo *et al.* 1992, Nigro 1993, Pranovi *et al.* 1993, Albertelli *et al.* 1994, Cattaneo-Vietti *et al.* 1997, Chiantore *et al.* 2000).

This scallop is long-lived and slow-growing and with intermittent recruitment (Ralph & Maxwell 1977, Stockton 1984, Berkman 1990, Cattaneo-Vietti *et al.* 1997). *Adamussium colbecki* is dioecious and becomes sexually mature at 5–7 years. It shows an annual gametogenic cycle and, in the Ross Sea, sexual maturity is reached late in the summer (Chiantore *et al.* 2002, Guidetti *et al.* 2004),

probably related to the water column food supply following the phytoplankton bloom.

Its growth rate is strongly size-dependent, with high inter-individual variability: it is higher for smaller individuals (< 40 mm in shell length), showing an average growth rate of 10 mm yr⁻¹, compared to 0.8 mm yr⁻¹ for large specimens (Cattaneo-Vietti *et al.* 1997, Chiantore *et al.* 2003, Heilmayer *et al.* 2003). The adults are free-living, while juveniles are byssally attached to adults' valves (Ansell *et al.* 1998).

The hypothesis tested in this work, addressing the LGP question regarding the role of persistent, large-scale ice structures in defining community composition along Victoria Land (Howard-Williams *et al.* 2006), is that *A. colbecki* populations are exchanging along the Victoria Land coast, between Terra Nova Bay and McMurdo Sound. Such hypothesis is supported by the planktotrophic behaviour of its larva (Berkman *et al.* 1991, Chiantore *et al.* 2002), by the water current movement features (Budillon *et al.* 2003), and, finally, by the effective swimming ability of this species (Ansell *et al.* 1998). In fact, it is well known that planktotrophic larvae of benthic invertebrates have a high dispersal ability, particularly those of polar species. For example, much information, for the Antarctic, is available for the sea urchin *Sterechinus neumayeri*

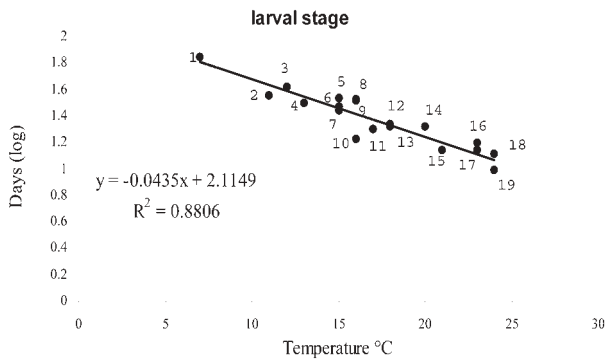


Fig. 1. Duration of larval stage in pectinids living at different sea water temperatures. 1. *Chlamys islandica* (Gruffydd, 1976), 2. *Patinopecten yessoensis* (Maru, 1985), 3. *Chlamys astata* (Hodgson & Burke, 1988), 4. *Patinopecten yessoensis* (Yoo & Imai, 1968), 5. *Placopecten magellanicus* (Culliney, 1974), 6. *Pecten maximus* (Comely, 1972), 7. *Pecten albicans* (Hotta, 1977), 8. *Chlamys astata* (Hodgson & Burke, 1988), 9. *Pecten maximus* (Gruffydd & Beaumont, 1972), 10. *Equichlamys bifrons* (Dix, 1976, Malakhov & Medvedeva, 1986), 11. *Chlamys asperrimus* (Rose & Dix, 1984), 12. *Amusium balloti* (Rose *et al.*, 1988), 13. *Pecten albicans* (Tanaka, 1984), 14. *Pecten maximus* (Sasaki, 1979), 15. *Argopecten irradians* (Loosanoff & Davies, 1963); 16. *Argopecten gibbus* (Costello *et al.*, 1973), 17. *Argopecten purpurea* (Illanes-Bucher, 1987), 18. *Argopecten irradians* (Sastry, 1965), 19. *Chlamys nobilis* (Ventilla, 1982). Confidence limits of the linear correlation coefficient are 0.85 and 0.97.

(Meissner) (Marsh & Manahan 2000, Podolsky *et al.* 1994 and references therein) and the sea star *Odontaster validus* (Koehler) (Pearse 1965, 1969, Bosch & Pearse 1990, Pearse *et al.* 1991 and references therein). Although *A. colbecki* veligers have been only occasionally been found in the water column and nothing is known about the extent of larval stage, the small eggs (Berkman *et al.* 1991, Chiantore *et al.* 2000) and measurements of larval prodissoconchs (Berkman *et al.* 1991) support a larval pelagic behaviour, but nothing is known about the effective larval duration. Comparing the duration of larval stage of pectinid species, at different temperatures (Fig. 1), it is possible to speculate that *A. colbecki* veliger could be in the water column for about 4–5 months before settling, giving the species a high dispersal capability.

Water currents such as the High Salinity Shelf Water formed in the Terra Nova Bay polynya, that moves southward along the bottom (Budillon *et al.* 2003), could effectively transport scallop larvae from north to south. In contrast, along the Victoria Land coast, there are some hydrographic barriers (such as the Drygalski Ice Tongue), that could prevent exchange between the north and south sides (Berkman & Tipton-Everett 2001, Berkman *et al.* 2005).

To test this hypothesis a molecular tool was used to compare population structure of this species, in order to

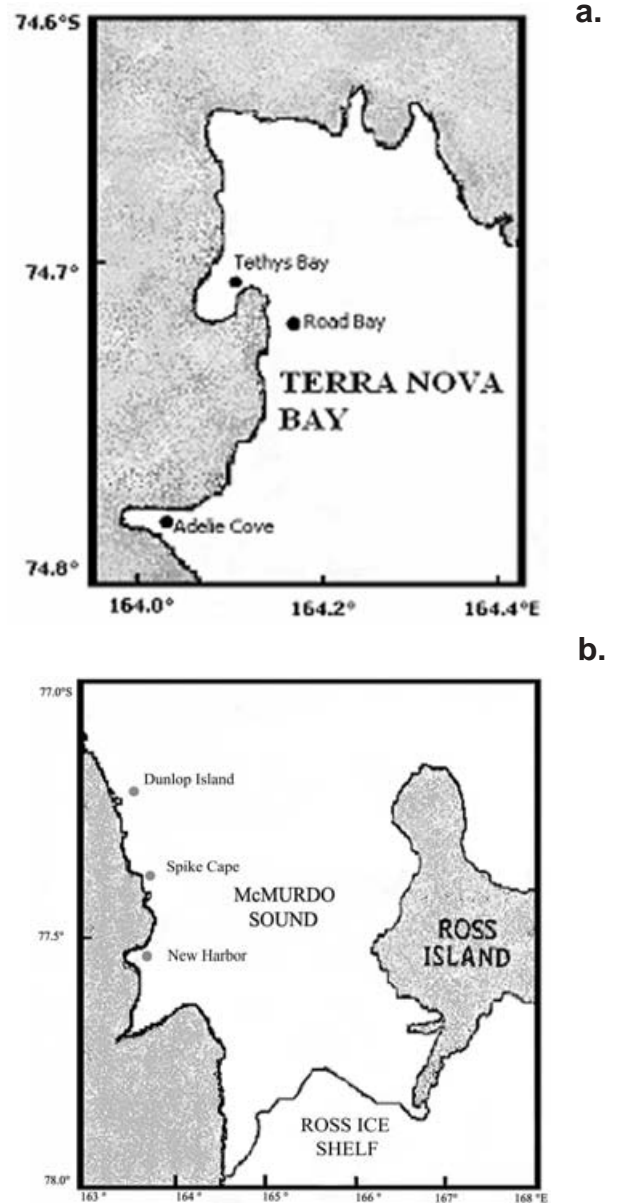


Fig. 2. Sampling sites for *A. colbecki* at **a.** Terra Nova Bay in 2001/02 and **b.** McMurdo Sound in 2002/03.

evaluate the likelihood of exchange. Similar studies have been carried out on other Antarctic marine organisms, such as the Antarctic krill *Euphausia superba* Dana (Zane *et al.* 1998) and the icefish *Chionodraco hamatus* Lönnberg (Patarnello *et al.* 2003). A circum-Antarctic survey of krill populations revealed little population differentiation, but mitochondrial DNA was used as marker, which is sometimes less sensitive to population subdivision even across large geographic distances. In this paper we investigated the population structure of *A. colbecki* by using the amplified fragment length polymorphism (AFLP) approach that scans polymorphism at restriction sites across the entire nuclear genome. This technique tends to be very

sensitive particularly at a small geographic scale, as genetic differentiation is expected to be not particularly pronounced; therefore a highly polymorphic marker such as AFLP seems to be more appropriate.

Materials and methods

Sample collection

Samplings were performed in Terra Nova Bay (Road Bay 74°41.93'S, 164°07.53'E; Tethys Bay 74°41.8'S, 164°04.8'E; and Adélie Cove 74°46.574'S, 163°58.160'E) (Fig. 2a) using a triangular dredge, at 40 m depth, close to the Italian Base (Mario Zucchelli Station) in 2001/02. Samples from the west McMurdo Sound were collected in 2002/03 by SCUBA and visual census (by videos surveys) from approximately 20 m depth in Dunlop Island (77°14.2'S, 163°28.0'E), Spike Cape (77°18.0'S, 163°34.0'E) and New Harbour (77°34.5'S, 163°31.7'E) (Fig. 2b).

Scallops were measured along the length axis, using a vernier calliper. Population structure was considered in terms of size frequency distribution. For each population mean, mode and median were calculated for juveniles and adults separately, where size-frequency distributions showed bimodal trends, and only one value was estimated for unimodal ones.

Genetic analyses were performed at all the sites only on 65 mm (± 2) long specimens, in order to test specimens putatively belonging to the same age class.

Animals were immediately dissected and DNA extraction was performed *in situ*, from a few milligrams of the adductor muscle, using Dneasy tissue kit (Qiagen), to avoid the DNA fragmentation, then frozen at -20°C .

Genetic analysis

Using amplified fragment length polymorphism (AFLP), a full set of markers were obtained from 141 individuals. Because of their geographic closeness and the small number of samples, the sites of Tethys Bay and Road Bay were considered together as a single population, hereafter called "Base". AFLP was carried out by the standard procedure (Vos *et al.* 1995) with the following modifications. High molecular weight genomic DNA was digested with a pair of restriction enzymes (*EcoRI/MseI*) and ligated to double-stranded adaptors *EcoRI* and *MseI* adapters in a single reaction. After digestion and ligation reactions, each sample was diluted tenfold and used as a template for the pre-selective PCR amplification. PCR pre-amplification was performed for 22 cycles at 94°C for 30 sec, 56°C for 1 min. and 72°C for 1 min. The pre-amplification products were diluted tenfold and used as template for the selective PCR amplification. The following PCR were performed using three primer pairs with three selective nucleotides: *EcoRI*-AAC/*MseI*-CAA, *EcoRI*-AAC/*MseI*-CAC, *EcoRI*-

ATT/*MseI*-CAT.

AFLP reactions were performed for 37 cycles with the following thermal profile: at 94°C for 30 sec, 65°C for 30 sec. and 72°C for 1 min. The annealing temperature in the first cycle was 65°C , subsequently reduced in each cycle by 0.7°C for the next 12 cycles, and continued at 56°C for the remaining 25 cycles AFLP products were electrophoresed in a ABI PRISM 3700 DNA Analyser (Applied Biosystems). Band scoring was performed manually on a digital representation of the gel obtained by the Genographer software (1999, Montana State University) (<http://hordeum.oscs.montana.edu/genographer/>). AFLP profiles were recorded in a matrix as presence (1) or absence (0) of bands (columns) in a specific individual (rows). Both polymorphic and monomorphic bands were scored.

In the analysis AFLP data were considered, disregarding their genetic base and making no assumptions about the Hardy-Weinberg equilibrium, as simple presence-absence data representing the phenetic similarity between nuclear genomes. The matrix was used to investigate the population heterogeneity.

Overall genetic heterogeneity was tested using an AMOVA (Analysis of MOlecular VARIance) approach (Excoffier *et al.* 1992) as implemented in the program Arlequin ver. 2.0 (Schneider *et al.* 2000). This approach performs a standard analysis of variance, in which the total variance is partitioned in covariance components due to inter-individual differences, inter-populations differences and, eventually, differences between groups of populations. Covariance components are used to calculate fixation indices (F or Φ , see below) within populations (indicated by subscript *-ct*), among populations within groups (*-sc*), or among populations (*-st*). Because AMOVA computed on the variance of gene frequencies is equivalent to a conventional F -statistic analysis *sensu* Cockerham (1969, 1973), we will indicate the corresponding fixation indices as F_{st} , F_{sc} , and F_{ct} . Alternatively, AMOVA allows us to take into account the number of mutations between haplotypes in the calculation of variance: in this case we will indicate fixation indices as Φ_{st} , Φ_{sc} and Φ_{ct} .

Statistical significance was assessed by comparing the observed distribution with a "null hypothesis" generated by a permutational approach (in this case with 10 000 permutations), in which individuals were randomly reallocated to each population. The same approach was applied to estimate the level of population genetic divergence, by calculating Φ_{st} (or F_{st}) and the associated probability level for each pair of populations reported as a pairwise population matrix. Significance threshold values were adjusted with a sequential Bonferroni correction (Rice 1989), that allows correction for sampling error associated with multiple tests in order to reduce the group-wide type I error rate. The pairwise genetic distance matrix was analysed using two-dimensional non-metric multi-

dimensional scaling (nMDS), an ordination procedure that finds those positions of n individuals in reduced space that best reflects their original genetic distances.

Results

Study sites

Three sites, spanning *c.* 12 km of coastline were investigated in the Terra Nova Bay area. Road Bay is very close to Tethys Bay (about 2 km) and Adélie Cove is located about 10 km southwards. Road Bay, up to 50 m depth, is characterized by sand and gravelly sand (fraction above 212 μm representing 94.2%) with an average scallop density of 58 ind m^{-2} (Chiantore *et al.* 2001). Inside Tethys

Bay (scallop density 23 ind m^{-2}) the slope is steeper with coarser sediments than the previous site. In Adélie Cove (scallop density 10 ind m^{-2}), a V-shaped bay located southward along the coast of Terra Nova Bay and isolated from the open ocean by a sill, fine sediments, particularly enriched in organic matter, are predominant. At all sites the sea ice breaks out every year (later in the season in Tethys Bay).

The west McMurdo Soundsites (that span *c.* 32 km of coastline) have different environmental characteristics, such as water circulation pattern, sea ice conditions and, above all, primary production. The southernmost site, New Harbour, is 24 km south of Spike Cape, and Dunlop Island is 8 km north of Spike Cape. At Dunlop Island (scallop density *c.* 12 ind m^{-1}) (Cummings *et al.* 2006) the bottom is a mix of cobbles, gravel and sand. Rocks, colonized by red encrusting algae, predominantly characterize the bottom of Spike Cape (where scallops were rare). The sea ice was *c.* 2.5 m thick during this investigation. New Harbour is a sandy embayment, dominated by the scallops but with a significant *Ophionotus* sp. presence. Berkman (1990) found that *Adamussium* densities were 40, 20 and 15 ind m^{-1} , at 10, 20 and 30 m depth respectively.

At New Harbour the sea ice only breaks out every 5–10 years (Norkko *et al.* 2005). During this investigation the ice was *c.* 3.5 m thick and the last known break-up was in 1999.

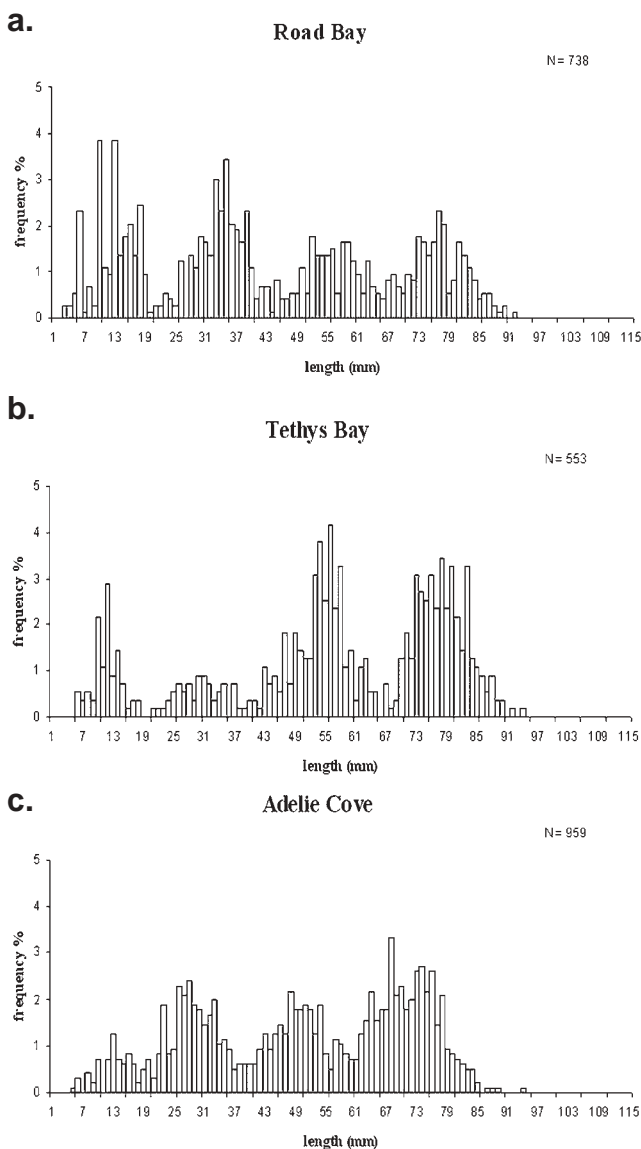


Fig. 3. Size frequency distribution of *Adamussium colbecki* at **a.** Road Bay, **b.** Tethys Bay and **c.** Adélie Cove, during 2001/02. Values were calculated on shell length.

Population structure

In the Terra Nova Bay area, populations studied show a multimodal size structure in all the sites. In Road Bay (Fig. 3a), during the summer 2001/02 average length \pm standard deviation is 24 mm \pm 11 for juveniles (shell length < 40 mm) and 66 mm \pm 13 for adults; younger individuals are well represented (53%). In Tethys Bay (Fig. 3b) (average length 20 mm \pm 10 and 67 mm \pm 13, for young and adults, respectively) and in Adélie Cove (Fig. 3c) (average length 26 \pm 8 and 63 \pm 12, young and adults, respectively) populations are mainly dominated by large-sized adults (79% and 66%, respectively), with a significant number of juveniles.

Table I shows means (with standard deviations) and medians of Terra Nova Bay populations for young and adult individuals separately. In all sites, a general consistency of

Table I. *Adamussium colbecki* population parameters recorded at Road Bay, Tethys Bay and Adélie Cove, during summer 2001/02. Values were calculated on shell length.

Site		Mean \pm st.dev (mm)	Median (mm)
Road Bay	Juv	23.7 \pm 11.0	26
	Ad	66.1 \pm 12.7	67
Tethys Bay	Juv	20.0 \pm 10.1	15
	Ad	66.5 \pm 13.1	70
Adélie Cove	Juv	25.8 \pm 8.2	27
	Ad	63.4 \pm 11.8	66

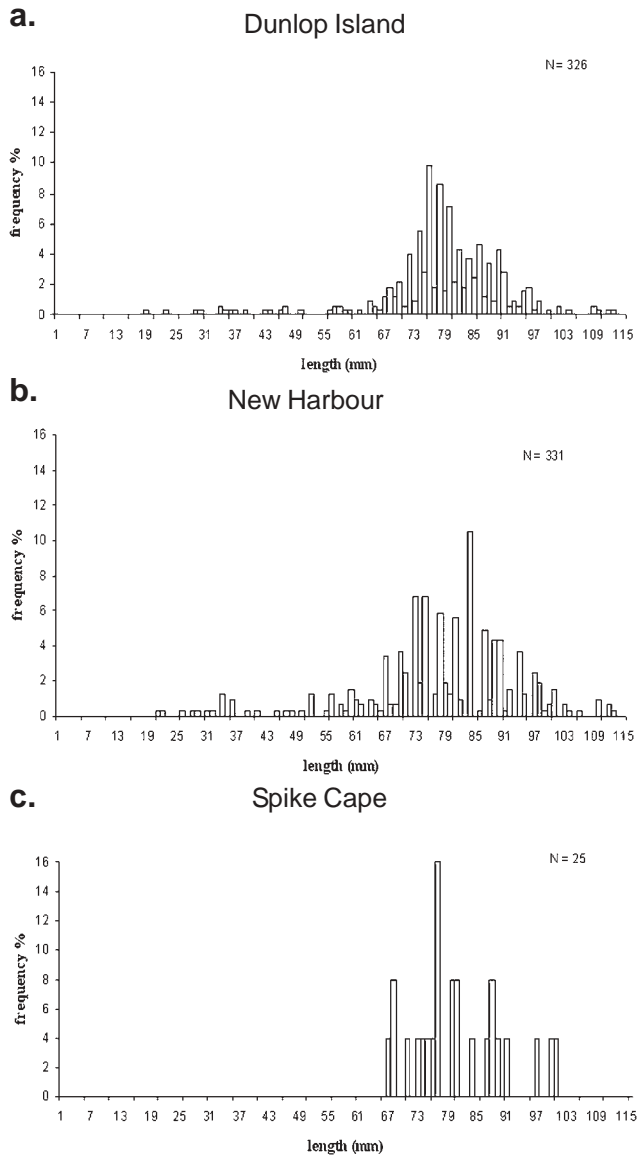


Fig. 4. Size frequency distribution of *Adamussium colbecki* at **a.** Dunlop Island, **b.** New Harbour and **c.** Spike Cape, during 2002/03. Values were calculated on shell length.

the large-sized individuals is evident, but some differences arise in the juveniles. Only in Road Bay is there a large presence of smallest individuals, while, in the other sites, recruitment did not occur in the sampling year.

In McMurdo Sound sites, during summer 2002/03, the *A. colbecki* populations show the dominance of large-sized individuals. Size distributions are always unimodal, with

Table II. *Adamussium colbecki* population parameters recorded at Dunlop Island, New Harbour and Spike Cape, during summer 2002/03. Reported values were calculated on shell length.

Site	Mean ± SD (mm)	Median (mm)
Dunlop Island	78.4 ± 13.2	79
New Harbour	78.0 ± 15.9	80
Spike Cape	80.1 ± 9.6	79

Table III. AMOVA analysis of the *A. colbecki* populations and fixation index statistics (ϕ statistics).

Source of variation %		ϕ Statistics
Total	100	$\phi S_T = 0.1787^*$
Among groups	14.3	$\phi C_T = 0.14302^*$
Within pops within groups	3.6	$\phi S_C = 0.04164^*$

P value < 0.0001 (after 10 000 permutations)

Table IV. Pairwise matrix reporting *F*_{st} values for each couple of *A. colbecki* populations.

Population	Dunlop Island	Spike Cape	New Harbour	Adélie Cove	Base
Dunlop Island	-				
Spike Cape	0.05644*	-			
New Harbour	0.06563*	0.02160*	-		
Adélie Cove	0.22501*	0.16427*	0.15742*	-	
Base	0.21333*	0.15227*	0.14951*	0.02535*	-

significant at *P* <= 0.05

Significance threshold values were adjusted with a sequential Bonferroni correction (Rice 1989) that allows correction for sampling error associated with multiple tests in order to reduce the group-wide type-I error rate

juveniles totally absent or extremely rare. In Dunlop Island (Fig. 4a) and New Harbour (Fig. 4b) the mean size is 78 mm (± 13 and ± 16 respectively), while in Spike Cape (Fig. 4c) it is a little bit higher (80 mm ± 10) (Table II).

Nuclear DNA analysis

Total sets of AFLP markers were obtained for 141 samples. Each of the three primer combinations used in AFLP

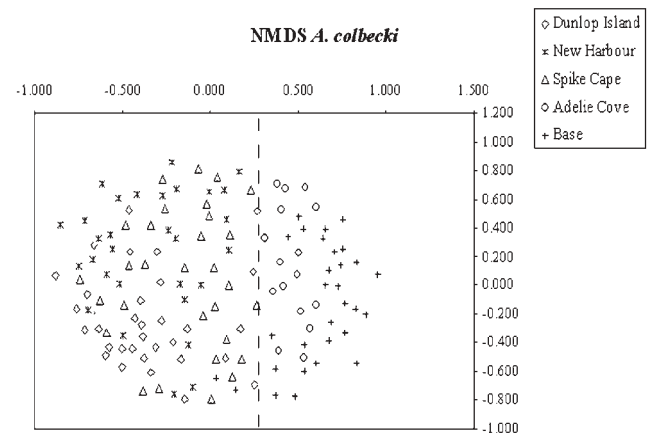


Fig. 5. Two-dimensional non-metric multidimensional scaling (nMDS). Genetic distances among individuals calculated on the base of AFLP profiles (presence/absence of bands shared between samples) were translated in an ordination procedure that finds those positions of *n* individuals in reduced space that best reflects their original genetic distances. Dunlop Island Spike Cape and New Harbour are in west McMurdo Sound; and “Base” (which grouped Road Bay and Tethys Bay) are in Terra Nova Bay.

analysis revealed a total of 193 polymorphic bands in the interval 200–450 BP.

A larger number of polymorphic loci is observed in Dunlop Island (84.45%) and New Harbour (84.97%) populations, while the number of polymorphic loci is smaller in Adélie Cove (64.76%).

The genetic distance matrix has been used to establish level of genetic divergence between populations. Table III shows that the hypothesis of panmixia (no population subdivision) must be rejected and that a substantial proportion of the overall variability can be explained by population subdivision among areas (14.30%).

ϕ_{st} analysis was carried out on each pair of populations to identify those samples which might account for deviation from panmictic conditions. In all cases the comparisons were significant (Table IV).

nMDS of the genetic distance matrix obtained from three primer pair combinations (Fig. 5) shows that all samples collected close together in McMurdo Sound are distinguished from samples collected in Terra Nova Bay. Differences between the two areas (McMurdo and Terra Nova Bay) are larger than those of populations within each area (Base, Adélie Cove and Dunlop Island, Spike Cape, New Harbour, respectively). In addition, the McMurdo sites data are more scattered than the Terra Nova Bay ones.

Discussion

Adamussium colbecki is numerically abundant in all studied sites, but differences have been found in the size-frequency distribution. Large-sized individuals are abundant in both McMurdo Sound and Terra Nova Bay. This could be due to the high longevity of this species, as well as a growth rate reduced with age (Berkman *et al.* 1990, Cattaneo-Vietti *et al.* 1997, Chiantore *et al.* 2003, Heilmayer *et al.* 2003). The presence of adults, belonging to different overlapping age classes, is characteristic of stable and K-selected populations (MacArthur 1960) and is linked to the coupling of high stability of the physical environment and the slow growth rate of the species. This leads to the evolution of efficient, stable populations with a low turn-over rate (White 1984) and large standing stocks, maximizing their share of food input under the constantly low temperature regime of the Southern Ocean (Brey & Clarke 1993).

In all Terra Nova Bay sites population structure shows a multimodal trend. In Road Bay young individuals are well represented; large-sized individuals mainly dominate populations in Tethys Bay and in Adélie Cove and successful recruitment events seem to be missing in recent years. In McMurdo, all population structures are characterized only by adult individuals, as shown by the unimodal trend observed in all three sites. In all sites no (or very few) juveniles are found, suggesting that successful recruitments are lacking for many years, or that the western McMurdo Sound is not a suitable recruitment area in

general, as other studies have already pointed out for other benthic organisms, such as the sea urchin *Sterechinus neumayeri* (Brey *et al.* 1995), the sea star *Odontaster validus* (McClintock *et al.* 1988), sponges (Dayton 1979) and other macroinvertebrates (Dayton 1989).

Such large differences between areas in juvenile abundance could be due to dispersal/settlement and larval availability, but also to different predation pressure on juveniles or food availability, as observed for other scallops from temperate waters (Broom & Mason 1978, Bayne & Newell 1983, McDonald & Thompson 1985), in this case linked to the extent of algal productivity under thicker sea ice with decreased light intensity moving south. Differences in population structure between McMurdo Sound and Terra Nova Bay could also be linked to the different sampling depth, but no data are available regarding the depth distribution of juveniles within the study sites.

Nuclear DNA markers, such as AFLPs data, provide information useful in characterizing the genetic structure of natural populations. By establishing the degree of differentiation between geographically isolated populations on the base of allele frequency distribution they allow us to analyse the exchange features of this species along the Victoria Land coast, and speculate about the existence of geographic/hydrographical barriers affecting larval distribution and the larval dispersal behaviour.

In our case, genetic analysis shows a differentiation between samples of Terra Nova Bay and McMurdo Sound. However, smaller differences are found between sites within the same geographic area, whereas genetic differences between populations of distant areas are an order of magnitude greater.

All this suggests that these populations may be effectively isolated from one another, notwithstanding the purported high dispersal capability of this species. This suggests that gene flow is very reduced or virtually absent, as the genetic variation observed among populations is not compatible with the hypothesis of *panmixia*, even at a small spatial scale. Such results are surprising given the pelagic habitat of the *A. colbecki* larva and its purported long duration in the water column. Yet, the larval transport along the coast may be affected not only by large geographical or hydrological barriers such as the Drygalski Glacier Ice Tongue and the Terra Nova Bay polynya, but also by smaller local barriers. In fact, at the small spatial scale of Terra Nova Bay, barriers could be represented by the embayments where the populations were sampled, that could be set apart from the general circulation pattern of surface and sub-surface waters in Terra Nova Bay, flowing counterclockwise along the Campbell Glacier, to the Gerlache Inlet and then turning south (Stocchino & Lusetti 1990, Stocchino & Manzella 1991), that should assure mixing of larvae from the northern to the southern sites. In particular, the slightly lower number of polymorphic loci observed in Adélie Cove could be explained by an isolation of the water column occurring in

the winter, due to the ice coverage in addition to the presence of a sill (Povero *et al.* 2001).

Alternatively, veligers could remain trapped under the pack ice during the winter, where food and shelter are available. Additional food supplies for Antarctic pelagic larvae are reported (Olson *et al.* 1987, Pearse *et al.* 1991), such as dissolved organic matter (Shilling & Bosch 1994) and bacterioplankton (Rivkin *et al.* 1986) are also abundant during the winter and it is possible that *Adamussium* larvae could rely on this kind of food under ice cover.

Conclusions

Demographic data reported in this work show that size frequency distributions are quite different from site to site along the Victoria Land Coast, even at a small spatial scale, and that large sized individuals are usually well represented.

Recruitment is a sporadic phenomenon, not synchronous in space and time and the hypothesis of *panmixia* among studied populations is rejected. On the basis of this evidence, we need to reconsider the effective dispersal potential of this species, testing the real duration of the larval stage and the effective transport by currents that could be limited to the short open sea season.

This work suggests an approach for future studies with which to analyse the degree of polymorphism of single cohorts to understand their fate and their affinity to local adult populations.

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