Movement and re-aggregation of blacklip abalone in response to intensive fishing

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FISHERIES RESEARCH & DEVELOPMENT CORPORATION

Project No. 95/165

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MOVEMENT AND RE-AGGREGATION OF BLACKLIP

ABALONE IN RESPONSE TO INTENSIVE FISHING

Final Report to Fisheries Research and Development Corporation

(FRDC Project 95/165)

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June 1998

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Contents

Appendices
   1. Intellectual Property
   2. Staff

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OBJECTIVES:

1. To determine the extent of migration and re-aggregation of a blacklip abalone population in response to fishing.

2. To describe differences between pre- and post-fishing spatial distribution patterns in a blacklip abalone population.

3. To determine the growth rates of a "stunted" abalone sub-stock.

NON-TECHNICAL SUMMARY:

Typically abalone are found clustered into aggregations of many individuals along gutters and ledges that dissect the surfaces of the reefs they inhabit. Commercial abalone divers take advantage of this clustering behaviour and specifically target aggregations to minimise the time spent searching for abalone and maximise their catch rates. This approach to abalone harvesting would be expected to progressively reduce the number and size of the aggregations to produce a less clustered pattern of distribution. Most methods used to detect changes in abalone abundance that result from fishing assume that abalone movement will have minimal effect on post-fishing patterns of distribution.

Abalone are generally viewed as relatively inactive organisms that occupy specific homesites from which they seldom move. Evidence for this lack of movement includes the oval shaped 'scars' of bare rock, free of algae and other immobile invertebrates, that remain after abalone are harvested. However there are many anecdotes describing the tendency for abalone to reform aggregations after fishing and during spawning periods. Presumably the latter promotes fertilisation success by increasing the quantities of sperm and eggs that mix in the water. It is unclear why abalone may aggregate into clusters outside spawning periods. If re-aggregation does occur after fishing, it is also unclear where these 'replacement' abalone come from. There is some speculation that small abalone may emerge from crevices and cryptic habitat. Other hypotheses include small-scale movements within aggregations or

4

migration from unfished areas. An understanding of how re-aggregation occurs after fishing and to what extent it occurs, is essential to determine its effect on estimates of abalone abundance and to estimate important population characteristics such as rates of natural mortality.

One reason why abalone may aggregate outside spawning periods is that the distribution pattern reflects the distribution of preferred habitat in terms of food availability. The high variability in growth that is characteristic of abalone is likely to be partly due to the availability of preferred habitat. Abalone populations with stunted growth contain many individuals that will not reach legal-size and thus represent lost yield to the fishery, whereas fast growing populations may be at greater risk of overfishing because many of their abalone will be caught before reaching reproductive maturity and having a chance to spawn.

Results were consistent with some recovery occurring after fishing among untagged individuals. This was reflected by smaller than expected decreases in post-fishing abundance. Changes in the fine-scale distribution pattern of abalone were consistent with re-aggregation occurring through a series of consecutive movements. Re-aggregation occurred as a combination of migration from unfished areas and emergence from cryptic habitat. Where emergence from crevices was a factor, larger abalone rather than smaller abalone appeared to be the prime source for this re-aggregation. Tagging appeared to counter re-aggregation by stimulating abalone to disperse. This was compounded by the repeated disturbance of tagged individuals during surveys. At Point Cook the majority of abalone movements were less than 10 m and the largest distance travelled by any tagged individual during the course of the study was 60 m in 7 months. The amount of movement varied with habitat quality and was affected by fishing. Prior to fishing the rates of dispersal, or movement beyond the experimental plots, were smaller in areas with more preferred habitat. The removal of 40% of the population from fished plots during experimental fishing caused a decrease in the proportion of abalone dispersing. Despite this, dispersal accounted for 40-60% of total tagged abalone disappearance from all experimental plots. Analysis of growth showed that at Point Cook virtually all abalone in this population have the potential to grow sufficiently large to enter the stock whereas at Flinders about 25% will not reach the legal minimum length. However, growth was highly variable over a scale of tens of metres.

Outcomes from this study have important consequences for abalone stock assessment. The results suggest that change-in-ratio and catch-per-unit-effort methods of

abundance estimation are inadequate because both methods assume that the only change in the population will be a reduction in the relative density of legal-size abalone. They also highlight the need to develop methods of abundance estimation that accommodate the impact of aggregating behaviour on blacklip abalone populations, and the need to measure dispersal when estimating natural mortality from tagging studies. If left unaccounted, dispersal beyond the study area will artificially inflate estimates of natural mortality. Substantial contributions from dispersal may explain why estimates of natural mortality from tagging studies often appear larger than anticipated.

The study outcomes also have important consequences for abalone fisheries management. The tendency for legal-size abalone to re-aggregate after fishing ensures that their vulnerability to capture will be maintained despite a reduced number of individuals in the stock. This means that abalone populations are more vulnerable to over-exploitation than populations of species whose densities are uniformly reduced by fishing. Fish populations that are uniformly reduced in density become more difficult to catch as stock numbers decrease. That this is not the case for abalone should come as no surprise given the global history of abalone stock collapses and should serve as a reminder to fishery managers of the need for a precautionary approach. Growth of the Point Cook population was inconsistent with the growth characteristics of a stunted stock because an increase of 1 cm in the legal minimum length would still leave 70% of the population available to the fishery. Similarly, 75% of the abalone at Flinders have the potential to enter the stock. Whilst growth in some abalone populations may be slow this does not necessarily mean that a population should be labelled as stunted.

6

Background

Blacklip abalone, *Haliotis rubra*, form the basis of a large and extremely important fishery in southern Australian waters. Despite the high economic value of the fishery, stock assessment of blacklip abalone has remained problematic. These difficulties are partly a product of the biology of the species and the way it is fished. Blacklip abalone occupy preferred homesites on reef complexes and often have a contagious spatial distribution that enables divers to target aggregations in order maximise catch rates (McShane, 1992 and 1994). The abalone are often found aggregated in gutters and have a tendency, particularly as juveniles, to occupy cryptic habitat provided by crevices that dissect the rocky substrate (Nash et al., 1994). Post-fishing observations indicate a tendency for abalone to reform aggregations through the movement of individual abalone into homesites vacated by harvested abalone. Abalone have also been observed to move in response to disturbance (Shepherd and Godoy, 1989), spawning (Shepherd, 1986) and food availability (Prince, 1989).

The tendency of blacklip abalone to live in aggregations renders them more vulnerable to overfishing by increasing their catchability. Divers are able to maintain high catch rates by moving from aggregation to aggregation and by relocating to a different area when catch rates drop below an acceptable level. If the abalone remaining after fishing then re-aggregate, a diver returning to the area may well harvest the area at a similar catch rate to the first excursion. These processes may all contribute to hyper-stability in catch rates and conceal real fluctuations in population size.

Previous studies of movement in Victorian blacklip abalone populations showed that the net movement of tagged abalone was only metres per month (McShane, 1990). However, these abalone were at liberty for several months between release and recapture to the extent that the observations of net movement provided no indication of short-term and total movement. Indeed, total movement over a period of several months may possibly be an order of magnitude greater than net movement.

During a recent FRDC-funded research project conducted by MAFRI to compare methods of abundance estimation (Gorfine et al. 1996), abalone were observed to move quickly into homesites vacated through harvesting. Repeated non-destructive surveys of unfished control sites revealed patterns of change that seemed to be related to the frequency of the surveys. In other words, the disturbance caused by the surveys resulted in abalone

relocating such that their spatial distribution had changed sufficiently to affect abundance estimates.

Hart and Gorfine (1997) tested the usefulness of mark-recapture by marking the shells of abalone *in-situ* and recapturing them during controlled fishing. Marked abalone were found to have increased catchability compared with unmarked abalone indicating that the abalone relocated in response to the disturbance caused by marking. However, the number of abalone that emigrated from experimental plots in response to marking could not be estimated within the scope of the experimental design. Other studies have also demonstrated increased initial movement of abalone immediately following disturbance. In laboratory trials Werner et al. (1995) found that young *H. discus hannai* disturbed by handling exhibited increased movement activity, and similar behaviour was observed in the field by Shepherd and Godoy (1989).

For this project we proposed the hypothesis that removal of abalone by fishing stimulates movements that result in reaggregation. Acceptance of this hypothesis would lead us to determine the source of reaggregating abalone. Three main sources of replacement abalone were hypothesised. The first was immigration of individuals from unfished areas outside the fished area. The second was emergence of abalone from cryptic habitat. In particular suggestions were advanced that emergent abalone would be of smaller shell size than those removed by fishing. The final hypothesis was the relocation of individuals from less dense areas within the fished areas to re-aggregate to areas of higher pre-fishing density.

Need

Understanding the nature of reaggregation is central to understanding the resilience of abalone to fishing, and crucial to the choice of tools used for stock assessment. Bias in estimates of abundance and population parameters that do not allow for re-aggregation can lead to inaccurate assessments of the state of stocks and consequently misguided management decisions. Understanding where the abalone come from to reform aggregations is essential as is knowledge of the time period for reaggregation. Changes in growth that may occur as re-aggregating abalone move to occupy habitat with improved food availability, or as density reduction reduces the competition for food are also important. It is of paramount importance that when fishery independent or fishery dependent methods are used to estimate

8

abalone stock abundance that the dynamics of movement are known and data interpreted accordingly.

Objectives

1. To determine the extent of migration and reaggregation of a blacklip abalone population in response to fishing.

2. To describe differences between pre- and post-fishing spatial distribution patterns in a blacklip abalone population.

3. To determine the growth rates of a "stunted" abalone sub-stock.

Whilst the project addressed all of the original objectives, the methodology necessitated that migration (movement of tagged abalone) was considered separately from re-aggregation, and that re-aggregation was considered as part of an examination of changes in spatial distribution patterns (grid counts). During the initial phases of the project it became evident that there was an opportunity to coincidentally study the effects of post-tagging dispersal on estimates of natural mortality. The methods and results presented below that pertain to dispersal were extracted from Dixon et al. (In press). The efficacy of the tagging method employed was also examined.

Methods

Experimental design

Experimental sites were selected off the coast of Victoria, Australia, at Point Cook and at Flinders (Figure 1). Both sites were subject to little illegal or recreational abalone fishing, and were closed to commercial fishing for six months prior to and throughout the experiment. The sites were chosen to represent extremes of habitat type and abalone distribution.

The Point Cook site (37°55.893' S, 144°47.104' E) was 3 – 4 m in depth and was not subject to strong swell or current. The reef consisted of basalt boulders, rarely > 1 m in height, on a sandy substrate. Conditions appeared anaerobic beneath the boulders and there was very little cryptic habitat that could not be thoroughly searched by a diver. The dominant macro-algae included *Ecklonia radiata*, *Caulerpa* spp., *Enteromorpha linza*, *Cystoseria* spp., and, during summer months, a thick mat of drift red algae (mostly *Jeannerettia pedicellata*). Abalone were abundant at Point Cook and were relatively evenly distributed. At Flinders (38°29.397' S, 145°01.274' E) the depth was 7 – 9 m and the site was prone to strong swells and currents. The reef consisted of fractured and stepped basalt platforms, often > 1 m in height, and interspersed by sand gutters. The fractured nature of the reef provided an abundance of unsearchable cryptic habitat. The dominant algae included *Phyllospora comosa.*, *Ecklonia radiata* and coralline algae. Abalone were less abundant at Flinders than at Point Cook and were more patchily distributed.

Four square plots were set up in fixed positions at each site during August 1996. Each plot measured 24 m x 24 m, and the four plots were separated from each other by 10 m corridors (Figure 2). At each site two plots were fished to assess the impact of fishing and two plots were left unfished to compare the fishing impact with unfished areas. Fished and control plots were chosen randomly, but were constrained to being diagonally opposed. Surveys were conducted prior to fishing, 3 – 4 weeks after fishing (to assess the impact of fishing), and 10 weeks later to assess the recovery from fishing. This design allowed for temporal and spatial comparisons between plots, both fished and control, and between sites.

Post-fishing changes in spatial distribution

Changes in abundance were assessed by counting all unconcealed abalone within the plots using an exhaustive 1 m x 1 m grid system. These grid counts were also used to calculate Morisita's index of dispersion (Krebs 1989):

$$I_d = n \left[\frac{\sum x^2 - \sum x}{\left(\sum x \right)^2 - \sum x} \right]$$

where I_d = Morisita's index of dispersion, n = sample size, $\sum x$ = sum of grid counts, and $\sum x^2$ = sum of grid counts squared.

This index is a useful descriptor of the degree of aggregation in observed spatial patterns. The significance of observed spatial patterns was tested using the standardised Morisita index of dispersion (described in Krebs 1989). This index allows comparisons between plots and sites because it is independent of both population density and sample size.

Differences in the spatial distribution of abalone were also studied by measuring the distance between abalone and their first, second and third nearest neighbours. The source individuals for these measurements were selected randomly from cells with the greatest and least abundance of abalone within each plot. A chi-square goodness-of-fit test was also used to compare the observed and expected distributions of nearest-neighbour distances (Campbell and Clarke 1971). These tests indicated the significance of any departure from random spacing. The shape of the observed distributions indicated any departure from a random pattern. The distribution of nearest neighbour distances at each survey was compared to assess temporal changes in the degree of aggregation.

During each survey the abundance of abalone outside each plot was estimated by making counts along fixed transects (Figure 2). These transects measured 24 m in length by 1 m in width. These counts were made to assess the extent of immigration into the plots.

Abalone lengths were recorded to assess fishing-induced changes in the size composition of the population. The extent of weed growth on shells was also noted. These data were collected under the assumption that abalone emerging from cryptic habitat were smaller and carried less algal cover than the unconcealed population.

Migration

To examine immigration and relocation, abalone were individually tagged. This was done with a rivet tag through a respiratory pore using a method modified from that of Prince (1991). All abalone were tagged and measured *in situ* to minimise disturbance and displacement. To spread the tagging within the plots across the range of conspicuous abalone sizes and across all habitats, divers attempted to tag every fifth abalone sighted. The positions of tagged abalone were then recorded within the grid to an accuracy of ± 0.1 m. This effectively provided position co-ordinates for all tagged abalone within each plot at a higher level of resolution that that available from cell locations alone. The 1322 and 819 abalone tagged within the plots at Point Cook and Flinders represented 19 and 18 per cent of the unconcealed populations, respectively.

To assess the extent of immigration into the plots after fishing, approximately 1400 abalone on the outer perimeters of the plots were also marked (Figure 2). Starting closest to each plot boundary and working outwards, all abalone encountered were marked until at least 170 had been either tagged or painted with a uniquely coloured paint-stick (50% for each marking method). Different colours were used to differentiate abalone occurring within and external to the experimental plots. Abalone between the inner borders of the plots were not marked so that interaction effects along the internal borders between plots were avoided. During successive surveys searches up to approximately 30 m beyond the plot boundaries were conducted to plot the positions of tagged abalone originating from within the plots.

The relocation of tagged abalone within the plots was examined by using grid cell abundance as an index of habitat quality. The assumption was that the greater the number of abalone initially resident within a grid cell, the better the habitat quality of that cell. The initial abundance in cells that tagged abalone occupied prior to moving was compared with that of the cells in which they settled. Abalone were determined to have settled when subsequent surveys revealed that they had moved less than one metre from their previous position.

Experimental fishing was for only untagged abalone above minimum size limits. The size limits used were less than the legal minimum lengths adopted for the Victorian abalone fishery (Point Cook: normally 100 mm, used 93 mm; Flinders: normally 110 mm, used 100 mm). These size limits made a greater proportion of the population available for fishing and,

hence, allowed a greater fishing impact. About 50% of the population at each site was over the respective size limits. Of the above-sized abalone, 20% were tagged and made unavailable for subsequent fishing. The remaining 80% of the population oversize (40% of total population) was fished until a reduction of 35% of total population abundance prior to fishing was achieved within each pair of fished plots. The same relative reduction in abundance was applied at both sites to allow between sites comparisons.

Effects of movement on estimates of natural mortality

Examination of the effects of movement on estimates of natural mortality requires estimation of the dispersal of tagged abalone from the experimental plots. However, dispersal cannot be estimated at study sites such as Flinders where there is cryptic habitat that may preclude observation of dispersed abalone. The absence of such cryptic habitat at the Point Cook study site provided an opportunity to effectively estimate dispersal. To estimate the number of abalone expected to disperse from the plots at Point Cook we first calculated distances moved by re-sighted tagged abalone. The frequency distribution of distances moved was then adjusted by predicting movements of individuals emigrating from the plots. We applied all predicted movements, in all possible directions of travel, to each initial tag position to estimate the probability of each individual moving beyond the boundaries of the plot in which it originated. The sum of each individual probability was the number expected to be lost through dispersal.

The position of each tagged abalone within a plot was recorded as an x and y co-ordinate. The distance travelled d_k for abalone k, from its initial position *(i)* to its finishing position *(f)* was calculated using the equation

$$d_k = \sqrt{((x_{fk} - x_{ik})^2 + (y_{fk} - y_{ik})^2)} \text{, where } i, f, k \in [1, n_{res}]$$ 1

and n_{res} is the total number of re-sighted tags.

A distribution of distances d_k for re-sighted tagged abalone was obtained from all movements within an experimental plot. From an initial tag position $x_{ik}y_{ik}$, a distance moved d_k in direction θ will result in the hypothetical finishing position $x_{hk}y_{hk}$. Distances d_k are biased against larger movements because the larger the movement d_k, the greater the probability that $x_{hk}y_{hk}$ will be outside of the plot of origin. Therefore, a predicted distribution of distances was calculated using the re-sighted distribution by obtaining the proportion of occasions $x_{hk}y_{hk}$ was outside a particular plot for all possible hypothetical movements ($1° \leq \theta \leq 360°$), assuming random direction of movement (Figure 3).

The displacement (x_{disp}, y_{disp}) of each hypothetical movement ($1° \leq \theta \leq 360°$) was obtained by assigning all absolute angles of θ from $x_{ik}y_{ik}$ and its actual distance moved d_k, (Equations 2-3).

$$x_{disp} = d_k \times \sin\theta \text{ and } y_{disp} = d_k \times \cos\theta,$$ 2
for $\theta \in (0°, 90°) \text{ or } \in (180°, 270°)$

$$x_{disp} = d_k \times \cos\theta \text{ and } y_{disp} = d_k \times \sin\theta,$$ 3
for $\theta \in (90°, 180°) \text{ or } \in (270°, 360°)$

The hypothetical finishing position $x_{hk} y_{hk}$ was compared with each of the four plots' boundaries to determine if it was inside the plot of origin (Equation 4).

14

Let $x_{hk} = x_{ik} \pm x_{disp}$ and $y_{hk} = y_{ik} \pm y_{disp}$.

Define $x_{min}, y_{min} = $ minimum x / y ordinate of the plot,

and $x_{max}, y_{max} = $ maximum x / y ordinate of the plot.   4

If $\left(x_{min} \le x_{hk} \le x_{max}\right)$ and $\left(y_{min} \le y_{hk} \le y_{max}\right)$

then the tagged abalone at $x_{hk} y_{hk}$ remained within the plot.

The probability P_{dk} of abalone k remaining within the plot having moved distance d was calculated to be

$$P_{dk} = \sum_{\theta=1}^{360} count / 360, \quad \text{where } count = 1, \text{ if } x_{hk}y_{hk} \text{ is inside the plot} \qquad 5$$

The predicted frequency of the distance d_k was defined by

$$freq_{dk} = 1 / P_{dk}. \qquad 6$$

The predicted and actual frequencies were summed across abalone k for each distance d to produce a frequency distribution function for all possible distances. Calculations from Equations 1-6 were repeated for all abalone re-sighted for each plot and survey. A frequency distribution function was created from all plots and surveys combined (Figure 4).

For each distance d_k and all possible directions, Equations 2-4 were repeated for all initial tagged positions, $x_{ia} y_{ia}$ (instead of $x_{ik}y_{ik}$), even if not re-sighted, for abalone a where $i, a \in [1, n_{tot}]$ and n_{tot} is the total number tagged in a plot. The number of times the individual was found inside and outside a plot (Equation 4) was multiplied by the predicted frequency at distance d_k (Equations 7 and 8).

$$freq_{in\_a, dk} = freq_{d_k} \times count \text{ where } count = \begin{cases} 1 \text{ if } x_{ha}y_{ha} \text{ is inside the plot} \\ 0 \text{ otherwise} \end{cases} \qquad 7$$

$$freq_{out\_a, dk} = freq_{d_k} \times count \text{ where } count = \begin{cases} 1 \text{ if } x_{ha}y_{ha} \text{ is outside the plot} \\ 0 \text{ otherwise} \end{cases} \qquad 8$$

The probability P_a of the theoretical finishing position for each initially tagged abalone, $x_{ha} y_{ha}$, being outside a plot for all possible movements was given by

$$P_a = \sum freq_{out\_a} / \sum (freq_{in\_a} + freq_{out\_a}) . \qquad 9$$

The expected dispersal (E_d) outside a plot and the expected remaining (E_r) within a plot for each survey were given by

$$E_d = \sum_{a=1}^{n_{tot}} P_a \quad \text{and} \quad E_r = n_{tot} - E_d \qquad 10$$

The number of tagged individuals expected and the number re-sighted were regressed against the median of the number of days at liberty for re-sighted individuals for each plot and survey. Their slopes were determined as the instantaneous rate of tag dispersal and disappearance respectively. Fishing mortality was assumed as zero as all legal fishing within 100 m of the site ceased six months prior and throughout the project. Cryptic loss was also assumed as zero as there was minimal cryptic habitat inaccessible to divers. Therefore the difference between the slopes represented disappearance due to M, tag loss and observer error.

Differences in dispersal rates were compared with the type of relief in each plot by expressing the number of tagged abalone expected to remain E_r as a percentage of the number tagged n_{tot}. The effect of experimental fishing was determined as the change in percentages between the second and third surveys.

Growth

Follow-up surveys to recover tagged abalone were conducted about 12-15 months after the final post-fishing survey to estimate growth. Shell length increments were analysed using the stochastic growth model developed by Troynikov (1998). This model accommodates heterogeneity in growth data and its software program estimates the quantiles of the Gompertz growth parameter for asymptotic length (L_∞), the growth parameter g, and Kulbeck's informative mean for goodness of fit comparisons among Weibull, gamma and log-normal density distributions. For Point Cook data, separate analyses were performed for each plot to determine the extent of differences between fished and un-fished plots. Whilst exhaustive searches for tagged abalone were conducted at Point Cook only limited searching was possible at Flinders. Consequently, for Flinders data a Leslie plot of sequential tag recovery rates against cumulative tag recovery was used to estimate the total number of tags

likely to be recovered. Comparisons of length frequency distributions were made among the entire study populations and the tagged samples to differentiate between the effects of bias and growth on the final length distributions of tagged abalone.

Results

Changes in Abundance

Changes in the total abundance of abalone counted within the plots were compared as a percentage of the initial abundance counted prior to fishing (Figure 5). At each site changes in abundance were consistent within each type of plot and were therefore combined for analysis. In all cases the observed change in abundance was different from that expected. If no movement had occurred after fishing a 35% reduction was expected in fished plots, and no change was expected in control plots. At both sites a decrease in abundance of less than 20% was observed in fished plots. An increase in abundance was observed in all control plots. At Point Cook the apparent recovery of fished areas was sustained but at Flinders the recovery slowed or possibly decreased.

Changes in Distribution

At both sites and during all surveys the distribution of abalone was found to be significantly aggregated (standardised Morisita index of dispersion > 0.5, therefore > 95% confident of aggregated pattern). Changes in the un-standardised Morisita index of dispersion indicated site-specific differences in distribution (Figure 6). The Flinders plots showed a consistently higher degree of aggregation. This was indicative of there being many areas with no abalone and a few areas with many. The lower degree of aggregation at Point Cook was indicative of a more homogenous spatial distribution. These initial distributions influenced the change in distribution observed after fishing. At Flinders the removal of abalone from aggregations made the size of aggregations less extreme and lowered the degree of aggregation. At Point Cook the even removal of abalone across the entire area created grid cells with no abalone thereby causing an increase in the degree of aggregation. The longer-term recovery after fishing generally showed a return towards the initial distribution (Figure 6).

The complete enumeration of all abalone within the plots meant that a Chi-square test of goodness-of-fit (Campbell and Clarke 1971) could be used to compare the observed and expected distributions of first, second and third nearest-neighbour distances. These tests indicated that significantly aggregated patterns existed in all plots at both sites during each survey ($p < 0.01$, $df = 5$). Prior to fishing the distribution of first, second and third nearest neighbour distances was similar in fished and control plots at each site (Figure 7 a and b). At both sites approximately 80% of abalone were located within 30 cm of their nearest neighbour. This aggregated pattern was more extreme at Flinders where about 50% of

abalone were located within 5 cm of their nearest neighbour (compared with about 40% at Point Cook). Distances to second and third nearest neighbours were also less at Flinders than at Point Cook. About 25% of second and 10% of third nearest neighbours were located within 5 cm of the source abalone at Flinders compared with 10% and < 5% respectively, at Point Cook. This pattern prior to fishing is indicative of the more aggregated pattern at Flinders and the more homogenous distribution at Point Cook.

The apparent impact of fishing was most noticeable at Flinders (Figure 7 b). In both control and fished plots the proportion of first, second and third nearest neighbours found close to the source abalone decreased during the first post fishing survey and the proportion located some distance from the source abalone had increased. This change was most noticeable in the fished plots. At Point Cook these changes were only noticeable in the fished plots (Figure 7 b) and to a lesser extent than at Flinders. Changes in the distribution of nearest neighbour distances in the control plots at Point Cook between the pre-fishing and first post-fishing survey were erratic. Between the first and second post-fishing surveys, changes in these distributions in control plots at Point Cook remained erratic.

Conversely, by the second post-fishing survey the distribution of first, second and third nearest neighbours at Flinders and in the fished plots at Point Cook had shown a general recovery towards the distribution found prior to fishing. At Flinders this recovery was most complete in the control plots. In fished plots the proportion of first, second and third nearest neighbouring abalone found within 5 cm of the source abalone was similar on the second post-fishing survey to that found prior to fishing. In contrast, the increase noted on the first post-fishing survey in the proportion of abalone located some distance from the source abalone decreased only marginally on the second survey.

Emergence

Categorising the shell cover of abalone proved to be difficult and imprecise. Therefore, these data were not used for analysis. Figure 8 shows the relative length–frequency distributions of the abalone in fished areas at each site. Length–frequency distributions before and after fishing did not show great change in the proportions of animals above and below the size limit.

Immigration

Figure 9 shows changes in the number of abalone counted on fixed transects around fished and control areas at each of the sites. At Point Cook there was a general and sustained decline in the number of abalone around fished areas after fishing. This result was not as apparent around control plots. At Flinders there was a decline in abundance around both fished and control areas but this decline was not as marked as at Point Cook.

The immigration of abalone tagged from outside the plots is illustrated for the Point Cook site in Figure 10. The movement of abalone into control plots was just as significant as the movement into fished areas. Whilst the number of tag movements at Flinders was not as great as at Point Cook, the results were similar.

Relocation

Figure 11 shows the number of abalone that moved and subsequently settled at each site plotted against the initial abundance of the cell in which they were tagged. At both sites abalone settled in cells of lower initial abundance than that of the cells in which they were tagged. This movement occurred in both control and fished plots but was more apparent in fished plots.

Dispersal from experimental plots

Annual rates of dispersal of tagged abalone at Point Cook ranged from 0.49 in the north west fished plot, to 0.78 in the north east control plot (Figure 4), contributing 40-60% of total tagged abalone disappearance for all plots. The remaining three components of tag disappearance (natural mortality, tag loss and observer error) ranged from 0.49 in the north west fished plot to 0.82 in the south east fished plot (Table 1).

The majority of abalone movements were less than 10 m (Figure 12). The largest movement detected between the first and second surveys (4 months) was less than 50 m. The maximum distance traveled by any tagged individual over the course of the study (7 months) was 60 m (Figure 12). Searches beyond plot boundaries failed to detect any movements greater than those measured within the plots.

The number of re-sighted tagged abalone, n_{res}, decreased between 50-55% from initial tagging (first survey) to the second survey (Table 2). Numbers re-sighted remained

fairly consistent or decreased only slightly after the second survey, decreasing by 5% from the second to fourth survey in the north east and south west plots, decreasing by 4% in the south east plot and an increase of 2% in the north west plot. The expected number of tagged abalone remaining, E_r, varied between plots after the second survey (Table 2). In the north east plot only 64% of tagged abalone were expected to remain after the second survey and in the south west plot 80% were expected to remain. From the second to fourth surveys only 3% to 8% more were expected to disperse outside of each plot (Table 2).

Pre-fishing dispersal varied depending on the amount of relief of the reef (Table 3). The south west control plot contained the highest proportion of medium to high relief (56%) and showed the lowest initial dispersal (20%) of the tagged population. In contrast, the north east control plot had the lowest amount of high relief (14%) and showed high initial dispersal (36%). Dispersal decreased in fished plots following fishing, by 2% and 3% in the south east and north west plots, respectively (Table 3). The south west control plot showed a small increase of 1%, whereas in the north east control plot dispersal increased by 8% after fishing.

Growth

Initial comparison of growth estimates for individual plots at Point Cook showed little difference that could not be attributed to sampling error so the data were pooled. Likelihood estimates for the distribution function parameters for the stochastic growth model were similar to the deterministic estimates in all instances (Table 4). Probability densities of asymptotic length (L_∞) approximated normal distributions and the Flinders values had a larger mean and variance than did the Point Cook values (Figure 13). Whilst the Flinders population had a larger mean L_∞, the rate of growth (g) was much slower than for the Point Cook population that grew much faster towards its relatively smaller asymptotic length. However, the Flinders result may be less reliable because of the larger errors in parameter estimates that reflect the relatively small sample size. Comparison of Kulbeck's informative mean for Weibull, gamma and log-normal distributions showed that the log-normal distribution provided the best fit to the data for both populations (Table 4).

Quantiles of L_∞ showed that less than 10% of the Point Cook population and about 25% of Flinders population would not reach the respective legal minimum lengths of 10 and 11 cm (Table 5). Proportions of tags recovered were 21% from Point Cook and 7% from Flinders (Table 6). In both instances the ratio of internal to peripheral tag recoveries was about 2:1. A Leslie plot of tag recovery rate against cumulative number of tags recovered

indicates that 111 tagged abalone would have been expected to be recovered from this site (Figure 14).

Examination of length frequency distributions of the entire study populations during each survey, and initial lengths of tagged samples at times of release and recapture, showed some bias towards larger individuals having been tagged at both sites. Whilst 23% of the prefished population at Point Cook and 9% at Flinders were larger than the LMLs, these proportions were 30% and 20% for their respective tagged samples. Recaptured tagged abalone had initial lengths that were 32% and 15% greater than the LMLs at time of release. The length-frequency distribution of initial lengths of the tagged sample at Flinders was narrower than the distribution for the entire population. However, these biases were less than the increases in the relative frequencies of larger abalone that could be attributed to growth after 12–15 months. Growth accounted for an increase of 42% at Point Cook and 11% at Flinders in the proportion of tagged abalone larger than the LML. Whilst the frequency of larger abalone in the entire Flinders study population decreased immediately after fishing there was little change at Point Cook.

Discussion

Changes in spatial distribution from post-fishing movement and re-aggregation

Many traditional methods of fisheries stock assessment assume that movement-driven changes in spatial distribution have little impact on estimates of abundance or important parameters such as catchability and natural mortality. Such methods have been applied in abalone population surveys despite many anecdotes describing the propensity for abalone to re-aggregate after fishing and during spawning (Hart and Gorfine 1997; McShane 1996; Shepherd 1986). Although there have been previous studies of abalone movement (Ault and DeMartini 1987; Newman 1966; Poore 1972; Prince 1992; Shepherd 1986) and the frequency of aggregations (McShane 1996; Shepherd 1986), a synthesis of these results has remained problematic. This study attempted to redress this deficiency by employing a combination of *in situ* tagging with fine-scale mapping of two distinctly different abalone populations. Controlled fishing of each population was conducted to test the hypothesis that removal of abalone by fishing stimulates movements that result in re-aggregation.

Experimental fishing clearly had an impact on the populations, evident as declines in the abundance of abalone counted in all fished areas. However, these reductions were less than those expected. Without fishing induced movement a 35% reduction in fished areas was expected and no change was expected in control areas. The increase of abundance in control areas, whilst not as great, may suggest a response to fishing at some distance. That these changes in abundance within the plots were the opposite of those shown outside the plots suggested that recovery of the populations after fishing was occurring.

Substantial movement was observed and both populations showed a trend to return to their original spatial distributions. However, understanding how this redistribution was achieved proved difficult because contradictory results were obtained from two parts of the study. Analysis of the movements of tagged abalone showed an apparent dis-aggregation during the recovery whereas the analysis of changes in the spatial distribution of abalone during the recovery suggested a re-aggregation. It was anticipated that the movement of tagged abalone would provide data that would best describe the nature of recovery of the abalone populations to fishing. It became apparent however, that these data were the least reliable as the number of tagged abalone available for this analysis was only a small proportion of the tagged population. Furthermore, the repeated disturbance during the tagging, fishing and re-surveying might have caused abalone to disperse, reducing the likelihood of recapture, and resulting in dis-aggregation. Increased movement activity has

been noted in other abalone species subject to disturbance (Shepherd and Godoy 1989; Werner et al. 1995).

Changes in the distribution of nearest neighbour distances appeared to better describe the recovery of the populations after fishing. These data represented the entire population under study and were therefore less likely to be affected by tagging induced disturbances. These data suggested that restocking of aggregations occurred at both sites but that it was less noticeable at Point Cook where the abalone displayed a more homogenous distribution. The post-fishing decrease in the frequency of larger abalone in the Flinders population that was not apparent at Point Cook is further evidence of a difference in the recovery process between the two sites. The attenuated recovery at Flinders suggests that reformed aggregations contained fewer individuals than they did prior to fishing and that sparsely populated areas surrounding aggregations were not quickly restocked following fishing. The recovery of a population through re-aggregation without complete restoration of the pre-fishing population densities has important implications for area-based population surveys because such a re-distribution of abalone will mask depletion caused by fishing. More-over the tendency for recruited abalone to re-aggregate ensures that catch rates will be maintained despite stock depletion. This hyperstability means that abalone populations can give the appearance of stability while actually decreasing. Populations of species whose catch rates decline as stock numbers decrease are less vulnerable to over-exploitation. This partly explains the global history of abalone stock collapses.

Smaller abalone were not the prime source of re-aggregation, particularly where emergence occurred from crevices. Whilst this result is contrary to the conclusions of other studies (Hart and Gorfine 1997; Hart et al. 1997; McShane and Smith 1989), it is consistent with the notion that smaller abalone seek the shelter afforded them by cryptic habitat until they attain sufficient size that the risks of emerging to occupy more exposed locations are outweighed by the benefits of improved food availability and the need to reproduce. Most of the observed movements involved relatively small displacements that when considered together with post-fishing changes in abundance suggest re-aggregation resulted from a series of contiguous displacements similar to a "domino effect". This implies that post-fishing spatial dynamics involves size-related competition for preferred home-sites.

Our results raise doubt about the validity of change-in-ratio methods that have sometimes been used for estimating abalone abundance (Nash et al. 1994). Our results

indicate that violation of the critical assumption of equal probability of recapture of two animal types (pre-recruits and recruits) is inevitable. Fine-scale hyper-stability in catch per unit effort (CPUE) is another consequence of re-aggregation and reduces the value of CPUE as an index of abundance except under conditions of severe depletion. This is not to suggest that instantaneous catch rate may not be sensitive to localised stock depletion. Immigration of abalone into fished areas, such as that indicated in this study, further undermines the assumptions of change-in-ratio analyses. This will be more apparent if immigration is most noticeable in recruits only.

A blacklip abalone population in a broad area can be viewed as comprising two parts, the aggregations that collectively constitute stock commercial abalone divers are adept at targeting, and the more sparsely distributed abalone that serve to re-supply and thus replenish aggregations after fishing. Although estimates of the numbers and sizes of aggregations provides a picture of the size of the stock, it is likely that these estimates tend to be hyper-stable whereas the density of sparsely distributed abalone may be a more sensitive indicator of the impact of fishing. Future research should be directed towards developing methods of abundance estimation that accommodate re-aggregation. Further analysis of our data using techniques developed for terrestrial ecosystems that estimate density using distances between nearest neighbours and distances from randomly selected sampling points offer promise for this purpose (Byth 1982; Byth and Ripley 1980). Here, the distances are considered as radii that define areas occupied by individuals distributed with varying degrees of aggregation. As the degree of aggregation increases, the distances between nearest neighbours decreases whilst the distances from randomly selected points tends to increase. The geometric mean between the overall density of nearest neighbours and the overall density relative to random points gives an estimate of density with less bias than more conventional estimates from quadrats and transects. Regardless of the survey methodology employed, the results of this study indicate that aggregating behaviour must be considered when assessing the impact of harvesting on blacklip abalone populations.

Effects of movement on estimates of natural mortality

Dispersal rates contributed between 40 to 60% of total tag disappearance in the four plots at Point Cook (Table 1). In this study dispersal had greater potential to bias estimates of natural mortality than did tag loss and observer error combined. Ignoring dispersal would have resulted in over-estimation of natural mortality by more than 200%. These high dispersal rates existed despite the fact that the majority of movements detected were less than

10 metres. Some studies have shown that abalone populations can be highly mobile, moving hundreds of metres within months and kilometres in their lifetime (Newman 1966, Ault and DeMartini 1987). In such circumstances, the contribution of dispersal to overall tag disappearance will increase, causing further bias to natural mortality estimates.

Beinssen and Powell (1979) modelled abalone dispersal by observing tag movements between 10×10 m blocks. Their technique was repeated by Shepherd (1986) for the greenlip abalone *H. laevigata,* but was unsuccessful because the assumption of random movement was violated. Shepherd (1986) found that *H. laevigata* migrated toward the direction of swell or main currents, using a technique described by Clavier and Richard (1984) for *H. tuberculata.* No such patterns were observed for *H. rubra* during this study, probably because Point Cook is not subject to any swell or currents. It could be then argued that our assumption of random movement is reasonable.

Beinssen and Powell (1979) alluded to a violation of their main assumption of localised movements. Within a month movements of up to 200 m were observed, three times greater than the maximum distance which could have been detected within their re-surveyed area. The maximum distance detectable within the Point Cook plots was 70 m and searches made beyond the plot boundaries roughly doubled this distance. Because the largest detected distance moved was less than 60 m over seven months the assumption of localised movement seems valid. Another assumption of our dispersal estimation method was that plotting disappearance and dispersal against the median number of days caused minimal bias to the estimates. This was necessary because each survey took several days to complete. It was considered a reasonable assumption because the majority of movements were small and the variation in the days at liberty was minimal relative to the time between surveys for each plot.

The position an abalone occupies on a reef is often referred to as a home-site (Momma and Sato 1969, Shepherd 1973, Tarr 1995). Home-sites such as crevices or gutters may be chosen because they provide protection from predators or they are sites that are likely to be acting as areas for entrapment of drift algae. Shepherd (1986) found that the magnitude of movements of greenlip abalone *H. laevigata* in Waterloo Bay, South Australia, were larger in areas with little cryptic habitat. In Shepherd's (1986) study cryptic habitat provided the greatest number of preferred home-sites, but at Point Cook cryptic habitat was scarce. Assuming that each abalone occupied a unique home-site, then the spatial density distribution of the pre-fished population should have reflected preferred habitat. The grid system used in

our experiment allowed categorising of cells by relief (height of the reef). Preferred habitat appeared to be of medium to high relief reef. Such reef accounted for only 37% of the total planar area but contained 60% of the total abalone population in this study.

Our results were consistent with Shepherd's (1986) findings, that movement, reflected by estimated dispersal, decreases as the area of preferred habitat increases (Table 3). The south west control plot contained the highest amount of medium and high relief and had the lowest percentage of initial dispersal. In contrast, the north east control plot had by far the lowest amount of high relief and had a higher initial dispersal. Initial dispersal was calculated from movements prior to any removal of abalone from the population.

The removal of 33% of the population during experimental fishing increased the amount of available home-sites/preferred habitat within the two fished plots. If dispersal increased over time, a reduced rate of increase would be expected. There was an estimated reduction in the percentage of dispersal at the two fished plots of both 2 and 3% respectively (Table 3). In the unfished control plots, a continued increase in dispersal was expected. The south west plot showed only a 1% increase, whereas in the north east plot dispersal continued to increase by 8%. This discrepancy appears to be due to the difference in the number of home-sites/preferred habitat available.

Although this study required substantially more searching effort than that available to most tag-recapture studies, carefully planned experiments which estimate dispersal and observer error can overcome the need for thorough searching of large areas. Searching small areas thoroughly will reduce observer error, but if tagged abalone movements are larger than the maximum dimension of the search area then the assumption of localised movements will be violated. Random sampling from a larger area would be preferable as it will ensure that the largest magnitudes of movement could be detected. If double counting exercises are used, estimates of observer error as well as dispersal may be achieved.

This study could only estimate dispersal due to emigration outside of the survey area, although further work is planned to estimate tag loss and observer error. At Point Cook the lack of cryptic habitat meant that disappearance of tagged abalone into crypsis was minimal. However at sites with more cryptic habitat the capacity for such disappearance will be greater. Therefore site selection should consider the complexity of the reef for potential losses due to crypsis as well as the number of available home-sites in relation to magnitude of

potential movement. The tagging method used in future studies should consider how tagging affects movement and tag induced mortality. We believe that an *in situ* tagging method is preferable because this study has shown that this approach reduces initial magnitudes of movement.

Past estimates of natural mortality could have benefited from a quantitative estimate of dispersal. We have shown that with a defined area of tag release and recapture and a distribution of population movements, estimation of dispersal can be achieved. Future tagging studies which aim to estimate natural mortality will need to consider all components of tag disappearance. Aside from natural mortality these include dispersal, cryptic loss, fishing mortality, tag loss, tagging induced mortality and observer error. Failure to account for any one of these components will over-estimate natural mortality.

Effects of tagging on movement

Higher initial dispersal rates may have been caused by disturbance due to tagging. Whilst *in situ* tagging may reduce initial tagging-induced dispersal, it is unlikely to eliminate the problem. Results from this study have shown that even small movements will considerably affect dispersal. Alternatively, initial tag loss may have been higher than tag loss from the second to fourth surveys. Treble and Day (1993) showed that the rate of tag loss for glue tags applied to the shell of limpets changed over time. The initial rate of tag loss was low while the glue maintained full adhesion, however as the glue reached a critical age its adhesive ability reduced rapidly and the rate of tag loss increased. In our opinion the opposite occurs with *in situ* rivet tags, as initial rates of tag loss may be relatively high while poorly inserted tags or weak shells have a high rate of shedding, leaving tags only in those animals tagged securely.

Tagging-induced disturbance appeared to increase the initial movements of tagged abalone during Beinssen and Powell's (1979) study. Approximately one third of movements greater than 50 metres occurred within one month of tagging during their three year study. Detected movements for this study did not exceed 50 m after the second survey, approximately four months after initial tagging.

When searches were conducted some 12 – 15 months after the second survey to recover tagged abalone for growth, the Flinders total recapture proportion was relatively low at about one third of the recapture proportion for Point Cook. Possible explanations for this

difference include tag loss, dispersal of tagged abalone into cryptic habitat, and overgrowth and obscuring of tags by epibiota. Indeed, one tagged abalone at Flinders was observed amongst many juveniles on the underside of a large boulder we overturned, and two others were only barely visible with most of their tags covered by encrusting coralline algae. Another explanation for the difference is the lower proportion of abalone tagged within the plots at Flinders compared with those tagged outside the plots. Given the two-fold higher probability of recapture for internal tags, less total tag recovery would be expected from Flinders regardless of other factors.

The tagging method adopted by Beinssen and Powell (1979) required the removal of the abalone from the substrate. Several studies have shown that disturbance of abalone by tagging induces abnormal movement (Forster 1967, Fournier and Breen 1983, Ault and DeMartini 1987). The tagging technique used in this experiment has the advantage of being an *in situ* method. Animals were never removed from the substrate and the tag was inserted into a pore in an operation taking less than a minute. This technique provided less stimulus for rapid initial movement, as the strong foot hold was never disrupted. It was observed that a low percentage of animals underwent rapid initial movement after *in situ* tagging compared to those that were removed and returned to the substrate in other studies (C.Dixon, personal observations).

Tagging methods may also influence overall rates of tag disappearance in three ways: tag loss, observer error and tag-induced mortality. A poor tagging method resulting in high tag loss will obviously result in high rates of tag disappearance. Perhaps just as important is the ease with which remaining tags are found. Inconspicuous tags may be missed resulting in higher rates of observer error. Thirdly, tagging methods which require removal of individuals from the substrate often cause mortality by injuring the foot. This mortality is difficult to differentiate from natural mortality. In this study all of these factors were minimised. The rivet tag reduced rates of tag loss (Prince 1991), the use of brightly coloured large plastic tags ensured that tags remained conspicuous throughout the period of the study and *in situ* tagging removed the possibility of damaging the foot.

Growth

More than ninety percent of the abalone at Point Cook and 75% of the abalone from Flinders have the potential to grow past their respective legal minimum lengths and enter the stock. This result seems at odds with the labelling of these populations as stunted, however

at the commencement of this study only a small proportion of each population appeared to have reached this potential. The reasons for this are unclear although knife-edge selection at the LMLs is plausible. This is supported by the changes in the length-frequency distributions of tagged abalone that could be attributed to growth rather than biases among tagged and recaptured samples. At Flinders the relatively small sample and the large growth increments of a small proportion of larger abalone may have combined to bias the result. If mortality has led to knife-edge selection at Flinders then recovery of this population is likely to be inexorably slow, however at Point Cook our results already show evidence of substantial recovery. In the absence of fishing mortality it seems likely that both populations will accumulate a large fishable stock of abalone. The classification of the Point Cook population as stunted is inappropriate and this classification may also be unreasonable for the Flinders population.

Benefits

There is a tendency towards decreasing funds available annually for abalone stock monitoring within the public sector with the expectation that the quality of stock assessment advice provided will be maintained through improved efficiency. Reducing bias and inaccuracies in assessment methods will help achieve better efficiency without incurring the additional costs associated with increased sampling.

Extension of the results to Tasmania and Western Australia should be particularly useful because both these States are in the process of selecting and testing methods for large-scale fishery independent monitoring. South Australia should benefit from application of the results to future studies of the effects of diver fishing behaviour. New South Wales and Victoria will endeavour to use the project outcomes in future development of spatially-structured fishery models, and Victoria will examine ways of modifying its current population surveys to obtain more spatially explicit observations.

Use of the *in-situ* tagging technique adopted for this study will most likely become the standard approach for future abalone mark-recapture studies in Australia.

Australia's valuable (AUD$125M) abalone industry will benefit from this study if abalone fishery assessment groups accommodate re-aggregation in their assessments of abalone stocks to provide greater certainty in estimating sustainable yields. We recommend that indices of aggregation be used in combination with abundance estimates, and that natural

mortality estimates be revised to make allowance for dispersal rates. This will better facilitate the adoption of risk-averse management that ensures benefits flow to the wider community by way of long-term sustainability.

Further Development

Although this study has demonstrated that re-aggregation does occur and that immigration into fished areas plays an important role in this regard, a number of questions remain unanswered. We were unable to isolate emergence from other processes, although if an effective barrier could be placed on the substrate to exclude immigration the propensity for emergence could be determined across a range of reef types. Dispersal in response to disturbance from tagging and measuring should also be investigated further in an attempt to produce more realistic estimates of natural mortality. The answer to the question of whether abalone relocate to areas of preferred habitat remains equivocal. Resurveying our study sites in the future and making more detailed observations of variability in habitat may help resolve this issue.

Conclusion

Abalone populations showed a trend to return to their original spatial distributions. Whilst this recovery may have occurred through an evenly distributed repopulation, the end result was reconstruction of the characteristic aggregated distribution. There was little or no evidence of emergence of undersize abalone. This is not surprising because if cryptic behaviour is primarily protection driven, it makes little biological sense to emerge before attaining a size that can survive in the open. Unfortunately an answer to the interesting question of preferential relocation remains equivocal. The apparent disaggregation of tagged abalone describes only a small proportion of the tagged population. Furthermore the repeated disturbance during the tagging, fishing and resurveying could well have induced this disaggregation. The time interval after fishing may also not have been long enough to allow a complete recovery. For all these reasons, it is planned to resurvey the experimental plots and hopefully get a better answer to the question of habitat driven relocation.

In satisfying the growth objective of this project we have called into question the process of labelling particular populations as stunted in the absence of supporting data. Such classifications may precipitate reductions in legal minimum lengths that will fail to effectively increase yields but may increase the risk of abalone fishing becoming unsustainable

Acknowledgments

References

Ault, J. S. and DeMartini, J. D. 1987. Movement and dispersion of red abalone, *Haliotis rufescens*, in Northern California. *California Fish and Game* 73:196–213.

Beinssen, K. and Powell, D. 1979. Measurement of natural mortality in a population of blacklip abalone *NotoHaliotis ruber. Rapport P. -v Reun. Cons. int. Explor. Mer.* 175:23–26.

Breen, P. A. 1986. Management of the British Columbia fishery for northern abalone (*Haliotis kamatschatkana*). *Canadian Special Publication in Fisheries and Aquatic Sciences* 92: 300–312.

Byth, K. 1982. On robust distance-based intensity estimators. *Biometrics* 38:127–135.

Byth, K. and Ripley, B. D. 1980. On sampling spatial patterns by distance methods. *Biometrics* 36:279–284.

Campbell, D. J. and Clarke, D. J. 1971. Nearest neighbour tests of significance for nonrandomness in the spatial distribution of singing crickets (*Teleogryllus commodus* [Walker]). *Animal Behaviour* 19:750–756.

Clavier, J. and Richard, O. 1984. Etude experimentale du deplacement de I'ormeau (*Haliotis tuberculata*) dans le milieu naturel. *Rev. Trav. Inst. Peches. Marit.* 46:79–92.

Dixon, C. D., Gorfine, H. K. and Officer, R. A. In press. Dispersal of tagged blacklip abalone, *Haliotis rubra*: implications for stock assessment. *Journal of Shellfish Research.*

Forster, G. R. 1967. The growth of *Haliotis tuberculata*: results of tagging experiments in Guernsey 1963-65. *Journal of the Marine Biology Association U.K.* 47:287–300.

Fournier, D. A. and Breen, P. A. 1983. Estimation of abalone mortality rates with growth analysis. *Transactions of the American Fisheries Society* 112: 403–411.

Gorfine, H. K., Hart, A. M. and Callan, M. P. 1995. Evaluation of methods to assess the abundance of blacklip abalone. FRDC Final Report 93/100.

Hart, A. M. and Gorfine, H. K. 1997. Abundance estimation of blacklip abalone (*Haliotis rubra*) II. A comparative evaluation of catch-effort, change-in-ratio, mark-recapture and diver-survey methods. *Fisheries Research* 29:171–183.

Hart, A. M., Gorfine, H. K. and Callan, M. P. 1997. Abundance estimation of blacklip abalone (*Haliotis rubra*) I. An analysis of diver-survey methods for large-scale monitoring. *Fisheries Research* 29:159–183.

Krebs, C. J. 1989. *Ecological Methodology*. Harper Collins, New York. 654 pp.

McShane, P. E. 1990. The fisheries ecology of Victorian abalone, Unpublished Ph.D. thesis. Department of Zoology, LaTrobe University.

McShane, P. E. 1992. Exploitation models and catch statistics of the Victorian fishery for abalone *Haliotis rubra. Fishery Bulletin* 90: 139–146.

McShane, P. E. 1994. Estimating the abundance of abalone (*Haliotis* spp.) stocks: examples from Victoria and southern New Zealand. *Fisheries Research* 19: 379–394.

McShane, P. E. 1996. Patch dynamics and effects of exploitation on abalone (*Haliotis iris*) populations. *Fisheries Research* 25:191–199.

McShane, P. E. and Smith, M. G. 1989. Direct measurement of fishing mortality in abalone (*Haliotis rubra* Leach) off Southeastern Australia. *Fisheries Research* 8:93–102.

Momma, H. and Sato, R. 1969. The locomotion behaviour of the Disc Abalone, *Haliotis discus hannai* Ino, and the Seibold's Abalone, *Haliotis sieboldi* Reeve, in the fishing grounds. *Tohoku Journal of Agricultural Research* 20:150–157.

Nash, W. J. 1995. The development of new techniques for assessing and managing the Australian abalone fisheries. DPIF, Tasmania. Final report FRDC, Grant 88/94.

Nash, W. J., Talbot, S. R., Cawthorn, A. J. and Ford, W. B. 1994. The population biology of abalone (*Haliotis* species) in Tasmania I. Blacklip abalone (*H. rubra*) from the north coast and the islands of Bass Strait. Tasmanian Sea Fisheries Division. Technical Report 48.

Newman, G. G. 1966. Movements of the South African abalone, *Haliotis midae. Invest. Rep and Div. Sea Fish and Rep. South Africa* 56:20 pp.

Peach, W. J. 1993. Combining mark-recapture data sets for small passerines. pp. 107–122. *In:* Lebreton, J.-D. and North. Ph. M. Marked individuals in the study of bird populations, Birkhäuser Verlag, Boston.

Poore, G. C. B. 1972. Ecology of New Zealand abalones, *Haliotis* species (Mollusca, Gastropoda). 2: Seasonal and diurnal movement. *New Zealand Journal of Marine and Freshwater Research* 6:246–258.

Prince, J. D. 1989. The fisheries biology of the Tasmanian stocks of *Haliotis rubra*. Unpublished Ph.D. thesis. Department of Zoology, University of Tasmania.

Prince, J. D. 1991. A new technique for tagging abalone. *Australian Journal of Marine and Freshwater Research* 42:101–106.

Prince, J. D. 1992. Using a spatial model to explore the dynamics of an exploited stock of the abalone *Haliotis rubra*. pp. 305–317 In *Abalone of the world: biology, fisheries and culture*, S. A. Shepherd, M. J. Tegner and S. A. Guzmán del Próo (eds.), Blackwell. Oxford.

Prince, J. D., Sellers, T. L.. Ford, W. B. and Talbot, S. R. 1988. Recruitment, growth, mortality and population structure in a southern Australian population of *Haliotis rubra* (Mollusca: Gastropoda). *Marine Biology* 100(1):75–82.

Shepherd, S. A. 1973. Studies on southern Australian abalone (genus *Haliotis*) I. Ecology of five sympatric species. *Australian Journal of Marine and Freshwater Research* 24:217–257.

Shepherd, S. A. 1986. Movement of the Southern Australian abalone *Haliotis laevigata* in relation to crevice abundance. *Australian Journal of Ecology* 11:295–302.

Shepherd, S. A. 1986. Studies on Southern Australian abalone (genus *Haliotis*) VII. Aggregative behaviour of *H. laevigata* in relation to spawning. *Marine Biology* 90:231–236.

Shepherd, S. A. 1990. Studies on southern Australia abalone (genus *Haliotis*) XII. Long term recruitment and mortality dynamics. *Australian Journal of Marine and Freshwater Research* 41:475–492.

Shepherd, S. A. and Godoy, C. 1989. Studies on southern Australian abalone (genus *Haliotis*). XI. Movement and natural mortality of juveniles. *Journal of the Malacological Society of Australia* 10:87–95.

Shepherd, S. A. and Breen P. A. 1992. Mortality in abalone: its estimation, variability and causes. pp. 276–304. In *Abalone of the world: biology, fisheries and culture*, S. A. Shepherd, M. J. Tegner and S. A. Guzmán del Próo (eds.), Blackwell. Oxford.

Shepherd, S. A. and Kirkwood G. P. and Sandland R. L. 1982. Studies on southern Australian abalone (genus *Haliotis*) III. Mortality of two exploited species. *Australian Journal of Marine and Freshwater Research* 33:265–272.

Sloan, N. A. and Breen, P. A. 1988. Northern abalone, *Haliotis kamtschatkana*, in British Columbia: fisheries and synopsis of life history information. *Canadian Special Publication in Fisheries and Aquatic Sciences* 103.

Tarr, R. J. Q. 1995. Growth and movement of the South African abalone *Haliotis midae*: a reassessment. *Marine and Freshwater Research* 46:583–590.

Treble, R. J., and Day, R. W. 1993. Detection and effects on mortality estimates of changes in tag loss. *Canadian Journal of Fisheries and Aquatic Sciences* 50:1435–1441.

Troynikov, V. S. In press. Probability density functions useful for parameterization of heterogeneity in growth and allometry data. *Bulletin of Mathematical Biology*.

Werner, I., Flothmann, S. and Burnell, G. 1995. Behaviour studies on the mobility of two species of abalone (*Haliotis tuberculata* and *H. discus hannai*) on sand: implications for reseeding programmes. *Marine and Freshwater Research* 46:681–688.

Tables

Table 1. The components of tagged abalone not re-sighted for all plots expressed as annual rates and dispersion expressed as a percentage of tagged abalone not re-sighted.

Annual rates of:	Fished plots		Control plots	
	NW	SE	NE	SW
Tagged abalone not re-sighted (observed)	0.98	1.54	1.38	1.31
Dispersion (expected)	0.49	0.72	0.78	0.53
Dispersion as a percentage of tagged abalone not re-sighted.	50%	47%	57%	40%
M + tag loss + observer error	0.49	0.82	0.60	0.78

Table 2. Numbers of tagged abalone expected to remain within each plot after dispersion, E_r, and number of abalone re-sighted, n_{tot}.

Plot	Plot Type	Expected remaining (E_r)				Number re-sighted (n_{tot})			
		1st survey	2nd survey	3rd survey	4th survey	1st survey	2nd survey	3rd survey	4th survey
NW	Fished	227	176	183	160	227	103	104	106
SE	Fished	277	198	203	174	277	137	117	124
NE	Control	362	232	203	222	362	177	136	158
SW	Control	456	366	360	328	456	228	224	207

Table 3. Effect of available preferred habitat on estimates of dispersion for fished and control plots.

Plot	Plot Type	% of medium and high relief	Prefishing dispersion (1st-2nd survey)	Postfishing dispersion (1st-3rd survey)	Postfishing change (2nd-3rd survey)
NW	Fished	38%	22%	19%	decrease 3%
SE	Fished	41%	29%	27%	decrease 2%
NE	Control	14%	36%	44%	increase 8%
SW	Control	56%	20%	21%	increase 1%

Table 4. Likelihood estimates of distribution function parameters for the stochastic Gompertz growth model for length increment data for Point Cook and Flinders *H. rubra* populations. E and SD are the mathematical expectation and standard deviation of L_∞. η and α are the parameters of the Weibull distribution, ρ and λ are the parameters of the gamma distribution; μ and σ are the parameters of the log-normal distribution.

Model	Parameter	Location	
		Point Cook	Flinders
"WG"	η	12.14 (5%)	6.68 (21%)
	α	117 (1%)	129 (5%)
	g	0.55 (6%)	0.12 (20%)
	$E(L_\infty)$	112	120
	$SD(L_\infty)$	10%	18%
"GG"	ρ	111.38 (11%)	40.82 (39%)
	λ	0.96 (12%)	0.33(43%)
	g	0.43 (6%)	0.11 (20%)
	$E(L_\infty)$	116	123
	$SD(L_\infty)$	10%	16%
"LNG"	μ	4.75 (<1%)	4.82 (1%)
	σ	0.10 (6%)	0.17 (22%)
	g	0.41 (7%)	0.10 (23%)
	$E(L_\infty)$	117	125
	$SD(L_\infty)$	10%	17%
Gompertz deterministic	L_∞	117 (<1%)	125 (1%)
	g	0.40 (1%)	0.10 (7%)
Sample size		439	72

WG abbreviates Weibull-Gompertz, GG abbreviates Gamma-Gompertz, and LNG abbreviates Lognormal-Gompertz. (* %) is statistical error.

Table 5. Kullback's informative mean Δ(M1, M2) for comparing models based on Weibull, gamma and Lognormal distributions (if Δ(M1, M2) > 0 then model M1 fits the data better; if < 0 then model M2 fits the data better).

Location	Δ(GG,WG)	Δ(LNG,WG)	Δ(LNG,GG)
Flinders	1.13×10^{-1}	1.27×10^{-1}	1.41×10^{-2}
Point Cook	1.01×10^{-1}	1.06×10^{-1}	4.30×10^{-3}

WG abbreviates Weibull-Gompertz, GG abbreviates Gamma-Gompertz, and LNG abbreviates Lognormal-Gompertz.

Table 6. Quantiles of the lognormal distribution of the asymptotic length (L∞) for each study site. Shaded cells represent that part of the population that will not reach the legal minimum length (LML) for fishing.

Location	LML	Quantiles								
		10%	20%	30%	40%	50%	60%	70%	80%	90%
Point Cook	100	103	107	110	113	116	119	122	126	131
Flinders	110	100	107	113	118	124	129	135	142	153

List of Figures

Figure 8. Relative length frequency distributions of abalone within fished plots at (a) Point Cook and (b) Flinders. The distribution prior to fishing is shown above the x-axis and the distribution after fishing is shown reflected below the x-axis for each site. Vertical lines indicate the size limits used at each site.

Figure 9. Changes in the abundance of abalone counted on fixed transects outside fished and control plots at (a) Point Cook and (b) Flinders over the course of the experiment.

Figure 10. Schematic diagram showing the minimum distance moved of peripherally tagged abalone that moved into the plots at Point Cook.

Figure 11. Position of moving and settled abalone relative to the initial abundance of the cell in which they were sighted.

Figure 12. Actual and predicted movement frequency distribution functions of tagged abalone at Point Cook.

Figure 13.   Probability densities of asymptotic length for Point Cook and Flinders populations.

Figure 14.   Leslie plot of tag recovery rate against cumulative number of tags recovered at Flinders.

Site locations:

Australia
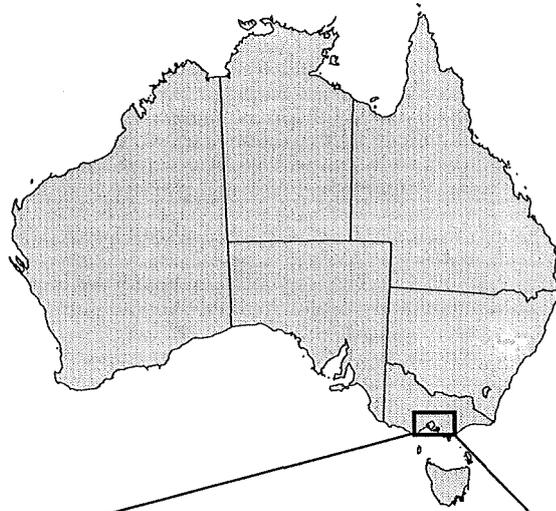
Point Cook

Flinders
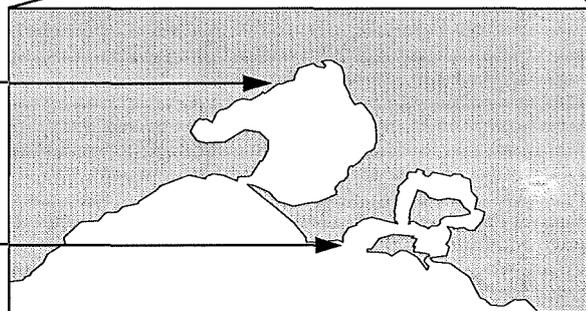
Figure 1. Locations of study sites on the central Victorian coast.
(Point Cook 37°55.893' S, 144°47.104' E; Flinders 38°29.397' S, 145°01.274' E)
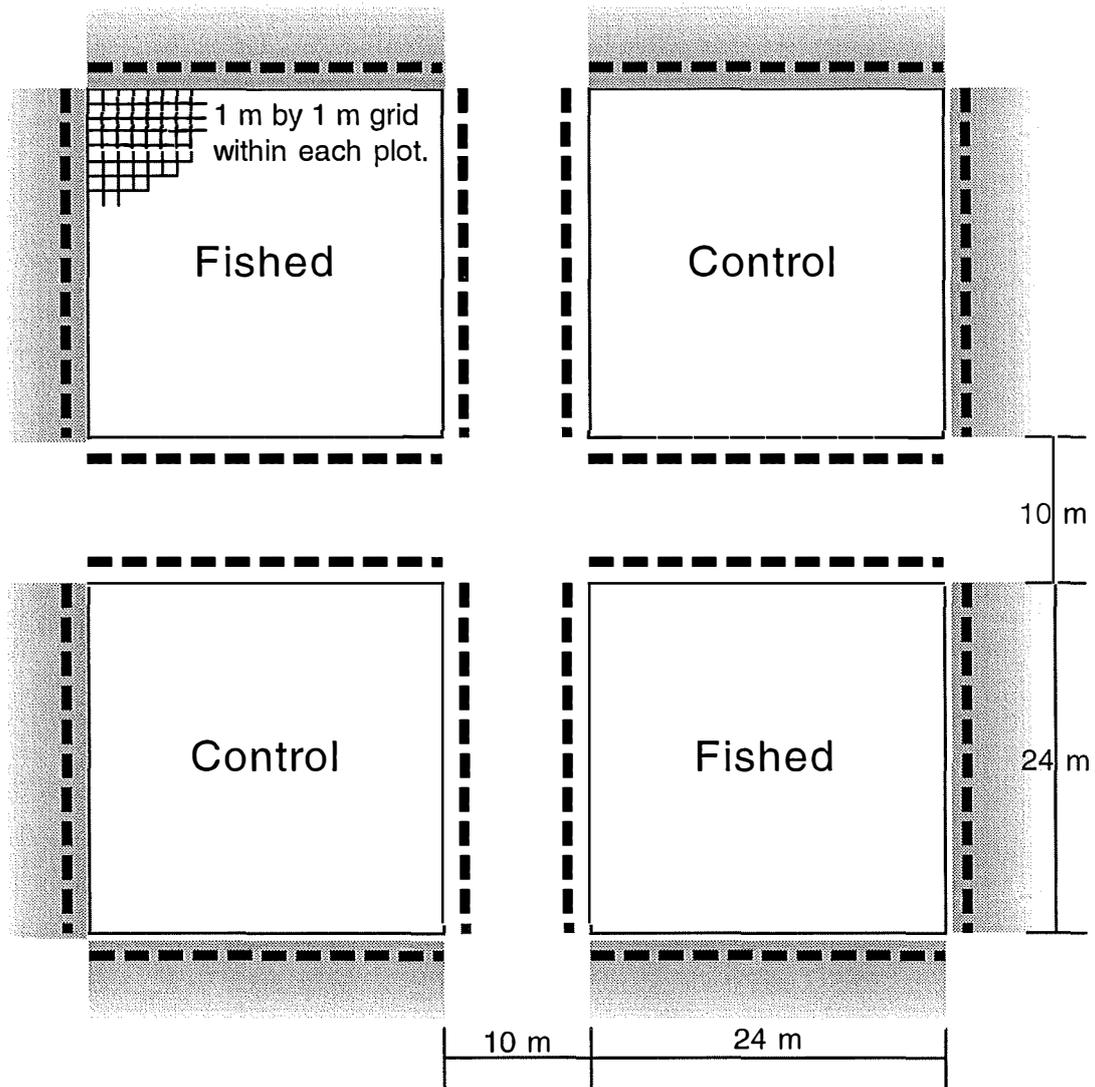
Figure 2. Diagram showing the set up of experimental areas at each site. Shaded areas outside the plots indicate areas in which abalone were mass marked. Dotted lines indicate the positions of fixed transects swum outside the plots.
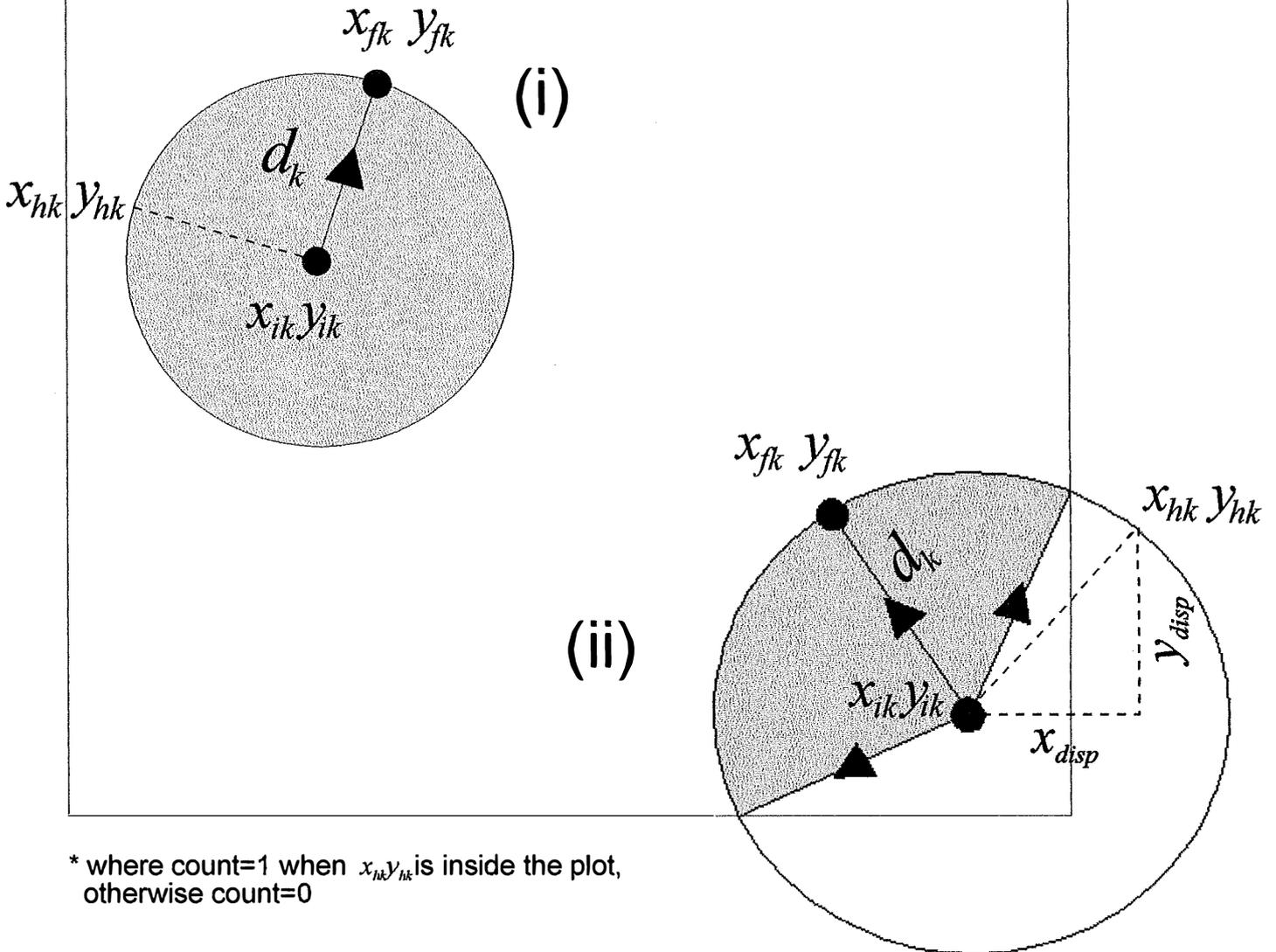
Figure 3. The probability P_k of a tagged abalone being re-sighted within a plot given its initial position $x_{ik}y_{ik}$ distance travelled d_k (assuming random direction of movement) and final position $x_{fk}y_{fk}$. Hypothetical finishing positions $x_{hk}y_{hk}$ which remain within the plot are shaded. Examples are shown for an abalone:

(i) which would remain within the plot regardless of the direction of movement, and,
(ii) When some directions of movement resulted in $x_{hk}y_{hk}$ being outside plot boundaries, determined by adding x_{disp} and y_{disp} to its initial position $x_{ik}y_{ik}$.

NW (F)

$$y = -0.49x + 5.41$$
$$R^2 = 0.88$$

$$y = -0.98x + 5.32$$
$$R^2 = 0.75$$

NE (C)

$$y = -0.78x + 5.85$$
$$R^2 = 0.88$$

$$y = -1.38x + 5.83$$
$$R^2 = 0.89$$

SW (C)

$$y = -0.53x + 6.12$$
$$R^2 = 0.99$$

$$y = -1.31x + 6.07$$
$$R^2 = 0.92$$

SE (F)

$$y = -0.72x + 5.62$$
$$R^2 = 0.96$$

$$y = -1.54x + 5.57$$
$$R^2 = 0.92$$

Ln (frequency)

Time (years)
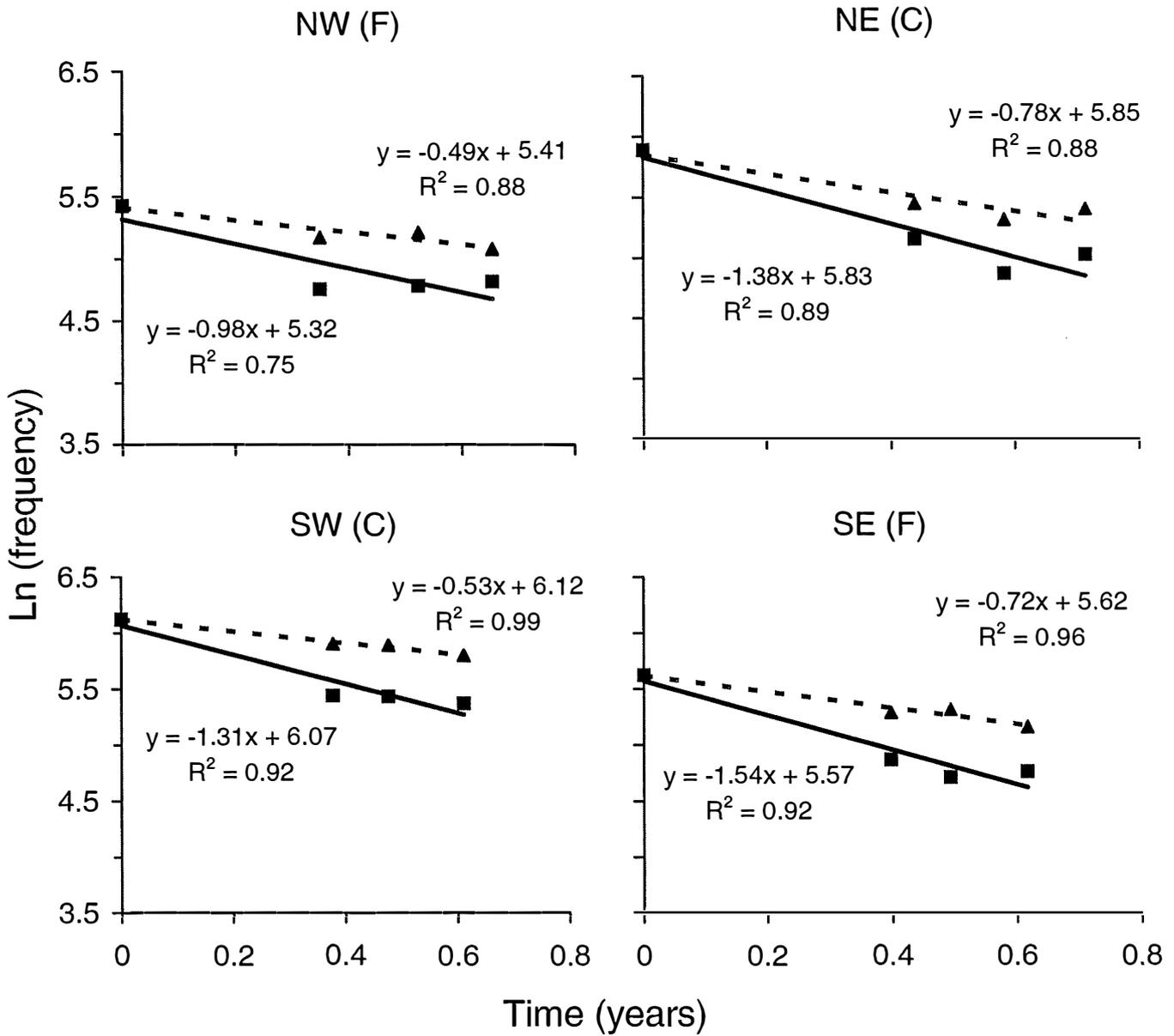
Figure 4. Regressions of the natural logarithm of the number of tags observed (■) and the number of tags expected (▲) after dispersal against time for each plot (NW, NE, SW, SE) at Point Cook. (F) = fished, (C) = control.
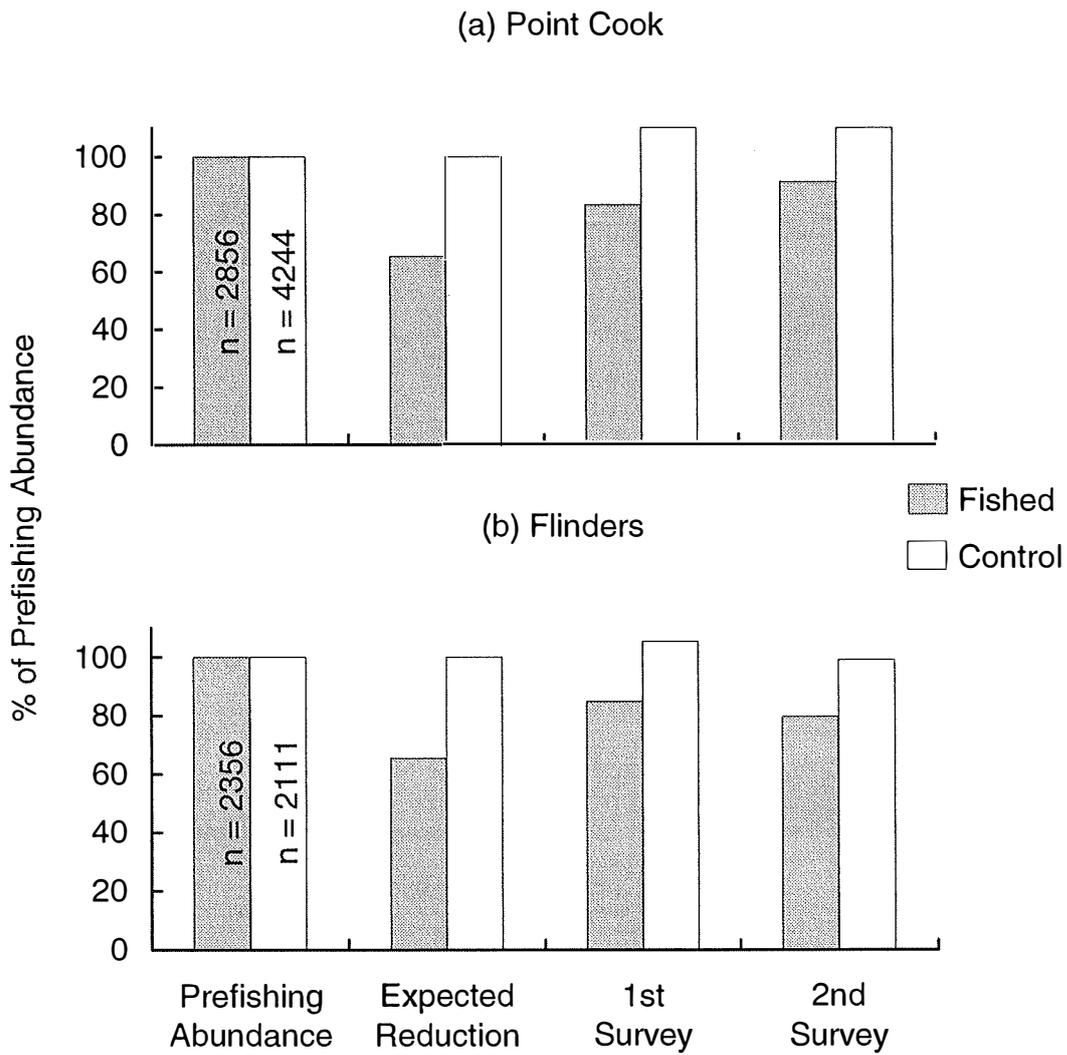
Figure 5. Changes in abundance of abalone within fished and control plots at (a) Point Cook and (b) Flinders over the course of the experiment.
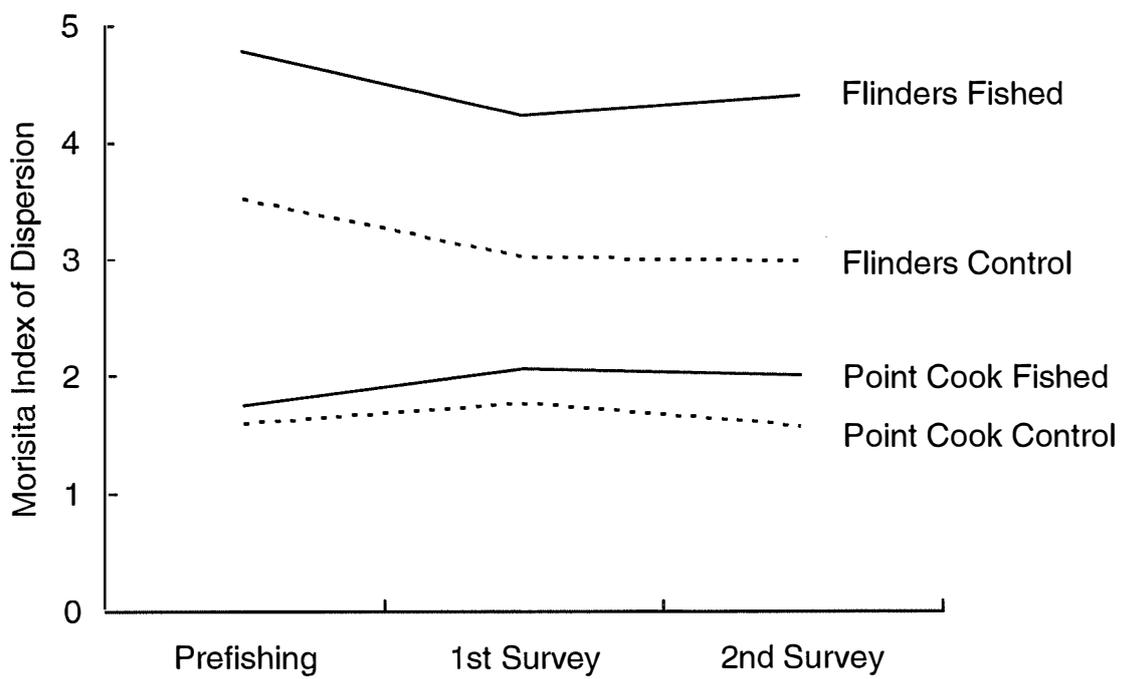
Figure 6. Changes in the un-standardised Morisita Index of Dispersion for abalone within fished and control plots at Point Cook and Flinders over the course of the experiment.
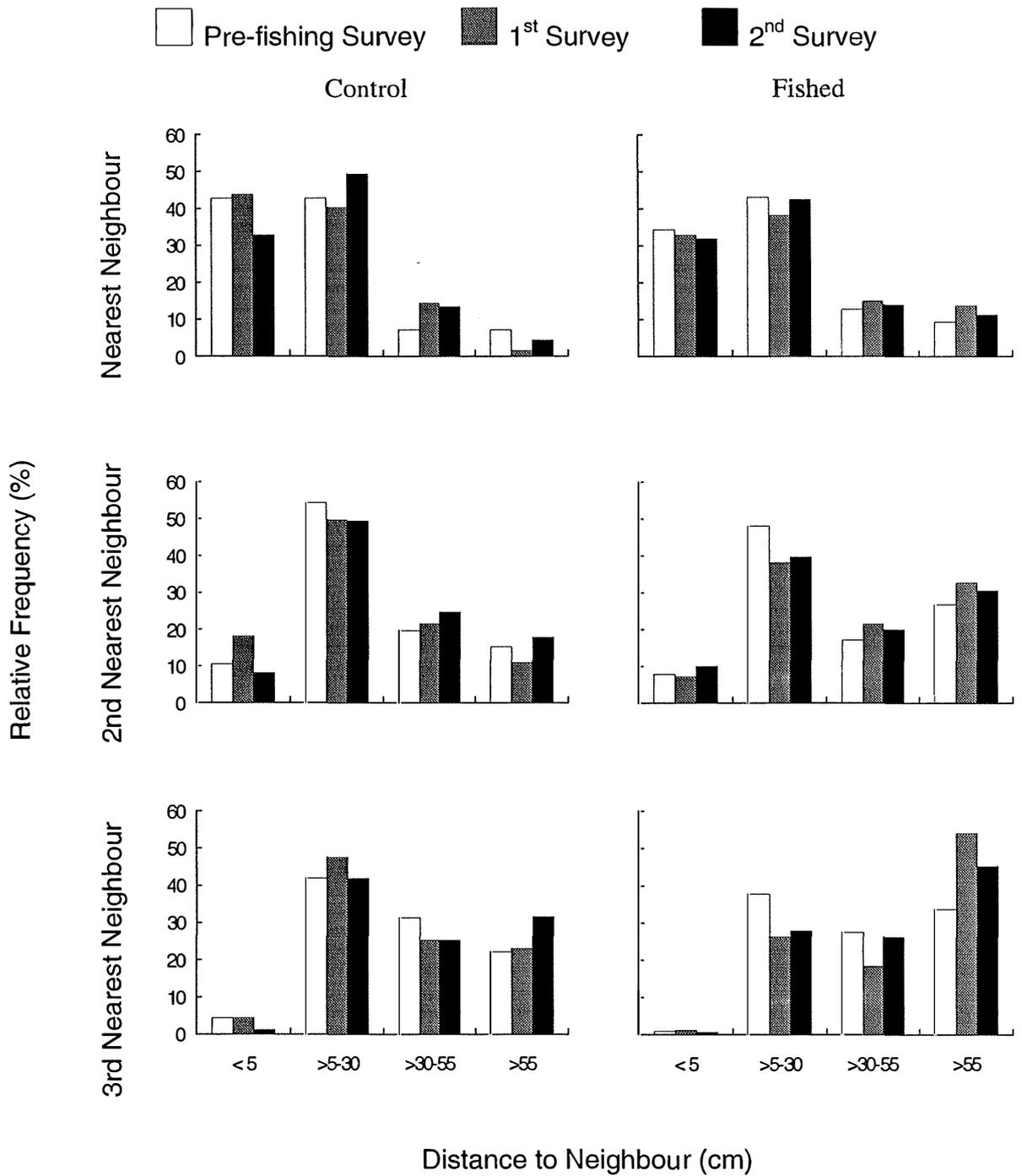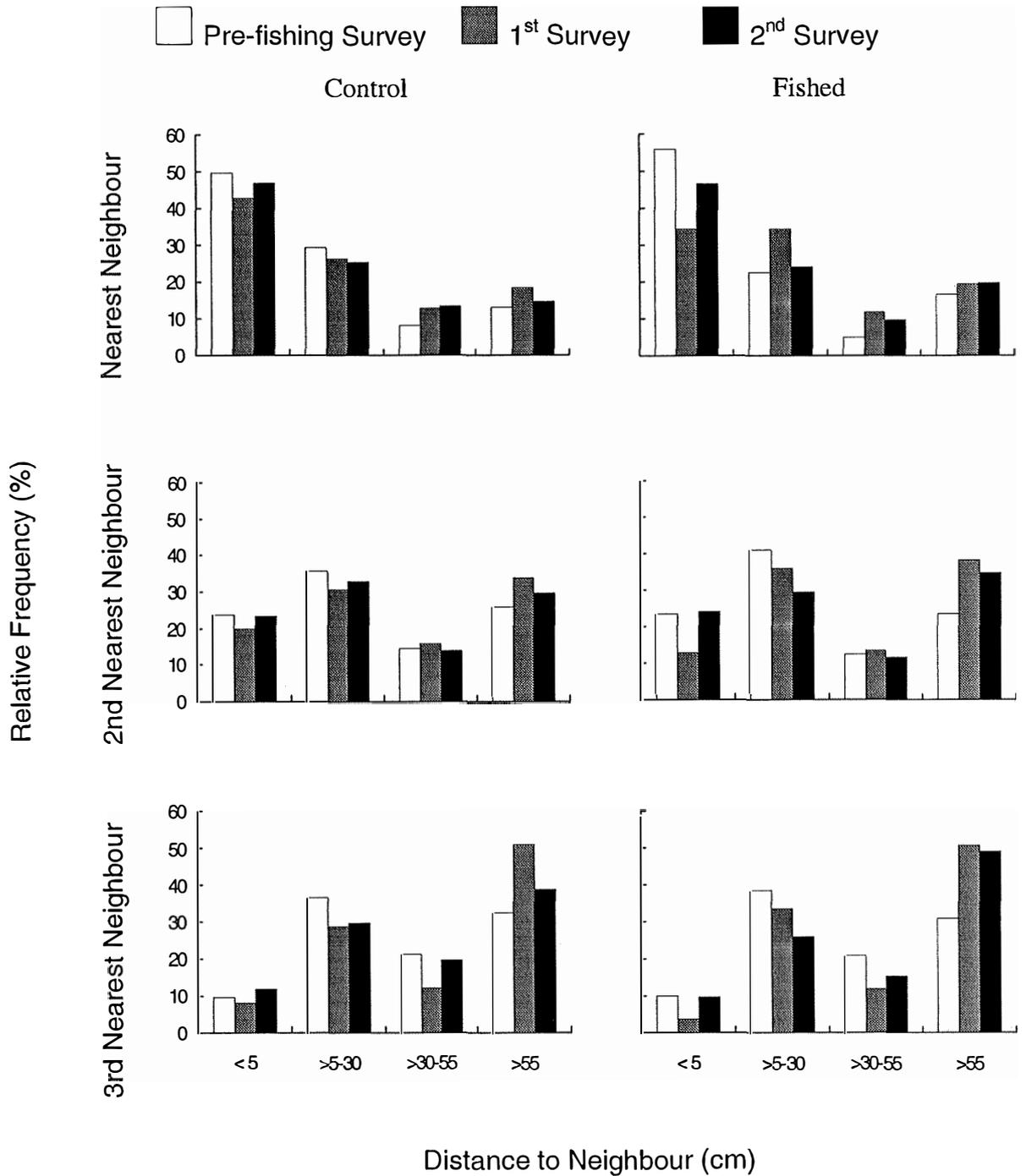
Figure 7(a). Relative frequency distributions of distances from abalone to their nearest, second nearest and third nearest neighbours at Point Cook prior to fishing and during each post-fishing survey.

Figure 7(b). Relative frequency distributions of distances from abalone to their nearest, second nearest and third nearest neighbours at Flinders prior to fishing and during each post-fishing survey.

Figure 8. Relative length frequency distributions of abalone within fished plots at (a) Point Cook and (b) Flinders. The distribution prior to fishing is shown above the x-axis and the distribution after fishing is shown reflected below the x-axis for each site. Vertical lines indicate the size limits used at each site.

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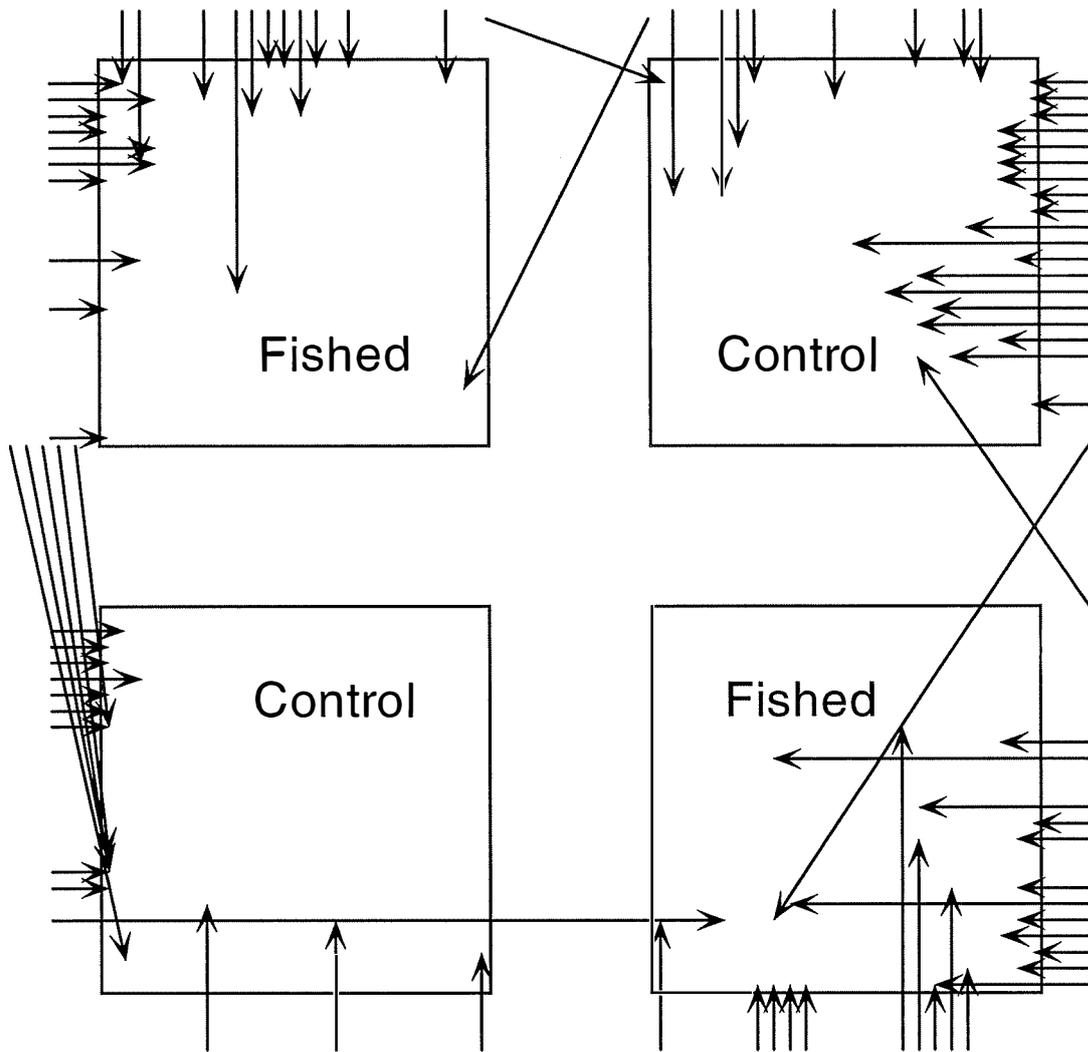
Figure 10. Schematic diagram showing the minimum distance moved of peripherally tagged abalone that moved into the plots at Point Cook.
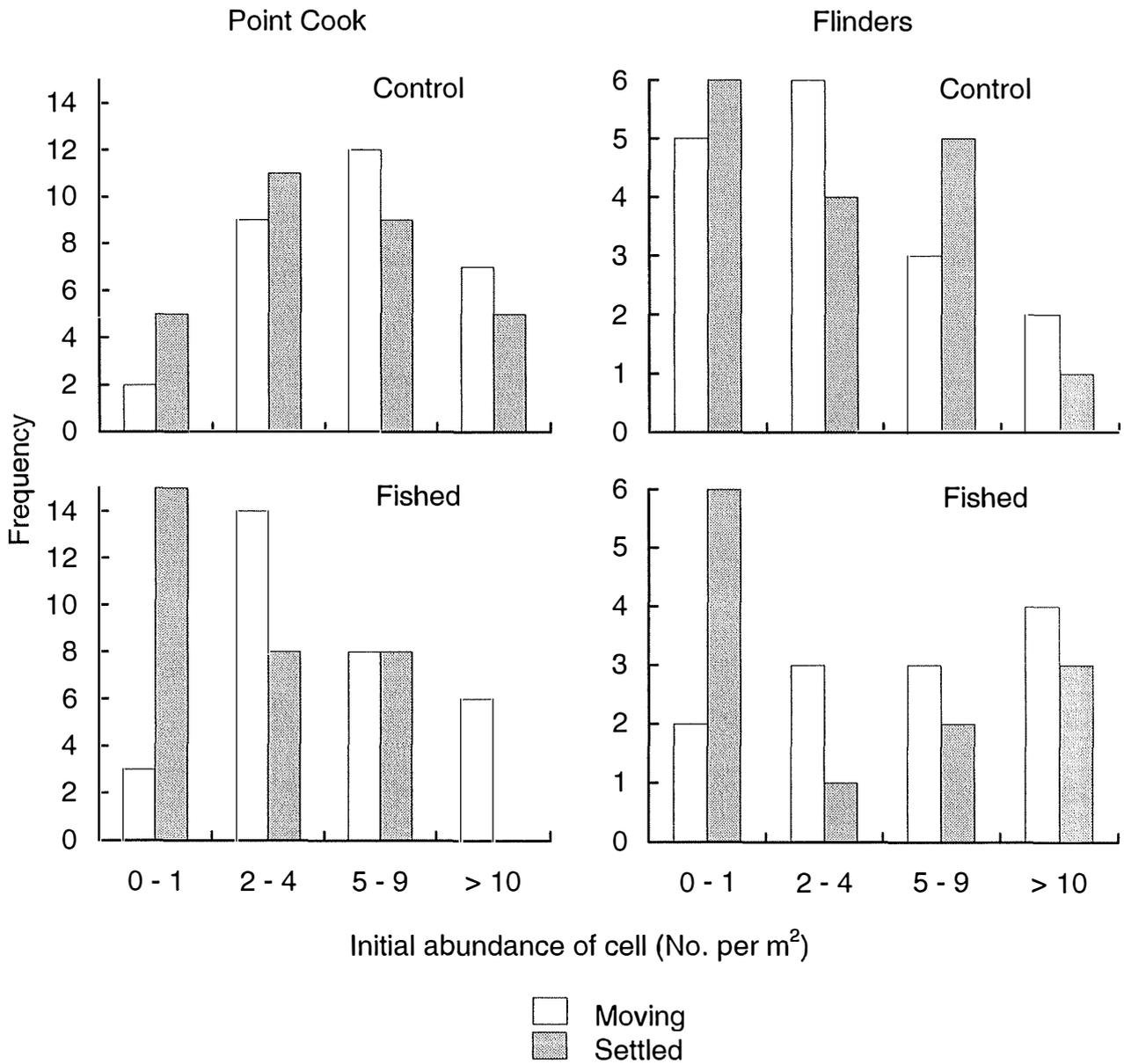
Figure 11. Position of moving and settled abalone relative to the initial abundance of the cell in which they were sighted.
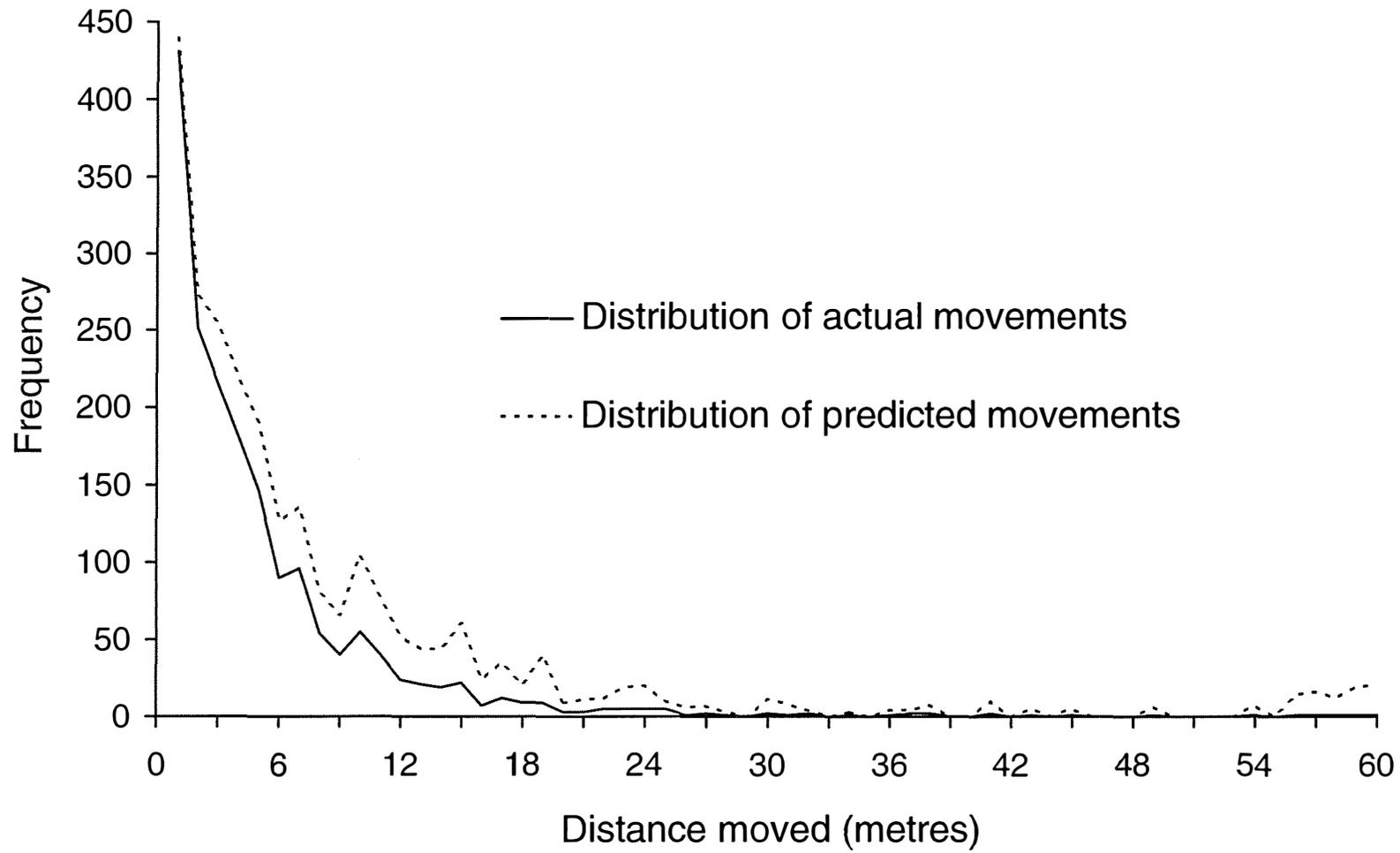
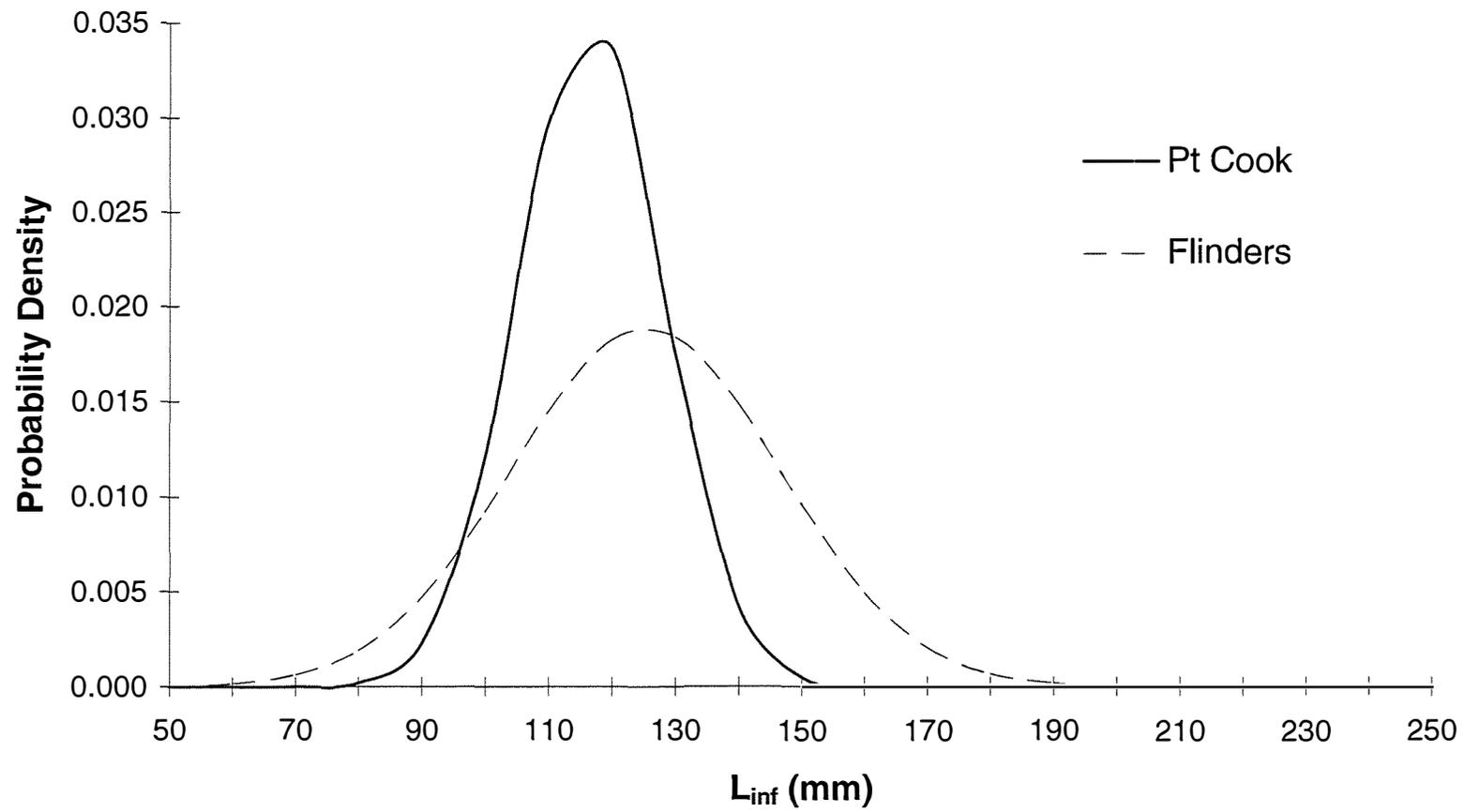**Figure 12.** Actual and predicted movement frequency distributions of tagged abalone at Point Cook.

Figure 13. Probability densities of asymptotic length for Point Cook and Flinders populations.
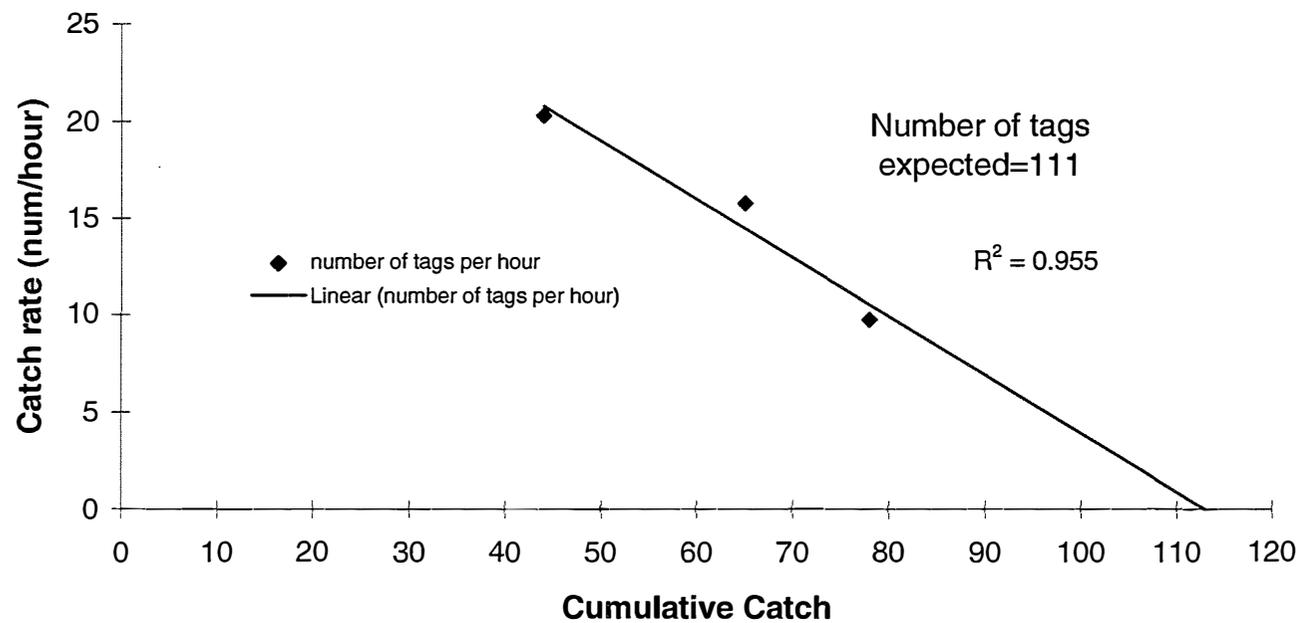
Catch rate of tagged abalone

Figure 14. Leslie plot of tag recovery rate against cumulative number of tags recovered at Flinders.

Appendices

Appendix 1:

Intellectual property

No intellectual property has arisen from the research that is likely to lead to significant commercial benefits, patents or licences. Intellectual property associated with the data produced during the project will be shared between MAFRI and FRDC.

Appendix 2:

Staff

Mr. Harry Gorfine	Principal Investigator	1 Jan 94 - 30 Jun 95	15%
Dr. Rickard Officer	Project Scientist	1 Apr 96 - 18 Oct 97	100%
Mr. Cameron Dixon	Technical Officer	1 Apr 94 - 30 Jun 95	75%
Mr. David Forbes	Contract Diver	1 Jul 96 - 30 Jun 97	20%
Mr. Rodney Knights	Contract Diver	1 Jul 96 - 30 Jun 97	15%
Mr. Bruce Waters	Contract Diver	1 Jul 96 - 30 Jun 97	15%
Mr. Michael Callan	Contract Diver	1 Jul 96 - 30 Jun 97	5%
Mr. Geoffrey Rodda	Charter Vessel Operator and Contract Diver	1 Jul 96 - 30 Jun 97	20%
Mr. Alistair MacDonald	Charter Vessel Operator	1 Jul 96 - 30 Jun 97	5%