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Genetic diversity and gene flow in collapsed and healthy abalone fisheries

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Abstract

Overexploitation of marine species invariably results in population decline but can also have indirect effects on ecological processes such as larval dispersal and recruitment that ultimately affect genetic diversity and population resilience. We compared microsatellite DNA variation among depleted and healthy populations of the black-lip abalone *Haliotis rubra* from Tasmania, Australia, to determine if over-fishing had affected genetic diversity. We also used genetic data to assess whether variation in the scale and frequency of larval dispersal was linked to greater population decline in some regions than in others, and if larval dispersal was sufficient to facilitate natural recovery of depleted populations. Surprisingly, allelic diversity was higher in depleted populations than in healthy populations ($P < 0.05$). Significant subdivision across hundreds of metres among our sampling sites ($F_{ST} = 0.026$, $P < 0.01$), coupled with assignment tests, indicated that larval dispersal is restricted in all regions studied, and that abalone populations across Tasmania are largely self-recruiting. Low levels of larval exchange appear to occur at the meso-scale (7–20 km), but age estimates based on shell size indicated that successful migration of larvae between any two sites may happen only once every few years. We suggest that genetic diversity may be higher in depleted populations due to the higher relative ratio of migrant to self-recruiting larvae. In addition, we expect that recovery of depleted abalone populations will be reliant on sources of larvae at the meso-scale (tens of km), but that natural recovery is only likely to occur on a timescale unacceptable to fishers and resource managers.

Keywords: connectivity, conservation, fisheries management, microsatellite DNA, larval dispersal, self-recruitment

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Introduction

The sustainability of exploited populations is a primary goal in the management of natural resources. In the marine realm, this can be especially challenging as most extractive industries operate remotely (i.e. trawling, trapping) and, due to the nature of the marine environment, exact estimates of population size, the geographical extent of populations and other important demographic parameters are almost impossible to obtain. While the management of some fisheries addresses biological sustainability requirements through quota systems or designation of no-take areas to protect brood stock, many marine fisheries around the world continue to decline or have collapsed through over-fishing (Hilborn *et al*. 2003). Indeed, current estimates indicate 29% of the world's fisheries have collapsed and are no longer economically viable, and these levels are predicted to rise (Worm *et al*. 2006).

One of the major issues associated with fisheries management is optimizing yield without compromising ecosystem or population processes (Fogarty *et al*. 1991; Caddy & Seijo 2005; Worm *et al*. 2006). Population decline beyond a critical point may be detrimental for at least two reasons. First, Allee effects, whereby fitness declines with population size, may result in reproductive and recruitment failure and severely constrain recovery potential of a population (e.g. Levitan & Sewell 1998). Second, over-fishing

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may lead to reduced genetic diversity in a population (Hauser *et al*. 2002), and small populations will also be susceptible to further loss of genetic diversity through drift (e.g. Allendorf & Luikart 2007).

In the absence of active intervention or enhancement, the recovery of collapsed fisheries will rely entirely on new recruitment. Understanding of the likely source and abundance of new recruits has therefore become a critical goal of fisheries science and management. For some fisheries, such as large fin-fish, direct tagging of individuals to understand emigration or immigration is possible (e.g. Davis & Stanley 2002; Block *et al*. 2005). However, for commercially important benthic invertebrate species the primary dispersal phase is usually a microscopic, pelagic larva which is difficult to tag and close to impossible to track. For such species, the application of genetic techniques has proven critical for understanding connectivity among populations (Hellberg *et al*. 2002).

Marine molluscs of the family Haliotidae, collectively referred to as abalone, represent one such group. Adult abalone are benthic, with small home ranges (Prince 1989), and the planktonic larvae are the primary dispersal phase (McShane 1992). Abalone are economically important, with commercial fisheries existing in seven countries, and form an important global industry worth around $US100 million. However, several major abalone fisheries have collapsed in recent decades with no, or only marginal, recovery. The most notable collapse was the Californian commercial abalone fishery which once produced > 2000 t/year but which was closed in 1997 and has still not recovered (Karpov *et al*. 2000). In fact, four of the five target species within that fishery are either listed as endangered or considered 'species of concern' (Micheli *et al*. 2008). Genetic and ecological studies have shown that, for many abalone species, larval dispersal is likely to be limited, and this has been cited as the major reason for slow recovery following over-fishing (e.g. Prince *et al*. 1987, 1988; McShane *et al*. 1988; Miner *et al*. 2006; Temby *et al*. 2007; Gruenthal & Burton 2008).

In Tasmania, Australia, black-lip abalone (*Haliotis rubra*) represents the largest wild abalone fishery in the world, supplying more than 25% of the global catch. Historically, the Tasmanian fishery production has remained relatively constant. However, despite conservative management, several depletion episodes over the past three decades have resulted in contractions of the fishery, with some reef systems failing to recover to prior productivity levels (Tarbath *et al*. 2007). It remains a mystery why, in Tasmania, some areas recover while others remain depleted. Do the different Tasmanian populations of *H. rubra* experience different dispersal or recruitment regimes? Or is the collapse of some regions linked to other biological or physical phenomena such as environmental change or loss of genetic variation?

Limited dispersal of *H. rubra* larvae is well accepted, although there is likely to be at least some occasional long-distance dispersal that has effectively maintained genetic homogeneity around Tasmania (Elliott *et al*. 2002; Temby *et al*. 2007). However, the frequency, directionality and distance of those dispersal events remain unknown. In this study, we compare genetic variation in two key areas of the Tasmanian abalone fishery — one that continues to be highly productive, and another that has failed to recover from a depletion episode in the mid 1980s — to determine if there is any evidence of a link between larval dispersal processes and recovery in the two regions. We also assess gene flow among abalone populations in the two regions to determine the level and directionality of connections among abalone populations and hence the role of dispersal in the future recovery of collapsed fisheries.

Materials and methods

Study sites and fishing background

Two regions were targeted for this study. The Actaeons region in southeastern (SE) Tasmania (Fishing Blocks 13 and 14, Fig. 1) represents a resilient, highly productive part of the abalone fishery. Annual catches from this region have been relatively consistent since 1975, averaging 289.9 ± 16.6(SE) and 177.4 ± 12.5(SE) tonnes for Blocks 13 and 14, respectively (Fig. 1). An abalone fishery reserve at George III Rock has existed in this region since 1985.

In contrast, parts of the northeastern (NE) region of Tasmania (Fishing Block 30, Fig. 1) have exhibited a classic boom-and-bust pattern, with annual catches peaking in the mid 1980s (298 tonnes) and subsequently declining to < 10% of the long-term average (Fig. 1). Block 30 was closed to commercial fishing in 2006 to facilitate recovery. Interestingly, this depleted area is adjacent to one of the most productive fishing grounds in the NE region (Fishing Block 31, Fig. 1).

Sample collection and population data

A total of 602 abalone was collected for microsatellite analysis. Sampling was according to a spatially replicated, hierarchical design so as to elucidate the spatial scale of population structure; 30–35 abalone were collected from each of three sites, within each of three locations across two geographical regions in Tasmania (18 sites in total; Fig. 1). Sites were areas typically 20 × 20 m in size, and replicate sites within each location were 100–200 m apart. The locations within each region were separated by 7–10 km (Fig. 1). Collections were made in June 2006 (NE region) and January 2007 (Actaeons, SE region). Two of the locations in the NE region (Dave's Fancy and Policemans Point) were classed as 'collapsed' (no longer capable of supporting a

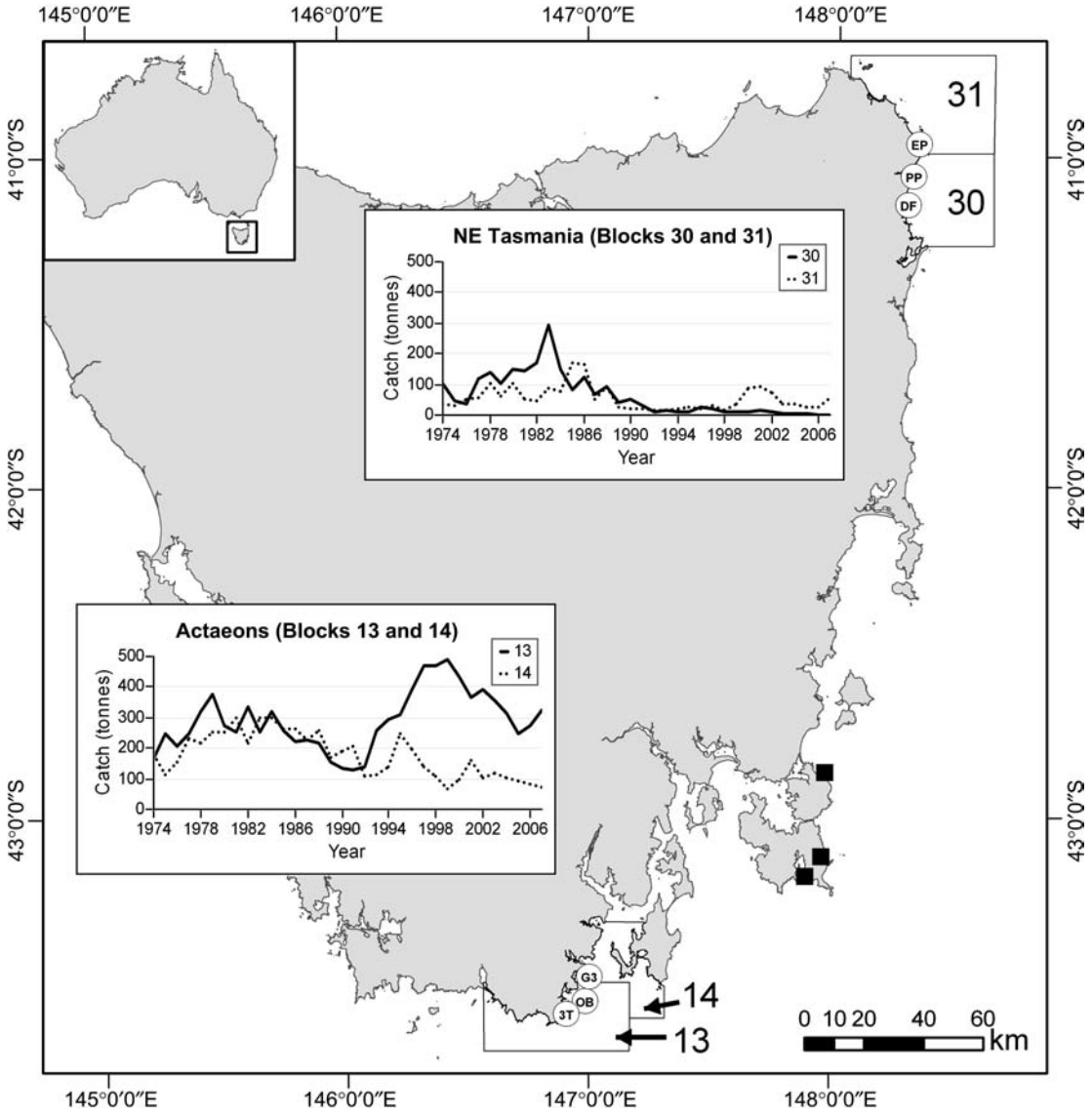

Fig. 1 Study locations and abalone (*Haliotis rubra*) catch history in Tasmania, Australia. The numbered areas represent four of the current fisheries management blocks in Tasmania, and the graphs show the total catches within relevant blocks since 1975 (from Tarbath *et al*. 2007). The coded circles denote each location within northeastern (NE) Tasmania and the Actaeons regions where we sampled abalone for this genetic study. In NE Tasmania (Blocks 30 and 31) the three locations are EP, Eddystone Point; PP, Policemans Point; and DF, Dave's Fancy. In the Actaeons (Blocks 13 and 14) the three locations are G3, George III Rocks; OB, Outer Breaks; and 3T, Three Tree Reef. Within each of the six locations we sampled from three sites (each separated by approximately 100–200 m). The squares denote three locations on the Tasman Peninsula sampled in an earlier study (Temby *et al*. 2007).

commercial fishery), whereas the remaining four locations (Eddystone Point in the NE region, and George III Rock, Outer Breaks and Three Tree Reef in the Actaeons) were classed as 'healthy' populations (i.e. continue to support a commercial fishery or in a no-take fishery exclusion area).

Within each site, abalone were collected from as small an area as possible, typically 20 m × 20 m, and in the collapsed populations, our collections included all emergent individuals within the area. A small sliver of foot muscle was removed from each abalone and preserved immediately in ethanol for genetic analysis. Abalone were then returned to the sampling site. Foot-muscle tissue samples were stored at –20 °C prior to DNA extraction.

The length of each abalone was measured to the nearest mm using a SciElex electronic measuring board (www.scielex.com.au). Abalone size data were used to classify the reproductive status of individuals whereby all

animals ≤ 80 mm length were considered immature (Tarbath *et al*. 2001). Immature animals in the NE region were classed in one of four cohorts based on estimated annual growth rates of 20 mm (Haddon *et al*. 2008).

Genotyping

Genomic DNA was extracted from each abalone sample using Qiagen DNEasy kits, according to the manufacturer's protocol. For each abalone, we amplified seven microsatellite loci representing a mix of di- [*cmrHr1.14* and *cmrHr1.24* (Evans *et al*. 2000)], tri- [*Hrub2.B01* (Baranski *et al*. 2006b)] and tetra- [*cmrHr2.14* (Evans *et al*. 2000), *Hrub6.C04, Hrub7.B11, Hrub9.H11* (Baranski *et al*. 2006a)] nucleotide repeats. The seven loci are distributed among ≥ six different putative chromosomes mapped by Baranski *et al*. (2006a) and are therefore unlikely to be linked.

Polymerase chain reaction (PCR) amplifications for all seven loci were in a final volume of 25 μL and contained 2.5 mM $MgCl_2$ (Promega), 5 pmol (locus *cmrHr1.24*) or 10 pmol (all other loci) of each primer (Sigma Genosys), 0.2 mM of each dNTP (Promega), PCR buffer (10 mM Tris-HCl, 50 mM KCL, 0.1% Triton X-100), 2 units TAQ polymerase (Promega) and ~50–100 ng of genomic DNA template. All forward primers were 5′ end-labelled with WellRED dyes (D2, D3 or D4). PCR products were sized by comparison to an internal size standard labelled with D1 on a Beckman Coulter CEQ8000XL automated sequencer. Loci with different labels and/or nonoverlapping size ranges were coplexed on the sequencer in the following combinations: (i) *cmrHr1.24/Hrub7.B11/Hrub6.C04*; (ii) *Hrub2.B01/Hrub9.H11*; and (iii) *cmrHr2.14/cmrHr1.14*. Forty-eight representative samples in two different loading ratios for each coplex combination, were initially analysed in order to spectrally calibrate sequencing software and assess genotyping error rates. Scoring discrepancies were only detected at locus *7.B11*, consequently data from this locus was not analysed further.

Alleles were scored according to the PCR fragment size. For all loci, the size of fragments and inferred number of repeats was compared against GenBank sequence and allele sizes recorded in other published studies that have utilized these loci (Evans *et al*. 2000; Elliott *et al*. 2002; Baranski *et al*. 2006a; Temby *et al*. 2007). In some instances, allele sizes recorded in our genotyping varied by one or two bases to that expected based on sequence data and/or the sizes recorded in other studies. This seems to be a common occurrence across microsatellite studies performed in different laboratories, at different times, labelled with different dyes and analysed on different systems with varying gel or capillary temperatures and migration algorithms (e.g. Presson *et al*. 2006; Pasqualotto *et al*. 2007). To enable a direct comparison specifically between the data generated here and that of Temby *et al*. (2007) from the Tasman Peninsula, allele-size adjustments were made at loci *cmrHr1.14* (+ one base), *cmrHr1.24* and *cmrHr2.14* (+ two bases).

Comparison of genetic diversity between collapsed and healthy populations

Where populations have declined due to fishing pressure, we might expect to see reduced levels of genetic variation. We tested the hypothesis that genetic diversity is lower in collapsed vs. healthy populations by ANOVA, based on: (i) allelic diversity [the total number of alleles across loci (tN_a) and the average number of alleles/locus (mN_a)]; (ii) the number of rare alleles (where frequency ≤ 0.05); and (iii) the expected heterozygosity (H_E).

We then assessed the genetic structure within all *Haliotis rubra* populations in two ways. First, we determined if the frequency of genotypes at each locus matched expectations of Hardy–Weinberg equilibrium for randomly mating populations with χ^2 tests using the software Genepop version 3.4 (Raymond & Rousset 1995) and following Bonferroni correction of significance levels to allow for multiple tests. We second calculated values of Wright's fixation index (f) to determine if departures from equilibrium represented heterozygote deficiencies (i.e. $f > 0$) or excesses (i.e. $f < 0$). Where heterozygote deficiencies were present, we tested for the presence of null alleles using Micro-checker (Van Oosterhout *et al*. 2004). Where there was evidence of null alleles, we adjusted allele frequencies (based on the Oosterhout correction algorithm), labelling the null allele size as the largest allele +1 repeat. The adjusted data set was then used for the remaining data analyses.

Connectivity and the scale of population subdivision

We used *F*-statistics, calculated as Weir and Cockerham's θ, to examine levels of genetic differentiation among all sites using FStat. Mean F_{ST} was calculated by jack-knifing over loci. Departures from panmixis among sites were tested using 95% CI calculated by bootstrapping over loci. Because microsatellites invariably lead to low F_{ST} estimates due to high amounts of within-population genetic variation, we also calculated a standardized measure of F_{ST} (F'_{ST}) according to the methods described by Hedrick (2005) and Meirmans (2006). Additionally, we used hierarchical *F*-statistic analyses to partition genetic variance; among sites within location (F_{SL}), among locations within regions (F_{LR}), and among locations (F_{LT}). We also analysed our data in combination with the data of Temby *et al*. (2007) for three loci *cmrHr1.14*, *cmrHr 1.24* and *cmrHr 2.14* to extend the geographical spread of our results (to include the Tasman Peninsula, Fig. 1) and to include an additional Tasmanian region where abalone populations are fished sustainably.

Migration and directionality of gene flow

We used assignment tests to determine the proportion of individuals self-recruiting to a population as well as to identify which individuals were first-generation migrants into each population (here, we consider migration to have occurred through larval dispersal and hence migrants to be individuals that have recruited into a population following the dispersal of a larva from a different population). Assignment tests were done in the software package Geneclass 2 (Piry *et al*. 2004) using the resampling algorithm of Paetkau *et al*. 2004 (with exclusion probability of 0.01), and they were based on the 'L_home' likelihood estimation (to account for the fact that not all possible source populations were sampled) and with the probability of assignment based on a threshold of $P < 0.05$ and on 10 000 simulated individuals. Data from the two regions (NE Tasmania and Actaeons) were analysed separately as we considered it unlikely that there would be direct larval dispersal between the two regions based on the results of F_{ST} analyses.

Individuals identified as first-generation migrants to each site were removed from the data set and then reassigned back to the remaining sample to determine their most likely population of origin. Where the re-assignment indicated that an abalone may have originated from more than one population, we considered the source population to be that with the highest probability of assignment. This data was then used to determine frequency and directionality of larval dispersal among sites. Using shell size as a proxy for age, we then determined the proportions of each generation (that would have recruited in the previous 3–6 years) that originated from self-recruitment or migration within the NE region. As most individuals sampled in the Actaeons were mature and could not be reliably aged based on shell size it was not possible to conduct this assessment in the SE region.

For the assignment tests we excluded Policemans Point Site 2, in the NE region, as we found no reproductive adults within this site (all animals seen and collected were < 80 mm length, Fig. 2), and we therefore assumed that all individuals were highly likely to be migrants. Instead, for Policemans Point Site 2 we used assignment tests to determine the likely source population for those individuals that were < 40 mm diameter and that were likely to have recruited to the site 12–24 months prior to our collections and during the period in which the area was closed to fishing. For these abalone, we considered it highly unlikely that the parents would have been removed from the site by fishers. Excluding natural mortality, the parents of these individuals were therefore likely to be from a different site. We used the results from this assignment test to determine the source and directionality of larval dispersal to Policemans Point Site 2.

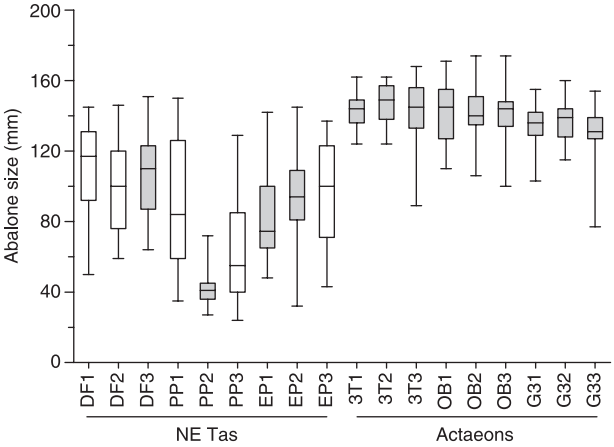

Fig. 2 Size structure of abalone, *Haliotis rubra*, from 18 study sites in Tasmania, Australia. Lines represent the maximum and minimum size of abalone at each site, while the bars represent the 25th and 75th quartile of size ranges, with the median indicated within each bar.

Results

Abalone size and age

The average size of abalone was smaller in the NE than in the SE populations (Fig. 2), and this is in part due to a higher proportion of smaller animals in the sample associated with less cryptic reef types. Growth rates and size at maturity are also slightly lower in the warmer waters of northern Tasmania (Tarbath *et al*. 2001) in comparison with the cooler southern areas. With the exception of Policemans Point Site 2, the maximum size of animals was similar across all sites, although few small animals were collected in the Actaeons region (Fig. 2), primarily due to the abundance of emergent adults and low probability of encountering cryptic juveniles during random collections in healthy populations.

At Policemans Point Site 2, all individuals were < 80 mm in length, and therefore classified immature. Almost half (46%) of these were from a cohort likely to have recruited between one and two years prior to collection (2004–2005), and another 43% from the previous year's cohort. It appears that recruitment prior to 2003 at this site was limited, given that our collections included all emergent animals (and most cryptic individuals) within the area.

Genetic diversity in collapsed vs. healthy populations

Although we expected that genetic diversity would be lower in areas where abalone had been heavily fished, we found, in fact, significantly higher levels of genetic variability in the collapsed populations compared with the healthy populations (Table 1). Both the total number of alleles (tN_a) and average alleles/locus (mN_a) were significantly higher in collapsed than

Table 1 Genetic diversity measures for abalone (*Haliotis rubra*) populations sampled in two regions of Tasmania, Australia. *N*, number of individuals genotyped; tN_a, the total number of alleles across loci; mN_a, the average number of alleles/locus; H_E, expected heterozygosity; N_E, northestern

	NE Tasmania			Actaeons											
	Dave's Fancy			Policemans Point			Eddystone Point			Three Tree Reef			Outer Breaks			Geroge III Rock		
	Site 1	Site 2	Site 3	Site 1	Site 2	Site 3	Site 1	Site 2	Site 3	Site 1	Site 2	Site 3	Site 1	Site 2	Site 3	Site 1	Site 2	Site 3
N	35	34	34	35	34	35	30	35	35	32	31	32	32	35	33	31	31	28
tN_a	52	49	40	44	44	47	40	42	44	41	44	45	39	45	48	39	44	40
mN_a	8.7	8.2	6.7	7.3	7.3	7.8	6.7	7.0	7.3	6.8	7.3	7.5	6.5	7.5	8.0	6.5	7.3	6.7
Private alleles	3	2	1	3	0	3	0	1	2	2	2	1	0	1	0	0	0	0
Rare alleles/locus	5.0	4.7	2.3	3.2	3.5	3.7	2.2	3.7	3.0	2.3	2.8	3.7	3.2	3.0	3.8	2.0	3.7	2.5
H_E	0.57	0.62	0.53	0.57	0.57	0.58	0.57	0.49	0.59	0.59	0.63	0.58	0.59	0.57	0.58	0.60	0.53	0.58

in healthy populations ($tN_a - F_{1,4} = 8.4$, $MS_{Residual} = 13.05$, $P = 0.04$; $mN_a - F_{1,4} = 8.4$, $MS_{Residual} = 0.363$, $P = 0.04$) although there was no significant difference in the levels of expected heterozygosity between collapsed and healthy populations ($H_e - F_{1,4} = 0.03$, $MS_{Residual} = 0.001$, $P = 0.87$). Surprisingly, more than half (57%) of all private alleles were found in populations considered to be collapsed, even though they represented only 35% of the total sample. A similar pattern was evident when we considered rare alleles, whereby collapsed populations had significantly more rare alleles (mean = 3.72 ± 0.4 SE) than healthy populations (mean = 2.99 ± 0.2 SE) ($F_{1,4} = 8.3$, $MS_{Residual} = 0.69$, $P = 0.045$).

Values of Wrights fixation index (f) were low across most abalone populations. Heterozygote excess was apparent in only 24 of 108 single-locus × population tests, and heterozygote deficits in 82 cases. However, in only 21 of these (all heterozygote deficits) were significant departures from Hardy–Weinberg equilibrium detected ($P < 0.05$), and only three of these remained significant after Bonferroni correction of significance levels. All three of these were heterozygote deficits at locus *Hrub6.CO4* (Table 2). Null alleles were predicted to exist at three loci; *Hrub6.C04*, *CmrHr2.14* and *CmrHr1.14*.

Connectivity among abalone populations

We found significant genetic subdivision among all abalone populations sampled, consistent with limited gene flow among sites ($F_{ST} = 0.026$, $P < 0.01$). When F_{ST} values were standardized to account for high within-population variation, levels of subdivision were moderate ($F'_{ST} = 0.065$, Table 3). Notably, however, most of this subdivision was being driven by a single locus — *CmrHr1.24* (Table 3) — suggesting that this locus may well be under selection (e.g. Slatkin 1995). When we recalculated *F*-statistics based only on five loci (i.e. excluding *CmrHr1.24*) we still found low but significant subdivision among all sites ($F_{ST} = 0.009$, $P < 0.01$, $F'_{ST} = 0.027$, Table 3).

Hierarchical *F*-statistic analysis indicated that most of the subdivision occured at our smallest sampling scale, i.e. among sites within locations ($F_{SL} = 0.026$, $P < 0.01$), and this was the case whether locus *CmrHr1.24* was included or excluded from the analysis (Table 3). Interestingly, although there was no significant subdivision between the two regions based on the six-locus analysis ($F_{RT} = 0.0003$), when we removed locus *CmrHr1.24* from the analysis we did detect small but significant subdivision between NE Tasmania and the Actaeons ($F_{RT} = 0.002$, $P < 0.05$) (Table 3).

An additional *F*-statistic analysis including abalone populations from the Tasman Peninsula extended the generality of these findings, although it was based on only three loci. There was significant subdivision among sites ($F_{ST} = 0.048$, $P < 0.01$), and hierarchical analysis again indicated that

Table 2 Values of Wright's fixation index (f) for *Halitotis rubra* at 18 sites in Tasmania, Australia. Positive values represent heterozygote deficits and negative values represent heterozygote excess. Significant departures from Hardy–Weinberg equilibrium are denoted as $^{*}P < 0.05$, $^{**}P < 0.01$ and $^{***}P < 0.001$. Figures in bold remain significant after Bonferroni correction of significance levels. N_E, northeastern

	NE Tasmania								
	Dave's Fancy			Policemans Point			Eddystone Point		
Locus	Site 1	Site 2	Site 3	Site 1	Site 2	Site 3	Site 1	Site 2	Site 3
6.CO4	0.44***	0.39*	0.18	**0.5*****	**0.43*****	**0.33****	0.26*	0.2*	0.25*
CmrHr2.14	0.12	0.12	0.33	–0.09	–0.02	0.18*	0.06	0.26	0.25*
9.H11	0	–0.06	–0.07	0.02	–0.05	–0.05	–0.01	0.06	0.01
CmrHr1.24	–0.07	0.08	0.12	0.13	0.03	–0.11	0	0.12	–0.06
CmrHr1.14	–0.08	0.16	0.28	0.34*	0.04	0.13	0.01	–0.04	0.12
2.B01	0.06	–0.1	0.1	0.04	0.04	0.01	0.02	–0.03	0.03

	Actaeons								
	Three Tree Reef			Outer Breaks			Geroge III Rock		
Locus	Site 1	Site 2	Site 3	Site 1	Site 2	Site 3	Site 1	Site 2	Site 3
6.CO4	0.25	0.37***	0.02	0.26	0.22	0.46***	0.19*	0.22	**0.72*****
CmrHr2.14	0.06	0.24*	0.07	0.12	0.13	0.14	–0.06	0.14	0.09
9.H11	–0.06	0.03	0.16	0.03	0.05	0.04	0.07	0.08	0.13
CmrHr1.24	0.25	–0.12	–0.03	0.06	0.09	–0.08	0.03	0.07	0.07
CmrHr1.14	–0.12	0.29***	0.09	0.04	0.05	0.15	–0.16	0.17	0.32
2.B01	–0.01	–0.04	0.11	0.14**	0.24	0.12	0.23	0.05*	–0.01

Table 3 Results from *F*-statistic analyses of 18 Haliotis rubra populations from two regions in Tasmania – NE Tasmania and Actaeons. Overall[1]– F_{ST} over all loci calculated based on six loci. Overall[2] – F_{ST} over all loci calculated excluding locus *CmrHr1.24*. Significant genetic subdivision is denoted as $^{*}P < 0.05$, $^{**}P < 0.01$

	6.CO4	*CmrHr2.14*	*9.H11*	*CmrHr1.24*	*CmrHr1.14*	*2.B01*	Overall[1]	Overall[2]
F_{ST}	0.023	0.005	0.001	0.2	0.012	0.001	0.026**	0.009**
F'_{ST}	0.056	0.017	0.004	0.28	0.019	0.009	0.065	0.027
Hierarchical analysis								
F_{SL}	0.023	0.006	0.0004	0.165	0.011	0.005	0.026**	0.008**
F_{LR}	0	0.0005	0.0001	0.001	0	0.005	0.0002^{ns}	0.000**
F_{RT}	0.0005	0.0009	0.0017	0	0	0.004	0.0003^{ns}	0.002*

most of the subdivision was at the smallest scale (among sites within locations, $F_{SL} = 0.047$, $P < 0.01$) with little variation either among locations or between regions (Table 4). Again, much of the subdivision was driven by locus *CmrHr1.24* although removal of this locus did not alter the conclusions or level of significance overall ($F_{ST} = 0.022$, $P < 0.01$) and, as seen in the two-region analysis, did result in significant subdivision at the regional scale ($F_{RT} = 0.003$, $P < 0.01$). As this final comparison was based only on two loci, results need to be treated with caution; however, it is pertinent that the same conclusions can be drawn from the two-locus data set from three regions as the five-locus data set from two regions.

Table 4 Results from *F*-statistic analysis among 27 *Haliotis rubra* populations from three regions in Tasmania: northeastern Tasmania, Actaeons and Tasman Peninsula. The analysis incorporates data on Tasman Peninsula abalone from Temby *et al*. (2007). Significant genetic subdivision is denoted as $^{**}P < 0.01$

	CmrHr2.14	*CmrHr1.24*	*CmrHr1.14*	Overall
F_{ST}	0.009	0.131	0.036	0.048**
F'_{ST}	0.03	0.197	0.062	0.093
Hierarchical analysis				
F_{SL}	0.009	0.117	0.038	0.047**
F_{LR}	0	0.002	0.019	0.005^{ns}
F_{RT}	0.001	0	0.005	0^{ns}

Table 5 Assignment of abalone, *Haliotis rubra*, to site of origin. Results show the proportion of individuals collected from each site that was assigned to each potential source population for the northeastern (NE) region of Tasmania. Italicised values represent the proportion of individuals sampled at each site that originated from the site (i.e. self-recruitment). Note the results for Policemans Point Site 2 are from a separate assignment test that assumed all abalone at the site were migrants due to the absence of reproductive adults at this site

	Source population								
Sample population	DF1	DF2	DF3	PP1	PP3	EP1	EP2	EP3	unassigned
Dave's Fancy 1	*97.1*							2.9	
Dave's Fancy 2		*97.1*			2.9				
Dave's Fancy 3			*94.1*		2.9				2.9
Policemans Point 1				*91.4*		2.9			5.7
Policemans Point 2		31.3				50.0		18.8	
Policemans Point 3					*100.0*				
Eddystone Point 1						*100.0*			
Eddystone Point 2		2.9			5.7		*91.4*		
Eddystone Point 3								*97.1*	2.9

Table 6 Assignment of abalone, *Haliotis rubra*, to site of origin. Results show the proportion of all individuals from each site that was assigned to each potential source population for the Actaeons region in southeastern (SE) Tasmania. Italicised values represent the proportion of individuals sampled at each site that originated from the site (i.e. self-recruitment)

	Source population									
Sample population	3T1	3T2	3T3	OB1	OB2	OB3	GIII1	GIII2	GIII3	Unassigned
Three Tree Reef 1	*96.9*									3.1
Three Tree Reef 2		*93.5*					3.2			3.2
Three Tree Reef 3			*90.6*				6.3			3.1
Outer Breaks 1				*96.9*			3.1			
Outer Breaks 2					*97.1*		2.9			
Outer Breaks 3						*93.9*	3.0		3.0	
George III Rock 1							*100.0*			
George III Rock 2			3.2					*96.8*		
George III Rock 3		3.4							*96.6*	

Migration

Assignment tests indicated that abalone populations were largely self-seeding; 90–100% of individuals in the Actaeons region and NE Tasmania region (excluding Policemans Point Site 2) were assigned to their parent population (Tables 5 and 6). Interestingly, of the 12 individuals identified as first-generation migrants in the Actaeons region, seven of those were assigned to sites at George III Rock, suggesting the abalone no-take reserve is an important source of larval recruits (Table 6). Two individuals migrated from Three Tree Reef to George III Rock while two other individuals could not be reliably assigned to any of the sampling sites and may have originated from an unsampled population (Table 6).

In the NE region, 11 individuals were identified as first generation migrants. Four of these were assigned to Policemans Point Site 3 and three others to Dave's Fancy Site 1 and Eddystone Point Sites 1 and 3, respectively. Four individuals could not be assigned to any of the sampled populations. Of the 16 abalone that had recently recruited to Policemans Point Site 2 (i.e. those ≤ 40 mm), most appear to have originated from the north (69%), with 11 assigned to sites at Eddystone Point. The remaining five abalone were all assigned to Dave's Fancy Site 2 (Table 5).

Interestingly, for the first-generation migration events identified through the assignment tests, there were no instances where larvae have dispersed successfully between sites within each of the locations. All migration events recorded were between sites in different locations, i.e. across 7–20 km (Fig. 3). In addition, for each of the two regions studied, the proportion of larvae that dispersed rather than self-recruited was relatively consistent among years. In the NE region, nine of the first-generation migrants could be confidently aged based on size. Of these, one, two, four and two individuals would have recruited over the

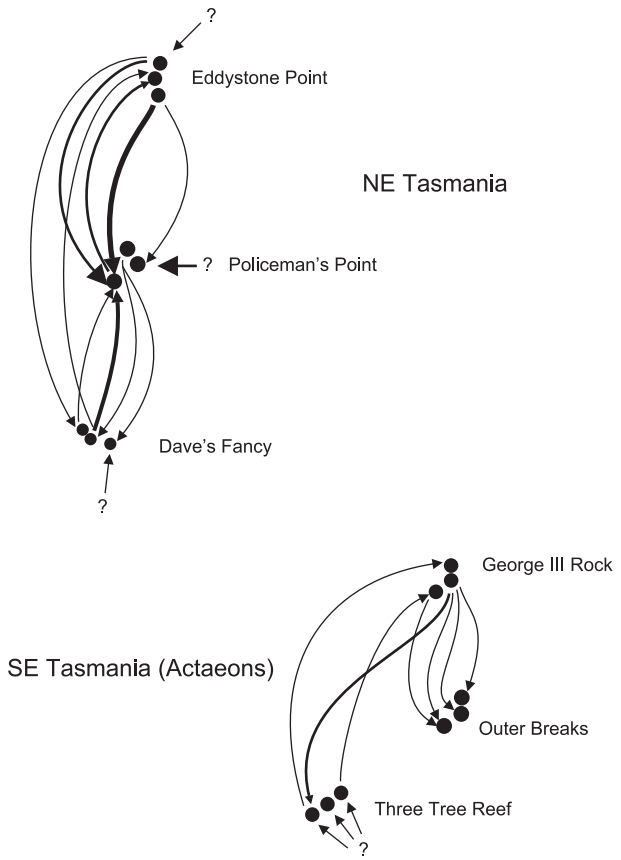

Fig. 3 Migration pathways of *Haliotis rubra* larvae among sites and locations, as indicated from assignment tests. The thickness of arrows is proportional to the number of larvae dispersing between sites where the thinnest line represents a single larva, and the thickest line represents eight larvae. '?' represent migrant larvae that could not be assigned to any of the sampled sites. Note that our results indicate that most larvae self-recruit (see Tables 5 and 6) with only 5–10% of all larvae successfully migrating between populations.

preceding three, four, five and six years, respectively. This represents 2%, 3%, 8% and 5% of each year–class across our entire sample (an average of 4.5% migration in each year).

Discussion

The failure of abalone populations in NE Tasmania to recover from depletion is unlikely to be linked to differing patterns of gene flow or larval dispersal within different regions. We found similar scales of population subdivision, based on microsatellite DNA data, both within the healthy fishery in the Actaeons region as well as the depleted NE region. These results are also consistent with our earlier findings from a third region, the Tasman Peninsula (Temby *et al*. 2007), indicating that small-scale population subdivision (i.e. across hundreds of metres) is most likely widespread in *Haliotis rubra*. Why some regions are apparently more resilient to fishing pressure than others remains unclear as all three regions in Tasmania have also been subject to identical management regimes since the inception of the fishery (in the early 1960s). Clearly, resilience is linked to factors other than differential larval dispersal or fishery management.

Scale of larval dispersal in H. rubra

Our results indicate that *H. rubra* populations are largely self-seeding. Certainly, self-recruitment is considered common in the marine environment and has been recorded across a diverse range of taxa (Swearer *et al*. 2002). Local recruitment in *H. rubra* as inferred from genetic data is consistent both with our knowledge of its larval biology (McShane 1992) and empirical field studies of dispersal (Prince *et al*. 1987; McShane *et al*. 1988). What is most surprising, however, is that, while most larvae appear to recruit to the parent population, there appears to be no short-distance larval dispersal (hundreds of metres between adjacent sites) but at least low levels of larval exchange at the meso-scale (across 7–20 km among locations).

Modelling studies by McShane *et al*. (1988) suggest that once abalone larvae exit the kelp canopy into the water column, they are likely to be advected tens of km away from the parent reef. This phenomenon may well explain why we find little genetic evidence that larvae disperse to adjacent sites but appear to travel occasionally between adjacent locations. In addition, models of dispersal distance in the New Zealand congener *Haliotis iris* similarly indicate that abalone larvae will disperse over tens of km (Stephens *et al*. 2006). Critically, however, our genetic data indicate that successful meso-scale dispersal events are rare. Back-calculation of the time since dispersal for each of our first-generation migrants based on the relationship between age and size suggest that, although low levels of migration occur within regions every year, successful dispersal may only occur once every few years between any two sites.

McShane *et al*. (1988) hypothesized that the likelihood of an abalone larva that is advected from the natal reef encountering and re-entering any reef system will be low, and this is certainly supported by our results. In fact, more larvae appear to successfully disperse between adjacent locations (i.e. 7–10 km) than between distant locations (15–20 km) (Fig. 3) emphasizing the declining probability of successful recruitment with increased dispersal distance. Indeed, our overall findings are consistent with the concept of bimodality of dispersal in marine larvae (e.g. Raimondi & Keough 1990; Krug 2001) whereby most larvae settle rapidly at competency and within the natal habitat, while others disperse but with associated risks including higher mortality and ultimately low successful long-distance dispersal rates.

Directionality of dispersal among locations shows no obvious trends except in the Actaeons where most migrants originate from George III Rocks. We currently have no knowledge of the small-scale hydrodynamics in the Actaeons region so cannot determine if this is related to local current patterns. However, the relatively large apparent export of larvae from George III Rocks may be related to the fact that this is a fishery no-take area that contains higher densities of mature abalone than any other site in the region (Mundy *et al*. 2006) and hence may contribute proportionally more individuals to the larval pool. Thus, marine protected areas may be important at least for local replenishment of abalone stocks and to contribute to the productivity of a fishery.

Does over-fishing lead to increased genetic diversity?

Despite our prediction that collapsed populations will suffer from loss of genetic variation, our results show that the depleted populations in NE Tasmania actually have higher numbers of private alleles, rare alleles and total alleles than the healthy populations in either the Actaeons or NE Tasmania. We propose two reasons for this unexpected result. First, as our data show, *H. rubra* populations are largely self-seeding. Thus, we would expect healthy abalone populations, like many marine invertebrates (Knowlton & Jackson 1993), to be subject to some level of inbreeding and have naturally reduced levels of genetic variation; indeed, heterozygote deficits were observed in some of our populations. The small amount of migration that we propose occurs among locations may, however, be sufficient to reduce the effects of inbreeding depression and partially allay the effects of drift.

Second, where populations have been depleted and the number of adults diminished, local reproductive output will be low (Allee effect) and, concurrently, local recruitment will also be reduced. Under these circumstances, we suggest that migrant larvae will represent a higher proportion of total larval recruitment. Given that the source of these migrants is likely to be varied both in space and through time (Fig. 3), the end result may be a local population with a more diverse genetic composition than those populations that are largely self-recruiting. Thus, although over-fishing in itself will not result in increased genetic diversity, the changed ratio of migrant to local larvae may well result in an apparently higher genetic diversity in recovering populations, at least in the short term. Obviously, it will be interesting to test whether, once these depleted populations have rebuilt to normal adult densities, a subsequent reduction of genetic diversity occurs following multiple generations of local recruitment and inbreeding.

Implications for management of abalone fisheries

Our study raises two issues that are central to the sustainable management of abalone fisheries, as well as having implications for many other benthic invertebrate fisheries worldwide. First, the fact that populations are largely self-seeding suggests that the decline of local populations of *H. rubra* will be linked to Allee effects, and especially reproductive and recruitment failure associated with a decline in adult abundance (e.g. Levitan & Sewell 1998; Babcock & Keesing 1999). Quite possibly, the collapse of abalone fisheries globally, e.g. in Canada, California and Japan (Bell *et al*. 2005) may also be linked to similar Allee effects suggesting management must address the prevention of Allee effects, rather than continue with the current focus on determination of a total allowable catch (TAC) independent from the ecological dynamics of the fishery. Even a conservative TAC is unlikely to prevent Allee effects because economic drivers and the tragedy of the commons encourage fishers to fish an area intensively, rather than to leave some animals behind (Prince 2003).

Second, successful dispersal of abalone larvae occurs only rarely (on average < 5% of a cohort will be migrants); and, typically, migrant larvae will disperse in the order of tens of km. Provided healthy abalone populations exist within a 10–20 km radius of a collapsed population, it is probably safe to assume that gradual recovery through the recruitment of migrant larvae will occur. This is evident in NE Tasmania where, because only a relatively small area of the coast suffered severe population decline, there appears to be sufficient healthy populations nearby that are providing a source of larvae (e.g. Eddystone Point to the north) — but notably, this is an effect we are only now beginning to see after more than 20 years. Thus, for the abalone fishery in NE Tasmania like other fisheries worldwide (Hutchings 2000), recovery without intervention will be possible, but may be on a timescale unacceptable to fishery managers and fishers.

For fisheries that have been less fortunate, and where whole regions have collapsed, the absence of a larval source at the meso-scale may well limit population recovery. For example in Canada, widespread depletion of the Pinto abalone *Haliotis kamtschatkana* has occurred and populations continued to decline seven years after the fishery was closed in 1990 (Jamieson 1999). Thus, in addition to management strategies that prevent Allee effects, fisheries will also need to be managed at the meso-scale to avoid regional depletion. In Tasmania, the abalone fishery is currently managed in geographical zones (i.e. east, west and north Tasmania) and reported at smaller management units (Blocks, see Fig. 1) that each cover more than 10 km of coastline. If over-fishing occurs at the scale of each of these blocks, then there is probably little chance of swift recovery. Resilience of abalone fisheries clearly lies both at the local scale where most recruits originate, but also at the meso-scale (tens of km) where more distant populations provide sporadic recruits. The relatively high number of successful migrants from the fisheries no-take area at George III Rock

to other SE locations illustrates the importance of healthy local populations in combination with marine protected areas for maintaining regional fisheries (Le Quesne *et al*. 2007).

Despite the important role that localized recruitment and sporadic larval dispersal will play both in the decline and recovery of Tasmania abalone populations, our results still fail to explain the differential recovery of a few locations in the NE region relative to other parts of the Tasmanian fishery. Habitat complexity may have an antagonistic effect on the dynamics of depletion in abalone populations. For example, the presence of cryptic habitat for juvenile stages is positively correlated with juvenile recruitment (Shepherd & Partington 1995). The collapsed NE reefs comprise a mix of low-complexity mudstone (Policemans Point) and more complex granite boulders (Fancy Reefs), suggesting no obvious relationship between habitat complexity and resilience in this area. Furthermore, while changes in subtidal assemblages have been seen following the collapse of abalone populations in California (Miner *et al*. 2006), broad-scale surveys in Tasmania have found only a very weak correlation between community composition and abalone abundance (r^2 = 0.02–0.3; J. Valentine unpublished data). Differential fishing pressure may also play a role, especially in areas around the Fancy Reefs which are easily accessible and adjacent to a major tourist destination and so potentially subject to higher levels of recreational fishing pressure than many other reefs.

Clearly, there is no simple explanation for the delayed recovery of abalone populations at some sites in the NE region of Tasmania, but further studies on the roles of habitat complexity coupled with accessibility may well shed more light on this dilemma. Importantly though, our genetic results indicate that ongoing larval dispersal from nearby healthy reefs should eventually result in the natural recovery of these populations, although it may well take many more decades before abalone densities approach those that existed prior to collapse of the fishery.

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This paper forms part of a larger study by Mundy & Miller on resilience and recovery of fished abalone populations in Tasmania. Karen Miller's research interests are on the early life-history and genetic connectivity of benthic marine invertebrates. Craig Mundy is a marine invertebrate ecologist currently leading the Abalone Research Group at TAF1. Ben Maynard is a recent PhD graduate whose research focuses on the application of molecular techniques to improving aquaculture and wild fisheries.
