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FINAL REPORT TO THE
FISHERIES RESEARCH AND DEVELOPMENT CORPORATION

THE DEVELOPMENT OF NEW TECHNIQUES FOR ASSESSING AND MANAGING THE AUSTRALIAN ABALONE FISHERIES

FRDC Grant 88/94

Warwick J. Nash

FISHERIES
RESEARCH &
DEVELOPMENT
CORPORATION

Department of
Primary Industry and Fisheries
TASMANIA

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EXECUTIVE SUMMARY

BACKGROUND

In studies of blacklip abalone (*Haliotis rubra*) in Tasmania conducted during 1983 to 1987, Jeremy Prince and his research team made several important findings concerning the biology and fishery management of this species. These include:

- Rate of deposition of growth layers in the shell is closely related to age, and may be used to determine the relationship between age and size (Prince *et al.*, 1988a). Sampling of populations may then be made to determine age structure and other demographic features.

- Experimental evidence was provided which suggests that larval dispersal is very limited, perhaps on the scale of tens of metres (Prince *et al.* 1987, 1988b).

- Catch rates are not closely related to abalone abundance except at high levels of exploitation (Prince 1992). Hence, monitoring of catch-effort statistics is not a useful means of detecting population changes (particularly declines).

When reviewing the findings of his work, Prince (1989: 145-6) concluded that an understanding of the population dynamics of *H. rubra* and of the sustainable levels of fishing might best be achieved by elucidating the relationship between spawning stock biomass and recruitment. It was as a result of this belief that the present study was proposed by Prince, and an application to the Fishing Industry Research and Development Council (FIRDC) for the funding of a stock-recruitment study was submitted shortly after I assumed the position of abalone biologist after Prince's departure.

When preparing the application, it was immediately apparent that the accuracy of measurement of the stock-recruitment relationship (SRR) depends on the accuracy with which abundance (or biomass) of both stock and recruits can be measured. The research proposal submitted to FIRDC therefore was intended to address the question of how accurately abalone abundance can be measured. (See below for the objectives of this study.)

The study was designed as a multi-State study: methods would be developed in Tasmania, and these methods would then be applied in other abalone-producing States (at least two of Victoria, South Australia and New South Wales). At each study site the

accuracy with which abundance could be measured would be determined; these sites would then be used to measure the relationship between stock and recruitment.

The general experimental procedure was to manipulate abalone densities at each of three sites (final densities to be high, medium and low) within a region, then to monitor subsequent recruitment rates at these sites. This would be repeated at four regions around Tasmania, and at a single site in other States. This experimental design relies critically on the validity of the finding of Prince *et al.* (1988b) that larval dispersal is limited to a scale of metres or tens of metres; if this were not the case then the abundance (or density) of the parental population from which recruitment was derived would be impossible to determine.

RESULTS

The results of the various aspects of this study have been prepared as draft papers and are presented as separate sections of this report. Estimation of abundance using three methods (strip transects, timed swims and depletion experiments) yielded, in general, similar estimates of abundance (Section 1). The precision of timed swim estimates was shown to be low because of high variability in swimming speeds between research divers, and between days and sites for individual divers. The accuracy of the abundance estimate obtained from the Leslie depletion experiments was found to vary greatly between sites; this was almost certainly dependent on the characteristics of the bottom (density of macroalgal cover and substrate heterogeneity): when searching was at random with respect to bottom features (no targeting of cracks, crevices and ledges in which abalone were likely to be found), the rate of decline of catch rates was linear; an unbiased estimate of abundance was then obtained. When searching was non-random, catch rates declined rapidly initially, then tailed off (hyperdepletion); if the depletion experiment had been terminated before catch rates had declined to zero, the population size would have been severely underestimated.

Strip transect estimates of abundance showed varying levels of precision, but in almost all cases the estimate was very similar to the final number of abalone found within the site during the depletion exercise. A double-survey method was used during the strip transect surveys to assess diver searching efficiency. It was shown that the number of abalone that may be overlooked by individual divers was substantial; this was highest at the Stinking Bay site, where an average of 40 percent of the abalone within a transect were overlooked. Density of algal cover and substratum complexity are important determinants of searching efficiency.

Major changes in abundance and size composition of abalone within the Port Arthur site over the course of this study showed that abalone movement may seriously affect estimates of abundance. In the absence of information on patterns of movement, these changes (particularly declines) may be wrongly attributed to overfishing (Nash 1992b).

The study sites were set up as a gridwork of squares so that rates of movement of tagged abalone could be measured. Rates of movement could then be used to estimate the number of untagged abalone, on subsequent mark-recapture visits, that were immigrants. Untagged abalone not accounted for as immigrants were then an estimate of the number of abalone present within the site during the previous mark-recapture exercise, but which were hidden under boulders or in crevices, or otherwise overlooked. An estimate of the probability of capture ('catchability') could then be obtained. The results of this study are presented in Section 2. An unexpected finding was that abalone movement is extensive, and is often directional. Linear distances travelled often exceeded the scale of *H. rubra* larval dispersal proposed by Prince *et al.* (1988b). This finding highlighted the deficiency of the study procedure in the original proposal to FIRDC: it would be impossible to manipulate abalone densities to either high or low level and maintain them at that level without frequent visits to do so. For this reason, this aspect of the study (experimental manipulation of abalone densities to artificially high or low levels) was abandoned as soon as the rate of movement became apparent.

Recent developments of mark-recapture-movement theory by terrestrial ecologists in the U.S.A. and France (Lebreton *et al.* 1992; Brownie *et al.* 1993; Nichols *et al.* 1993) have allowed a detailed analysis of the mark-recapture results of this study to be made.

Partially to address the objectives of this study, but also in an attempt to understand why some abalone populations are more resilient to fishing than others (Nash 1991), settlement rates of abalone larvae were measured at George III Reef. Using methods developed in commercial abalone hatcheries, larval settlement rates to conditioned artificial surfaces were monitored for a 12-month period (Section 3). Settlement rates as high as 2,500 larvae.m^{-2} were achieved (Nash *et al.* in press); this is the first time that such a study has been successful. Good agreement between settlement rate patterns and reproductive seasonality (measured by histological analysis of gonad samples collected monthly) was obtained (Section 4).

Measurement of growth and ageing was made at each of the three Tasmanian sites (Section 5). Growth was measured from a large number of length increment measurements at each site. Growth rates (expressed per unit time) were maximal for 60 to 80 mm-diameter abalone (depending on the site), indicating that the relationship

between age and length is sigmoid. Growth of abalone larger than size at maximal growth rate was shown to fit the von Bertalanffy growth function. Marginal increment analysis (measurement of the timing of shell layer deposition) indicated that shell growth rings are deposited annually at the three sites in south-east Tasmania. This rate has been confirmed only for abalone ≥ 80 mm maximum shell diameter.

The inter-State components of the study were not successful in achieving the stated objectives, but were successful in other ways. Since the gridwork site configuration used in Tasmania requires at least two surveys, conducted several weeks or months apart, to estimate catchability, this approach could not be used inter-State, since the time available for this component of the study was limited to no more than one month per State. The effect of abalone movement on the estimation of catchability could be overcome only by using as sites isolated patch reefs, at which immigration or emigration would be negligible (since abalone are hard-bottom dwellers, and generally do not move across sand). Unfortunately, suitable patch reefs containing abalone in useful densities could not be found.

The work that was done in South Australia was useful in demonstrating that the size distribution and abundance of *H. rubra* is closely related to position with respect to prevailing weather direction (Section 6). Abalone size and abundance were measured at several transects placed radially around each of three emergent rocky reefs in Rivoli Bay. It was found that abalone were in highest abundance on the lee side of these reefs, and juvenile abalone predominated on the lee side as well. The implications of these findings for distribution patterns of larval settlement are considered.

Several hundred abalone were tagged and released at one reef in Rivoli Bay for growth studies. Some of these were recaptured in early 1995, five years after tagging. These mark-recapture results are being used to estimate age-size relationships, and the shells have been retained by the South Australian Research and Development Institute for analysis to elucidate the relationship between number of shell growth rings and age.

The work that could be conducted in New South Wales was to a large extent determined by the severe decline of *H. rubra* populations that has occurred there. The various aspects addressed by the research team included an assessment of the legal minimum size limit (with respect to size at onset of sexual maturity), a re-survey of one of the study sites of the early 1980s, and measurements of *H. rubra* abundance and size composition at several sites between Eden and the Victorian border (Section 7). A comparison of the results of the present study with those conducted at the study site 10 years earlier showed that there was little change in abundance of abalone smaller than

the size limit, suggesting that the perceived overfishing problem may have been one of growth overfishing rather than recruitment overfishing. Other evidence indicated that this was likely to be an oversimplified interpretation, since the sea urchin *Centrostephanus rogersii* occurs in New South Wales waters in exceedingly high numbers. The impact of *C. rogersii* on *H. rubra* is likely to be adverse because (i) it has substantially removed the macroalgae from large areas of the bottom, thereby removing both food and shelter from predation; and (ii) juvenile *C. rogersii* were often observed occupying the cracks and crevices normally occupied by juvenile *H. rubra*, with juvenile *H. rubra* sometimes observed in the open outside the juvenile urchins, which is very uncharacteristic behaviour of juvenile abalone. It therefore seems unlikely that abalone populations in southern New South Wales can increase through fishery management intervention (reduction of fishing mortality) unless the abundance of *C. rogersii* is substantially reduced.

Finally, the ultimate objective of this study as expounded by Prince (1989)—to determine the relationship between stock and recruitment and to use this relationship to set harvest rates that optimise recruitment rates—is appraised (Section 8). It is argued that, because of the high fecundity of abalone, a close relationship between stock and recruitment is unlikely to exist. In addition, fine-scale geographic variation in recruitment rates (Nash 1991) indicates that, even if a close SRR relationship could exist, its usefulness for management would be limited because of the inability to manage a fishery with the fine spatial resolution required. The usefulness of the stock-recruitment approach to management of abalone fisheries therefore seems small.

FUTURE DIRECTIONS AND RECOMMENDATIONS

1 This study (Section 1) has shown that the timed swim method of estimating abundance is prone to large error variance because of variation in diver swim rate while searching. Depletion methods are likely to yield abundance estimates that are severely biased (underestimates) because of unequal catchability of abalone. Strip transect methods may yield accurate estimates of abundance with a precision that would be adequate for adoption as a management tool for long-term monitoring of abundance, if the following conditions are met:

- transects are of a size that is suitable for abalone densities; that is, large enough that the mean number of abalone per transect unit is substantially greater than zero, so that confidence limits may be satisfactorily narrow;

- spatial patchiness is not so great that the number of transects required to achieve the required level of precision is not impractically large;

- temporal variation in catchability is not so large that it masks true trends in abundance; or catchability on each survey is measured using the double-survey method, and abundance estimates adjusted accordingly.

2 It is argued (Section 8) that the ultimate objective of this study—to determine the spawning stock biomass/density at which recruitment rates are maximal, and then to manage the fishery in ways that maintain stock densities at or near this level—is unlikely to be a useful approach to managing abalone fisheries because of the high fecundity of this animal, and because evidence from population surveys conducted in Tasmania indicates that recruitment rates vary greatly on a fine spatial scale. There is therefore no single stock biomass/density at which recruitment rates are maximal, and the fine spatial scale at which the stocks must be managed to achieve maximal recruitment rates would be impossible to achieve.

3 Two other avenues to abalone fishery assessment and management have been explored in Tasmania during the course of this study and subsequently. These are the change-in-ratio method to estimate abundance and fishing mortality, and egg-per-recruit analysis.

4 The change-in-ratio (CIR) method has been applied to the stunted *Haliotis rubra* fishery in Bass Strait to estimate abundance, biomass and fishing mortality. It has been shown that this method yields estimates of abundance, on a spatial scale of 10–30 kilometres of coastline, with quite narrow confidence limits (± 10 percent of the estimate) with relatively little survey effort. The accuracy of the estimates obtained is affected by growth, natural mortality and recruitment between the surveys conducted before and after the fishing exercise. If the fishing season is short, the time between the pre- and post-fishing surveys is short enough that the effect of these factors is negligible. If the size composition of the sampled populations is relatively uniform throughout the study area, then the precision will be high (*i.e.*, the confidence limits will be narrow). Both of these conditions were satisfied in the Bass Strait fishery. When the estimates of abundance and fishing mortality obtained are considered in conjunction with estimates of other population parameters that have been collected (Nash *et al.* 1994), a detailed assessment of the Bass Strait abalone fishery has been obtained.

Importantly, the CIR method yields estimates of abundance of immediate pre-recruits as well as recruits, which is critical for the detection of recruitment declines.

The CIR method may be applied more widely in abalone fisheries if the requisite conditions listed above are met (a short intense fishing season and uniform size composition throughout the region that is to be assessed). These conditions are to a large extent met in the Tasmanian west coast fishery, where fishing is of short duration (the summer months) because of the adverse weather conditions that apply for most of the year. As a precursor to conducting this study, preliminary surveys will be conducted in the region to examine the heterogeneity of size composition.

5 Egg-per-recruit (EPR) analyses have been used to assess abalone fisheries (Sluczanowski 1986; Tegner *et al.* 1989; Nash 1992a; Shepherd *et al.* 1991. Although the method does not take into consideration the relationship between stock and recruitment, it yields estimates of population egg production levels relative to what they would have been in the absence of fishing. EPR analyses carried out on fisheries that have collapsed can provide valuable information on the levels of egg production at which recruitment failure is likely. Egg production in the collapsed Mexican abalone fishery had declined to 6 to 17 percent of pre-fishing levels (Shepherd *et al.* 1991).

An assessment of *Haliotis rubra* by EPR analysis carried out in several parts of Tasmania yielded egg production estimates of 44 to 74 percent of pre-fishing levels (Nash 1992a), suggesting that Tasmania's stocks are not in serious danger of recruitment overfishing. It is proposed that this method be utilised more widely.

A drawback of the EPR method is that it is essentially an equilibrium-based model. If conditions (*e.g.*, climatic or environmental) that affect rates of recruitment change, the level of egg production required to maintain the stock may change; the EPR approach will not be sufficient to detect this. Only direct monitoring methods will, highlighting (yet again) the importance of implementing long-term monitoring programs, using procedures that reduce bias and maximise precision within budgetary constraints.

REFERENCES

Breen, P.A. (1986). Management of the British Columbia fishery for northern abalone (*Haliotis kamtschatkana*). In: G.S. Jamieson and N. Bourne (editors), *North Pacific Workshop on Stock Assessment and Management of Invertebrates. Canadian Special Publication on Fisheries and Aquatic Sciences* 92: 300-312.

Brownie, C., J.E. Hines, J.D. Nichols, K.H. Pollock and J.B. Hestbeck (1993). Capture-recapture studies for multiple strata including non-Markovian transitions. *Biometrics* 49: 1173-1187.

Lebreton, J.-D., K.P. Burnham, J. Clobert and D.R. Anderson (1992). Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecological Monographs* 62: 67-118.

Nash, W.J. (1991). Recruitment rate variation complicates abalone management. *Fishing Today* 3(6): 25-27.

Nash, W.J. (1992). An evaluation of egg-per-recruit analysis as a means of assessing size limits for blacklip abalone (*Haliotis rubra*) in Tasmania. *In* S.A. Shepherd, M. Tegner and S.A. Guzmán del Próo (eds): *Abalone of the World: biology, fisheries and culture*. pp. 318-338. Blackwell: London.

Nash, W.J. (1992b). Some recent findings and future directions for abalone research in Tasmania. *Fishing Today* 5(5): 29-31.

Nash, W.J., J.C. Sanderson, J. Bridley, S. Dickson and B. Hislop (in press). Post-larval recruitment of blacklip abalone (*Haliotis rubra*) on artificial collectors in southern Tasmania. *Australian Journal of Marine and Freshwater Research.*

Nash, W.J., T. Sellers, S. Talbot, A. Cawthorn and W. Ford (1994). The population biology of abalone (*Haliotis* species) in Tasmania. I. Blacklip abalone (*H. rubra*) from the north coast and the Furneaux group of islands. *Sea Fisheries Division Technical Report* 48: 69 pp.

Nichols, J.D., C. Brownie, J.E. Hines, K.H. Pollock and J.B. Hestbeck (1993). The estimation of exchanges among populations or subpopulations. *In* J.-D. Lebreton and P.M. North (eds): *Marked Individuals in the Study of Bird Population*. pp. 265-279. Birkhäuser Verlag: Basel.

Prince, J.D. (1989). The fisheries biology of the Tasmanian stocks of *Haliotis rubra*. *Ph.D. dissertation, University of Tasmania.* 174 pp.

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

Prince, J.D. (1993). A stock reduction analysis of the Mexican abalone (Haliotid) fishery. *Fisheries Research* 16: 25-49.

Prince, J.D., T.L. Sellers, W.B. Ford and S.R. Talbot (1987). Experimental evidence for limited dispersal of haliotid larvae (genus *Haliotis*; Mollusca: Gastropoda). *Journal of Experimental Marine Biology and Ecology* 106: 243–263.

Prince, J.D., T.L. Sellers, W.B. Ford and S.R. Talbot (1988a). A method for ageing the abalone *Haliotis rubra* (Mollusca: Gastropoda). *Australian Journal of Marine and Freshwater Research* 39: 167–175.

Prince, J.D., T.L. Sellers, W.B. Ford and S.R. Talbot (1988b). Confirmation of a relationship between the localized abundance of breeding stock and recruitment for *Haliotis rubra* Leach (Mollusca: Gastropoda). *Journal of Experimental Marine Biology and Ecology* 122: 91–104.

Shepherd, S.A., S.A. Guzmán del Próo, J. Turrubiates, J. Belmar, J.L. Baker and P.R. Sluczanowski (1991). Growth, size at sexual maturity, and egg-per-recruit analysis of the abalone *Haliotis fulgens* in Baja California. *The Veliger* 34: 324-330.

Sluczanowski, P.R. (1986). A disaggregate model for sedentary stocks: the case of South Australian abalone. *Canadian Special Publication of Fisheries and Aquatic Sciences* 92: 393-401.

Tegner, M.J., Breen, P.A. and Lennert, C. (1989). Population biology of red abalones, *Haliotis rufescens*, in Southern California and management of the red and pink, *H. corrugata*, abalone fisheries. *Fishery Bulletin U.S.* 87: 313- 339.

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1 OBJECTIVES OF THE STUDY AS SET OUT IN FIRDC APPLICATION 88/94

The overall objective of this project is to lay the foundation for an extended study of the stock-recruitment relationship in abalone populations, so that this relationship can be used to develop a new model for assessing and managing exploited stocks of abalone. This project will develop and verify the techniques necessary for such a study, as well as establish the research sites upon which the study would be based. The goal is to assess the feasibility of conducting an extended study in the future.

Specifically, the individual objectives are:

1 to choose four localities around Tasmania and one each in Victoria and New South Wales which represent the range of habitats typically inhabited by abalone;

2 within each locality, to choose three sites which will be experimentally manipulated to provide low, medium and high population densities;

3 to measure stock abundance with three different methods (transects, Leslie fishdowns and mark-recapture);

4 to develop and use a computer simulation model to test the robustness of the three methods;

5 to conduct a reproductive study of the different areas in order to determine whether accurate estimates of population fecundity can be derived.

METHODS OF COMMUNICATING THE RESULTS OF THIS STUDY TO INDUSTRY, FISHERY MANAGERS AND THE SCIENTIFIC COMMUNITY

The findings of this study have been communicated in the following ways:

1 The abalone fishing industry

1 Oral and written results at meetings of the Abalone Liaison Committee (Tasmania).

2 Oral presentations at annual general meetings of the Tasmanian Abalone Divers Association.

3 Oral presentation at a special general meeting of the NSW Abalone Fishermen's Association (in Eden, New South Wales).

4 The following publications in fishing industry magazines:

Nash, W.J. (1992). Some recent findings and future directions for abalone research in Tasmania. *Fishing Today* 5(5): 29-31.

Nash, W.J. (1993). Future plans for abalone research. *Fishing Today* 5(6): 27-29.

2 The scientific community

1 Oral and written presentations to the Demersal Mollusc Research Group (that meets at least once per year to discuss research and identify important research objectives for fishery management).

2 Oral presentations at the Second International Symposium on Abalone Biology, Fisheries and Culture, held in Hobart in February 1994. These papers were:

- Larval settlement of blacklip abalone (*Haliotis rubra*) to conditioned artificial substrates in the sea. (presented by Craig Sanderson)
- Growth and ageing of blacklip abalone (*Haliotis rubra*) in southern Tasmania. (presented by Warwick Nash)

3 Oral presentation at the North Pacific Symposium on Invertebrate Stock Assessment and Management, held in Nanaimo, British Columbia in March 1995:

- Estimation of abundance, catchability, survival and movement of blacklip abalone (*Haliotis rubra*) by mark-recapture in three spatially stratified study sites. (presented by Warwick Nash)

4 The following publications in scientific journals and conference proceedings:

Nash, W.J. 1992. What do abalone spat settlement studies measure? The effects of substrate attractiveness on abalone larval settlement rate to artificial surfaces. *In* D.A. Hancock (ed.) *Recruitment Processes. Australian Society for Fish Biology Workshop, Hobart, 21 August 1991.* pp. 26-32. Bureau of Rural Resources Proceedings No. 16, AGPS, Canberra.

Nash, W.J., J.C. Sanderson, J. Bridley, S. Dickson and B. Hislop (in press). Post-larval recruitment of blacklip abalone (*Haliotis rubra*) on artificial collectors

in southern Tasmania. *Australian Journal of Marine and Freshwater Research.*

Nash, W.J. (in prep.). Estimation of abundance, catchability, survival and movement of blacklip abalone (*Haliotis rubra*) by mark-recapture in spatially stratified sites. *Canadian Special Publication of Fisheries and Aquatic Sciences.*

3 The Tasmanian Department of Primary Industry and Fisheries

1 Oral presentations to the Research & Assessment and Wild Fisheries Management Branches:

- The Abalone Liaison Committee;
- The Abalone Research Reviews (presented annually);
- The Abalone Research Advisory Group (which meets annually or bi-annually)

SECTION 1.: ESTIMATION OF ABUNDANCE OF BLACKLIP ABALONE (HALIOTIS RUBRA) BY THREE TECHNIQUES: STRIP TRANSECTS, TIMED SWIMS AND DEPLETION EXPERIMENTS

WARWICK J. NASH, J. CRAIG SANDERSON, SIMON R. TALBOT AND ANDREW CAWTHORN

SECTION 1. Estimation of abundance of blacklip abalone (*Haliotis rubra*) by three techniques: strip transects, timed swims and depletion experiments

Warwick J. Nash, J.Craig Sanderson, Simon R. Talbot and Andrew Cawthorn

INTRODUCTION

Following several years of study of blacklip abalone (*Haliotis rubra*) in Tasmania, Prince (1989) concluded that one of the most important aspects of the fishery-related biology of this species remaining to be understood was the relationship between spawning stock biomass and recruitment. Prince believed that an understanding of the nature of this relationship would enable fishery biologists and managers to identify the spawning stock density (or biomass) which maximised the rate of recruitment to the fishery. A management goal would then be to maintain adult densities at or near this optimum level.

The accuracy with which the stock-recruitment relationship can be measured depends on the accuracy with which the abundance or biomass of both spawning stock and recruits to the fishable stock can be measured. The purpose of the present study was therefore to determine the accuracy with which abundance of *H. rubra* can be measured.

There are two components to the estimation of abundance:

- With what precision and accuracy can the visible fraction of a population be measured? and

- What fraction of a population is visible or accessible to survey personnel during a survey?

In order to answer the first question, three different abundance estimation techniques were used: strip transects, timed swims and depletion experiments (the topic of this Section). The second question was addressed using multiple mark-recapture methods using a spatial design which allowed information on abalone movement to be incorporated into the analysis (the topic of Section 2). The second question seeks to measure the probability of capture (the 'catchability') of adult abalone in relation to

habitat complexity and other factors, and to determine whether catchability is temporally constant within a site.

The timed swim method of assessing abalone abundances was adopted because it is simpler and easier to carry out timed swim surveys than strip transect surveys. If it can be shown that the timed swim results are comparable with those of the more precise strip transect method, then the extensive surveys necessary to monitor abundance, and changes in abundance, will be much more easily and rapidly carried out. In addition, this method has been used extensively to survey *Haliotis rubra* stocks and to assess abalone fishing pressure in Victoria (McShane and Smith 1989); an evaluation of the method is therefore desirable.

Depletion methods of estimating abundance were also employed because they could easily be incorporated into the study with only slight increase in survey effort; Prince (1989) used depletion methods to estimate abundance of *H. rubra* at George III Rock. This study therefore allowed a comparison with Prince's results at this site to be made; it also extended the comparison to two other sites.

METHODS

Overall study design

Three sites in southern Tasmania were chosen in which to conduct this study (Figs. 1, 2). The primary criteria by which sites were chosen were substrate complexity and abalone abundance. Since probability of capture is likely to be determined to a large degree by the availability of cracks, crevices and sub-boulder habitat in which abalone may hide, the sites chosen ranged from relatively flat rocky substrate (low complexity: George III Rock), to moderately complex (small to medium-sized boulders: Stinking Bay), to highly complex (medium to very large boulders: Shag Rock Bay).

In a complete Cormack-Jolly-Seber type study, multiple mark-recapture methods may be used to estimate abundance, survival rate, capture probability, births/recruitment/ immigration and deaths/emigration (Cormack 1964, Jolly 1965, Seber 1965, Pollock *et al.* 1990). The robust design of Pollock (1982) enables death and emigration to be estimated separately; similarly, it allows births (or *in situ* recruitment) to be estimated separately from immigration. An alternative approach, adopted here, is to subdivide the mark-recapture area into smaller areas; the position of tagged abalone on each mark-recapture survey is recorded, allowing movement (both rate and direction) to be

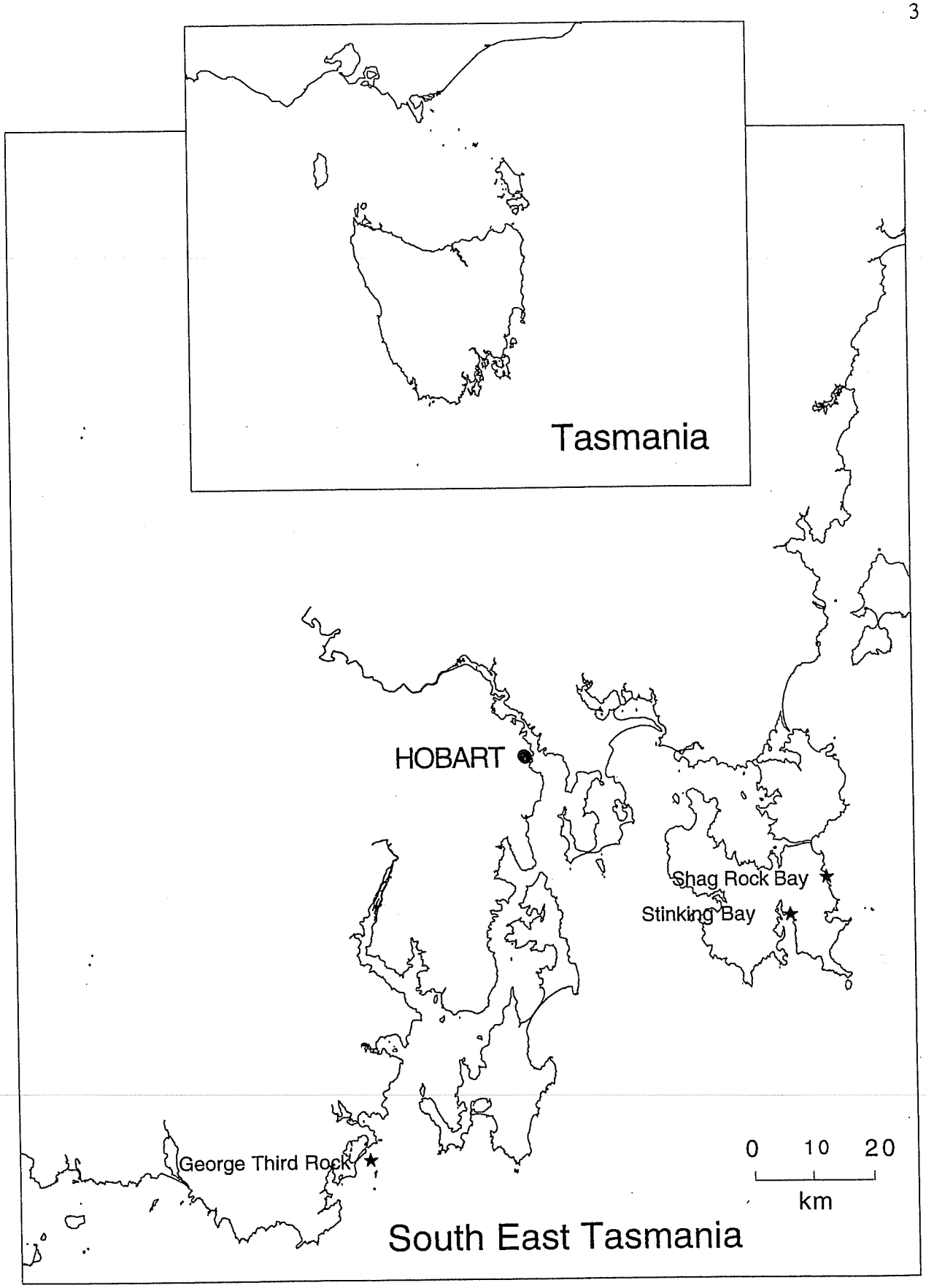


Figure 1. Location of the study sites in southern Tasmania.

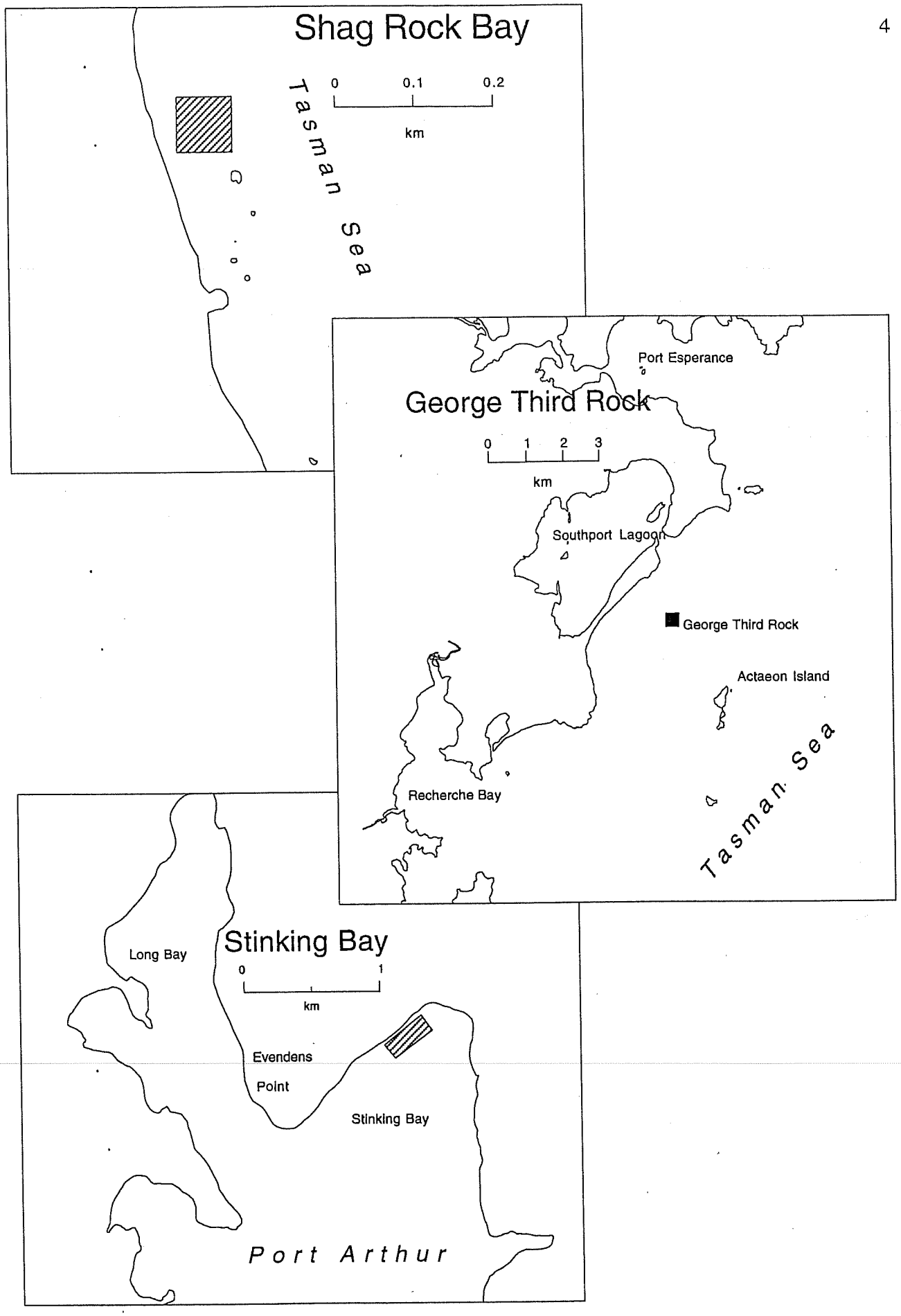


Figure 2. Location and orientation of the study sites.

measured. Movement estimates may then be used to calculate expected numbers of migrants, and thence the numbers of births, deaths, immigrants and emigrants. This method, similar to that used by Beinssen and Powell (1979) to measure rates of natural mortality of blacklip abalone, is described further in Section 2.

Each study site was therefore divided into a gridwork of cells (Fig. 3). During the initial survey, all abalone ≥80 mm maximum shell diameter were tagged with a uniquely numbered tag and released in the grid of capture. On the following visit, the grid position of each tagged abalone within the site was recorded, and all untagged abalone were tagged and released in the grid of origin, as in the first survey. This procedure was repeated several times at each site.

Survey procedure

It was desirable to complete the survey of a site in as short a time as possible in order to minimise within-survey immigration of abalone. Thus, all eight field personnel were involved in surveying a site when possible. All surveys were conducted using surface-supplied breathing apparatus (hookah). Two 5.5-m outboard motor-powered aluminium dinghies were used in all surveys.

Strip transects

Transect sampling methods may take one of two general forms: strip transect censuses, in which all individuals of the target species are counted; and line transects (or distance sampling), in which the distance of each individual from the transect line is measured (usually to a pre-determined maximum sighting distance). Quadrats are a form of strip transect census. Despite the advantages of the line transect method—more extensive statistical analyses are possible (Buckland *et al.* 1993), and detection probabilities less than 1 are allowed—this method was not used here for several reasons: (i) measuring the distance of abalone from the transect line would have been extremely arduous, time-consuming and virtually impossible because of high macroalgal density at two of the sites (George III Rock shallow site and Stinking Bay), where it was often difficult to see abalone even 1.5 m from the transect line; (ii) the topographic complexity (large-boulder bottom) at the Shag Rock Bay site made it often impossible to measure the perpendicular distance between an abalone an the transect line, especially when both could not be seen simultaneously; and (iii) an important assumption of the distance sampling method—that the probability of detection of an individual under the transect line is 1—was clearly violated, as a double-survey method (described below) demonstrated. (Analytical methods when this detection probability is less than 1 are an area of current methodological

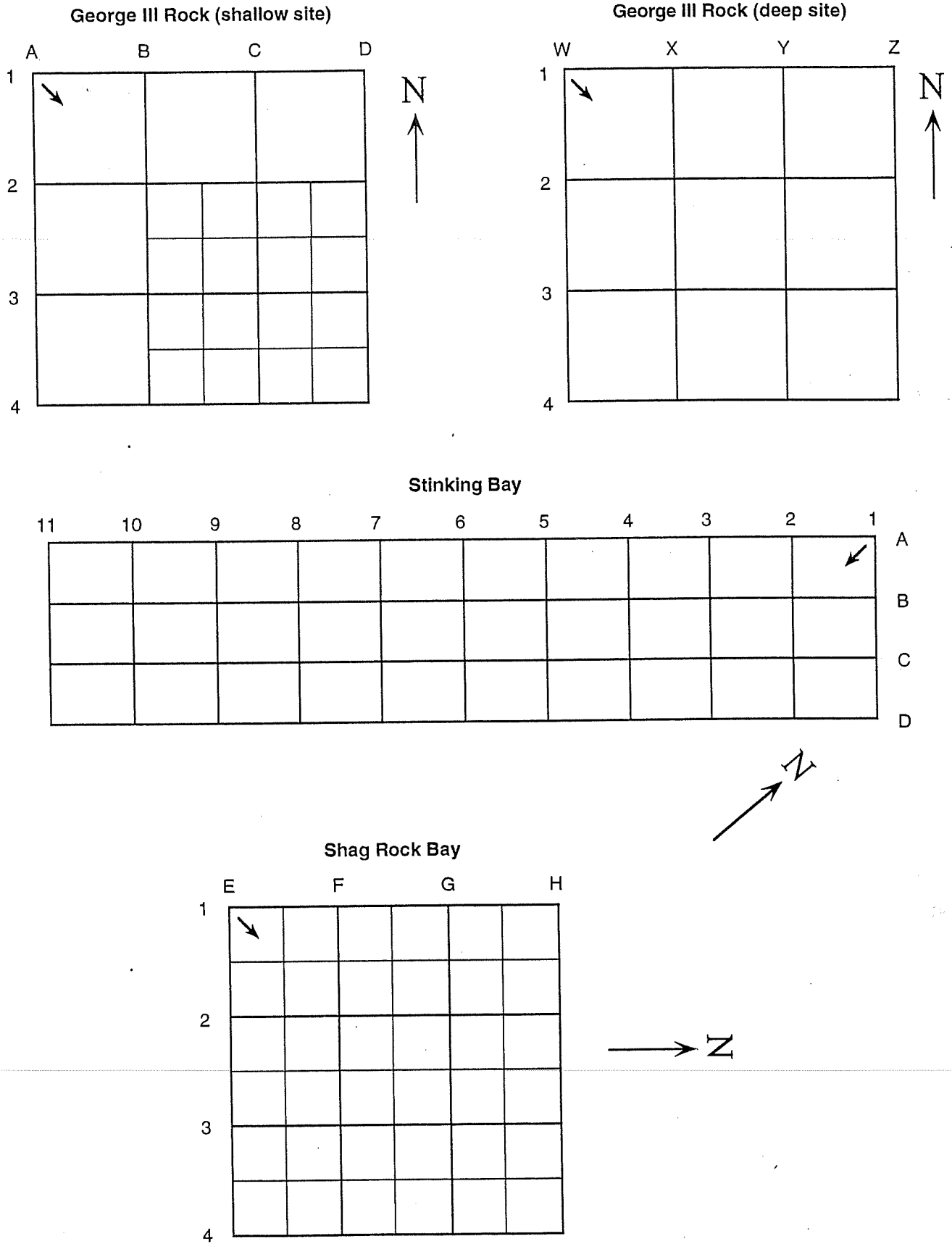


Figure 3. Diagrams showing the grid design of each of the study sites. Grid cells are labelled by the coordinates indicated by the arrows (*e.g.*, the top left cell at the Shag Rock Bay site is cell E1).

development: Buckland *et al.* 1993.) Thus, the strip transect census method was adopted as one of the abundance estimation methods in this study.

Strip transect censuses were conducted along the boundaries of each gridded site – a total of 48 transects at the two George III Rock sites and the Shag Rock Bay site and 66 transects at the Stinking Bay site (Fig. 3). All abalone ≥80 mm diameter were counted in a 1.2 m-wide strip either side of the transect line at the shallow George III Rock site, and in a 1.5 m-wide strip at the remaining three sites. A narrower transect was searched at the shallow George III Rock site because the density of the bull kelp (*Durvillaea potatorum*) made searching extremely difficult. Tag number and position of any tagged abalone seen were recorded while conducting the censuses.

An advantage of this type of transect configuration is that it allows the precision of various transect shapes and sizes to be calculated from a single set of transects (Fig. 4). Its disadvantage is that autocorrelation of counts between contiguous transects is likely (contiguous transects being more likely to have similar counts than non-contiguous transects), resulting in negatively biased estimates of the variance. Autocorrelation was therefore tested for by comparing the counts in contiguous transects.

Diver searching efficiency

In the early phases of this study, most strip transects were each surveyed by one diver, and a small number of transects were surveyed by several divers in order to compare diver searching efficiencies. In later surveys, an assumption implicit in strip transect censuses – that all individuals are detected – was addressed by adopting a double-survey method. Diver searching efficiency was estimated using divers working in pairs: the divers each searched one side of the transect line then changed sides and searched the strip just searched by his/her partner. Each transect was therefore searched twice. While searching the first transect, all abalone seen were marked on the shell with builders' crayon. When searching the second transect, the numbers of chalked and unchalked abalone were recorded separately. The number of abalone in each transect was then estimated using the method of Magnusson *et al.* (1978). Nichols *et al.* (1986) provide an alternative method for analysing these data.

The necessary equations are:

$$\hat{P}_1 = B/(B + S_2)$$

$$\hat{P}_2 = B/(B + S_1)$$

$$\hat{M} = S_1 S_2 / B$$

$$\hat{N} = \frac{(S_1 + B + 1)(S_2 + B + 1)}{(B+1)} \quad (1)$$

where $\hat{P}_1$ and $\hat{P}_2$ are the estimated proportions of abalone seen within a transect by the first and second diver, respectively; B is the number of abalone seen by both divers; S_1 and S_2 are the number of abalone seen by only the first or second diver, respectively; $\hat{M}$ is the estimated number of abalone overlooked by both divers; and $\hat{N}$ is the estimated total number of abalone within the transect. This estimator is unbiased when $S_1 + S_2 + 2B \geq \hat{N}$, which was the case here. An unbiased estimator of the variance of $\hat{N}$ is calculated as

$$\mathrm{Var}(\hat{N}) = \frac{S_1 S_2 (S_1 + B + 1)(S_2 + B + 1)}{(B+1)^2 (B+2)}.$$

Two estimates of the mean $\hat{P}_i$ for a site are available, namely the pooled estimate:

$$\overline{\hat{P}}_1 = \frac{\sum B}{\sum B + \sum S_2} \quad (2)$$

and

$$\overline{\hat{P}}_2 = \frac{\sum B}{\sum B + \sum S_1}; \quad (3)$$

and the average:

$$\overline{\hat{P}}_1 = \frac{\sum_j P_{1j}}{j}$$

and

$$\overline{\hat{P}}_2 = \frac{\sum_j P_{2j}}{j}$$

where j is the number of transects surveyed by the double-survey method.

Timed swims

Timed swims were conducted during the first survey at three of the four sites (not the deep George III Rock site). Timed swim experiments were initiated in the shallow site at George III Rock, where bull kelp predominates. Initially, each diver carried out a series of at least twenty 5-minute timed swims, counting abalone as he/she swam, taking care to survey the entire area of the square as evenly as possible.

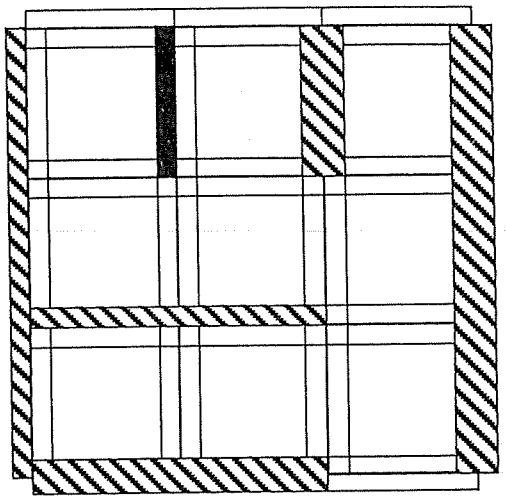


Figure 4. Strip transects of different sizes and dimensions (cross-hatched), formed by joining unit-sized strip transects (black), either end to end or side by side. This was done to determine which transect size and shape gave maximum precision. See text for details.

The distances covered in 10 of each diver's timed swims were determined using a General Oceanics flowmeter attached to a manta board. This method has been employed extensively in Great Barrier Reef waters in surveys of crown-of-thorns starfish, giant clams, beche-de-mer (Pearson 1980) and trochus (Nash 1981). The flowmeter was calibrated in still-water conditions by replicate tows in a 50-m swimming pool. The flowmeter impeller completed 4,000 revolutions per 112 m traversed.

The revolution count at the beginning and end of each 5-minute swim was recorded by a second diver swimming closely above the searching diver. The distance covered was later calculated by multiplying the number of revolutions by 0.028 (112 ÷ 4 000).

Width of area searched has been set at 1.5 m in the relatively open habitat at the deep site (the same as the strip transect width), and at 1.2 m in the dense bull kelp habitat. The area covered, and hence abalone density, per 5-minute swim can then be calculated. Transect width in the bull kelp habitat was determined by practice: in the densest stands of bull kelp the width that could be scanned was at times less than 1 m, while in more open areas the width which could be scanned thoroughly without weaving from side to side to search was about 1.5 m. The average width of area searched by timed swim was judged to be close to 1.2 m.

Flowmeter measurement of distance covered by the searching diver, and number of abalone seen in each 5-minute period, were made by a second diver, who followed closely behind with the flowmeter held directly above the searching diver.

Timed swims may provide an unbiased estimate of abundance only if the diver swims randomly across the bottom. If the diver targets good abalone habitat when searching, the estimates of abundance will be positively biased. To avoid bias, divers swam as nearly as possible in a straight line, and resisted the temptation to divert along good habitat (such as ledges) or to count abalone that fell outside the pre-determined transect width. When the boundary of the square was reached, the diver changed direction and continued searching in a different part of the square.

Validation of flowmeter accuracy

Under static water conditions (no tidal current or swell) the flowmeter accurately measures distance traversed through the water. Since ideal conditions seldom prevailed, the accuracy of the flowmeter under normal field conditions was determined by swimming a known distance (30 m along boundaries of cells in the shallow George III Rock site) under normal working conditions.

The flowmeter was swum twice in each of the cardinal compass directions (north, south, east and west) along the grid cell boundaries shown in Fig. 5. Care was taken to swim in a manner similar to that used when measuring the distance swum by a searching diver: slowly, with no attempt to swim either against or with the surge of the swell; swimming was done mainly in the brief lull between surges. It was observed that there was negligible rotation of the impeller when the diver drifted passively with the swell. This swimming pattern was possible because the searching diver was not swimming so fast that continuous swimming by the flow-metering diver was necessary.

Depletion experiments

Depletion experiments provide unbiased estimates of abundance if the rate of decline of catch rate with cumulative catch is linear. This occurs when the probability of capture is the same for all individuals within the target population, and constant throughout the experiment. Many depletion studies are ceased when the catch rate declines to some pre-determined proportion (*e.g.*, 50 percent) of the initial catch rate. In this study, the objective was to continue the experiment to full depletion; the assumption of constant catchability for each individual could then be examined.

The fishdown procedure was as follows: abalone were collected in consecutive 5-minute periods. Divers worked in pairs, with one diver harvesting abalone (depleting the population) while the second diver kept time for his/her partner. All abalone ≥ 80 mm maximum shell diameter were collected. At the end of each 5-minute period, the partner would exchange the searcher's bag for an empty bag and swim the previous bag back to the boat, where the boat crew counted the abalone in each bag, measured each abalone to the nearest millimetre, then tagged them. The abalone were then hung over the side of the dinghy in open-weave mesh bags for return to the bottom in the grid cell of origin at the end of the fishdown.

The grid cells within a site were each fished down separately. Depletion estimates were therefore obtained for each cell; these were later pooled to yield an estimate of abundance for the entire site. In the first fishdown at each of the four sites, each cell was searched until no abalone had been seen for 30 minutes—that is, for six consecutive 5-minute fishdown periods. In subsequent fishdowns each cell was searched until no abalone had been found for 15 to 20 minutes (three to four consecutive 5-minute periods). It was judged that 30 minutes was unnecessarily long at the Port Arthur site because of the small cell size (generally 12 m by 12 m). In

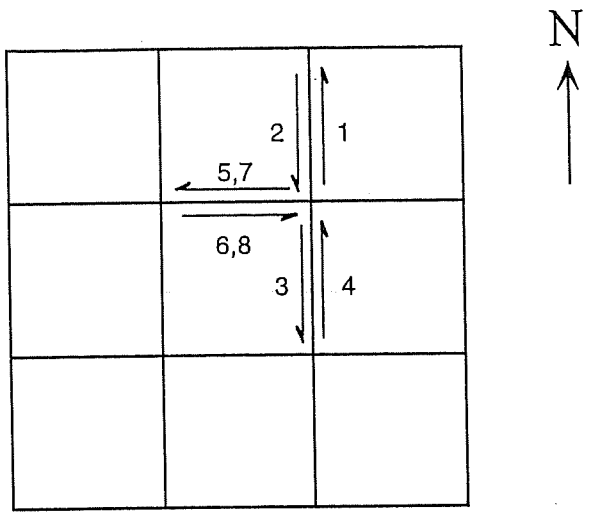


Figure 5. Flowmeter calibration at the shallow George III Reef site. The numbers show the sequence in which the transects were traversed.

addition, the cells at the shallow George III Rock site and the Shag Rock Bay site were divided into four with ropes and each cell quadrant was searched separately; the shorter time period of 15 to 20 minutes was deemed adequate for these cells. Upon completion of a fishdown of a cell, a fresh diver (or a diver who had been searching in a different cell) generally searched the cell for a further 10 to 15 minutes; a fresh diver often yielded additional abalone.

At the deep George III Rock site the two-diver team method was abandoned in favour of single divers, with numbers of abalone in each 5-minute period written on an underwater slate. This was possible because of the relative paucity of abalone at this site.

Analytical methods

Strip transects

The precision of the abundance estimates at each site is determined from the formula

$$p = \frac{s}{\bar{x} \cdot \sqrt{n}} \qquad (4)$$

(Southwood 1978), where p = the precision, s = standard deviation of the counts per transect around the mean count ($\bar{x}$) per transect, and n = number of transects.

Optimal transect dimensions are determined by precision and the cost/effort to set up transects of different sizes. Some studies (e.g. Morin 1985) have found that optimal transect dimensions are also density-related. The literature on this topic is large, and will be reviewed in more detail later.

Transects of different sizes and shapes were constructed by combining contiguous unit-sized transects into larger transects (Fig. 4) and summing the counts of abalone from these transects.

Statistical distributions of strip transect data

The dispersion of abalone within the study sites may be random, clumped or uniform. Various measures of dispersion may be used to determine the type of dispersion; in this section it is determined by examining the goodness of fit of the abalone strip transect data to the Poisson and negative binomial distributions. The Poisson distribution adequately describes the dispersion of individuals within a population when the spatial pattern is random. Goodness of fit of the strip transect data to the

major deterrent is the almost daily presence of commercial abalone divers at the nearby Actaeon Islands, from which boats on George III Rock are clearly visible.

George III Rock lies midway between the Actaeon Islands and Southport Lagoon in southern Tasmania (Fig. 2). It is an area of almost continuous rocky bottom approximately 850 m long and 900 m wide (Prince 1989), with sand gutters intruding into the reef at depths greater than 11 m.

George III Rock is a shallow, dome-shaped reef, rising to within approximately 2 m of the surface near the centre of the reef. The shallow portion of the reef is covered predominantly by bull kelp (*Durvillaea potatorum*), as well as a diversity of red and brown macroalgae (Sanderson 1990). Bull kelp is replaced by cray weed (*Phyllospora comosa*), which forms dense stands at 6 to 8 m depth. A band of string kelp (*Macrocystis pyrifera*) lies beyond the *Phyllospora* at a depth of 7 to 11 m. The extent of *Macrocystis* cover is temporally variable; at the commencement of the study in mid-1989 it was relatively low, but by the end of the study in mid-1992 it had increased substantially to form a circle around the reef dome. Beyond the *Macrocystis*, the bottom slopes off gradually on all sides to a maximum depth of 18 to 20 m. Algal cover is predominantly low red and green macroalgae. Two study sites were set up on this reef, one in each of the two major habitats.

Shallow site

The square study site was set up around the shallow point of the reef, with the boundaries aligned north-south and east-west. The 90m x 90m square was divided into nine 30m x 30m cells using galvanised steel chain, fastened to heavy weights (iron railway wheels at the four corners of the outer square, and car tyres filled with concrete and lengths of steel at the remaining 12 cell boundaries).

Depth range is from 1.5 to 7 m, and the rocky substratum is mostly continuous rock pavement. Some small areas of coarse sand in low-lying gutters break up the bottom, with very low (>5 percent) cover by small boulders. The site is exposed to the south and south-east, although it is protected to some extent from the full force of the prevailing winds by the Actaeon Islands.

The predominant macroalga in the site is bull kelp (*Durvillaea potatorum*), a large plant with a stipe up to about 10 cm diameter and thick leathery fronds up to about 4 m long and 50 cm wide. Encrusting coralline algae are the predominant sub-storey plant form under the bull kelp.

Deep site

The deep site lies approximately 150 m south-west of the shallow site, with a depth range of 8 to 16 m. This site had a similar configuration to the shallow site, but was larger (150m x 150m), and was divided into nine 50m x 50m cells. Cover was primarily by low red (especially *Plocamium dilatatum*) and brown (*Ecklonia radiata*, *Cystophora* sp. and *Acrocarpia* sp.) macroalgae (Sanderson 1990). The north-eastern boundary of the deep site extended into the *Macrocystis* zone.

Stinking Bay

Stinking Bay forms the northern limit of the Port Arthur embayment (Fig. 2). It faces south, but is relatively protected from rough weather by its position at the back of the bay, the narrowness of the bay, and because strong winds do not commonly come directly from the south. Although wave energy at the site is not great, the sea can rise to a short, steep chop, making boat work (tagging, measuring and data recording) difficult and uncomfortable. Under these conditions searching the shallows (<2 m) becomes impossible, and visibility near the sand edge becomes very poor because of suspended sediment in the water. As much as possible, surveys were not conducted under these conditions.

The northern end of the western shore of Stinking Bay was protected from diving or harvesting of abalone, except for research purposes. The western shore of Stinking Bay is approximately 1.5 km long, and the northern portion closed to diving is approximately 700 m long. The study site lies approximately in the centre of the closed area.

Rocky reef extends from the shoreline to the sand edge, which at the northern end of the study site is approximately 40 m off shore; the reef widens to the south, and is about 70 m wide at the southern limit of the site. Maximum depth at the sand edge is 7 m at the northern end and 11 m at the southern end of the site. The reef continues to widen and deepen toward the south, and near Evendens Point the sand edge is approximately 90 m off shore and 17 m deep.

The substratum within the study site comprises small (0.2 to ~1.5 m diameter) boulders. Algal cover is dense throughout the site. The site was divided into three zones on the basis of algal composition and apparent abalone abundance: shallow, middle and deep. Abalone density was clearly highest in the shallow zone, lowest in the middle zone and intermediate in the deep zone. The shallow zone is bounded at its offshore margin by a line of string kelp (*Macrocystis pyrifera*) at a depth of 2 to 4 m.

Cray weed (*Phyllospora comosa*) is abundant at depths <2 m. Encrusting coralline algae are also common.

Algal cover in the middle and deep zones is a mixture of brown, green and red species. Commonly occurring species are *Ecklonia radiata*, *Cystophora* spp. and *Acrocarpia* spp.; *Caulerpa* sp. becomes increasingly common toward the sand edge in the deep zone. Algal cover in these two zones is low (<1 m) but very dense. Sediment levels increase toward the sand edge.

The site was subdivided into 30 grid cells (10 along the shore by 3 across the shore: Fig. 6). Heavy weights (car tyres filled with concrete and lengths of steel) were placed at the grid cell boundaries; galvanised iron chain, used to delineate the grid cells, was secured to the tyres. The shallow zone was 12 m wide, the deep zone extended 12 m shoreward from the sand edge, and the middle zone was of variable width (depending on the width of the rocky bottom), and widened toward the south. The grid cells were 10 m wide, giving a total length for the study site of 100 m (Fig. 6).

Shag Rock Bay

Lying on the eastern side of Tasman Peninsula, Shag Rock Bay is exposed to open-sea conditions, which can be very rough. In even moderate seas it is impossible for a diver to maintain position on the bottom at a depth of 15 m. Relatively low-swell conditions were essential to work this site.

A narrow boulder-strewn strip of shore is bounded by an almost vertical cliff rising approximately 200 m high above the bay. Subtidally, the bottom slopes gradually to a depth of 5 to 7 m, then more steeply to a depth of about 25 m within 200 m of the shoreline. Water depth within the study site ranges from 7 m to 18 m. The site was set up as a 90m x 90m square, subdivided into nine 30m x 30m grid cells (Fig 3). When conducting surveys at this site, each cell was further subdivided with ropes into four 15m x 15m squares to aid searching.

The bottom comprises large to very large (2 to 5 m diameter) boulders, with smaller boulders that are moveable (not wedged into cracks between other boulders) at depths greater than about 14 m. *Phyllospora comosa* is common in the shallower (7 to 9 m) portions of the site. Red macroalgal species (*Plocamium* spp., *Phacelocarpus* spp.) predominate, with high cover of the boulders by encrusting coralline algae.

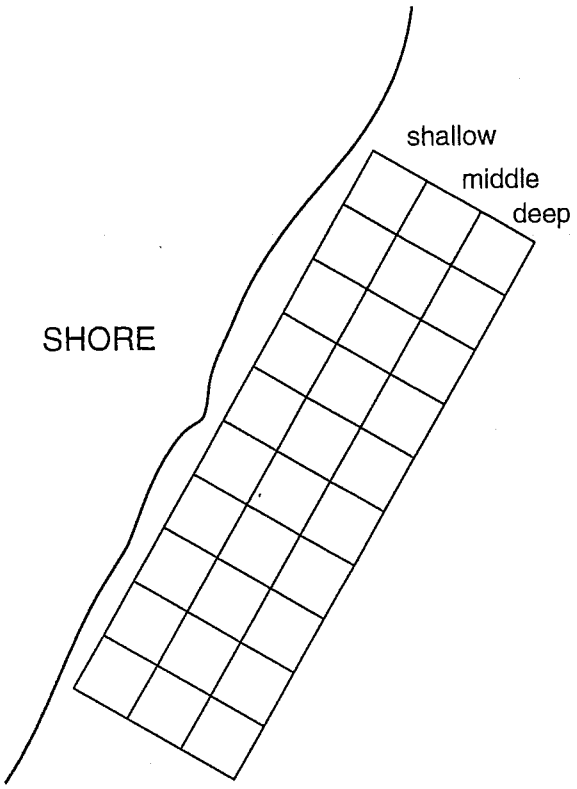


Figure 6. Diagram of the Stinking Bay study site, showing the shallow, middle and deep zones into which the site was divided.

Strip transects

The frequency distribution of the number of abalone per unit transect at the four study sites is shown in Figs. 7, 8 and 9. The modal number of abalone per unit transect was zero at the deep George III Rock site, and greater than zero at all other sites. Abundances were highest at the shallow George III Rock site and the shallow zone at Stinking Bay (not shown). At the deep George III Rock site abalone were most commonly found at the 'sand edge' on the sides of boulders; elsewhere within the site they were found primarily among red and brown algae and in cavities between boulders. At Stinking Bay abalone abundances were highest in the shallows (<2 m depth), moderate at the sand edge, and low in the middle of the reef, where *Caulerpa*, *Ecklonia*, *Cystophora* and other brown algal species were predominant.

Autocorrelation between contiguous transects was found to be statistically significant ($P<0.05$) for all laterally contiguous transects (*e.g.*, 30m x 1.5m transects at the Shag Rock Bay site) but not for other transect configurations. Autocorrelation occurs because contiguous transects are more likely to contain similar habitat, and therefore similar numbers of abalone, than non-contiguous transects. The condition of independence of counts is therefore violated and variances will be negatively biased. Transects contiguous at their narrow margins (their 'ends') showed no autocorrelation, probably because the area of shared habitat was much less. To avoid autocorrelation, all analyses described below are of transects that have been pooled laterally; for example, into 30m x 3m transect at Shag Rock Bay.

These data were then fitted to the Poisson and negative binomial distributions. The strip transect data for the following sites did not differ significantly from the Poisson distribution ($p>0.05$): survey no. 4 at the shallow George III Rock site, and surveys 3 to 6 at Shag Rock Bay (Table 1). (Expected values less than 3 were pooled prior to analysis.) Variance-to-mean ratios were highly significantly greater than 1 ($p<0.001$) at most sites and surveys, indicative of the aggregated distribution of blacklip abalone. This was especially so at the deep George III Rock site and at Stinking Bay (all surveys). Values of the standardised Morisita index of dispersion were greater than 0.5 at most surveys and sites (Table 1), again showing significant clumping ($p<0.05$). Good fit ($p>0.05$) of the transect data to the negative binomial distribution was found at all sites except Shag Rock Bay (third survey) (Table 1). Data for survey 4 at the shallow George III Rock site at surveys 4, 5 and 6 at Shag Rock Bay fit both the Poisson and negative binomial distributions. (The negative binomial exponent k is a measure of the degree of clumping; low values reflect clumping, and as k increases toward infinity the negative binomial distribution tends toward the Poisson distribution: Elliott 1977).

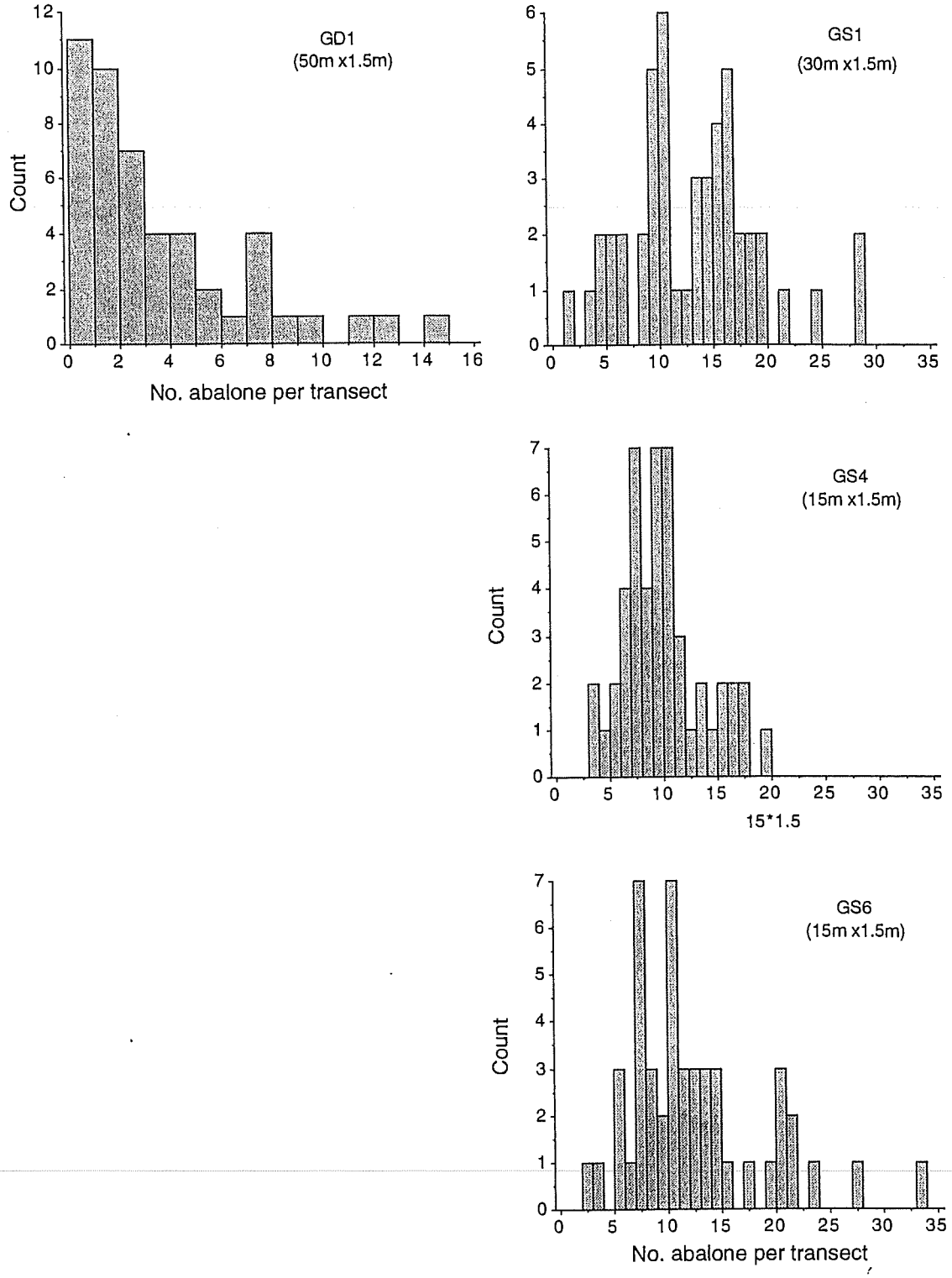


Figure 7. Frequency distribution of the number of abalone found per unit transect (in parentheses) at (GD) the deep George III Reef site, and (GS) the shallow George III Reef site, during each survey. Survey number is indicated by the digit appended to the site code (*e.g.*, GS1). Note that the unit transect size in surveys 4 and 6 at the GS site is half that in survey 1.

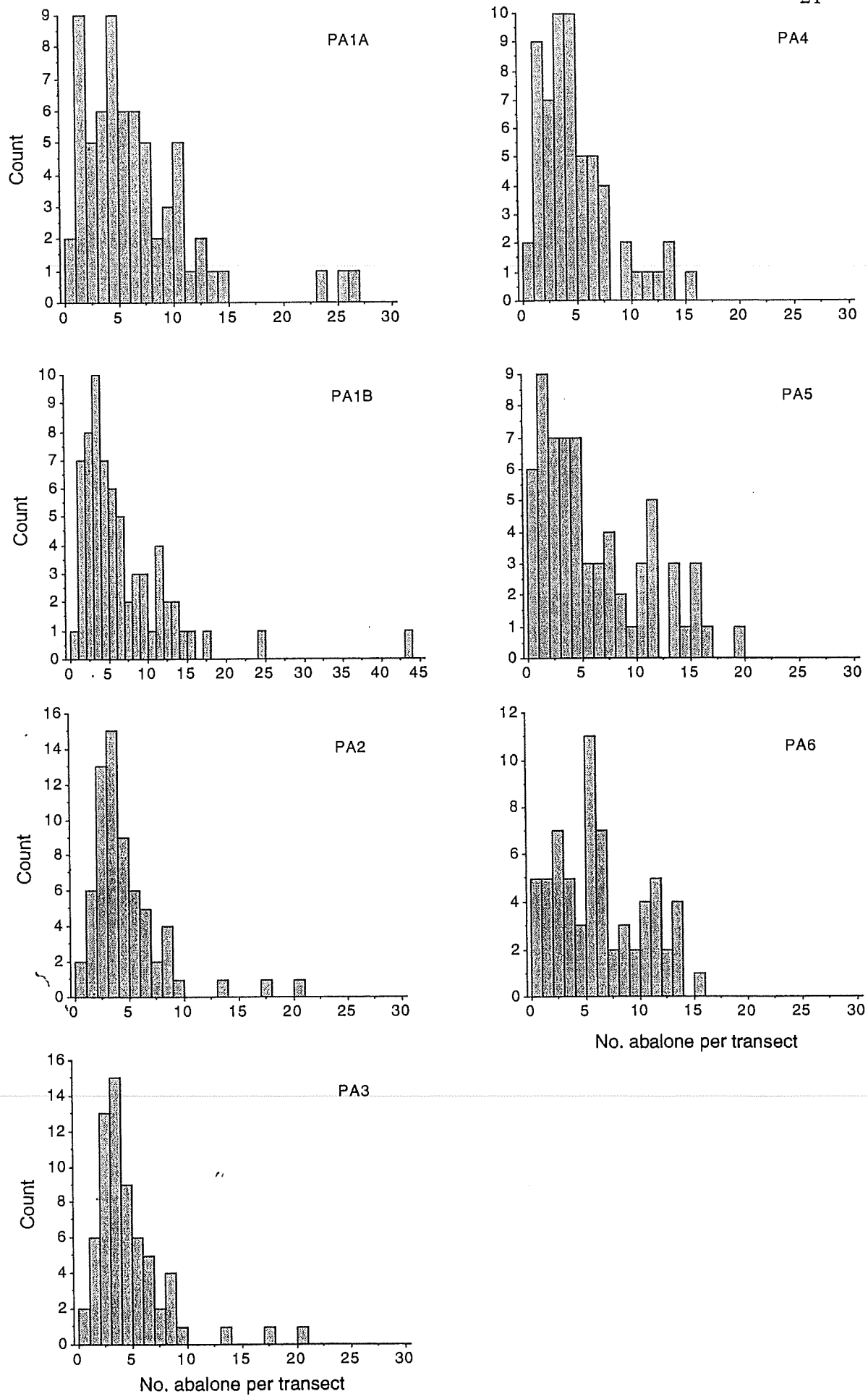


Figure 8. Frequency distribution of the number of abalone found per unit transect (12m x 1.5m) at the Stinking Bay site. Survey number is indicated by the digit appended to the site code (*e.g.*, PA1A).

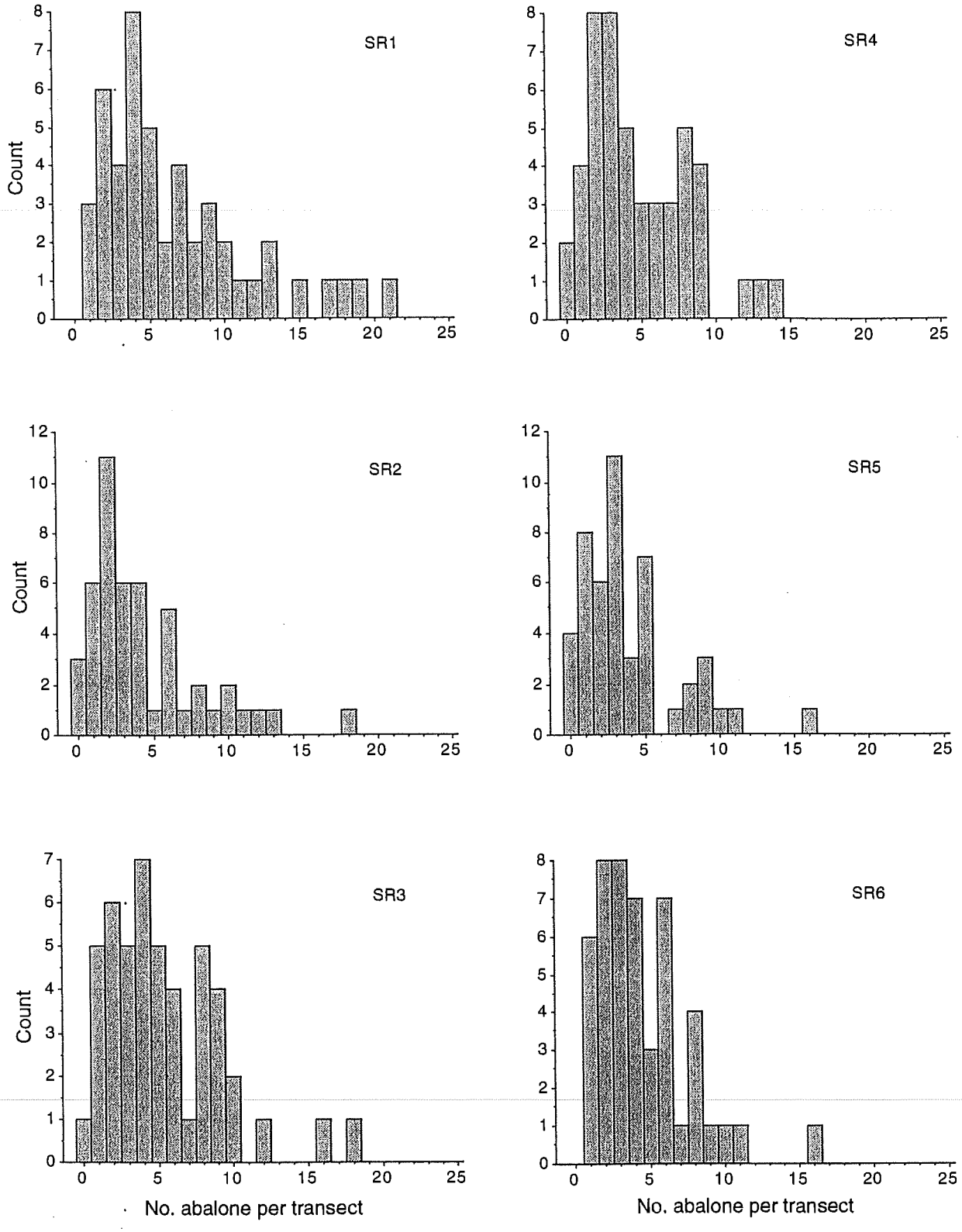


Figure 9. Frequency distribution of the number of abalone found per unit transect (30m x 1.5m) at the Shag Rock Bay site during each survey. Survey number is indicated by the digit appended to the site code (*e.g.*, SR1).

Table 1. Goodness of fit of strip transect count data of blacklip abalone (*Haliotis rubra*) to the negative binomial distribution. Dispersion pattern, estimated by the standardised Morisita index, is also shown. n=number of transects; $\bar{x}$=mean number of abalone per transect. p_1=goodness of fit to the negative binomial distribution; k=negative binomial exponent; I_d=standardised Morisita index of dispersion; p_2=significance level of departure of abalone dispersion toward clumping from random; df=degrees of freedom; ns=not significant; p_3=significance level of fit to the Poisson distribution after pooling theoretical frequencies less than 3.

Site	Survey no.	Transect size (m)	n	$\bar{x}$	95% C.L. ($\bar{x}$) lower	95% C.L. ($\bar{x}$) upper	k	p_1	I_d	p_2	p_3
George III Rock (deep site)	1	50x3	24	3.868	2.178	6.585	1.232	.856	.517	<0.05	.000
George III Rock (shallow site)	1	30x3	24	23.683	19.708	28.342	7.684	.149	.502	<0.05	.020
	4	15x3	24	18.705	16.714	20.830	77.845	.780	.231	ns	.795
	6	-"-	24	22.341	18.751	26.504	8.860	.291	.502	<0.05	.368
Stinking Bay	1A	12 x 3	33	12.212	8.672	15.753	1.985	.739	.509	<0.05	.000
	1B	-"-	33	12.818	8.818	16.819	1.933	.261	.510	<0.05	.000
	2	-"-	33	8.424	6.501	10.347	3.878	.331	.504	<0.05	.000
	3	-"-	33	12.150							
	4	-"-	60	8.933	6.751	11.116	3.315	.788	.505	<0.05	.000
	5	-"-	33	11.394	8.319	14.469	1.754	.280	.507	<0.05	.000
	6	-"-	33	11.667	9.163	14.171	2.342	.129	.504	<0.05	.000
Shag Rock Bay	1	30 x 3	24	12.021	9.458	15.146	5.128	.576	.503	<0.05	.000
	2	-"-	24	7.019	4.974	9.737	2.693	.661	.507	<0.05	.000
	3	-"-	24	9.630	7.584	12.095	5.835	.014	.503	<0.05	.027
	4	-"-	24	8.619	6.747	10.875	5.853	.111	.502	<0.05	.146
	5	-"-	24	6.439	4.691	8.681	3.429	.908	.504	<0.05	.396
	6	-"-	24	8.329	6.777	10.113	11.285	.231	.500	<0.05	.172

Estimates of precision for the various strip transect configurations at the four sites are given in Figs. 10, 11 and 12, and Tables 2, 3, 4 and 5. A brief description of the estimation of precision is appropriate here. For a given amount of research effort, the researcher has a choice of surveying a large number of small transects or a small number of large transects. The most suitable transect configuration is the one that minimises the precision estimate (p) (equation 4). It is clear from equation 4 that p increases as the number of transects decreases, and decreases as the mean number of individuals per transect increases. $\bar{x} \cdot \sqrt{n}$ always increases with increasing transect size when contiguous transects are summed to make larger ones, as was done here, so a survey conducted using large transects can yield a lower p value than one using small transects only if s is substantially less for the large transects. This will depend on the scale of aggregation relative to the transect dimensions.

The pattern of precision estimates at different transect dimensions is interesting. At the deep George III Rock site precision is higher (*i.e.*, p is lower) for the 50m x 1.5m and 150m x 1.5m transects than, respectively, the 50m x 3m and 150m x 3m transects (Fig. 10), reflecting the significant autocorrelation present between laterally contiguous transects. Precision is only slightly less for the 150m x 1.5m transects than the 50m x 1.5m transects, even though there were only one-third as many of them; this is because between-transect variation in counts was reduced substantially at the larger transect size, reflecting the spatial scale at which abalone are clustered. A similar pattern was seen at the shallow George III Rock site on surveys 1 and 4, but this pattern did not exist during survey 6 (Fig. 10). On visit 4, precision increased (p decreased) with increasing transect size, indicating that between-transect variation in counts was substantially less in the larger transects, the reduction in s being greater than the reduction in $\bar{x} \cdot \sqrt{n}$. This was not the case on visit 6, where p increased with increasing transect size. This suggests that abalone were more aggregated during survey 4 than survey 6 (at the scale of the transects used). A possible reason for this decline in aggregation is that, as abundance increased within the site (which it did substantially; see below), abalone became more evenly distributed throughout the site. It is clear from this analysis that the use of contiguous transects, and calculation of precision for various transect configurations, can help elucidate spatial dispersion patterns of abalone, notwithstanding the potential bias of autocorrelation.

The pattern of precision estimates with transect size at the Stinking Bay site (Fig. 11) was similar to that at the deep George III Rock site (Fig. 10): comparing the precision estimates of the 12m x 3m and 36m x 3m transects, the decrease in between-transect variation in counts (s) with increasing transect size was not as large as the decrease in $\bar{x} \cdot \sqrt{n}$ on most surveys. Unlike the shallow George III Rock site, the abalone

population did not increase over the course of the study, so the dispersion-homogenising effect of increasing population density postulated for the shallow George III Rock site could not occur. The decline in p for the 12m x 3m transects from 0.16 at survey 1B to 0.11 at the final survey reflects the decline in abundance in the shallow zone over this period (Table 4); this decline effectively reduced the variation in abundance between transects.

Precision estimates were almost constant at all transect configurations at the Shag Rock site within a survey (Fig. 12). They also showed little change over the course of the study. When these results are combined with the downward trend in abundance (see below), they suggest that abalone dispersion became less clumped between the first and final surveys.

An examination of the coefficient of variation (CV) (calculated as $\frac{s}{\bar{x}} * 100$) for the various transect configurations at the four sites (Tables 2 to 5) reveals a marked reduction in the CV with increasing transect size at all sites and surveys. These help explain the pattern of precision estimates obtained, described above.

Estimates of abundance obtained by strip transect surveys are shown in Figs. 13, 14 and 15. At the shallow George III Rock site, abundance was estimated to have nearly doubled between the first and final surveys (from 2,280 to 4,298) (Fig. 13). At Stinking Bay, abalone abundance in the shallow zone reduced by half (but not statistically significantly) from 754 to 373 between surveys 1B and 2, then fluctuated between 420 and 685 for the remainder of the study (Fig. 14A). Abundances remained fairly stable in the middle and deep zones throughout the study. When abundances for the entire site are examined (all zones pooled), there was an estimated 35 percent decline in abundance between surveys 1B and 2 (although this is not statistically significant; Fig. 14B), but otherwise appeared fairly stable. There appeared to be a general decline in abundance at the Shag Rock Bay site over the course of the study (Fig. 15), although this decline reached statistical significance ($p<0.05$) only when surveys 1 and 5 are compared. (Confidence limits for Shag Rock Bay visit 3 (Fig. 15) are approximate only, as they are based on the negative binomial distribution which does not adequately fit the data.)

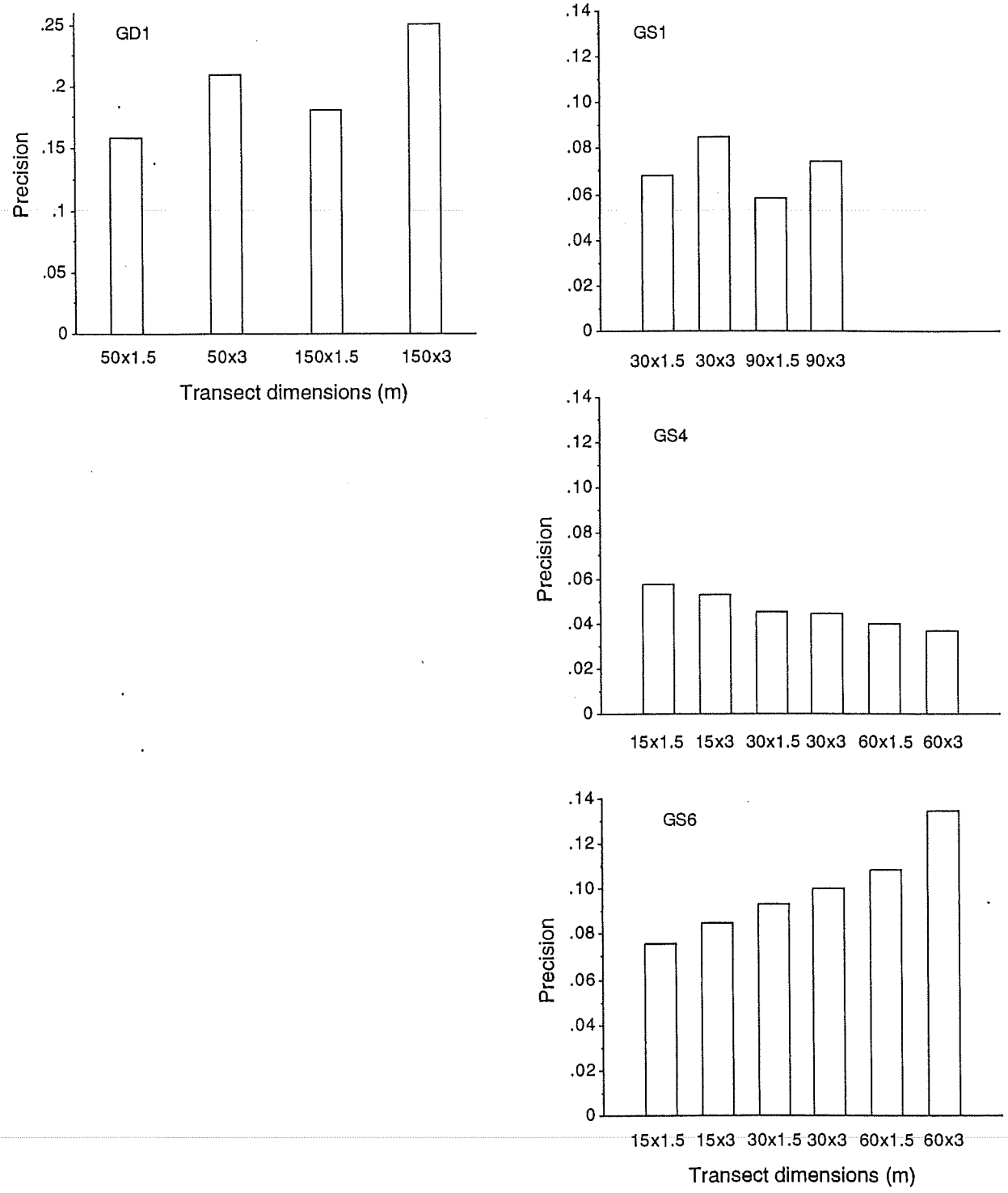


Figure 10. Precision estimates for different transect dimensions at (GD) the deep George III Reef site, and (GS) the shallow George III Reef site, during each survey. Survey number is indicated by the digit appended to the site code (*e.g.*, GS1).

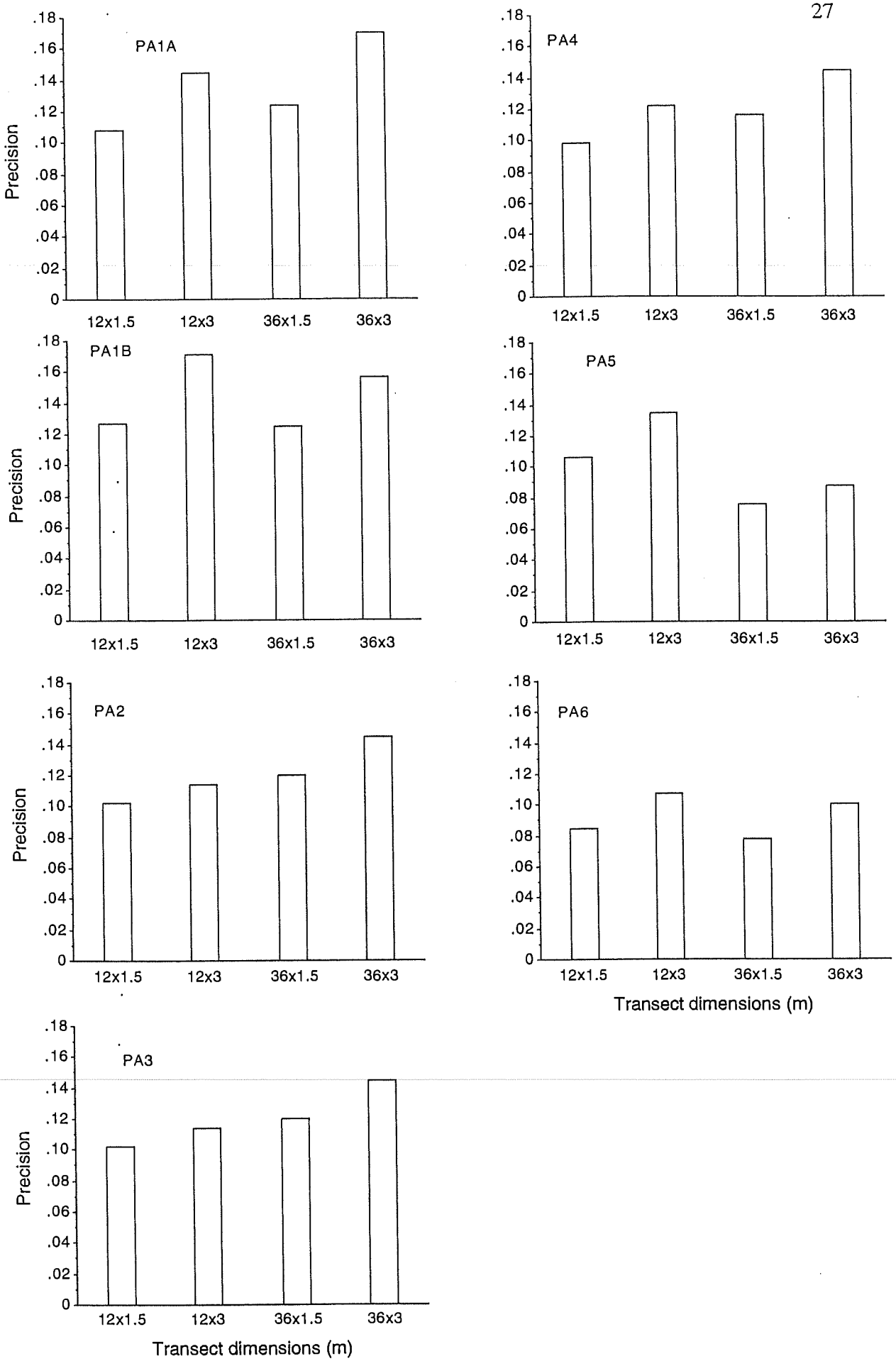


Figure 11. Precision estimates for different transect dimensions at the Stinking Bay site during each survey. Survey number is indicated by the digit appended to the site code (*e.g.*, PA1).

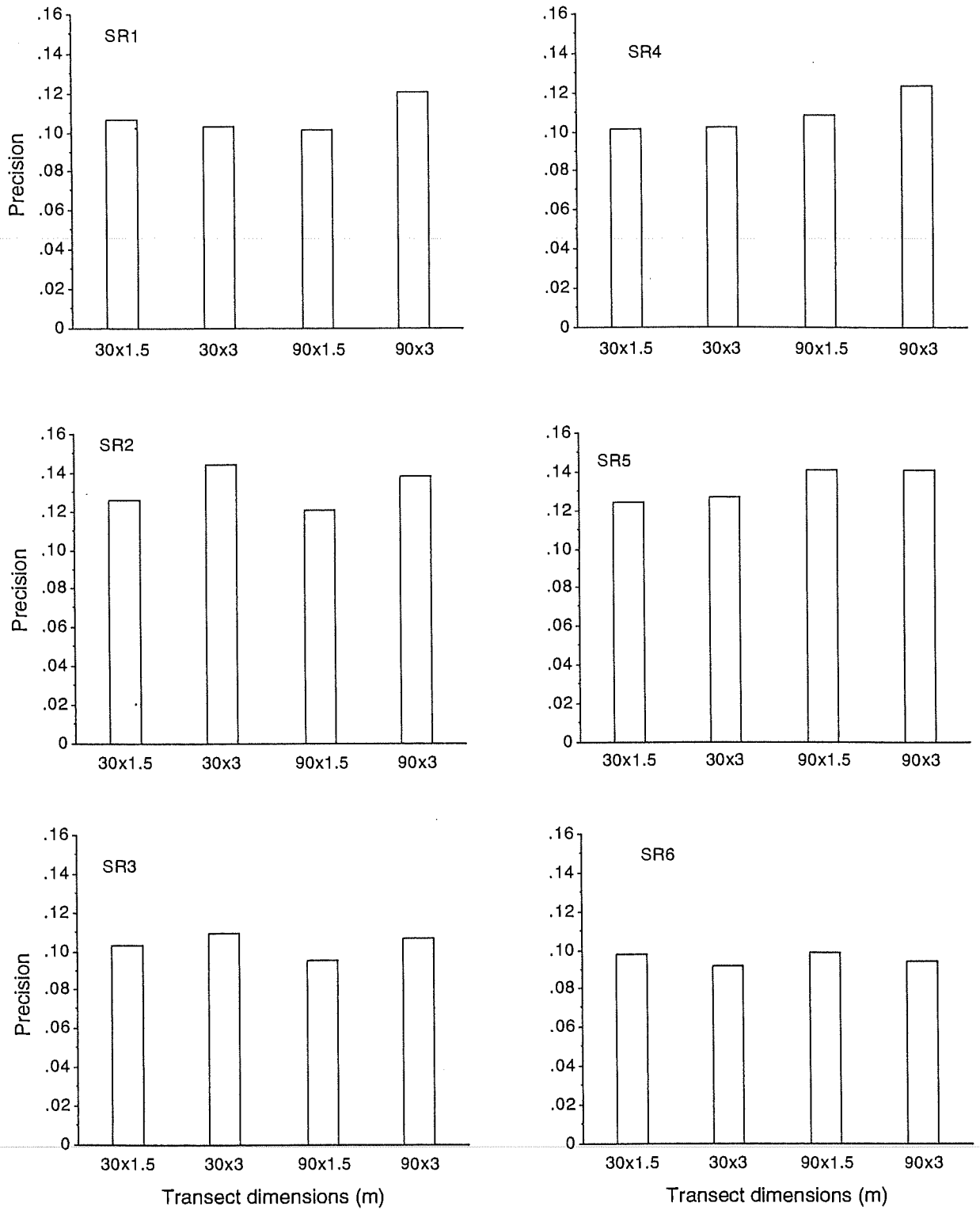


Figure 12. Precision estimates for different transect dimensions at the Shag Rock Bay site during each survey. Survey number is indicated by the digit appended to the site code (*e.g.*, SR1).

Table 2. Numbers of abalone per transect at the deep George III Rock site at each survey, for several transect dimensions. *n*=number of transects, *p* = precision, CV = coefficient of variation.

Survey no.	Transect dimensions (m)	*n*	*p*	CV
1	50 * 1.5	48	0.159	110.2
1	50 * 3	24	0.210	102.6
1	150 * 1.5	16	0.182	72.8
1	150 * 3	8	0.252	71.3

Table 3. Numbers of abalone per transect at the shallow George III Rock site at each survey, for several transect dimensions. Symbols as in Table 2.

Survey no.	Transect dimensions (m)	*n*	*p*	CV
1	30 * 1.5	48	0.068	47.0
1	30 * 3	24	0.085	41.8
1	90 * 1.5	16	0.059	23.5
1	90 * 3	8	0.079	22.4
4	15 * 1.5	48	0.057	39.4
4	15 * 3	24	0.053	26.1
4	30 * 1.5	24	0.045	22.0
4	30 * 3	12	0.044	15.2
4	60 * 1.5	12	0.040	13.7
4	60 * 3	6	0.037	8.9
6	15 * 1.5	48	0.076	52.9
6	15 * 3	24	0.085	41.8
6	30 * 1.5	24	0.093	45.6
6	30 * 3	12	0.100	34.8
6	60 * 1.5	12	0.109	37.8
6	60 * 3	6	0.135	33.1

Table 4. Numbers of abalone per transects at the Stinking Bay site at each survey, for several transect dimensions. Symbols as in Table 2.

Survey no.	Row	Transect dimensions (m)	n	p	CV
1A	shallow	12 * 1.5	22	0.139	65.4
	shallow	12 * 3	11	0.186	61.8
	middle	12 * 1.5	22	0.194	91.2
	middle	12 * 3	11	0.274	90.7
	deep	12 * 1.5	22	0.120	56.5
	deep	12 * 3	11	0.138	45.6
	all	12 * 1.5	66	0.108	87.4
	all	12 * 3	33	0.145	83.3
	all	36 * 1.5	22	0.124	58.2
	all	36 * 3	11	0.170	56.2
1B	shallow	12 * 1.5	22	0.163	76.7
	shallow	12 * 3	11	0.194	64.2
	middle	12 * 1.5	22	0.146	68.7
	middle	12 * 3	11	0.194	64.2
	deep	12 * 1.5	22	0.141	66.2
	deep	12 * 3	11	0.161	53.5
	all	12 * 1.5	66	0.125	101.3
	all	12 * 3	33	0.156	89.6
	all	36 * 1.5	22	0.127	59.5
	all	36 * 3	11	0.171	56.7
2	shallow	12 * 1.5	22	0.196	92.1
	shallow	12 * 3	11	0.207	68.8
	middle	12 * 1.5	22	0.134	62.7
	middle	12 * 3	11	0.184	60.9
	deep	12 * 1.5	22	0.102	47.9
	deep	12 * 3	11	0.115	38.3
	all	12 * 1.5	66	0.102	82.7
	all	12 * 3	33	0.114	65.6
	all	36 * 1.5	22	0.120	56.3
	all	36 * 3	11	0.145	48.1

Table 4 - cont'd.

Survey no.	Row	Transect dimensions (m)	n	p	CV
4	shallow	12 * 1.5	22	0.136	60.7
	shallow	12 * 3	11	0.169	53.5
	middle	12 * 1.5	22	0.207	92.4
	middle	12 * 3	11	0.248	78.6
	deep	12 * 1.5	22	0.150	67.1
	deep	12 * 3	11	0.183	57.7
	all	12 * 1.5	66	0.098	76.1
	all	12 * 3	33	0.122	66.9
	all	36 * 1.5	22	0.116	52.1
	all	36 * 3	11	0.145	45.9
5	shallow	12 * 1.5	22	0.094	44.1
	shallow	12 * 3	11	0.088	29.2
	middle	12 * 1.5	22	0.256	120.2
	middle	12 * 3	11	0.355	117.9
	deep	12 * 1.5	22	0.144	67.7
	deep	12 * 3	11	0.180	59.6
	all	12 * 1.5	66	0.106	85.9
	all	12 * 3	33	0.135	77.5
	all	36 * 1.5	22	0.076	35.6
	all	36 * 3	11	0.088	29.2
6	shallow	12 * 1.5	22	0.082	38.2
	shallow	12 * 3	11	0.068	22.6
	middle	12 * 1.5	22	0.184	86.4
	middle	12 * 3	11	0.259	85.8
	deep	12 * 1.5	22	0.128	60.1
	deep	12 * 3	11	0.146	48.3
	all	12 * 1.5	66	0.085	69.0
	all	12 * 3	22	0.107	61.6
	all	36 * 1.5	22	0.078	36.5
	all	36 * 3	11	0.101	33.4

Table 5. Numbers of abalone per transects at the Shag Rock Bay site at each survey, for several transect dimensions. Symbols as in Table 2.

Survey no.	Transect dimensions (m)	n	p	CV
1	30*1.5	48	0.107	73.9
1	30*3	24	0.103	50.5
1	90*1.5	16	0.101	40.6
1	90*3	8	0.121	34.3
2	30*1.5	48	0.126	87.4
2	30*3	24	0.144	70.7
2	90*1.5	16	0.121	48.3
2	90*3	8	0.138	39.0
3	30*1.5	48	0.103	71.0
3	30*3	24	0.109	53.6
3	90*1.5	16	0.095	38.1
3	90*3	8	0.107	30.4
4	30*1.5	48	0.101	69.8
4	30*3	24	0.102	49.8
4	90*1.5	16	0.108	43.3
4	90*3	8	0.123	34.7
5	30*1.5	48	0.124	85.6
5	30*3	24	0.127	62.1
5	90*1.5	16	0.141	56.6
5	90*3	8	0.141	39.9
6	30*1.5	48	0.098	68.0
6	30*3	24	0.092	45.3
6	90*1.5	16	0.099	39.5
6	90*3	8	0.094	26.6

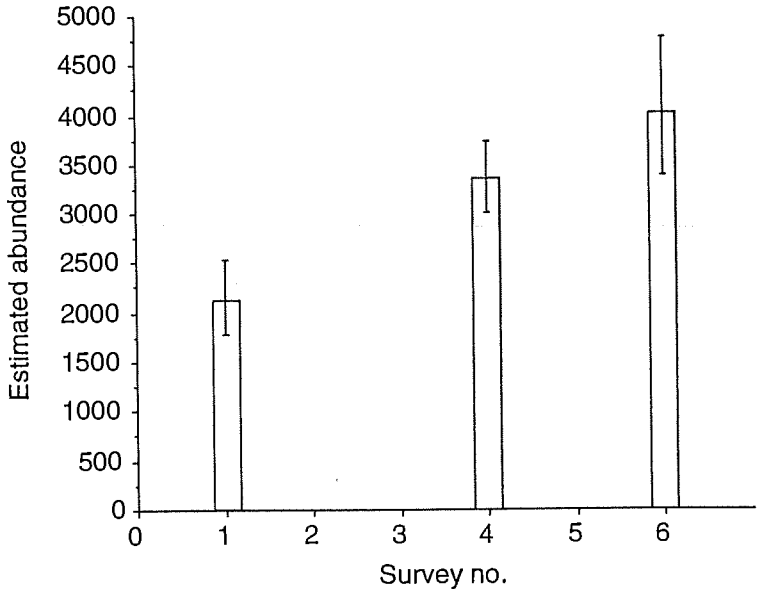


Figure 13. Abundance of blacklip abalone (*Haliotis rubra*) at the shallow George III Reef site at surveys 1, 4 and 6, estimated by strip transect. Error bars are 95% confidence limits for 30m x 3m transects.

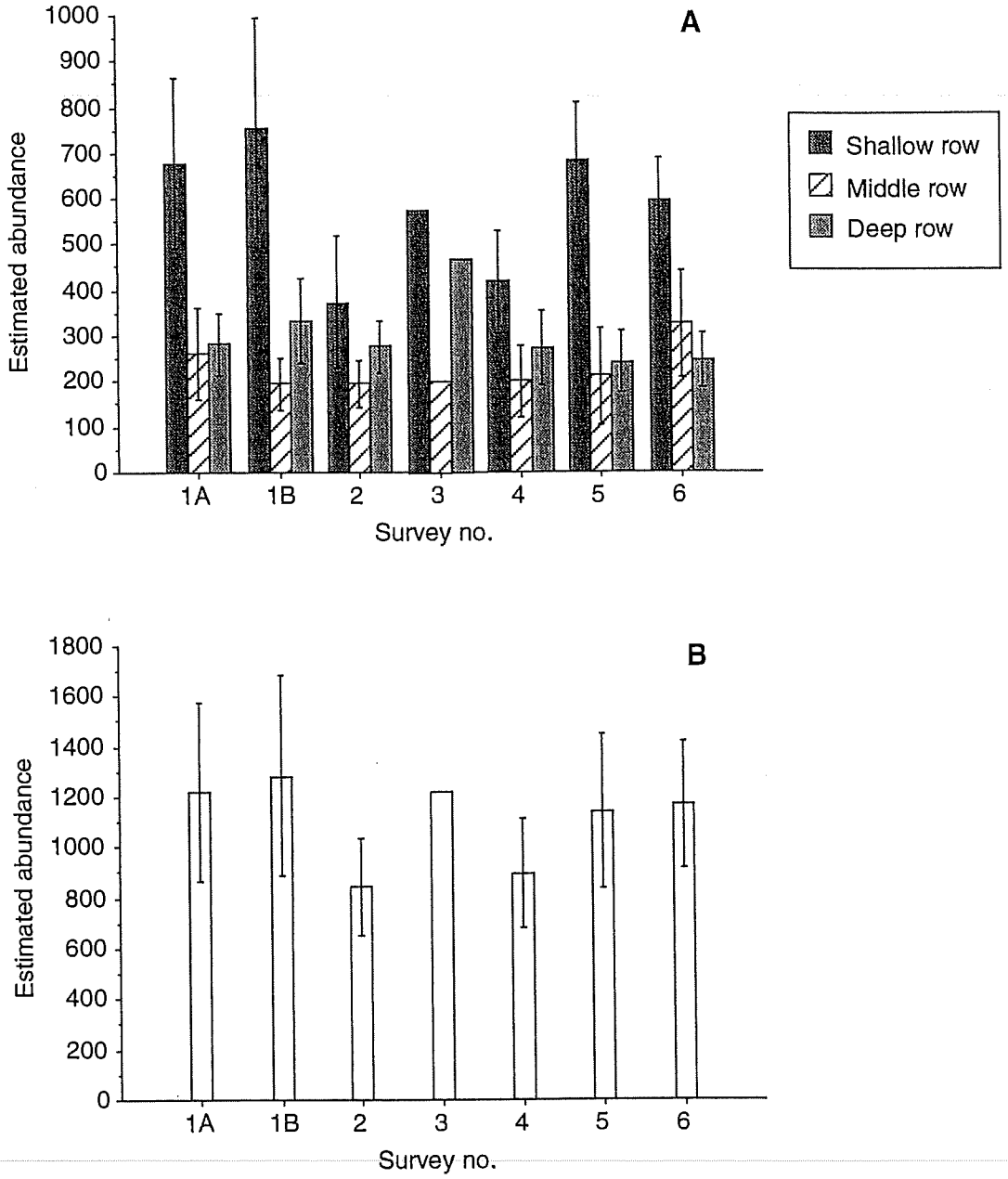


Figure 14. Abundance of blacklip abalone (*Haliotis rubra*) at the Stinking Bay site at each survey, estimated by strip transect. (A) Abundance in each of the three zones (shallow, middle, deep) separately, using 12m x 3m transects; (B) Estimated total abundance at each survey, using 12m x 3m transects. Error bars are 95% confidence limits.

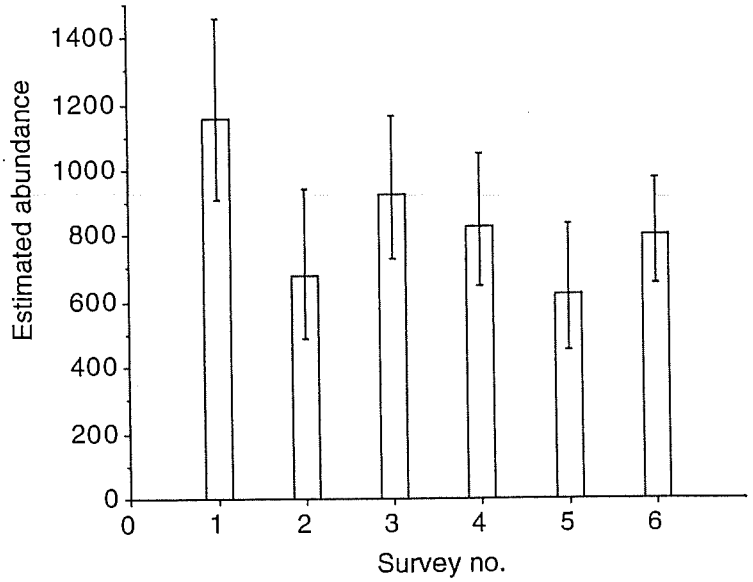


Figure 15. Abundance of blacklip abalone (*Haliotis rubra*) at the Shag Rock Bay site at each survey, estimated by strip transect. Error bars are 95% confidence limits for 30m x 3m transects.

Diver searching efficiency

Diver searching efficiency varied considerably between sites, ranging from 60 percent at Stinking Bay to 90 percent at George III Rock; Shag Rock Bay was intermediate at 70 percent (Table 6). (The efficiency values described here refer to those for the pooled estimates for the first diver to search a transect; *i.e.*, the first set of $\hat{P}_1$ figures in Tables 6 and 7.) The pooled and average mean diver efficiencies were very similar; some of the variation was because efficiency estimates for some transects could not be calculated because of division by zero (the divisor in equations (2) and (3) above).

Searching efficiencies were similar for first and second divers at the George III Rock site (*i.e.*, $\hat{P}_1 = \hat{P}_2$), but at Stinking Bay and Shag Rock Bay the efficiency of the second searcher was 14 and 9 percent lower than that of the first searcher, respectively (Table 6). The most likely reason for this is that a small proportion of abalone at these two sites disappeared before the arrival of the second diver, either by moving beyond the transect boundary or into crevices within the transect.

In order to test the response of abalone to being chalked on the shell, 50 abalone at each of two sites within the George III Rock site were chalked after the completion of this study. Only one of these abalone disappeared into a crevice, and a second changed orientation without any lateral displacement. The response of the remainder was to clamp down on the rock or to show no noticeable response at all. This low (1 to 2 percent) movement response is consistent with the similarity of the $\hat{P}_1$ and $\hat{P}_2$ values at George III Rock (Table 6). No such observations of movement response were made at Stinking Bay and Shag Rock Bay; however, the dissimilarity between the $\hat{P}_1$ and $\hat{P}_2$ values at these two sites is most likely because of disturbance by the first searcher.

Search efficiencies of individual divers varied between 0.808 and 0.947 at George III Rock (referring to the pooled $\hat{P}_1$ estimates), between 0.514 and 0.750 at Stinking Bay, and between 0.167 and 0.864 at Shag Rock Bay (Table 7). The anomalously low searching efficiency of diver 7 at Shag Rock Bay (0.167) is because of low total counts by either diver 7 or his partner, the absence of any chalked abalone seen by diver 7 and the low number of transects ($n = 3$) searched by this diver at Shag Rock Bay. If diver 7 is excluded from the Shag Rock Bay analysis, searching efficiencies varied between 0.521 and 0.864 (Table 7), and variation in searching efficiency between sites was statistically significant ($p<0.05$) but variation between divers within a site was not ($p>0.05$) (1-way ANOVA).

Table 6. Mean diver searching efficiency at each site, estimated by the double-survey method.

Site	Pooled		Average	
	$\hat{P}_1$	$\hat{P}_2$	$\hat{P}_1$	$\hat{P}_2$
George III Rock	0.893	0.908	0.880	0.922
Stinking Bay	0.598	0.514	0.603	0.538
Shag Rock Bay	0.693	0.634	0.647	0.625

Table 7. Search efficiency of individual divers, when either the first ($\hat{P}_1$) or the second diver ($\hat{P}_2$) to search a transect, estimated by the double-survey method. n = no. of transects searched.

Site	Diver	Pooled			Average		
		$\hat{P}_1$	$\hat{P}_2$	n	$\hat{P}_1$	$\hat{P}_2$	n
George III Rock	1	0.886	0.897	20	0.892	0.909	20
	2	-	-	0	-	-	0
	3	0.893	0.923	18	0.840	0.997	19
	4	0.896	0.984	8	0.912	0.978	8
	5	0.947	0.947	12	0.943	0.904	12
	6	0.938	0.909	8	0.939	0.924	8
	7	0.808	0.798	11	0.790	0.782	10
	8	-	-	0	-	-	0
Stinking Bay	1	0.644	0.303	8	0.584	0.201	6
	2	0.616	0.537	14	0.645	0.555	18
	3	0.555	0.693	34	0.599	0.777	24
	4	0.545	0.411	9	0.572	0.462	9
	5	0.643	0.400	2	0.675	0.600	3
	6	0.514	0.349	19	0.435	0.347	19
	7	0.707	0.623	10	0.752	0.593	11
	8	0.750	0.509	12	0.727	0.518	23
Shag Rock Bay	1	-	-	0	-	-	0
	2	0.683	0.559	11	0.660	0.508	12
	3	0.864	0.689	18	0.856	0.818	15
	4	0.521	0.742	9	0.525	0.691	9
	5	0.651	0.642	14	0.542	0.542	17
	6	-	-	0	-	-	0
	7	0.167	0.188	3	0.167	0.143	3
	8	0.680	0.733	3	0.681	0.823	4

On some occasions the second diver to search a transect found abalone on or immediately adjacent the transect line that had not been chalked by the first diver. This demonstrates that an assumption of the line transect method (probability of detecting an animal on the transect line equals 1; see Introduction) is violated.

An important assumption of the double-survey method is that the counts of the two searchers are independent. This assumption may be violated in two ways: disturbance caused by chalking may reduce the probability of sighting by the second diver (as described above), and the chalk mark may increase conspicuousness of the abalone. The difference between $\overline{\hat{P}}_1$ and $\overline{\hat{P}}_2$ values at both Stinking Bay and Shag Rock Bay suggests that chalking was a source of bias at these two sites. This affects the efficiency estimates of both divers ($\hat{P}_1$ and $\hat{P}_2$) and $\hat{N}$. A simple test of the possible magnitude of the bias was carried out on the Stinking Bay data by assuming that 15 percent of the abalone chalked by the first diver disappeared before the second diver could encounter them. This caused a 5.5 percent increase in search efficiency of diver 1 ($\hat{P}_1$), a 15 percent increase for diver 2 ($\hat{P}_2$), and a decrease in $\hat{N}$ of 5.2 percent. Because all divers were the second searcher in about as many transects as they were first searcher (because divers searched in pairs and swapped transects), it is therefore concluded that (i) the difference between $\hat{P}_1$ and $\hat{P}_2$ in Tables 6 and 7 is probably because of disturbance of chalked abalone by diver 1, and (ii) the magnitude of bias in $\hat{P}_1$ caused by abalone disturbance is small enough to be safely ignored. Mean searching efficiency of diver 1 ($\overline{\hat{P}}_1$) was therefore used to adjust abundance estimates, rather than both $\overline{\hat{P}}_1$ and $\overline{\hat{P}}_2$ (equation 2) above.

The second potential source of assumption violation is believed to be minor because, although clearly visible on the shells, the chalk marks do not act as a 'beacon' to alert the diver to abalone that otherwise may not have been seen. This is particularly so for blue and red crayon, which are dull colours underwater.

Timed swims

Validation of flowmeter accuracy

The length of each boundary surveyed by flowmeter (Fig. 5) was only approximately 30 m because the concrete-filled tyres used to mark the corners of the gridded site were lodged where they were unlikely to be moved by the swell, which was not

always at the 30-m mark. A suitable evaluation of flowmeter accuracy is therefore the similarity of duplicate swim estimates along each boundary rather than how close the estimates are to 30 m. Estimates of the distance swum ranged from 23.7 m to 33.6 m, with a mean of 28.1 m (Table 8). The largest difference between paired estimates was 7.9 m (23.7 m and 31.6 m) along the C1-C2 boundary and the smallest was 0.6 m (33.0 and 33.6 m) along the C2-C3 boundary (Fig. 5). The mean difference, expressed as relative to the mean of each pair of estimates, was 15 percent.

Table 8. Examination of flowmeter accuracy in measuring 30-m distances along cell boundaries at the shallow site at George III Rock. Transect coordinates and the swimming sequence are shown in Fig. 5.

Swim no.	Transect	Distance (m)	Time taken (min.sec)
1	C2-C1	27.1	1.50
2	C1-C2	31.8	1.40
3	C2-C3	33.0	2.05
4	C3-C2	33.6	1.50
5	C2-B2	23.7	1.25
6	B2-C2	31.6	1.30
7	C2-B2	24.9	1.22
8	B2-C2	28.2	1.22

Diver swim rate variation

Considerable variation in the distance swum in 5-minute timed swims occurred, both between divers and between swims by individual divers, at all sites (Tables 9 to 14, Figs. 16, 17 and 18). There was also large variation in swim speeds between sites, being highest at the shallow George III Rock site (Table 9) and lowest at Stinking Bay (Table 11). There were highly significant differences between divers in the distances they swam in 5 minutes at each site (1-way ANOVA; p=0.0001).

It is apparent from the swim rate patterns shown in Figs. 16, 17 and 18 that the swimming characteristics of individual divers varies greatly from site to site. Diver 3, for example, swam at a relatively constant rate at the shallow George III Reef site (Fig. 16), but had both a wider spread and a lower average swim speed at Stinking Bay (Fig. 17). Other divers (*e.g.*, Diver 4) exhibited similar variation; Diver 1, on the other hand had a relatively constant (and slow) swim rate at all three sites.

The mean distances swum during 5-minute searches, the number of these searches conducted and the number of abalone seen in each 5-minute swim were used to estimate the number of abalone at each site (Tables 10, 12, 14). Two estimates of abundance ($\hat{N}_1$ and $\hat{N}_2$) were calculated, the first using only the timed swims which had their distance measured by flowmeter, and the second using both flow-metered and non-flow-metered swims; the mean swim rate during the metered distances was applied to the non-metered swims. Average $\hat{N}_1$ and $\hat{N}_2$ values differed by 7, 4 and 11 percent at the shallow George III Rock, Stinking Bay and Shag Rock Bay sites respectively. There was large variation in estimated abundance between divers at each site, ranging between 1640 and 3057 at the shallow George III Rock site (Table 10), between 272 and 876 at Stinking Bay (Table 12) and between 400 and 1604 at Shag Rock Bay (Table 14).

An event at the Shag Rock Bay site illustrates one of the problems with the timed swim method. Two divers (4 and 5) with low abundance estimates compared to the other divers (Table 14) conducted a further set of timed swims, measured by flow meter, the following day. Their swim rates halved and their estimates of abundance increased more than twofold (Table 14, Figs. 18, 19). The reasons for this and the implications for the timed swim method of estimating abundance are discussed further below.

Table 9. Distances covered by each of six research divers in ten 5-minute swims at the shallow George III Rock site, as measured by flowmeter. sd = standard deviation; CV = coefficient of variation.

	Distance swum (m)			
Diver	Min.	Max.	Mean (sd)	CV
1	23.3	56.5	38.9 (13.2)	33.9
3	33.6	58.8	47.1 (8.2)	17.5
4	39.6	90.1	56.4 (16.1)	25.3
5	26.6	72.0	56.4 (13.4)	23.8
10	14.8	49.8	30.7 (11.7)	37.9
12	33.8	62.1	46.2 (9.3)	20.1

Table 10. Estimated number of abalone in the shallow George III Rock site, calculated for each diver from his/her measured distances covered in 5 minutes while searching for abalone, as determined by flowmeter. $\hat{N}_1$ = estimated no. of abalone in the site (from flow-metered swims); $\hat{N}_2$ = estimated no. of abalone in the site (from metered and non-metered swims combined).

Diver	Mean distance swum per 5 min. (m)	Mean area per 5 min. swim (m^2)	Mean no. abalone per 5 min. swim		$\hat{N}_1$	$\hat{N}_2$
			Metered	All		
1	38.9	46.6	17.6	18.2	3057	3161
3	47.1	56.5	21.2	20.3	3041	3465
4	63.9	76.7	23.3	24.2	2460	2555
5	56.4	67.7	13.7	14.6	1640	1888
10	30.7	46.1	12.3	13.2	2701	3575
12	46.2	55.5	13.9	8.7	2029	1273
				Average=	2488	2653

Table 11. Distances covered by each of seven research divers in ten 5-minute swims at the Stinking Bay site, as measured by flowmeter. sd = standard deviation; CV = coefficient of variation.

Diver	Distance swum (m)			CV
	Min.	Max.	Mean (sd)	
1	3.5	13.6	8.2 (3.4)	41.2
3	20.6	72.4	34.1 (17.2)	50.4
4	8.0	26.6	18.6 (6.8)	36.5
5	24.4	51.4	33.9 (8.4)	24.8
6	17.3	30.9	24.0 (4.4)	18.5
7	11.2	21.7	16.8 (4.0)	23.8
8	15.0	37.4	26.5 (7.4)	27.8

Table 12. Estimated number of abalone in the Stinking Bay site, calculated from the abalone counts and mean distance traversed per 5 min of each diver, as determined by flowmeter. Area covered per 5 minute swim was calculated by multiplying mean area covered/5 min. by 1.5, assuming a search width of 1.5m. All divers had 10 of their 5-min swim distances measured by flowmeter. Symbols as in Table 10.

Diver	Mean distance swum per 5 min. (m)	Mean area per 5 min. swim (m^2)	Mean no. abalone per 5 min. swim		$\hat{N}_1$	$\hat{N}_2$
			Metered	All		
1	8.2	12.3	3.0	2.6	876	745
3	34.1	51.2	6.1	5.8	429	404
4	18.6	27.9	4.6	4.7	593	600
5	33.9	50.8	5.0	4.7	354	333
6	24.0	36.0	3.3	3.8	330	380
7	16.8	25.2	2.4	2.0	343	278
8	26.5	39.7	3.0	3.6	272	322
				Average=	457	437

Table 13. Distances covered by each of seven research divers in ten 5-minute swims at the Shag Rock Bay site, as measured by flowmeter. sd = standard deviation; CV = coefficient of variation.

Diver	Distance swum (m)			CV
	Min.	Max.	Mean (sd)	
1	22.4	31.0	26.7 (3.1)	11.7
3	44.3	89.8	60.7 (15.6)	25.6
4 #1	28.2	61.9	43.6 (10.1)	23.2
4 #2	13.0	26.4	21.0 (3.7)	17.7
5 #1	37.6	59.6	47.2 (7.1)	15.1
5 #2	18.5	37.7	31.6 (6.1)	19.4
6	13.7	35.1	24.9 (6.4)	25.7
9	24.5	47.0	33.8 (7.6)	22.4

Table 14. Estimated number of abalone in the Shag Rock Bay site, calculated from the abalone counts and mean distance traversed per 5 min of each diver, as determined by flowmeter. Area covered per 5 minute swim was calculated by multiplying mean area covered/5 min. by 1.5, assuming a search width of 1.5m. All divers had 10 of their 5-min swim distances measured by flowmeter. Symbols as in Table 10.

Diver	Mean distance swum per 5 min. (m)	Mean area per 5 min. swim (m^2)	Mean no. abalone per 5 min. swim		$\hat{N}_1$	$\hat{N}_2$
			Metered	All		
1	26.7	40.1	5.2	5.4	1051	1091
3	60.7	91.1	10.5	10.7	934	952
4 #1	43.6	65.4	4.9	5.5	607	906
4 #2	21.0	31.5	5.8	5.5	1485	906
5 #1	47.2	70.8	3.5	6.4	400	756
5 #2	31.6	47.5	9.4	6.4	1604	756
6	24.9	37.4	5.1	4.7	1104	1018
9	33.8	50.7	6.8	5.9	1085	934
				Average=	1034	915

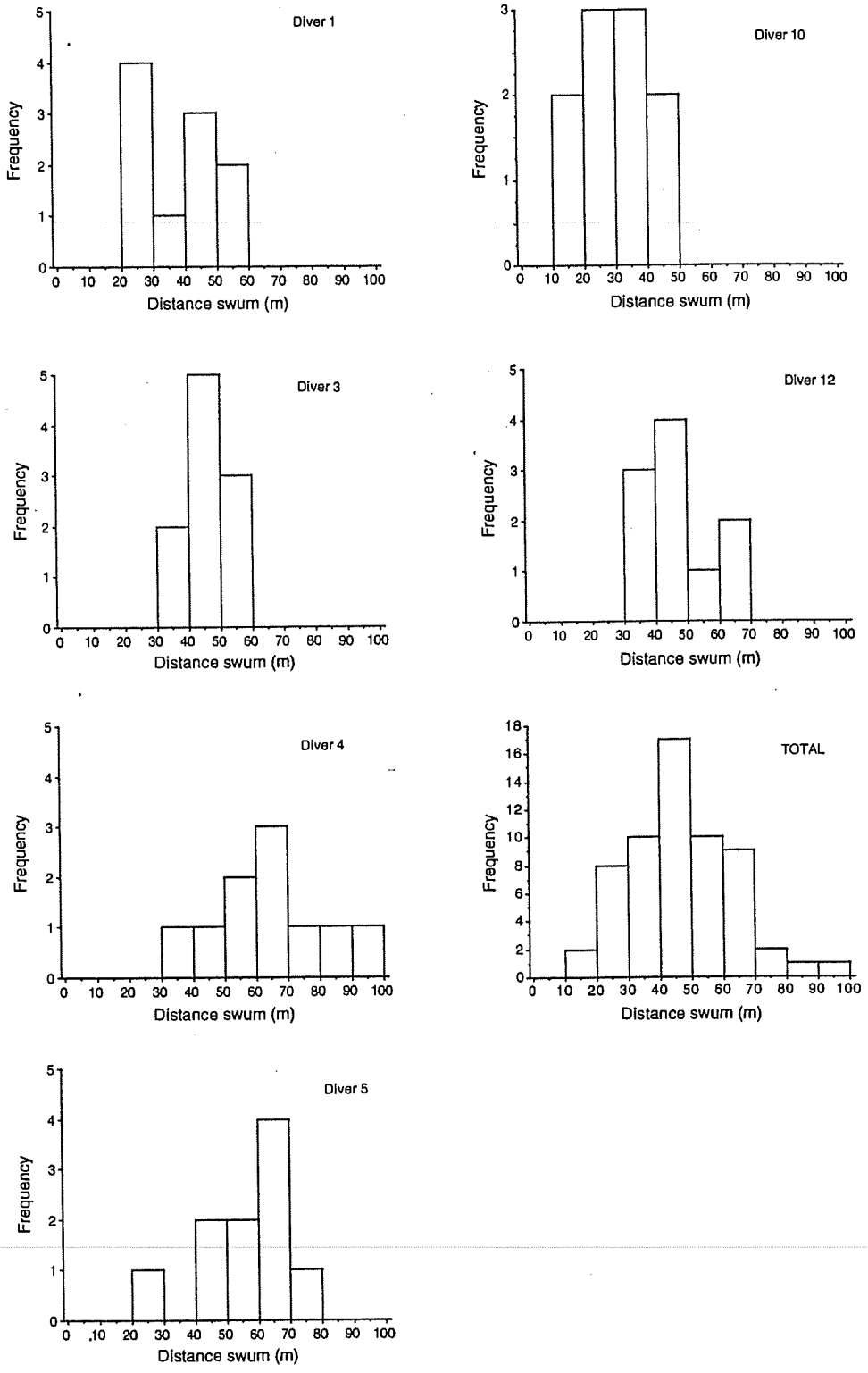


Figure 16. Frequency distribution of distance swum by six divers in ten 5-minute intervals while searching for abalone at the shallow George III Rock site.

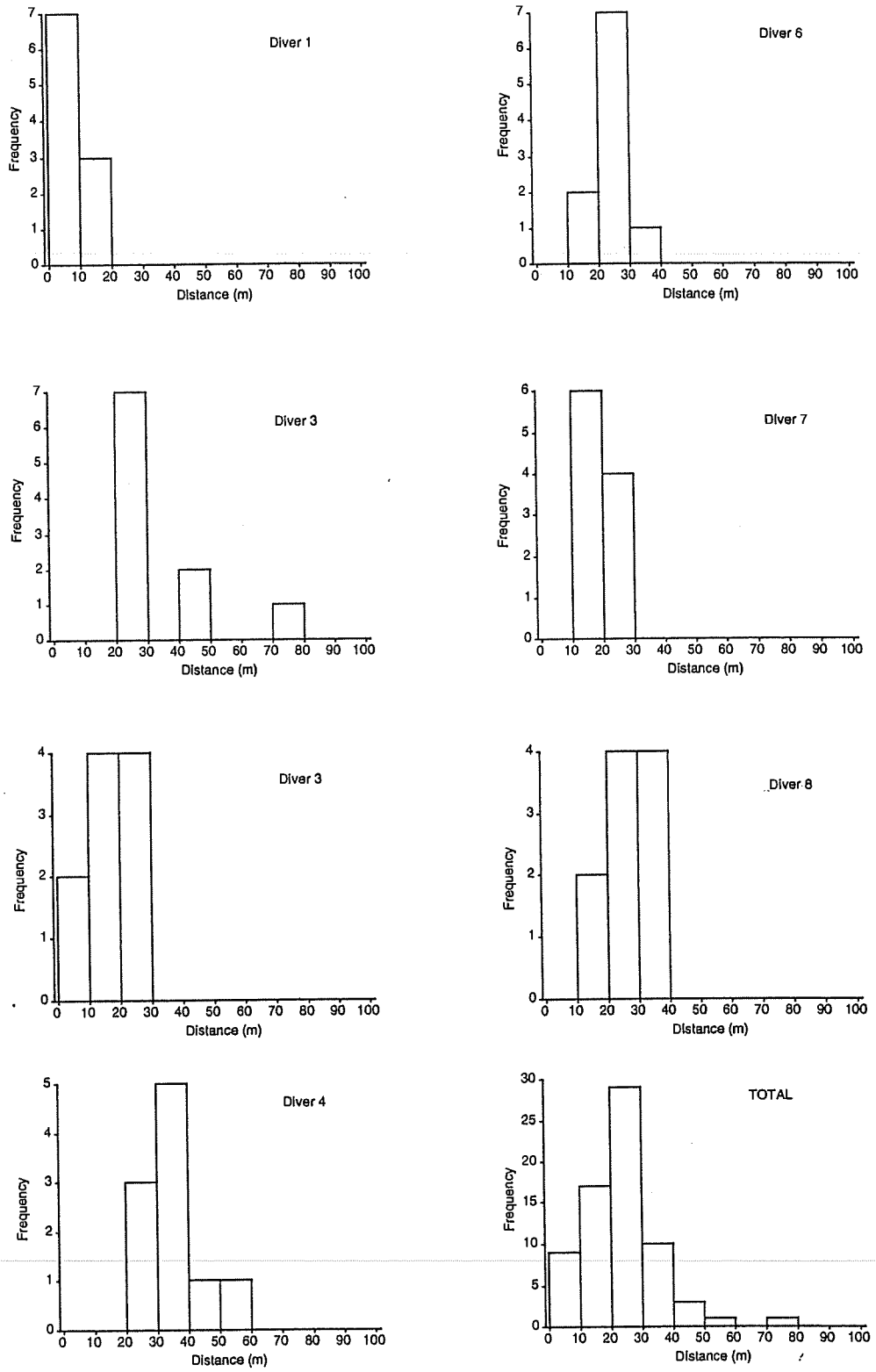


Figure 17. Frequency distribution of distance swum by seven divers in ten 5-minute intervals while searching for abalone at the Stinking Bay site.

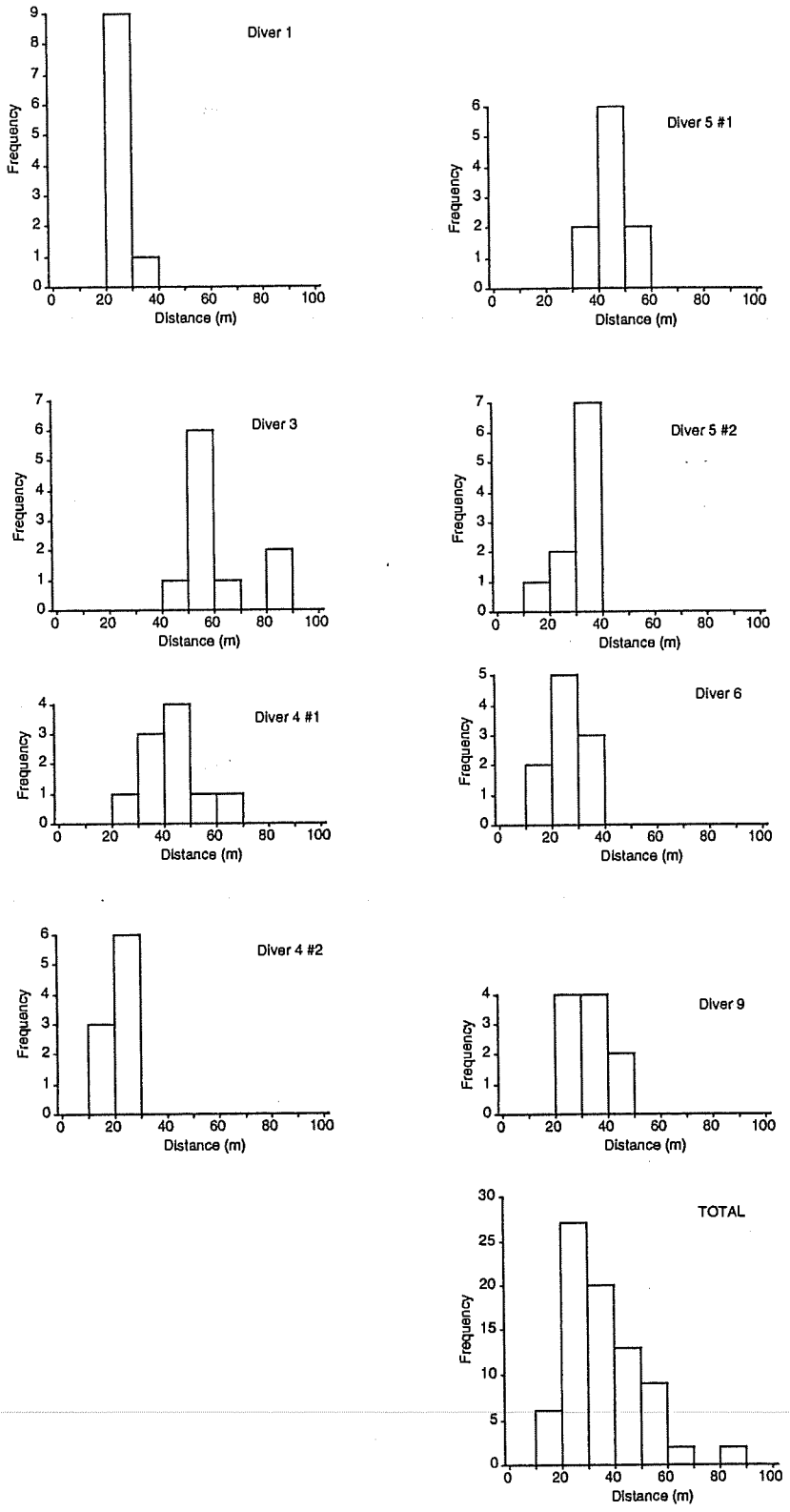


Figure 18. Frequency distribution of distance swum by six divers in 10 5-minute intervals while searching for abalone at the Shag Rock Bay site. Two divers (4 and 5) conducted two sets of metred timed swims. See text for details.

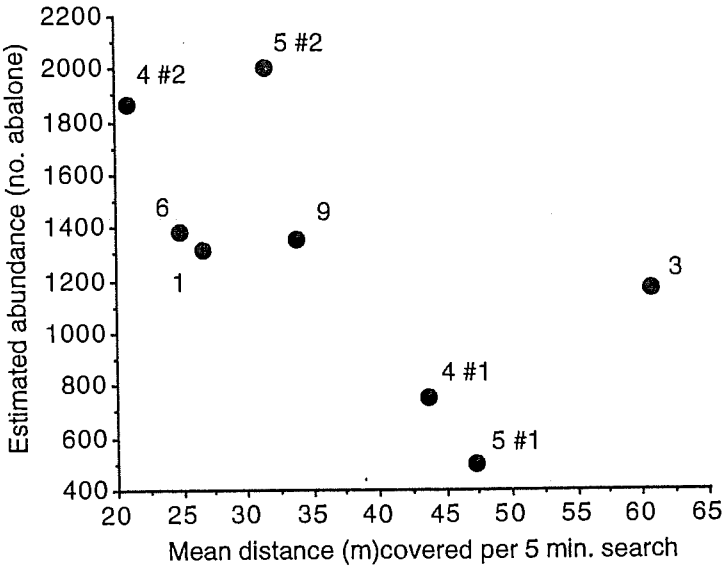


Figure 19. Relationship between timed swim searching speed and estimated total number of abalone at the Shag Rock Bay site. Numbers signify diver number. Divers 4 and 5 conducted two sets of timed swims at both high and low searching speeds.

Depletion experiments

The results of the depletion experiments for only the first survey at each site (when there were no tagged abalone) are discussed here. During subsequent surveys, divers recorded tag numbers of tagged abalone on slates underwater (rather than bringing them to the boat for this purpose) to avoid disturbing the abalone; this was done to minimise bias in movement results, important for the estimation of true survival rates from the mark-recapture analyses (see Section 2). Depletion rates of the second and subsequent surveys at each site are therefore not directly comparable with those of the first surveys described here because of the additional time spent recording tag numbers.

The total number of abalone removed from the sites in the depletion experiments ranged from 703 at Shag Rock Bay to 2,256 at the shallow George III Rock site (Table 15). These were tagged, measured and released as part of the study of survival and catchability rates, described in Section 2. The Leslie depletion curves for the four sites are shown in Fig. 20. Each of the graphs in this figure shows the catch rate expressed as a mean over all cells within each site. For the Stinking Bay site, depletion plots are shown separately for the shallow, middle and deep zones (as well as for the total site) because these zones contain distinctly different habitat and markedly different abalone densities.

Table 15. Estimates of abundance obtained from the depletion experiments. N = number of abalone removed at each site; $\hat{N}$ = population estimate obtained by fitting a regression line to all data points; $\hat{N}_{trunc}$ = population estimate obtained by truncating the data when the catch rate had declined to at least 50 percent the initial rate. n = number of data points in Fig. 20 used to calculate $\hat{N}_{trunc}$.

Site	N	$\hat{N}$	$\hat{N}_{trunc}$	Bias (%)	n
George III Rock (deep)	1028	-	323	-69	5
George III Rock (shallow)	2256	2220	1491	-34	8
Stinking Bay	1110	1057	846	-24	5
Shag Rock Bay	703	699	462	-34	4

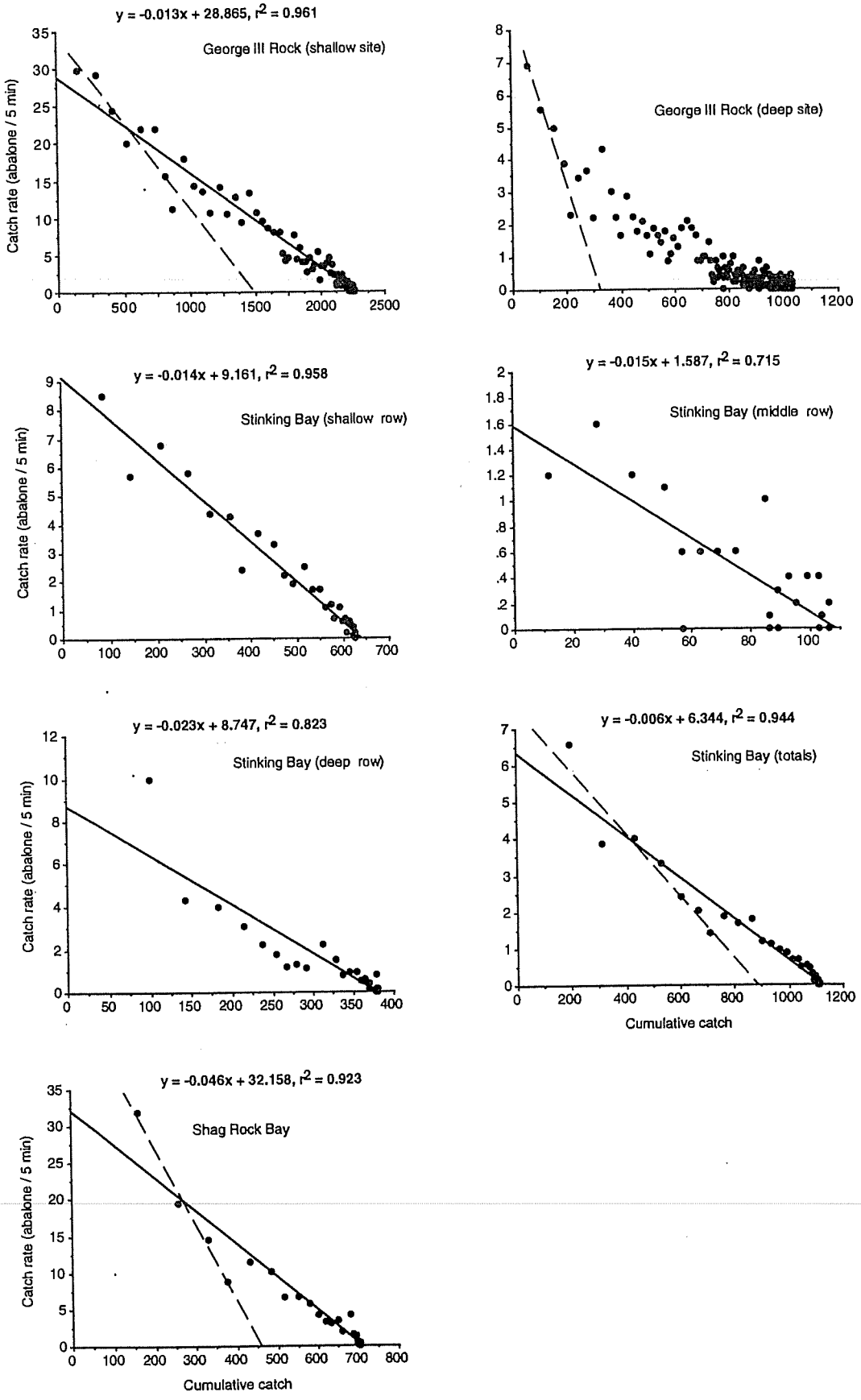


Figure 20. Depletion plots for blacklip abalone (*Haliotis rubra*) at the four study sites. Broken regression lines are fitted to the data points up until the catch rate has declined to at least half the initial catch rate. *x*-intercept is estimated abundance within the site.

Catch rates declined approximately linearly at the George III Rock (shallow) site, but departures from linearity occurred at the remaining three sites (Fig. 20). Non-linearity was most pronounced at the George III Rock (deep) site and Stinking Bay (deep zone), and to a lesser extent at Shag Rock Bay.

At both the deep George III Rock site and the deep zone of Stinking Bay, abalone are found in highest densities on the sides of rocks very close to the sand edge. Divers targeted the sand edge habitat first, resulting in a relatively rapid initial decline in catch rate, followed by a less steep decline as less suitable habitat was searched. The initial catch rate decline is particularly pronounced at the deep Stinking Bay zone, where the catch rate declined very rapidly within one or two sampling intervals before declining at a much slower rate. The non-linear nature of this catch rate decline contributes substantially to the depletion pattern for Stinking Bay as a whole (Fig. 20), where the first data point is an outlier from an otherwise linear decline.

The approximately linear decline in catch rate at the shallow George III Rock site is because the dense bull kelp (*Durvillaea potatorum*) that almost covers this site prevented the targeting of suitable abalone habitat (cracks, crevices and ledges) by searching divers. Fishing was therefore effectively random with respect to abalone habitat because the bottom could not be seen clearly by a diver until he/she had penetrated the bull kelp canopy.

Most depletion experiments do not aim to deplete the study populations to zero, but are ceased when catch rates have declined to some pre-determined proportion of the initial catch rate. To test the effect of this experimental procedure at our four study sites, total population size estimates were obtained by 'terminating' the experiment when the catch rate had declined to half the initial rate. At the deep George III Rock site, for example, the regression line was fitted to the first five data points (Fig. 20). Truncation of the depletion experiment at the 50 percent initial catch rate mark would have resulted in underestimation of total population size at all four sites (Table 15). This bias, estimated as $(N-\hat{N}_{trunc})/N$ (where N is the number of abalone removed at each site and $\hat{N}_{trunc}$ is the population estimate obtained by truncating the data when the catch rate had declined to at least 50 percent the initial rate) ranged from 24 percent at Shag Rock Bay to 69 percent at the deep George III Rock site.

Given the reasonably large variation in consecutive catch rates observed, it is unlikely that a biologist would cease a study of this sort until catch rates had declined by more than 50 percent; however, the shape of the depletion plots for all except the shallow

George III Rock site indicates that population abundance would be severely underestimated unless the depletion experiment continued until catch rates approached zero. Alternatively, earlier cessation of a depletion study might be justified if a diver's searching behaviour were constrained so that the bottom were covered in a systematic way (for example, in lanes); this would cause searching to be random with respect to abalone habitat.

Comparison of abundance estimates obtained by the three methods

The abundance estimates obtained by the three methods described here during the first survey at each site are shown in Table 16. The total number of abalone removed from each site during the first depletion exercise is also shown. None of these estimates has been adjusted for by the searching efficiency factor (Table 6), which is likely to apply to all methods (although perhaps not all to the same extent because of different levels of searching intensity by the various methods); it therefore does not aid the comparison. Confidence limits are not given for the timed swim estimates because they include variation in diver swim rate, and are therefore difficult to calculate; but they are large.

The strip transect estimates of abundance did not differ significantly from the total number of abalone removed in the depletion experiments at all but the Shag Rock Bay site, where the estimate was 54 percent larger than the number removed (Table 16). The estimate for the deep George III Rock site is derived from a mean of 6.250 abalone per 50m x 3m transect; this is the 'raw' mean. The mean and confidence limits for this site shown in Table 1 were transformed back to the original scale after inverse hyperbolic sine transformation; the transformed mean shown in Table 1 (3.868) differs markedly from the 'raw' mean, which was an exceptional case.

Because the depletion experiments were continued until no abalone were found for a 20 to 30-minute period, it is not surprising that the abundance estimate obtained by this method is very similar to the total number of abalone removed (Table 16). The truncated estimate ($\hat{N}_{trunc}$) differs greatly from the total number of abalone removed at all sites. It is clear that the non-linear nature of the Leslie depletion plots makes accurate estimation of abundance by this method virtually impossible unless catch rates have been reduced very substantially; it therefore is not a practical or reliable method for assessing and monitoring abalone fisheries.

The timed swim method yielded abundance estimates that were closest to the total number removed at the shallow George III Rock site (10 percent greater), exceeded this number by 41 percent at Shag Rock Bay, and underestimated it by 59 percent at Stinking Bay (Table 16). It is believed that timed swims greatly underestimate abundance at Stinking Bay because highest abundances were localised in a small fraction of the site (the shallow zone at depths <2 m). Since the direction of timed swim surveys was selected at random, it was not unlikely that a disproportionally small fraction of the narrow, high-density shallow zone would be traversed during these surveys. In general, the greater the degree of aggregation, the greater the risk of bias. An additional factor is likely to be lower searching efficiency during the timed swims than either strip transect or depletion searches because searching intensity is higher in these latter two methods. This may be particularly important at the Stinking Bay site because of the low visibility and dense algal cover.

Table 16. Estimates of abundance of blacklip abalone (*Haliotis rubra*) at three study sites obtained by three methods, and the total number of abalone removed during the depletion experiments.

	Method						
	Strip transects			Timed swims	Depletion		
		95% C.L.					
Site	$\hat{N}$	lower	upper	$\hat{N}$	$\hat{N}$	$\hat{N}_{trunc}$	No. removed
George III Rock (deep site)	938	-	-	-	-	323	1028
George III Rock (shallow site)	2131	1773	2551	2488	2220	1491	2256
Stinking Bay	1282	882	1682	457	1057	846	1110
Shag Rock Bay	1082	851	1363	1034	699	462	703

DISCUSSION

Strip transects

Abundance and distribution

The different shapes of the frequency distributions of numbers of abalone per transect between the deep and shallow sites (Fig. 7) may be explained as a function of abalone density: When densities are low, most transects will have only a small number (in this case one or two) abalone. At high densities, on the other hand, it is unlikely that any transect will have a small number of abalone; the modal number will be somewhat higher. Thus, the two curves are qualitatively similar, and differ only in their position along the x–axis; as the mean density of abalone decreases, the modal number will shift toward the left until, at very low densities, the mode is 0 abalone per transect.

In this study, the George III Rock site was divided for experimental purposes into two habitat types: the string kelp habitat and the bull kelp habitat. Although many more habitats (boulder bottom, bedrock, sand patches, sand edges, etc.) could be identified, it was not possible to stratify the site to this detail because these many habitats were interspersed on a very fine scale. It was therefore not possible to determine, even approximately, the area occupied by each of these. If this were possible, it is certain that within-stratum variation in counts would have been substantially reduced, since casual observations showed that, in the shallow bull kelp locality, the majority of the abalone were under ledges or in crevices, and in the deep string kelp locality, most were on boulders adjacent to sand ('sand edges').

Hence, the variation about the mean at each locality (Table 1) could not have easily been reduced, and the confidence limits about the estimates of population size are unavoidably large, particularly for the string kelp (*Macrocystis pyrifera*) locality.

Use of strip transects rather than line transects

Statistical methods for the analysis of line transect data are well developed (Buckland *et al.* 1993), and in many respects line transects are more amenable to statistical analysis than strip transects. Nevertheless, strip transects were adopted in this study for reasons related to the complexity of the abalone habitat and the density of the macroalgae at the study sites.

One important assumption of line transect estimation is that animals lying along the transect line have a capture (or sighting) probability of 1. Recovery of unchalked

abalone on the transect line by diver 2 during double-surveys demonstrates that this assumption is violated;line transect methods would therefore have been inappropriate in this study.

It is assumed in line transect sampling that the transect line is placed on the bottom randomly with respect to the target animal's distribution. The rate of attenuation of numbers of animals observed with distance from the transect line is a measure decreasing sightability. Yet in the case of abalone, the transect width that could be reliably searched in practice was no more than 1.5 m either side of the transect line. At the shallow George III Rock site this was because the bull kelp (*Durvillaea potatorum*) is very dense, and very difficult to search in; at the Shag Rock Bay site because of the complexity of the bottom (a confusing number of crevices between the large boulders). Because of the extreme topographic complexity of the bottom in Shag Rock Bay, it would have been virtually impossible to measure accurately the distance from the transect line to each abalone. Similarly, it would have been impossible at the shallow George III Rock site because of the often-turbulent conditions under which the survey work was done and the density of the bull kelp, which would have made the use of a measuring stick or tape to measure perpendicular distance between the transect line and the abalone virtually impossible and totally impractical.

Zahl (1989) has described a line-transect method for estimating abundance when the probability of sighting under or on the transect line is unknown. This method, which requires searching each transect at two different intensities (*i.e.*, at different swimming speeds), would have been unsuitable in our study for the reasons of habitat complexity and algal density just described.

Diver searching efficiency

It was not anticipated that searching efficiencies as low as 60 percent would occur in strip transect searches, where searching intensity is high and confined to a narrow strip of bottom. Searching may be particularly thorough when divers work in pairs and both search the same transects, because the desire to compare well with his/her partner promotes careful searching. Low efficiencies could not be attributed to diver inexperience because some of the divers had considerable experience searching for abalone; moreover, differences between divers were relatively small. Searching efficiency is affected by algal density, sea condition (rough or calm), underwater visibility, bottom complexity, shell camouflage and water temperature. The low (60 percent) searching efficiency at the Stinking Bay site is attributable to dense algal cover, often high turbidity and difficulty of searching complex boulder habitat in the shallows.

One result (not shown here) was variation in searching efficiency between surveys at individual sites. This was most pronounced at Stinking Bay, where seasonal variation in algal density was sometimes extreme. An unidentified species of filamentous green algae that blooms in summer months makes searching particularly difficult.

One factor believed to affect divers' searching efficiency is water temperature. Although no attempt was made to measure the importance of this, it was commonly observed, especially during winter months when water temperatures were 10 to 12°C, that a diver would find several more abalone from a grid square thought to be completely depleted, after 20 to 30 minutes out of the water and a warm drink.

The double-survey method provides a simple, effective way of measuring the relative searching efficiency of divers. It can be applied in a range of habitats and, importantly, it can be repeated at the same sites using the same divers to determine searching efficiency trends of individual divers—for example, whether searching efficiency increases with experience or whether searching efficiency varies widely between surveys. It is noteworthy that, despite the wide range of experience of the research divers used in this study, searching efficiency did not differ greatly between divers. This is an encouraging result for the use of strip transect methods to estimate abalone abundance.

The major assumption of the method is that chalked abalone do not disappear before the second diver has completed his/her search; this can be confirmed by chalking a sample of abalone and examining them for a few minutes each to determine the proportion that move. Alternatively, since individual divers are the second diver to search a transect about as often as they are the first diver, any difference in searching efficiency of diver 1 and diver 2 (*i.e.*, $\hat{P}_1$ and $\hat{P}_2$) is probably because of the effects of chalking, in which case $\hat{P}_1$ is unbiased.

Variation in searching efficiency between surveys has important implications for assessing long-term trends in abundance. It reduces the ability to detect temporal changes in abundance because error-associated variation is increased. The double-survey method may be used to estimate searching efficiency at each sampling occasion; these estimates may then be used to adjust strip transect density estimates. It is suggested that the reduction of error-associated variation in abundance between surveys will increase the sensitivity of transect methods to detect real changes in abundance through time.

Timed swims

Flowmeters accurately measure the distance swum when water movement is zero; meaningless readings may be obtained if used in strong currents (Nash 1981). Care was taken, therefore, to conduct the flowmeter measurement of distance swum by each diver in different habitat types and abalone densities at times of relatively calm weather and minimal tidal currents.

Although still-water conditions seldom prevail at the study sites (especially Shag Rock Bay and the shallow George III Rock site), the test of flowmeter accuracy demonstrated that, although there may be some deviation in individual flowmeter measurements, these are evened out when all 20 transects for a diver are summed. This is because the timed swims were done in several directions relative to the tidal current and swell. It is concluded that the area covered in any particular timed swim cannot be calculated with certainty, but the area for all timed swims combined can be estimated with reasonable accuracy.

A major shortcoming of the timed swim method is that variation in swimming speed introduces an additional error term into the estimated variance; this error term is difficult to calculate (and very wide) because of variable diver swim rate and the inconsistency of individual divers' swim rate patterns from one survey to the next. At least some of the variation in swim rate by individual divers measured by flow meter was because of measurement inaccuracy (Table 8). Nevertheless, the pronounced differences between divers, and the differences in swim rates between sites by individual divers (Figs. 16, 17, 18) are unlikely to be caused by errors of measurement.

An important source of bias not often discussed in the abundance estimation literature is competition between survey divers. It can be difficult for a diver to resist 'topping up' his/her count with abalone seen, for example, just outside the strip transect boundary, particularly if his/her counts have been lower than those of other divers on the team. Searching in pairs can reduce this over-counting when each transect is searched sequentially by two divers.

Timed-swim searching appears to be especially prone to competition-induced overcounting. This may have occurred during the survey at the Shag Rock Bay site. Unlike strip transects, in which a fixed, marked area of the bottom is to be searched thoroughly at each diver's own pace, the rate of swimming affects both the area of

bottom covered and diver searching efficiency, and thence the estimated abalone density.

Contrary to what may have been divers' perceptions, the abundance estimate is *inversely* related to swimming speed—that is, the divers with the highest swimming speeds obtained the lowest abundance estimates (Fig. 19) because searching efficiency declines with swimming speed; slow divers are likely to search more thoroughly. This is not necessarily strictly true since it also depends on searching skill. If the divers carrying out the survey at the Shag Rock Bay site were of equal efficiency, the inverse relationship between swimming speed and estimated abundance would be a close one. The outlying point, which shows a high abundance estimate for a high swimming speed for diver 3 suggests that this diver is a more efficient searcher. This is supported by other evidence (not shown) from his pattern and rate of fishing down cells in the Leslie depletion experiments.

Divers 4 and 5 conducted a second set of flow-metered timed swims because their first set yielded low estimates of abundance compared to the other divers (Fig. 19). The second set were swum at a deliberately slow speed because it was suspected that the low estimates from their first set were because of high swimming speeds (and therefore relatively low searching efficiency) induced by competition between these two divers. Unexpectedly, their abundance estimates from the second set of timed swims were substantially higher than those of the other divers. Possible causes of this are: (i) a higher proportion of abalone were found by divers 4 and 5 on their second survey; (ii) divers 4 and 5 concentrated their searching in parts of the site where abalone were particularly abundant (that is, they avoided the extreme shallows and the deep); or (iii) some sort of overcompensation by these divers to try to improve their counts occurred. The first possibility implies their searching efficiency increased markedly—and to a level higher than the other divers—which is unlikely. Changes in abalone catchability (caused by better weather conditions or increased conspicuousness of the abalone) between the two search days is ruled out because other divers who conducted timed swim searches over two days did not show the same variation in their abundance estimates. One of these two divers later admitted that, on this second set of surveys, the area searched might have been wider than the agreed 1.5 m because of the desire not to obtain a low estimate of abundance in these second surveys. Although this is an extreme case, it illustrates the effect that between-diver competition may have on the accuracy of abundance estimation by the timed swim method.

Another source of bias in timed swim abundance estimation is that the width of the search area is only estimated, and is likely to vary both between divers and type of bottom searched (wider search area in more open bottom with less macroalgae, for example). The inaccuracy this introduced into the estimate of abundance does not exist with the strip transect method.

Another factor which may affect timed swim abundance estimates is that divers may unwittingly search areas in which abalone are more likely to occur, such as crevices between boulders and areas of bottom with more open algal cover (more encrusting coralline algae).

Bias may also occur if the entire site were not covered by a diver during his timed swims, and if abalone were more abundant in some parts of the site than others. A diver may, for example, spend more time in that part of the region of highest abundance. It was not always possible to ensure that this source of bias was avoided. Evidence concerning the importance of this factor is inconclusive.

In summary, there are several possible sources of bias and error associated with the timed swim method which do not arise with the strip transect method. The most important of these are variable swimming speed, reduced searching efficiency at high swim speeds, and variable (estimated) search path width.

Depletion experiments

Depletion experiments yield accurate (unbiased) estimates of abundance if all animals within the study area have equal probability of capture. On a Leslie depletion plot, this means a linear rate of decline in catch rates when plotted against cumulative catch until all animals are removed. Unequal catchability will yield an underestimate of population size unless the proportion of the population removed is very large; in many cases this is impractical or impossible, particularly if the spatial scale of the study is large (*e.g.*, tens of kilometres of coastline). The slope of the depletion plot may change because the less catchable (*i.e.*, hidden or camouflaged or non-aggregated) abalone are generally found last; or searchers become less efficient in their searching with time, either through boredom, tiredness or inability to maintain a high level of concentration.

In our studies, the first reason is most likely. Evidence for this is that, when searching was random with respect to bottom type (*i.e.*, at the shallow Georges site), the Leslie depletion plot was in fact linear until all abalone had been removed, despite the

difficulty of searching this bull kelp-dominated site, which tested the patience and endurance of all searchers.

In a Leslie depletion experiment carried out at George III Rock in 1987, Prince (1989) found the decline in catch rate with cumulative catch to be linear. This may be attributed, at least in part, to the fact that the fishdown undertaken by Prince ceased when catch rates were still substantially higher than those at the end of the current set of fishdowns. If we had ceased our depletion experiments before the catch rates had declined to none per 30 minutes' searching, our plot for the lower-density deep site would appear linear also.

These results demonstrate that, unless there is other independent evidence that the Leslie depletion relationship is linear, it is not possible to ensure that an accurate estimate of abundance has been obtained unless the depletion experiment has been continued until the catch rates have declined to zero.

The decline in catch rate as the depletion experiment proceeded showed considerable variation around the regression line, particularly at the deep George III Rock site (Fig. 20). This may be attributed to the clumped distribution of abalone and the heterogeneous nature of the bottom, and the searching behaviour of the diver: when fishing down of a cell commences, the diver usually swims rapidly until promising habitat, or an aggregation of abalone, is located. Unless the diver is lucky, this is likely to occur after some time has elapsed because the grid cells at all except the Stinking Bay site are large. The catches at the beginning of the fishdown will then be less than those once an aggregation is located. Some of this non-declining variation may be removed by pooling pairs of 5-minute catches to give catches for 10-minute periods (not shown here).

From experience, it was found thorough depletion of a site requires the alternation of two searching strategies, known by some commercial abalone divers as 'scratching' and 'creaming'. The former describes slow, careful searching of the bottom, and the latter describes fairly rapid swimming above the bottom and scanning for abalone from a distance.

An evaluation of the three abundance estimation techniques

Depletion methods do not provide unbiased estimates of abundance unless the decline of catch rate with cumulative catch is linear; this is unlikely to occur unless abalone catchability is uniform. Because of the aggregating behaviour of abalone, however,

catchability is seldom uniform. Depletion methods are therefore an unreliable method of estimating abalone abundance.

Timed swims may provide unbiased estimates of abundance if divers' searching patterns are random (no targeting of aggregations or preferred habitat) and the width of bottom searched is constant. The large variability in swim rates by research divers that has been found in this study indicates, however, that confidence limits on abundance estimates are likely to be very wide. The timed swim method also appears more prone than other methods to bias caused by diver competitiveness.

Strip transects yield relatively unbiased estimates of abundance. If the double-survey method is adopted as part of the survey procedure, temporal variation in search efficiency caused by weather conditions or abalone conspicuousness can be used to adjust density estimates, thereby reducing error-associated variation in abundance. Despite these advantages, only relatively large changes in abundance can be detected with confidence. An additional factor that affects the interpretation of abundance estimation results is abalone movement, which has been shown in this study to be both extensive and size-related (see Section 2).

All of the methods examined have various sources of bias or inaccuracy associated with them. The evidence from this study, however, indicates that the strip transect method is the most suitable for assessing blacklip abalone abundance.

REFERENCES

Beinssen, K. and D. Powell (1979). Measurement of natural mortality in a population of blacklip abalone, *Notohaliotis ruber*. *Rapp. P.V. Cons. Int. Expl. Mer* 175: 23-26.

Buckland, S.T., D.R. Anderson, K.P. Burnham and J.L. Laake (1993). *Distance Sampling: Estimating abundance of biological populations*. Chapman and Hall: London. 446 pp.

Cormack, R. M. (1964). Estimates of survival from the sighting of marked animals. *Biometrika* 51: 429-438.

Elliott, J.M. (1977). Some methods for the statistical analysis of sampling of benthic invertebrates. *Freshwater Biological Association Publication No.* 25: 1-142.

Jolly, 1965. Explicit estimates from capture-recapture data with both death and immigration—stochastic model. *Biometrika* 52: 225-247.

Krebs, C.J. (1989). *Ecological Methodology*. Harper & Row: New York. 654 pp.

Magnusson, W.E., G.J. Caughley and G.C. Grigg (1978). A double-survey estimate of population size from incomplete counts. *Journal of Wildlife Management* 42: 174-176.

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

Morin, A. (1985). Variability of density estimates and the optimization of sampling programs for stream benthos. *Canadian Journal of Fishery and Aquatic Sciences* 42: 1530-1534.

Myers, J.H. (1978). Selecting a measure of dispersion. *Environmental Entomology* 7: 619-621.

Nash, W.J. (1981). A survey of trochus stocks on selected reefs of the central Great Barrier Reef. *Unpublished report to Applied Ecology Pty. Ltd.: Canberra.* 38 pp.

Nichols, J.D., R.E. Tomlinson and G. Waggerman (1986). Estimating nest detection probabilities for white-winged dove nest transects in Tamaulipas, Mexico. *Auk* 103: 825-828.

Patil, G.P., E.C. Pielou and W.E. Walters (1971). *Spatial Patterns and Statistical Distributions.* Pennsylvania State University Press: University Park, Pa.

Pearson, R.G. (1980). Assessment and management of fisheries for sessile invertebrates. *In* J.L. Munro (Ed.): *UNESCO Seminar on Marine and Coastal Processes in the Pacific*, 123-157. (UNESCO: Paris.)

Pollock,. K.H. (1982). A capture-recapture design robust to unequal probability of capture. *Journal of Wildlife Management* 37: 757-760.

Pollock, K.H., J.D. Nichols, C. Brownie and J.E. Hines (1990). Statistical inference for capture-recapture experiments. *Wildlife Monographs* 107: 97 pp.

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

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

Sanderson, J.C. (1990). Subtidal macroalgal studies in east and south-eastern Tasmanian coastal waters. *Unpublished M.Sc. thesis, University of Tasmania*: Hobart.

Seber, 1965. A note on the multiple-recapture census. *Biometrika* 52: 249-259.

Smith-Gill, S.J. (1975). Cytophysiological basis of disruptive pigmentary patterns in the leopard frog *Rana pipiens*. II. Wild type and mutant cell specific patterns. *Journal of Morphology* 146: 35-54.

Southwood, T.R.E. (1978). *Ecological Methods*. 2nd edition. Methuen: London.

Zahl, S. (1989). Line transect sampling with unknown probability of detection along the transect. *Biometrics* 45: 453-470.

SECTION 2.: ESTIMATION OF ABUNDANCE, CATCHABILITY, SURVIVAL AND MOVEMENT OF BLACKLIP ABALONE (*HALIOTIS RUBRA*) BY MULTIPLE MARK-RECAPTURE-MOVEMENT METHODS IN THREE SPATIALLY STRATIFIED STUDY SITES

W. J. NASH, J.C. SANDERS, S.R. TALBOT, A. CAWTHORN, J BRIDLEY AND B. HISLOP

2 Estimation of abundance, catchability, survival and movement of blacklip abalone (*Haliotis rubra*) by multiple mark-recapture-movement methods in three spatially stratified study sites

W.J. Nash, J.C. Sanderson, S.R. Talbot, A. Cawthorn, J. Bridley and B. Hislop

INTRODUCTION

In Section 1, three methods of estimating abundance (strip transects, timed swims and depletion experiments) were compared and evaluated. A double-survey method was used to estimate the searching efficiency of individual divers at each site and a mean diver searching efficiency for each site. In this Section, capture probability is estimated using multiple mark-multiple recapture methods. The subdivision of each site into grid cells, described in Section 1, also allows the pattern and extent of movement of abalone at each site to be estimated. The movement information could then be used in the estimation of survival rates.

The movement-mark-recapture results for the Stinking Bay site were presented orally at the *North Pacific Symposium on Invertebrate Stock Assessment and Management*, held in Nanaimo, British Columbia in March 1995. This aspect of the study is being prepared as a paper to be published as part of the proceedings of the symposium in the *Canadian Special Publication of Fisheries and Aquatic Sciences* series.

METHODS

Field methods

Overall experimental design

The determinants of capture probability of abalone include substratum complexity, density of macroalgal cover, water clarity, water turbulence (affecting ability to search) and the degree of abalone shell camouflage. The three sites were chosen for their range of substratum complexity (from simple to complex) in order to estimate the range of capture probabilities that may be encountered. The study sites are described in Section 1.

In order to measure the proportion of abalone in the sub-boulder habitat, multiple mark-recapture methods were used. Untagged abalone that are recovered within the study site on a second visit following tagging of all abalone within the site may have come from several sources: they may have moved into the site since the previous

survey; they may have been within the site, and visible, during the first survey but were overlooked; or they may have emerged from the sub-boulder habitat since the first survey. The gridwork arrangement of squares at the study sites (described in Section 1), allows estimates of immigration and emigration rates to be obtained. These estimates may then be used to determine the number and proportion of untagged abalone that were either present in the site in the above-bottom habitat in the previous survey, but overlooked, or that had emerged from the sub-boulder habitat since the previous survey. The proportion of untagged abalone that were overlooked may be estimated by the double-survey procedure described in Section 1. This experimental procedure is an extension of that described by Beinssen and Powell (1979).

Tagging

The tagging exercise was conducted in conjunction with the Leslie depletion experiment described in Section 1. The tagging was done one grid at a time. All abalone collected from a single grid were taken back to the dinghy as the depletion experiment proceeded. These were suspended in open-mesh bags over the side of the dinghy until ready for tagging. The abalone were then tagged and again suspended over the side of the dinghy until all abalone from that grid had been tagged; they were then returned to the grid from which they had been removed and individually held on the bottom by the diver until they had adhered to the substrate. Care was taken to place the abalone on suitable substrate (solid rock devoid of sediment, and preferably encrusted with coralline algae). Smaller abalone were placed in crevices or under boulders when possible. Maximum shell diameter, tag number, respiratory pore into which the tag was inserted and grid cell of origin and shell condition were recorded. Shell condition was also recorded using the following categories: clean, animal (sponge, bryozoan, tubicolous polychaete) or plant (encrusting coralline or fleshy macroalgae). Shell condition could be used to assign each abalone to either cryptic or emergent habitat.

The tagging method described by Prince (1991) was used. The tags used were individually numbered Floy™ laminated disc tags, with a central perforation by which the tag was attached to a respiratory pore with a nylon rivet. The first 50 abalone tagged in each grid were double-tagged in order to estimate the rate of tag loss. The tags were placed in the most proximal perforate respiratory pores where possible, since Prince (1991) found that the majority of tags lost from double-tagged abalone were from the more distal pores.

Recapture of tagged abalone

On all surveys subsequent to the first, each site was searched intensively, grid cell by grid cell, to recover tagged abalone. Tag number and position within the site of each tagged abalone were recorded underwater. The tagged abalone were disturbed as little as possible to reduce the effects of handling on movement, survival and catchability to a minimum. All dead tagged shells were retrieved, and the grid and date of recovery recorded. All untagged abalone were taken to the dinghy, tagged, then returned to the grid of origin as described above.

Six tag-release-recapture surveys were conducted at the shallow George III Rock, Stinking Bay and Shag Rock Bay sites, and two at the deep George III Rock site. Dates of these surveys are shown in Table 1. The time interval between consecutive surveys was judged to be long enough to allow thorough mixing of tagged abalone with untagged abalone (both emergent and cryptic). The fourth survey of the Shag Rock Bay site was abandoned part-way through because of logistical problems. Tag-recapture results from this visit are not easily incorporated into the mark-recapture analysis; the approach adopted here was to combine the fourth and fifth surveys into a single (extended) survey (renamed the fourth survey); the sixth survey then became the fifth survey. The deep George III Rock site was abandoned after only two mark-recapture surveys because of insufficient resources to continue this study at four sites; mark-recapture surveys took longest to complete at this site because of its size and depth. Similarity of movement patterns between this and the shallow George III Rock site (see Results) justified the abandonment of the deep site.

The shallow George III Rock site was further modified at the start of the third survey by reducing it in size from the original 90m x 90m to 60m x 60m. This was done by using only the four southeastern-most squares of the original nine, and was necessitated because of the heavy work load maintaining and surveying the sites. It was judged that abalone within the site were sufficiently abundant for adequate mark-recapture sample sizes to be obtained.

The possibility of overlooking abalone (both tagged and untagged) was minimised by employing various methods at the different sites: at the deep site on George III Reef, each 50m x 50m grid was subdivided, using rope, into lanes two to four metres wide (depending on substrate complexity); at the shallow George III Reef site, rope could not be used because of the density of the bull kelp (*Durvillæa potatorum*) so lanes were marked out by attaching a line of buoys to the bull kelp fronds. Searching was conducted by two divers in each lane; divers would generally start searching from opposite ends of a lane, and upon completion move to the next lane. It was found that

using two divers per lane reduced the number of abalone that were overlooked, because of greater searching time per lane, and also because it helped maintain divers' vigilance.

Table 1. Dates of mark-recapture surveys at the four study sites.

Site	Start date	Finish date	Survey no.
George III Rock	27.Jun.89	3.Aug.89	1
(deep site)	10.Nov.89	27.Feb.90	2
George III Rock	16.Aug.89	20.Sep.89	1
(shallow site)	7.Nov.89	15.Feb.90	2
	6.Feb.91	15.Feb.91	3
	2.Sep.91	6.Sep.91	4
	18.Oct.91	5.Nov.91	5
	3.Feb.92	13.Feb.92	6
Stinking Bay	18.Sep.90	24.Sep.90	1
	5.Dec.90	13.Dec.90	2
	8.Apr.91	20.Apr.91	3
	29.Jul.91	9.Aug.91	4
	25.Nov.91	30.Dec.91	5
	20.Feb.92	10.Mar.92	6
Shag Rock Bay	30.Oct.90	27.Nov.90	1
	18.Apr.91	1.May.91	2
	14.Aug.91	26.Aug.91	3
	9.Dec.91	13.Dec.91	4
	13.Jan.92	24.Jan.92	5
	16.Mar.92	2.Apr.92	6

Searching for abalone during the initial survey at the two George III Rock sites and the Stinking Bay site continued until no abalone were found for six consecutive 5-minute periods. This was judged to be unnecessarily thorough, and was replaced by

three 5-minute periods on subsequent surveys, and at the Shag Rock Bay site on all surveys.

Strip transect searches outside the site

At the completion of the final fishdown at the shallow George III Rock and Stinking Bay sites, strip transect searches for tagged abalone were conducted outside the site. The purposes of these were to measure diffusion rates outside the site. These results were used to complement the movement information obtained by studying within-site movement. Tag numbers of all tagged abalone were recorded.

At the shallow George III Reef site, 100-m long transects were aligned radially at each of the cardinal and sub-cardinal points of the compass. The transects extended from the periphery of the square (60m x 60m), and searches were conducted in a 1.5m strip either side of each transect. Divers worked in pairs, one either side of the transect line. Tag numbers of all tagged abalone found were recorded for each 10-m increment of the transect. In addition, the number of untagged abalone seen was recorded for each 10-m increment. All tagged abalone were brought back to the dinghy and measured to the nearest mm, then released within the study site. Exact position of release was recorded.

Any tagged abalone found wider than 1.5 m from the transect line were also examined, and estimated distance from the transect line and distance along the transect line (*i.e.*, which 10-m increment it was adjacent) recorded. Depth, dominant algal species and substratum complexity were recorded for each 10-m increment.

The bottom outside the Stinking Bay site was searched in March 1992. The number of untagged abalone within each area was recorded as well as the tag numbers of the tagged abalone, in order to use the decline in the ratio of tagged to untagged abalone as an additional measure of the movement rate of tagged abalone from the site. The bottom outside the study site was divided into strips using shore markers: the first marker outside the site on the south side was 15 m from the site, and subsequent markers were 30 m apart. To the north of the site the first marker was 20 m from the site, and subsequent markers were 30 m apart. Width of the cells searched was 12 m in the shallow and deep zones and variable (~15-20 m) for the middle zone. These cells were searched less intensively than those within the site because of time limitations. Each cell was therefore searched with equal intensity: the 30-m wide square was searched by two divers for 60 minutes. The narrow squares either side of the site were fished for proportionally less time to provide the same searching intensity as in the 30-m wide squares (*i.e.*, for 30 minutes per diver pair in the 15-m

wide square, and for 40 minutes per diver pair in the 20-m wide square). Although the outside-site squares were not searched as intensively as the within-site squares, the very low recovery rate of tagged abalone at the end of each 60-minute search indicated that searching was reasonably thorough.

The two 30-m wide strips of bottom immediately inside the southern boundary of the research reserve were also searched to provide an estimate of long-distance dispersal. These two areas were searched with the same intensity as the other outside-site areas.

Dive team composition was chosen so that searching efficiency was approximately equal among the teams, since diver efficiency may affect the total counts of abalone harvested in each square in the allotted time. It would not, however, affect the *ratio* of tagged to untagged abalone.

Analytical methods

Tag loss analysis

The number of double-tagged abalone found on each mark-recapture visit containing either the first or second tag, or both, was recorded. Some tagged abalone were recaptured several times within a visit; for these, only the number of tags present on the final within-survey recapture was recorded.

Rate of tag loss was estimated using the methods described by Seber (1982:94-95). For a more recent review of double-tagging methods see Wetherall (1982). The rate of tag loss was $\log_e(x+1)$-transformed (since values were <1). If the rate of tag loss is constant through time, the regression of tag loss (log-transformed) against time since tagging will be linear. To simplify the analyses, time at liberty (between tagging and recapture) was recorded as the time interval between the midpoints of each visit. The purpose of this was to avoid the situation of there being many time intervals with few data cases; sampling error would have produced a large variation in capture rates of double-tagged abalone, which would in turn result in a wide scatter of points on the tag-loss graph. Treating each mark-recapture visit as a point in time allows all double-tag recaptures within a visit to be pooled; this approximation is unlikely seriously to affect the estimation of tag loss because the time between survey is long relative to the duration of each survey.

Estimation of movement, catchability and survival rates

Methods for estimating survival and catchability of animals in mark-recapture studies have been developed by Cormack (1964), Jolly (1965) and Seber (1965). The

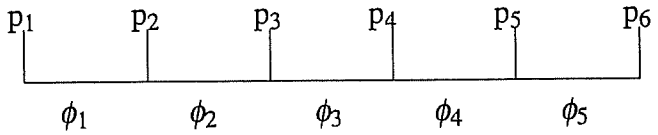
theoretical and mathematical bases for estimating these parameters have been described extensively in the literature, most recently by Burnham *et al.* (1987), Pollock *et al.* (1990) and Lebreton *et al.* (1992), among others.

The capture history of each tagged abalone was developed using the codes shown in Table 2. Codes 0, 1 and 2 are common to all mark-recapture procedures; codes 3 and 4 are used in the mark-recapture computer programs JOLLY and JOLLYAGE of Pollock *et al.* (1990); code 5 has not been used in the analysis of live recaptures because the development of theoretical methods to use both live recaptures and dead recoveries has been developed very recently (Burnham 1993).

Table 2. Capture history codes for tagged abalone used in this study.

Code	Definition
0	Not found during a survey
1	Found during a survey
2	Found on a survey but removed from the site (usually because of mortal damage – broken shell or cut foot)
3	Not captured in a survey, but resighted after the survey and before the next survey
4	Captured and released in a survey and resighted after the survey and before the next survey
5	Found dead

Under the full Cormack-Jolly-Seber (CJS) model, both survival and capture probability vary between surveys; if several groups (*e.g.*, males and females) are being compared, survival and capture probability vary between groups as well. The notation and analytical methods of the CJS model are described comprehensively by Lebreton *et al.* (1992). As explanation, the survival and capture probability parameters for a six-survey study are shown in Fig. 1; the parameters that can be estimated are also shown.



Estimable parameters are:

p_2 p_3 p_4 p_5
ϕ_1 ϕ_2 ϕ_3 ϕ_4
$\phi_5 p_6$

Figure 1. Survival (ϕ) and capture probability (p) parameters for a six-survey mark-recapture study. p is estimated for each survey and ϕ is estimated for the time interval between consecutive surveys. ϕ_5 and p_6 are not separately estimable; only their product is.

Goodness of fit of the mark-recapture data at each site to the CJS model was evaluated using TEST 1 and TEST 2 of program RELEASE (Burnham *et al.* 1987). If fit of the entire data set for a site was poor, the data were subdivided by sex and/or size and these data subsets examined for goodness of fit using RELEASE. Program CR (based on the program SURGE of Lebreton *et al.* 1992) was then used to examine the goodness of fit of variants of the full CJS model to the data.

Model selection

The ease with which a large number of models may be fitted to mark-recapture data (using programs such as CR), the primary issue in the analysis of capture-recapture data is that of proper model selection (Burnham and Anderson 1992). This becomes especially important in the analysis of multiple interrelated data sets (e.g. 2–3 age-or size classes and several sampling occasions, as in this study), when the number of possible survival (ϕ) and recapture (p) parameters may exceed 100. One or more of these parameters may be common across sex or age classes or years, while others are sex- or age- or time-specific. Choosing the most suitable model among the many models to which the data may fit then becomes a fairly complex procedure.

The 'global' model used as the basis for these analyses is the most general model that includes all reasonable effects possible in the data. More parsimonious reduced-parameter models that are nested in the global model are then fitted to the data and compared with more complex models. Burnham and Anderson (1992) and Lebreton *et al.* (1992) recommend the use of Akaike's Information Criterion (AIC) as the basis for model selection in the analysis of capture-recapture data. Anderson *et al.* (1994)

evaluated AIC and several other tests with respect to their usefulness in selecting the most appropriate model when mark-recapture data are overdispersed; these other tests were based on modifications of the AIC. Overdispersion (extra-binomial variation) can be caused by heterogeneity of true capture and survival rates among individuals and/or failure of the statistical independence of the fates of individuals (Burnham *et al.* 1987; Lebreton *et al.* 1992). The model-selection procedures recommended by Anderson *et al.* (1994) were used when poor fit of the CJS model to subsets of the mark-recapture data occurred.

The AIC is calculated as

$$\mathrm{AIC} = -2\log[\mathcal{L}(\hat{\theta})] + 2K$$

where $\log[\mathcal{L}(\hat{\theta})]$ is the maximised log-likelihood for a given model and K is the number of free parameters in the model.

The amount of overdispersion in the data is measured by the variance-inflation factor c. The pooled chi-square test statistics (TEST 2 + TEST 3) of RELEASE (Burnham *et al.* 1987), with corresponding pooled residual degrees of freedom rdf (= df2 + df3), provides a robust estimator of c (Burnham et al. 1987: 246):

$$\hat{c} = \frac{\text{TEST 2 + TEST 3}}{\text{rdf}}. \qquad (1)$$

When the CJS model provides a good fit to the data, $\hat{c} = 1$; $\hat{c}$ increases as the degree of overdispersion increases.

A modified form of the AIC with a small-sample bias correction is given by

$$\mathrm{AIC}_c = \mathrm{AIC} + \frac{2(K+1)(K+2)}{n-K-2}$$

where n = sample size. When $\hat{c} = 1$, AIC and AIC_c perform equally well in model selection (Anderson et al. 1994). When $\hat{c} > 1$, modifications to AIC and AIC_c based on quasi-likelihood theory are applicable:

$$\mathrm{QAIC} = -\{2\log[\mathcal{L}(\hat{\theta})]/\hat{c}\} + 2K$$

and

$$\mathrm{QAIC}_c = \mathrm{QAIC} + \frac{2(K+1)(K+2)}{n-K-2}.$$

QAIC and $QAIC_c$ are similar in performance (Anderson et al. 1994); both were used here on overdispersed data to examine the consistency with which they selected the same model.

When $\hat{c}$ was greater than 1, estimates of sampling variances and covariances for ϕ and p were computed by multiplying the model-based variances and covariances by $\hat{c}$ (Anderson et al. 1994).

Movement analysis

The position (grid cell) of release or recapture of each tagged abalone was recorded. Movement patterns between consecutive visits were then determined. Estimates of survival and catchability obtained by Cormack-Jolly-Seber (CJS) analysis are affected by the degree of movement of tagged animals into and out of the study site. The survival parameter estimate obtained by CJS analysis is in fact the true survival rate multiplied by the probability of not emigrating permanently from the site; when emigration occurs the survival rate is underestimated. True survival rate can only be obtained in this situation when emigration rates can be measured; the survival estimates can then be adjusted accordingly.

The movement-mark-recapture program MSSURVIV (Brownie *et al.* 1993, Nichols *et al.* 1993) yields estimates of the transition probabilities ϕ_i^{rs}, the probability of being alive and in stratum s at time i+1, for an animal alive and in stratum r at time i. It is necessary to estimate the rates of movement between strata, however, to obtain estimates of actual survival rates. Methods to measure emigration rates of abalone from each of the study sites are presently being developed with the assistance of a statistician.

The present version of MSSURVIV does not allow auxiliary variables (such as rates of tag loss or survey effort expended) to be incorporate into the analyses as described by Pollock *et al.* (1984). The mark-recapture program SURGE of Lebreton *et al.* (1992) does allow the incorporation of auxiliary variables (as does CR, the program used here). Movement itself may be treated as an auxiliary variable.

Handling and tagging-induced mortality

The effect of handling or tagging on abalone survival rates was examined using program CR by comparing the survival between surveys i and i+1 of abalone tagged and released at survey i with previously-tagged abalone that were sighted (but not handled) at survey i. Similarly the effect of handling on capture probability was

examined by comparing capture probabilities at survey i+1 of abalone tagged and released at survey i with previously-tagged abalone that were sighted (but not handled) at survey i. Arnason and Mills (1987) discuss the effects of handling and tagging on mortality rates, how to measure it, and its effects on Jolly-Seber estimates of abundance, survival and recruitment. Pollock *et al.* (1990) incorporate the analytical methods of Brownie and Robson (1983) to detect the effects of handling into their programs JOLLY and JOLLYAGE.

RESULTS

Tag loss

The mid-survey dates used to calculate time between tag and recapture are shown in Table 3. The pattern of tag loss varied markedly between respiratory pores and between sites (Fig. 2; Table 4). Tags in the first respiratory pore (*i.e.*, furthest from the growing margin of the shell) had the highest retention rate at all sites. Each data point in the graphs shown in Fig. 2 is derived from all recaptures of double-tagged abalone at that particular site and date, tagged in that particular respiratory pore. Since sampling error is inversely related to sample size, data points derived from a small number of recaptures are more likely to be inaccurate. Hence, each data point was assigned a weighting value equivalent to the sample size. Parameter values of the weighted regression equations are given in Table 4, and the weighted regression lines only are shown in Fig. 2. Regression lines were fitted to the data using the following equation:

$$\log_e(y + 1) = a + b.x \qquad (2)$$

where y = P(tag retention) [= 1–P(tag loss)], x is time at liberty between tagging and recapture (in days), and a and b are y-intercept and slope of the fitted regression line, respectively.

At the Stinking Bay site, retention rate of tags in pores 2, 3 and 4 were very similar, but much lower than tags in pore 1 (~25 percent tag loss per year, compared with 10 percent per year: Table 4). Rates of tag retention were different for all respiratory pores at the shallow George III Rock site. Except for tags in respiratory pore 3, the data points suggest a regular decline in the retention rate with time. The regression line for tag retention in pore 1 has a positive slope, indicating an increase in the proportion of tags retained with time since tagging. This is clearly impossible, and reflects sampling error. Regression lines for tags in respiratory pores 1 and 2 at the

Shag Rock Bay site also have a positive slope. The data points are scattered widely about all four regression lines, indicating that the accuracy of estimating the proportion and number of abalone within this site that had lost all tags is low. The situation is much more satisfactory at the shallow George III Rock and Stinking Bay sites; however, these results illustrate the importance of using a tagging method for which the rate of tag loss is very low.

The reason for the distinctly higher rate of retention of tags in respiratory pore 1 at Stinking Bay is unknown, but may be because this pore is filled in with nacre soonest; the inner side of the rivet holding this tag would become securely fixed sooner than tags in more distal respiratory pores. If this were the case, however, the tag retention rate would be expected to decrease steadily with respiratory pore position tagged, rather than be essentially identical for tags in pores 2, 3 and 4.

Table 3. Mid-harvest dates used to calculate time at liberty between tagging on the first survey at each site and each subsequent survey.

Site	Survey no.	Mid-harvest date	Time at liberty (days)
George III Rock	1	3.Sep.89	0
(shallow site)	2	27.Dec.89	115
	3	10.Feb.91	525
	4	4.Sep.91	731
	5	1.Nov.91	789
	6	7.Feb.92	887
George III Rock	1	15.Jul.89	0
(deep site)	2	1.Jan.90	170
Stinking Bay	1	21.Sep.90	0
	2	9.Dec.90	79
	3	10.Apr.91	201
	4	7.Aug.91	320
	5	6.Dec.91	441
	6	6.Mar.92	532
Shag Rock Bay	1	14.Nov.90	0
	2	24.Apr.91	161
	3	19.Aug.91	278
	4	12.Dec.91	393
	5	18.Jan.92	430
	6	25.Mar.92	497

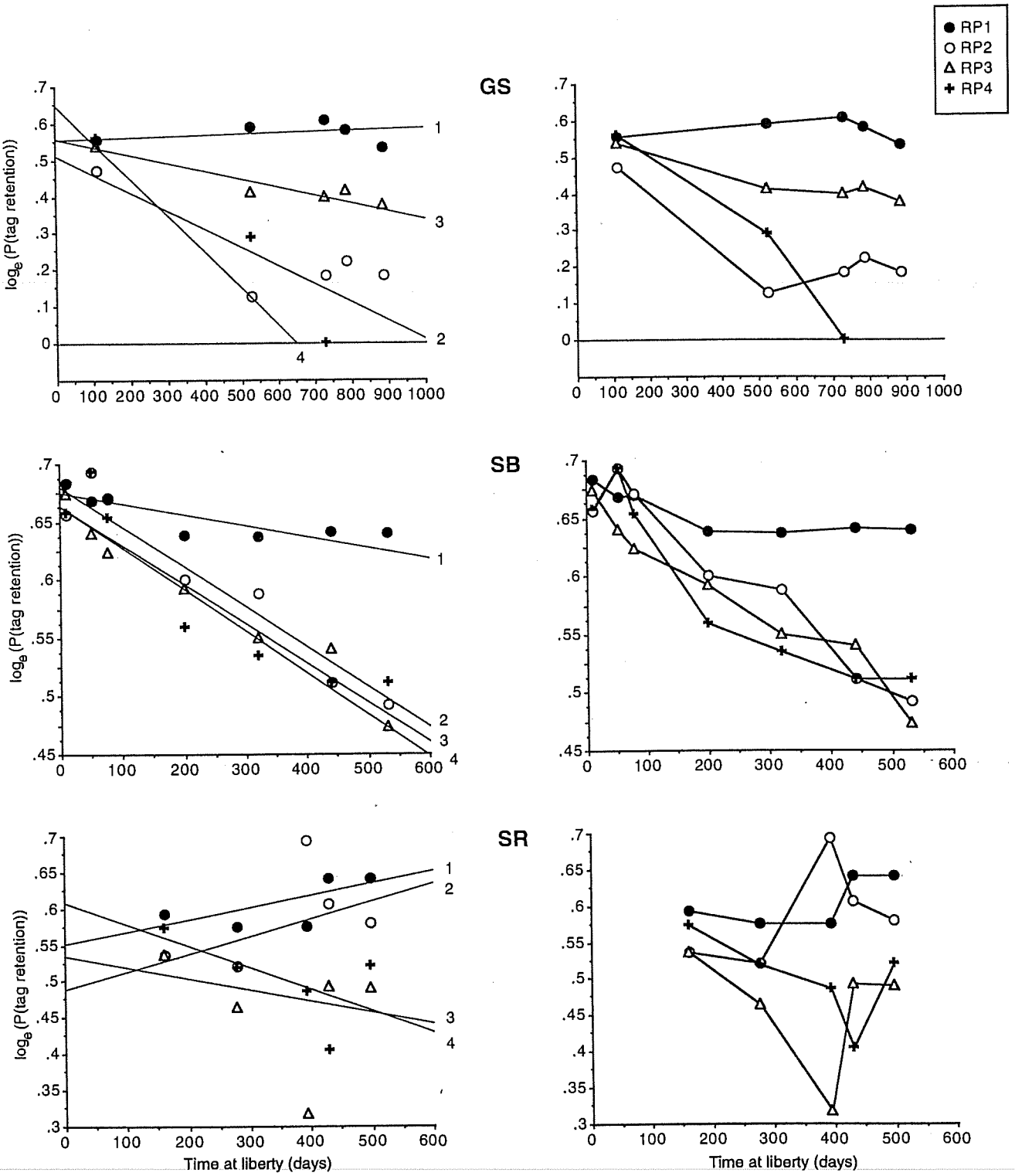


Figure 2. Decline in tag retention with time since tagging at three of the study sites, for tags in respiratory pores 1 to 4. Graphs in the left column show the weighted regression lines fitted to data points for each of the respiratory pores. The graphs in the right column show the same data points joined by lines for ease of distinguishing between them. Numbers at the end of the regression lines refer to respiratory pore number. GS=shallow George III Rock site; SB=Stinking Bay; SR=Shag Rock Bay.

Table 4. Rate of tag loss from respiratory pores 1 to 4 of *Haliotis rubra* at each of the study sites. *a* and *b* are the *y*-intercept and slope of regression equation (2) above. Regression analyses were weighted by sample size (see text for details). RP=respiratory pore.

Site	RP no.	*a*	*b*	Tag loss.yr^{-1} (%)
George III Rock	1	0.554	0.0000368	23.6
(shallow site)	2	0.513	-0.0004979	60.7
	3	0.560	-0.0002196	38.4
	4	0.650	-0.0010000	67.0
Stinking Bay	1	0.675	-0.0000940	10.2
	2	0.680	-0.0003432	25.9
	3	0.663	-0.0003362	28.4
	4	0.664	-0.0003583	29.6
Shag Rock Bay	1	0.551	0.0001669	15.6
	2	0.488	0.0002435	22.0
	3	0.534	-0.0001551	38.8
	4	0.608	-0.0002979	35.3

Modelling survival and capture probability

Poor fit of the tag-recapture data may occur if survival rates or capture probabilities, or both, are size-dependent. Size-dependence may be reflected in the size composition of the sampled population through time. The size frequency compositions of the populations at each survey are shown in Figs. 3, 4 and 5. The first graph for each site reflects the size composition of the entire abalone population ≥80 mm, as all abalone within the site were collected for measuring and tagging. The final graph is also for the entire population because it comprises both tagged and untagged abalone found during the final survey. The remaining graphs show the size composition of only the untagged fraction of the population. (Tagged abalone had their tag numbers and position within the site recorded, but were otherwise not disturbed.)

No marked change in size composition was observed at the shallow George III Rock site (Fig. 3). There is an increase in the relative abundance of smaller (80-120 mm) abalone during surveys 2, 3 and 4, but the first and final size compositions are similar. A marked increase in the number of small (80-120 mm) abalone (in both relative and absolute terms) occurred between the second and third surveys at Stinking Bay that persisted until at least the end of the study (Fig. 4). The marked reduction of larger abalone after survey 2 at Stinking Bay is not because of disturbance because these

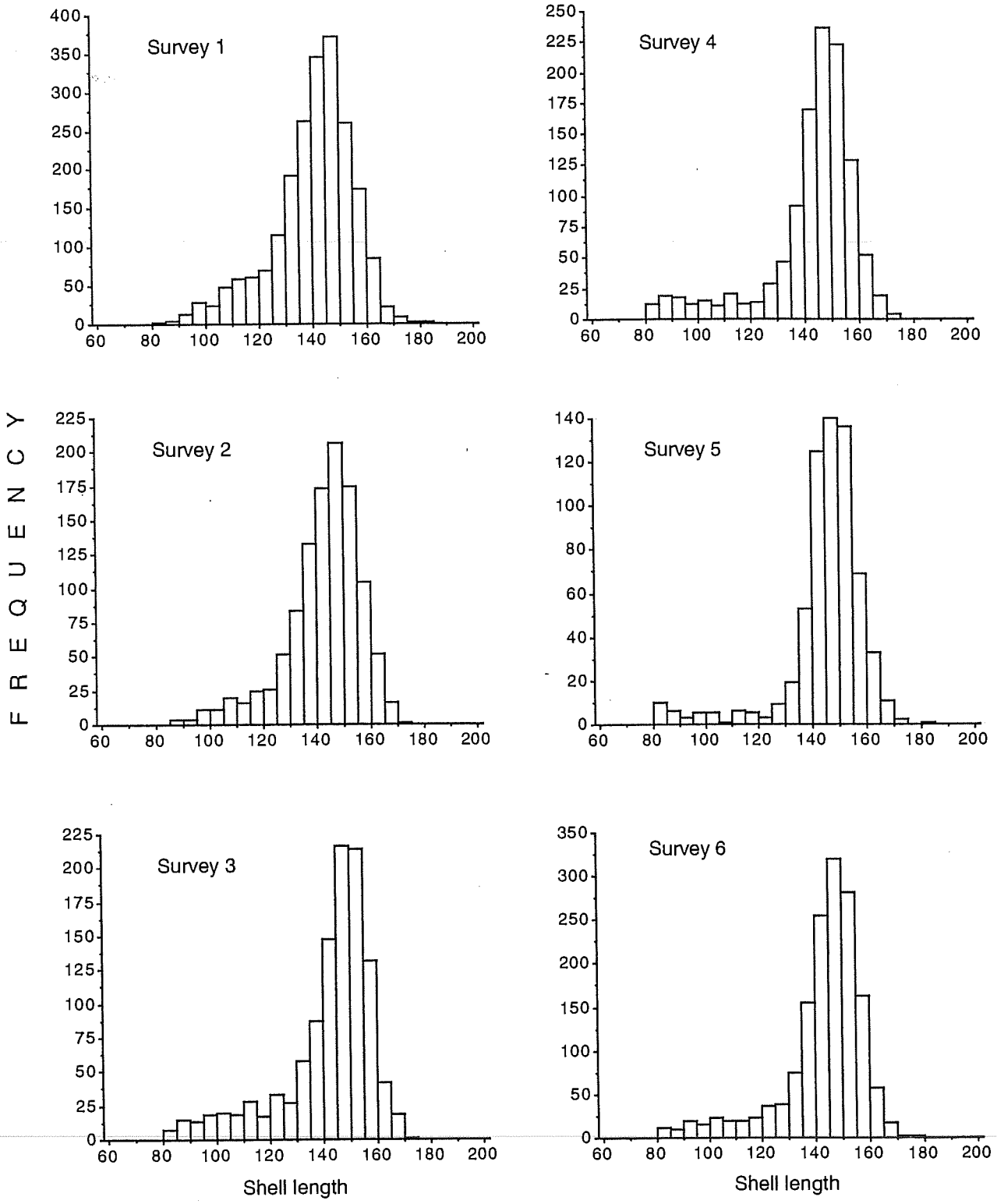


Figure 3. Size-frequency composition of the blacklip abalone (*Haliotis rubra*) population at the shallow George III Rock site at each survey.

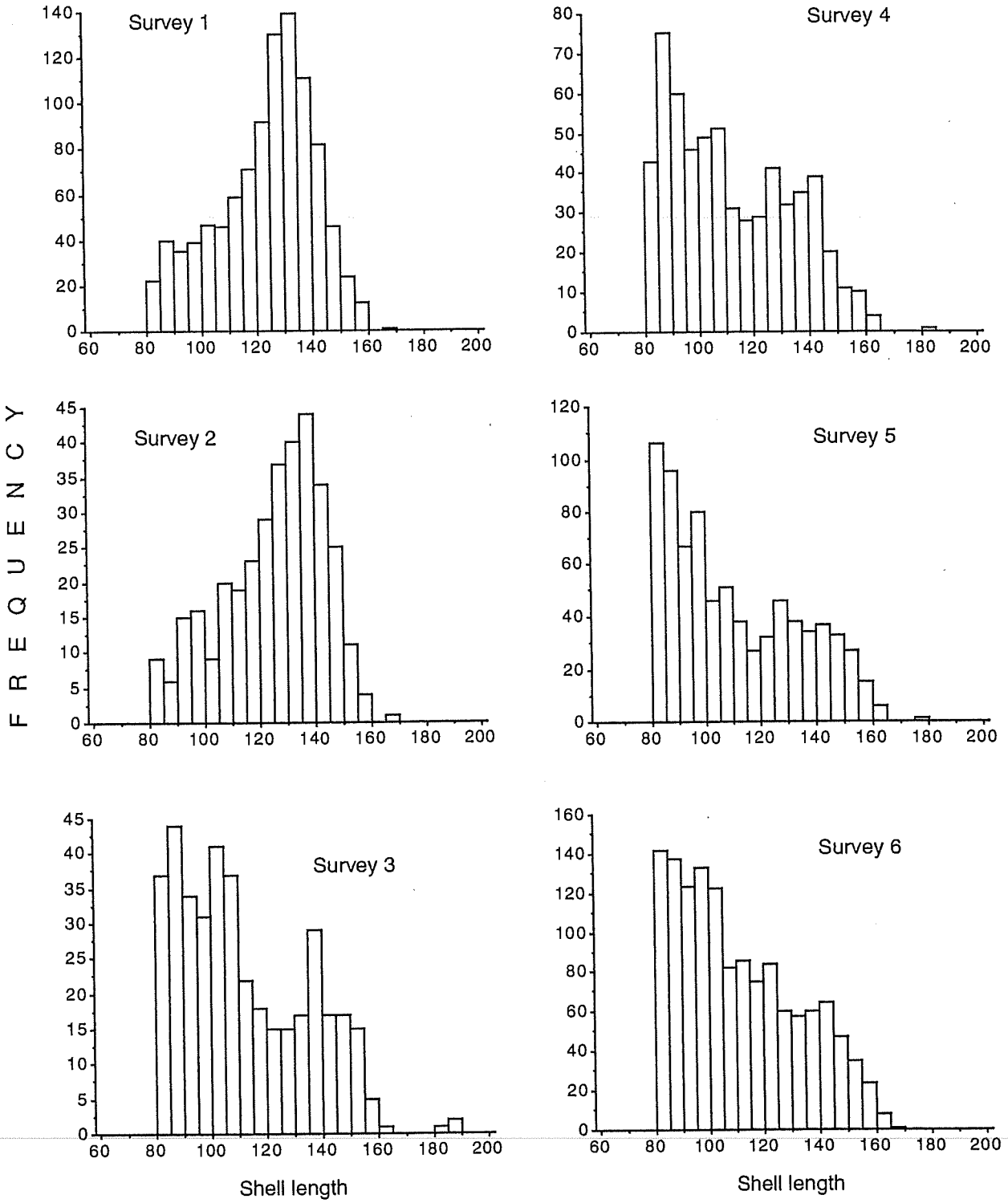


Figure 4. Size-frequency composition of the blacklip abalone (*Haliotis rubra*) population at the Stinking Bay site at each survey.

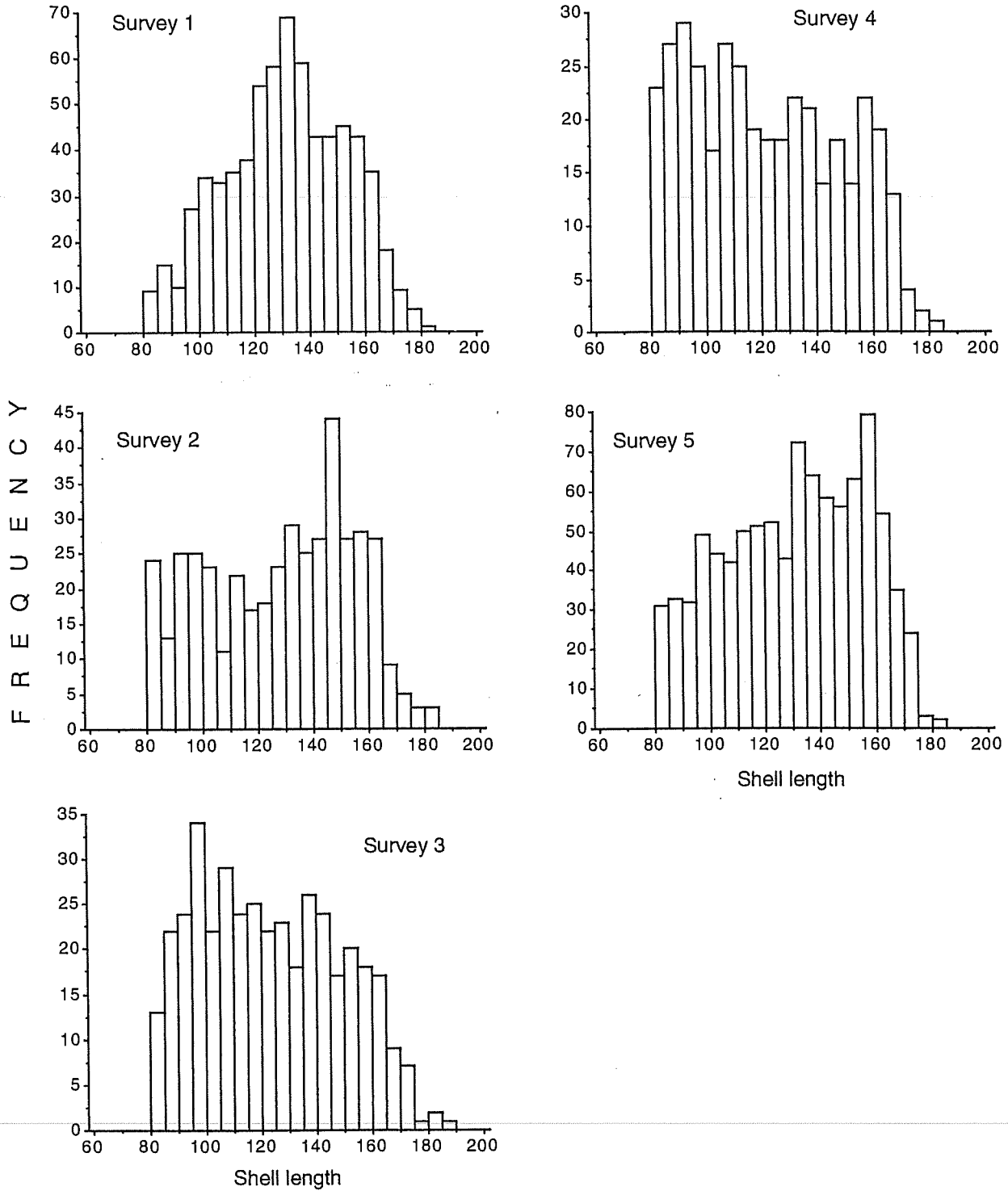


Figure 5. Size-frequency composition of the blacklip abalone (*Haliotis rubra*) population at the Shag Rock Bay site at each survey.

untagged abalone had not been seen or handled on previous surveys. These size-frequency plots suggest appropriate size groups into which the mark-recapture data may be divided for analysis.

George III Rock (shallow site)

The data for this site have been analysed partially. Further snalyses on subsets of the data, as carried out on the Shag Rock Bay data (see below), will be done.

Stinking Bay

The tag-recapture data for Stinking Bay are summarised in reduced *m*-array format (Burnham *et al.* 1987) in Table 5. The entire tag-recapture data set for Stinking Bay provides a poor fit to the CJS model, as measured by TESTs 2 and 3 of RELEASE (Table 6). The change in size composition between surveys 2 and 3 (Fig. 4) suggested that subdividing the data into two sets (one for small abalone, one for large) may yield a good fit, of each data subset, to the CJS model. The data were therefore subdivided into the size classes 80-120 mm and >120 mm and re-examined using RELEASE. This yielded a good fit of the 80-120 mm size class to the CJS model, but not the >120 mm class.

The data were therefore subdivided into three size classes (80-120 mm, 121-145 mm and >145 mm) and re-examined using RELEASE. The >145 mm size class fitted the CJS model well, but the 121-145 mm group did not. The data for the three size groups are summarised in *m*-array format in Table 7. Goodness of fit results obtained using RELEASE are shown in Table 8.

Table 5. Tag-recapture results for the Stinking Bay site (entire data set), summarised in reduced *m*-array format.

		Recaptures, $m_{i,j}$					
i	R_i	j=2	3	4	5	6	r_i
1	980	316	114	80	38	14	562
2	663		233	87	29	10	359
3	718			208	83	25	316
4	986				246	111	357
5	1153					382	382
m_j		316	347	375	396	542	
z_j		246	258	199	160	0	

Table 6. Estimation of goodness of fit of the Stinking Bay mark-recapture data (entire data set) to the CJS model.

Summary of TEST 3 (Goodness of fit) Results

Group	Component	Chi-square	df	P-level	Sufficient Data
1	3.SR2	13.9641	1	0.0002	Yes
1	3.SR3	0.0117	1	0.9139	Yes
1	3.SR4	4.4651	1	0.0346	Yes
1	3.SR5	0.1702	1	0.6800	Yes
Group 1	3.SR	18.6110	4	0.0009	
1	3.Sm2	1.5439	3	0.6722	Yes
1	3.Sm3	2.3892	4	0.6646	Yes
1	3.Sm4	5.2067	3	0.1573	Yes
Group 1	3.Sm	9.1398	10	0.5189	
Group 1	TEST 3	27.7508	14	0.0154	

Summary of TEST 2 (Goodness of fit) Results

Group	Component	Chi-square	df	P-level	Sufficient Data
1	2.C2	22.5956	3	0.0000	Yes
1	2.C3	0.3513	2	0.8389	Yes
1	2.C4	2.6478	1	0.1037	Yes
Group 1	TEST 2	25.5947	6	0.0003	

Goodness of Fit Results (TEST 2 + TEST 3) by Group

Group	Chi-square	df	P-level
1	53.3455	20	0.0001

Table 7. Tag-recapture results for the Stinking Bay abalone, divided into three size groups (80-120 mm, 121-145 mm, >145 mm), summarised in reduced *m*-array format.

Small abalone (80-120 mm)

		Recaptures, $m_{i,j}$					
i	R_i	j=2	3	4	5	6	r_i
1	374	118	69	39	18	11	255
2	244		91	38	15	6	150
3	394			115	58	19	192
4	582				180	86	266
5	773					281	281
m_j		118	160	192	271	403	
z_j		137	127	127	122	0	

Medium abalone (121-145 mm)

		Recaptures, $m_{i,j}$					
i	R_i	j=2	3	4	5	6	r_i
1	533	180	39	39	19	3	280
2	360		127	42	13	4	186
3	259			78	21	6	105
4	327				54	17	71
5	283					68	68
m_j		180	166	159	107	98	
z_j		100	120	66	30	0	

Large abalone (>145 mm)

		Recaptures, $m_{i,j}$					
i	R_i	j=2	3	4	5	6	r_i
1	65	18	6	2	1	0	27
2	52		15	7	1	0	23
3	59			15	3	0	18
4	64				11	8	19
5	88					31	31
m_j		18	21	24	16	39	
z_j		9	11	5	8	0	

Table 8. Estimation of goodness of fit of the Stinking Bay mark-recapture data (three size groups: 80-120 mm, 121-145 mm, >145 mm) to the CJS model.

Summary of TEST 3 (Goodness of fit) Results

Group	Component	Chi-square	df	P-level	Sufficient Data
1	3.SR2	0.4193	1	0.5173	Yes
1	3.SR3	0.0396	1	0.8423	Yes
1	3.SR4	2.9920	1	0.0837	Yes
1	3.SR5	0.0421	1	0.8375	Yes
Group 1	3.SR	3.4930	4	0.4789	
1	3.Sm2	0.7573	3	0.8597	Yes
1	3.Sm3	2.6558	4	0.6170	Yes
1	3.Sm4	10.6802	3	0.0136	Yes
Group 1	3.Sm	14.0934	10	0.1688	
Group 1	TEST 3	17.5863	14	0.2263	
2	3.SR2	14.5143	1	0.0001	Yes
2	3.SR3	0.0344	1	0.8529	Yes
2	3.SR4	2.2318	1	0.1352	Yes
2	3.SR5	0.4202	1	0.5168	Yes
Group 2	3.SR	17.2007	4	0.0018	
2	3.Sm2	0.2943	2	0.8632	Yes
2	3.Sm3	0.5533	2	0.7583	Yes
2	3.Sm4	0.5491	2	0.7599	Yes
Group 2	3.Sm	1.3967	6	0.9661	
Group 2	TEST 3	18.5974	10	0.0457	
3	3.SR2	0.3705	1	0.5427	Yes
3	3.SR3	0.1219	1	0.7270	Yes
3	3.SR4	5.9228	1	0.0149	Yes
3	3.SR5	0.0286	1	0.8657	Yes
Group 3	3.SR	6.4439	4	0.1684	
3	3.Sm2	0.6033	1	0.4373	Yes
3	3.Sm3	0.0475	1	0.8275	No
3	3.Sm4	0.1148	1	0.7348	No
Group 3	3.Sm	0.7656	3	0.8577	
Group 3	TEST 3	7.2095	7	0.4074	
All Groups	TEST 3	43.3932	31	0.0688	

Summary of TEST 2 (Goodness of fit) Results

Group	Component	Chi-square	df	P-level	Sufficient Data
1	2.C2	4.2242	3	0.2382	Yes
1	2.C3	1.3014	2	0.5217	Yes
1	2.C4	0.6433	1	0.4225	Yes
Group 1	TEST 2	6.1689	6	0.4045	
2	2.C2	24.2477	3	0.0000	Yes
2	2.C3	1.4326	2	0.4886	Yes
2	2.C4	0.3617	1	0.5475	Yes
Group 2	TEST 2	26.0421	6	0.0002	
3	2.C2	0.0060	1	0.9380	Yes
3	2.C3	0.0109	1	0.9167	No
3	2.C4	4.6888	1	0.0304	No
Group 3	TEST 2	4.7057	3	0.1947	
All Groups	TEST 2	36.9167	15	0.0013	

Table 8 – cont'd.

Goodness of Fit Results (TEST 2 + TEST 3) by Group

Group	Chi-square	df	P-level
1	23.7552	20	0.2532
2	44.6395	16	0.0002
3	11.9152	10	0.2908
Total	80.3098	46	0.0013

The data for the small (80-120 mm) and large (>145 mm) abalone that each show a good fit to the CJS model were then analysed using program CR. Numerous models were examined (Table 9). Incorporating searching effort into the model did not improve the fit. Similarly, models that included the effect of handling on either survival or capture probability did not improve the fit. Best fit was obtained for model ϕ_{s+t}, p_{s+t}; that is, where both survival and capture probability varied between size groups and between sampling periods, but with no size x time interaction. All model-selection methods (AIC, AIC_c, QAIC and $QAIC_c$) selected the same model, so only AIC values are shown in Table 9 for simplicity. The parameter estimates obtained from this model are shown in Table 10, and graphically in Fig. 6.

The survival rate patterns obtained (Fig. 6) were not expected. For all sampling intervals survival rates were much higher for the small size group than the large size group. The opposite pattern seems more likely because of size-related predation pressure. Moreover, survival rates as low as 7.5 percent per year for the large size group (during sampling interval 4) were estimated—equivalent to a rate of instantaneous natural mortality (M) of 2.6, which is simply not believable. Even when adjusted for tag loss, using a tag loss rate of 10 percent (assuming all tags were in respiratory pore 1—a fair approximation because ~80 percent of them were), the mean over all sampling intervals of large abalone (19 percent) is increased to 21 percent ($M = 1.56$), which is still not believable.

For comparison, the rate of instantaneous mortality (Z) was obtained using the size composition of the population and the von Bertalanffy growth parameters $L\infty$ and K (obtained by growth increment analysis; see Section 5), derived using the method of Beverton and Holt (1956):

$$Z = \frac{K \cdot (L_\infty - \bar{L})}{\bar{L} - L'},$$

where L' is the size at full recruitment to the emergent (fished) population and $\bar{L}$ is the mean size of fully recruited animals in the population. The population sample

Table 9. Results of capture-recapture models and of comparisons between models for blacklip abalone (*Haliotis rubra*) at the Stinking Bay site. The full model ($\phi_{s\cdot t}, p_{s\cdot t}$) includes variation between size classes (s) and sampling periods (t). Searching effort (e) was also incorporated into the models. The size classes used in the analysis were small (80-120 mm) and large (≥145 mm). For each model are given the number of estimable parameters (np), the deviance (DEV) and the Akaike Information Criterion (AIC). Comparison between models was by likelihood ratio test.

Model	*np*	DEV	AIC	Comparison
I. Basic models				
(1) ($\phi_{s\cdot t}, p_{s\cdot t}$) (CJS model by size class)	18	5373.854	5409.854	(fits the data)
(2) (ϕ_t, p_t) (CJS model for pooled data)	9	5420.472	5438.472	Overall difference between size classes: (2) vs. (1): χ^2_9=46.518, P = .0000
II. Modelling capture rate				Parallelism over time on p:
(3) ($\phi_{s\cdot t}, p_{s+t}$)	15	5376.118	5406.118	(3) vs. (1): χ^2_3=2.264, P = .5195
(4) ($\phi_{s\cdot t}, p_t$)	14	5377.188	5405.188	(4) vs. (3): χ^2_1=1.070, P = .3009
(5) ($\phi_{s\cdot t}, p_s$)	12	5381.856	5405.856	(5) vs. (4): χ^2_2=4.668, P = .0969 (6) vs. (4): χ^2_3=5.512, P = .1379
(6) ($\phi_{s\cdot t}, p$)	11	5382.700	5404.700	(6) vs. (5): χ^2_1=0.844, P = .3583 (7) vs. (4): χ^2_1=0.793, P = .6727 (7) vs. (6): χ^2_1=4.719, P = .0298
III. Modelling survival rate				
(7) (ϕ_{s+t}, p_{s+t})	12	5377.981	**5401.981**	
(8) (ϕ_t, p_{s+t})	11	5406.843	5428.843	
(9) (ϕ_s, p_{s+t})	8	5406.604	5422.604	
(10) (ϕ, p_{s+t})	7	5433.192	5447.192	
(11) (ϕ_s, p_t)	9	5408.787	5426.787	
(12) (ϕ_s, p_s)	4	5411.155	5419.155	
(13) (ϕ, p_t)	6	5446.363	5458.363	
IV. Models incorporating search effort				(14) vs. (7): χ^2_1=1.784, P = .1817
(14) ($\phi_{s\cdot t}, p_{s+e}$)	13	5379.765	5405.765	
(15) ($\phi_{s+e}, p_{s\cdot t}$)	13	5391.072	5417.072	
(16) (ϕ_{s+e}, p_t)	8	5399.715	5415.715	
(17) (ϕ_{s+e}, p)	4	5411.870	5419.870	
(18) (ϕ_{s+e}, p_{s+e})	6	5408.707	5420.707	
(19) ($\phi_{s+e}, p_{s\cdot e}$)	7	5408.663	5422.663	
(20) ($\phi_{s\cdot e}, p_{s+e}$)	7	5407.796	5421.796	
(21) ($\phi_{s\cdot e}, p_{s\cdot e}$)	8	5407.254	5423.254	
(22) ($\phi_{s\cdot e}, p_t$)	9	5396.748	5414.748	

Table 10. Estimates of survival (ϕ) and capture probability (p) for the small (80-120 mm) and large (>145 mm) size groups at the Stinking Bay site for each of the survey periods, as shown in Fig. 1. *s.d.* = standard deviation.

Size group	Parameter	estimate	95% confidence interval		*s.d.*
small	ϕ_1	0.570	0.354	0.743	0.034
small	ϕ_2	0.733	0.487	0.879	0.042
small	ϕ_3	0.384	0.263	0.510	0.040
small	ϕ_4	0.352	0.253	0.457	0.035
large	ϕ_1	0.194	0.052	0.425	0.079
large	ϕ_2	0.398	0.141	0.676	0.094
large	ϕ_3	0.088	0.036	0.182	0.061
large	ϕ_4	0.075	0.032	0.149	0.055
small	p_2	0.356	0.301	0.414	0.029
small	p_3	0.380	0.324	0.439	0.029
small	p_4	0.414	0.359	0.471	0.029
small	p_5	0.442	0.389	0.497	0.028
large	p_2	0.394	0.287	0.512	0.058
large	p_3	0.419	0.308	0.538	0.060
large	p_4	0.454	0.344	0.569	0.058
large	p_5	0.483	0.371	0.596	0.059

used for this analysis was all abalone collected from within the site during the first mark-recapture survey (*i.e.*, immediately after fishing had ceased with the closure of the site for research). A second estimate of Z was obtained using the size composition of the population at the end of the final mark-recapture survey (nearly two years after the site had been closed to fishing). Z values were converted to annual survival rates as $S = e^{-Z}$ and compared with the survival estimates shown in Table 10 and Fig. 6. This comparison is shown in Fig. 7. The appropriate comparison is with the mean survival rate of the large size group (similar in size to those used in the B-H method. Survival rate estimates derived by the B-H method are much higher than the mark-recapture estimates, despite the fact that the B-H estimates are of a population subjected to fishing as well as natural mortality.

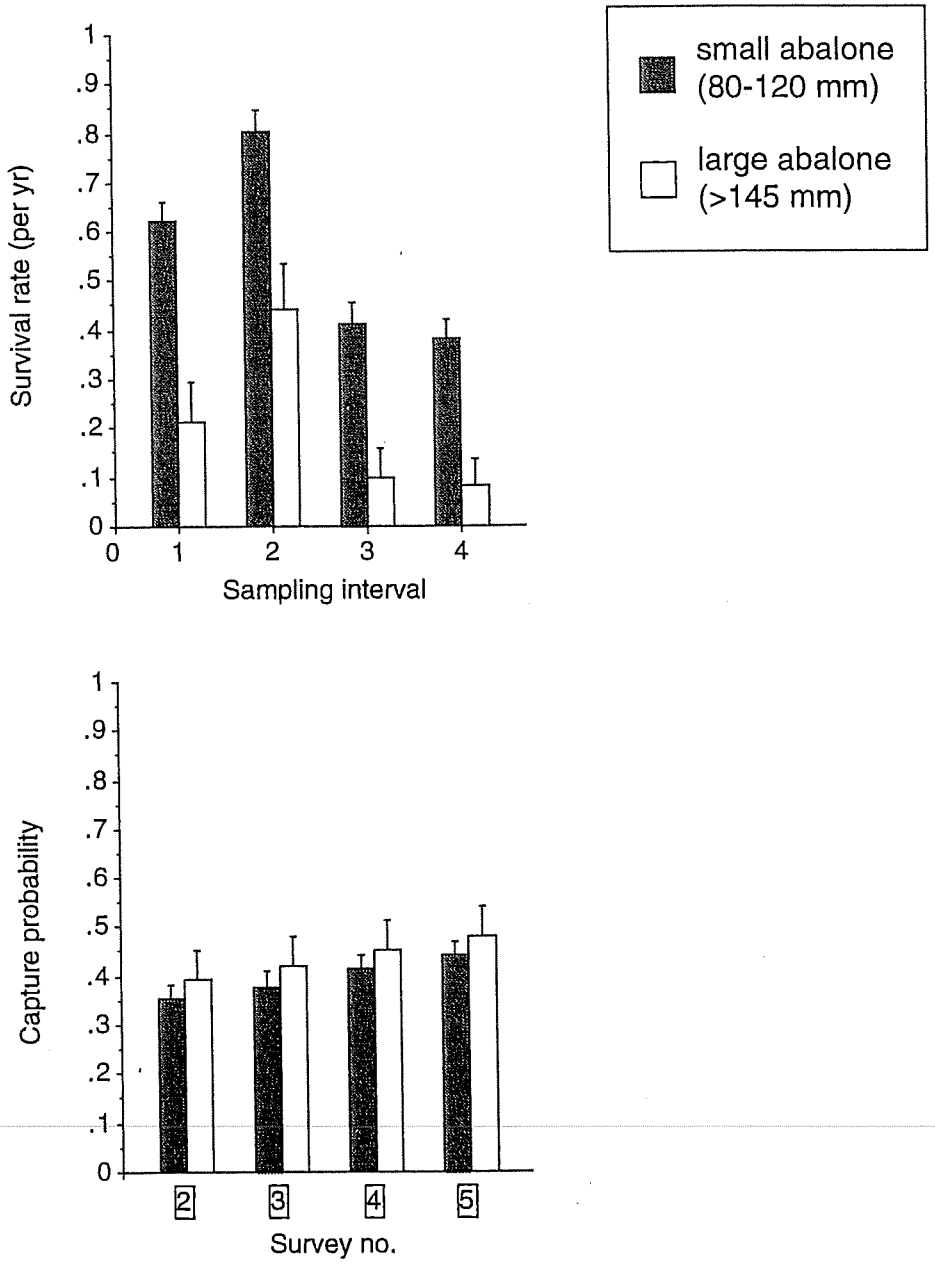


Figure 6. Rates of survival rates and capture probability for small abalone and large abalone separately at the Stinking Bay site. Sampling interval and survey no. are as shown in Fig. 1.

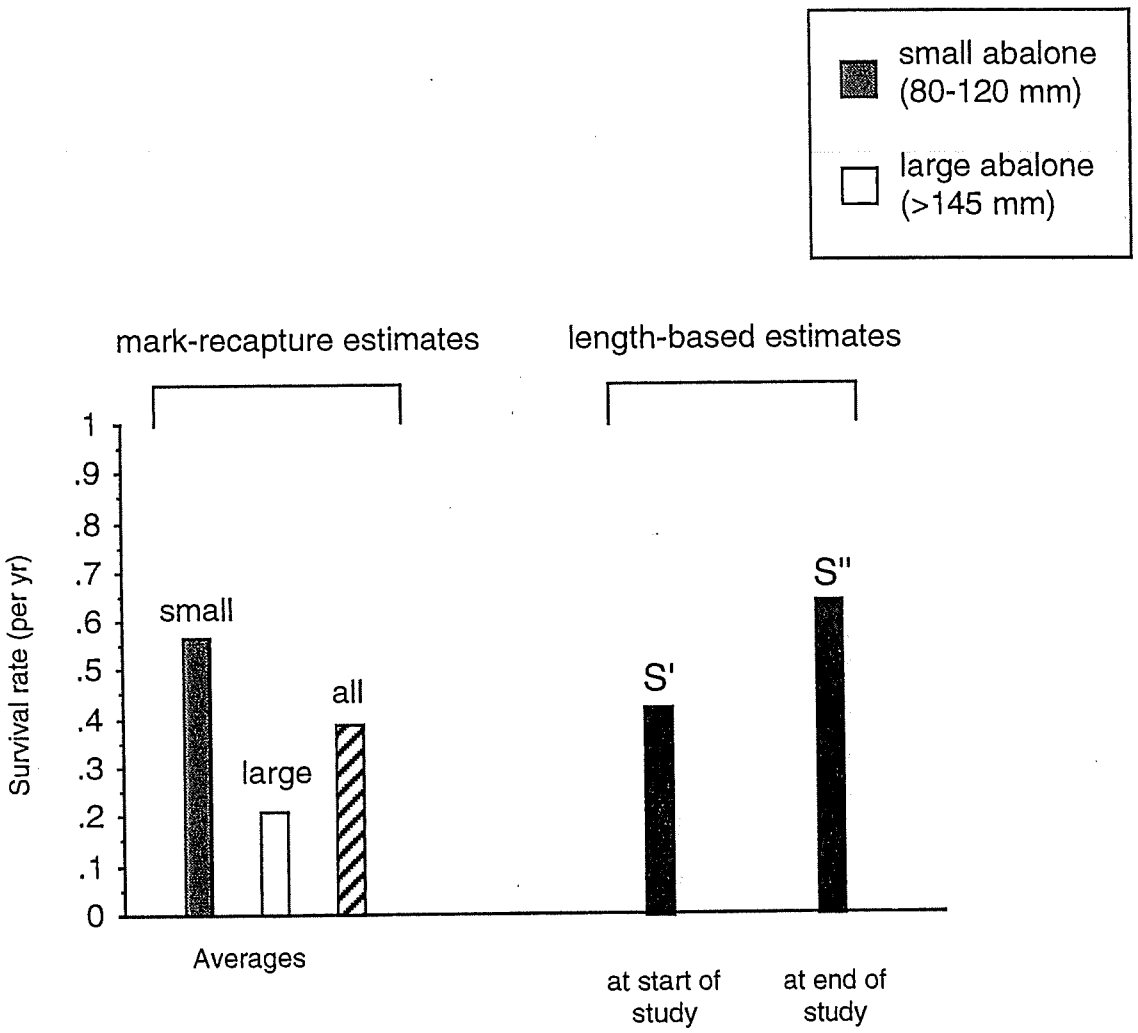


Figure 7. A comparison of survival estimates for Stinking Bay abalone, obtained by mark-recapture and length-based methods. Length-based estimates were obtained from the length composition of the poulation at the beginning (S') and the end (S") of the study.

The most likely reason for the low survival rate estimates derived by mark-recapture methods is that this estimate is the true survival rate times the probability of not emigrating permanently from the site. The movement paterns described below show clearly that movement of blacklip abalone was extensive at all sites, and at the two George III Rock sites and the Stinking Bay site, movement had a strong directional component. Although the movement rates have yet to be measured statistically, it is likely that the rates of movement at the Stinking Bay site are sufficient to explain the low survival rate estimates obtained.

Shag Rock Bay

The mark-recapture results for the Shag Rock Bay *Haliotis rubra* population are summarised in reduced *m*-array format in Table 11. Goodness of fit of the Shag Rock Bay mark-recapture data to the Cormack-Jolly-Seber (CJS) model was estimated using TESTs 2 and 3 of RELEASE (Burnham et al. 1987). The overall fit was poor ($p<0.0001$: Table 12), with good fit shown for only one component (3.Sm2) of TEST 3 and one component (2.C2) of TEST 2. The variance-inflation factor $\hat{c}$ (equation 1 above) was very high (10.4; derived from the chi-square GOF results in Table y), indicating an extreme degree of overdispersion of the data.

The survival and capture rate estimates for these data obtained under the CJS model are shown in Table 13. Survival rates averaged 0.660 (range 0.611 to 0.704) and recapture rates averaged 0.542 (range 0.438 to 0.637).

Poor overall fit indicates that one or more of the following factors are occurring: heterogeneity in survival rate or capture probability between individuals; lack of independence between individuals; or a behavioural response to tagging and/or handling. Heterogeneity in survival rate or capture probability between individuals may be tested in several ways. Following Burnham *et al.* (1987), the Shag Rock Bay abalone population was divided into two groups: those that were seen on only one occasion after tagging and those that were seen repeatedly. These two groups are analogous to the transient and resident groups of Lazuli buntings (birds) described by Burnham et al. (1987: 348ff). It is unlikely that transience in abalone is the same as in birds; rather than being temporary residents within the study area, it is more likely that the distinction is on the basis of cryptic behaviour: some abalone (the transients) are essentially cryptic animals (spending more time under boulders where they are less vulnerable to capture) while others (the residents) are emergent (living in relatively exposed areas).

Table 11. The reduced *m*-array for *Haliotis rubra* from Shag Rock Bay (entire data set). The statistics m_j and z_j are also shown.

		Recaptures, $m_{i,j}$				
i	R_i	j=2	3	4	5	r_i
1	683	211	78	45	16	350
2	611		245	51	18	314
3	724			288	70	358
4	844				401	401
m_j		211	323	384	505	
z_j		139	130	104	0	

Table 12. Estimation of goodness of fit of the Shag Rock Bay mark-recapture data (entire data set) to the CJS model.

Summary of TEST 3 (Goodness of fit) Results

Group	Component	Chi-square	df	P-level	Sufficient Data
1	3.SR2	46.1892	1	0.0000	Yes
1	3.SR3	14.8521	1	0.0002	Yes
1	3.SR4	9.7155	1	0.0019	Yes
Group 1	3.SR	70.7567	3	0.0000	
1	3.Sm2	1.0277	2	0.5982	Yes
1	3.Sm3	7.9520	2	0.0188	Yes
Group 1	3.Sm	8.9797	4	0.0616	
Group 1	TEST 3	79.7365	7	0.0000	

Summary of TEST 2 (Goodness of fit) Results

Group	Component	Chi-square	df	P-level	Sufficient Data
1	2.C2	21.7701	2	0.0000	Yes
1	2.C3	2.2535	1	0.1333	Yes
Group 1	TEST 2	24.0236	3	0.0000	

Goodness of Fit Results (TEST 2 + TEST 3) by Group

Group	Chi-square	df	P-level
1	103.7600	10	0.0000

Table 13. Bias-adjusted estimates of survival (ϕ_i) and recapture (p_i) rates for the Shag Rock Bay *Haliotis rubra* data under the CJS model (model $H_{4\phi}$), output from program RELEASE.

Parameter	Estimate	s.e.	95% C.I.	
Phi(1)	0.452	0.033	0.363	0.551
Phi(2)	0.280	0.031	0.208	0.366
Phi(3)	0.305	0.026	0.247	0.371
p(2)	0.438	0.029	0.382	0.494
p(3)	0.551	0.027	0.498	0.605
p(4)	0.637	0.027	0.584	0.690

The data in Table 11 accordingly were partitioned into two *m*-arrays: new captures and previous captures (Table 14). Homogeneity of the two data sets was examined using TEST 1 of RELEASE (Burnham et al. 1987). This is an overall test of equality of all survival and capture probabilities between groups. The transient and resident groups were quite different ($p<0.0001$; Table 15).

The 'transient' and 'resident' fractions of the Shag Rock Bay *Haliotis rubra* population each showed good fit to the Cormack-Jolly-Seber model (Table c). The data were in reduced *m*-array format (Table a) and so TEST 3 is not possible; GOF testing was by TEST 2 only.

The survival and capture rate estimates for these data obtained under the Cormack-Jolly-Seber model are shown in Table d. Survival rates averaged 0.570 for the 'transients' and 0.715 for the 'residents'. Recapture rates averaged 0.564 for the 'transients' and 0.724 for the 'residents'.

Table 14. Partitioned *m*-arrays for the Shag Rock Bay *Haliotis rubra* data. The data for abalone recaptured only once appear at the top, followed by abalone recaptured after being re-released. The statistics m_j and z_j are also shown.

		Recaptures, $m_{i,j}$			
i	R_i	j=3	4	5	r_i
2	400	129	30	11	170
3	401		129	44	173
4	460			196	196
m_j		129	159	251	
z_j		41	55	0	
2	211	116	21	7	144
3	323		159	26	185
4	384			205	205
m_j		116	180	238	
z_j		28	33	0	

Table 15. Comparison of 'transient' and 'resident' fractions of the Shag Rock Bay *Haliotis rubra* population.

Component	Chi-square	df	P-level	Sufficient Data
1.R3	9.7155	1	0.0019	Yes
1.T3	6.3375	1	0.0117	Yes
1.R2	14.8521	1	0.0002	Yes
1.T2	0.9065	1	0.3410	Yes
1.R1	46.1892	1	0.0000	Yes
TEST 1	78.0008	5	0.0000	

Table 16. Estimation of goodness of fit of the 'transient' and 'resident' fractions of the Shag Rock Bay *Haliotis rubra* populations to the CJS model. Group 1 = transients, Group 2 = residents.

Summary of TEST 2 Results

Group	Component	Chi-square	df	P-level	Sufficient Data
1	2.C2	0.0000	1	1.0000	Yes
2	2.C2	1.9776	1	0.1597	Yes
All Groups TEST 2		1.9776	2	0.3720	

Table 17. Bias-adjusted estimates of survival (ϕ_i) and recapture (p_i) rates for the 'transient' and 'resident' fractions' of the Shag Rock Bay *Haliotis rubra* population under the Cormack-Jolly-Seber model (model $H_{3\phi}$) output from program RELEASE. **NOTE: The survival rate estimates and their CL's still need to be converted to rates per year.**

Parameter	Estimate	Standard Error	95% Confidence Intervals Lower	Upper
		Estimates for Group 1 Transient Group		
Phi(1)	0.559310	0.039748	0.481404	0.637216
Phi(2)	0.580011	0.040049	0.501514	0.658508
p(2)	0.575804	0.045975	0.485693	0.665914
p(3)	0.551927	0.040935	0.471693	0.632160
Phi(3)p(4)	0.426087	0.023056	0.380896	0.471278
Corr(Phi(1),Phi(2))		-0.284112		
		Estimates for Group 2 Resident Group		
Phi(1)	0.780920	0.041834	0.698926	0.862915
Phi(2)	0.649862	0.034520	0.582202	0.717521
p(2)	0.703514	0.045048	0.615220	0.791809
p(3)	0.744372	0.037157	0.671543	0.817200
Phi(3)p(4)	0.533854	0.025457	0.483959	0.583750
Corr(Phi(1),Phi(2))		-0.240623		

Correlation and Ratio of Survivals between Groups

Parameter	Estimate	Standard Error	95% Confidence Intervals Lower	Upper
S(1,2,Phi(1))	0.714170	0.063558	0.589597	0.838743
Corr(1,2,Phi(1))		0.000000		
S(1,2,Phi(2))	0.890003	0.077535	0.738035	1.041971
Corr(1,2,Phi(2))		0.000000		

Movement

The movement rate data are in the process of being analysed statistically to obtain estimates of the probability of emigrating permanently from the study sites. These values will be used to correct the mark-recapture estimates of survival. Patterns of movement at the two George III Rock sites and the Stinking Bay site are shown in Figs. ?? to ??. The Stinking Bay movement data were simplified by pooling the site grids into three (north, middle and south), and using movement patterns between these three zones to illustrate the scale and directionality of abalone movement at this site.

DISCUSSION

This has yet to be done. The movement-mark-recapture analysis of the Stinking Bay data is being prepared for publication in the *Canadian Special Publication of Fisheries and Aquatic Sciences* series.

REFERENCES

Anderson, D. R., K. P. Burnham, and G. C. White (1994). AIC model selection in overdispersed capture-recapture data. Ecology 75: 1780–1793.

Brownie, C., J.E. Hines, J.D. Nichols, K.H. Pollock and J.B. Hestbeck (1993). Capture-recapture studies for multiple strata including non-Markovian transition probabilities. *Biometrics* 49: 1173-1187.

Burnham, K.P. (1993). A theory for combined analysis of ring recovery and recapture data. *In* J.-D. Lebreton and P.M. North (eds) *Marked Individuals in the Study of Bird Population*. pp. 199-213. Birkhäuser Verlag: Basel.

Burnham, K. P., and D. R. Anderson (1992). Data-based selection of an appropriate biological model: the key to modern data analysis, p. 16–30. *In* D.R. McCullough and R.H. Barrett [eds] Wildlife 2001: populations. Elsevier, London, England.

Burnham, K. P., D. R. Anderson, G. C. White, C. Brownie, and K. H. Pollock (1987). Design and analysis methods for fish survival experiments based on release-recapture. *American Fisheries Society Monograph* 5: 1-437.

Hilborn, R., 1990. Determination of fish movement patterns from tag recoveries using maximum likelihood estimators. *Canadian Journal of Fisheries and Aquatic Sciences* 47: 636-643.

Lebreton, J.-D., K. P. Burnham, J. Clobert, and D. R. Anderson. 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecological Monographs* 62: 67–118.

Nichols, J.D., C. Brownie, J.E. Hines, K.H. Pollock and J.B. Hestbeck (1993). The estimation of exchanges among populations or subpopulations. *In* J.-D. Lebreton and P.M. North (eds) *Marked Individuals in the Study of Bird Population*. pp. 265-279. Birkhäuser Verlag: Basel.

Pollock, K.H., J.E. Hines and J.D. Nichols (1984). The use of auxiliary variables in capture-recapture and removal experiments. *Biometrics* 40: 329-340.

Pollock, K.H., J.D. Nichols, C. Brownie and J.E. Hines (1990). Statistical inference for capture-recapture experiments. *Wildlife Monographs* 107: 97 pp.

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

Seber, G.A.F. (1982). *The Estimation of Animal Abundance*. Griffin: London.

Wetherall, J.A. (1982). Analysis of double-tagging experiments. *Fishery Bulletin* 80: 687-701.

SECTION 3.: POST-LARVAL RECRUITMENT OF BLACKLIP ABALONE (*HALIOTIS RUBRA*) ON ARTIFICIAL COLLECTORS IN SOUTHERN TASMANIA

W. J. NASH, J.C. SANDERSON, J. BRIDLEY, S. DICKSON, B. HISLOP

POST-LARVAL RECRUITMENT OF BLACKLIP ABALONE (HALIOTIS RUBRA) ON ARTIFICIAL COLLECTORS IN SOUTHERN TASMANIA

W. J. Nash, J. C. Sanderson, J. Bridley, S. Dickson, B. Hislop

Sea Fisheries Division, Department of Primary Industry and Fisheries, Crayfish Point, Taroona, Tasmania 7053, Australia

Running title: Patterns of abalone post-larval recruitment

Post-larval recruitment of blacklip abalone (Haliotis rubra) on artificial collectors in southern Tasmania.

Abstract

Recruitment rates of blacklip abalone (Haliotis rubra) post-larvae were measured at fortnightly intervals for a year in southern Tasmania on larval collectors made of transparent, corrugated plastic. The settlement plates were conditioned prior to use in a flow-through seawater system in a two-stage process: a film of diatoms (mainly Nitzschia and Navicula species) was first established on the plates which were then grazed by juvenile H. rubra. This allowed second-phase algae (principally Myrionema species) to become established. The plates were then periodically deployed at a depth of ~7 m. Larval settlement occurred mainly during the austral winter and early spring. A peak settlement rate of 1408 post-larvae per collector (2347 post-larvae m^{-2}) occurred in mid-August. Methods of measuring larval or immediate post-larval abundance are reviewed with regard to their use in the assessment and management of abalone fisheries.

Introduction

Abalone species and populations vary greatly in their vulnerability to overfishing. Poor recruitment to fishable size might occur because of infrequent spawning, as a result of low fertilisation success at low adult densities, because settlement or recruitment at high levels occurs only occasionally even when egg production levels are high, or because settled larvae suffer high mortality before they recruit to the adult population. The decline of populations of H. rufescens in California and H. kamtschatkana in British Columbia occurred despite the reasonably high levels of egg production conserved (Breen 1986; Tegner et al. 1989). Similarly, Shepherd and Partington (1995) have described the decline of a H. laevigata population in Waterloo Bay, South Australia, despite a size limit that conserved 50% of the virgin stock egg

production (S.A. Shepherd, personal communication). Sainsbury (1982) and McShane (1993) reported that the low levels of recruitment of H. iris were inconsistent with the abundance of older animals, and concluded that high recruitment rates occur only sporadically, thus allowing only relatively low levels of fishing pressure in many areas. In contrast, H. rubra can sustain relatively high levels of fishing pressure (McShane 1992).

Regional differences in susceptibility to fishing pressure also exist within abalone species. For example, experienced abalone divers in Tasmania refer to 'non-recovery bottom', on which initially-abundant H. rubra populations did not regenerate after short (1 to 2 year) periods of intense fishing. These contrast with other areas which have sustained intense fishing for more than 20 years.

A knowledge of the factors affecting spawning and larval settlement is essential to untangle the determinants of recruitment success. By identifying patterns of larval abundance (both in the plankton and immediately after settlement) it will be possible to assess whether recruitment strength is determined by larval abundance, larval settlement rates, high post-settlement survival rates or a combination of these (Nash 1991).

This paper describes a method for measuring rates of post-larval recruitment of H. rubra to conditioned artificial surfaces, and describes the patterns of post-larval recruitment over a 12-month period in southern Tasmania. The merits of this and other sampling methods of larvae and newly settled abalone are then compared.

Methods

The larval settlement collectors used were a modification of a crevice-type puerulus (juvenile rock lobster) collector described by Booth and Tarring (1986). Each collector consisted of four 25 cm x 30 cm horizontal plates made from sheets of

transparent polycarbonate held rigid in a metal frame and attached to a heavy base consisting of a car tyre filled with iron and concrete (Fig. 1). The collector plates were 45 to 55 cm above the substratum. Three four-plate collectors were used in each sampling period. The collector unit was attached to the base by a removable pin to facilitate rapid deployment and retrieval.

The settlement collector plates were conditioned in a two-stage process, as described by Suzuki et al. (1987): in the first stage, plates were conditioned for two weeks in an open-air tank supplied with vigorously aerated flowing seawater filtered to 20 µm. A film of diatoms (mainly Nitzschia and Navicula species) became established on the plates within approximately two weeks. The plates were then transferred to another aerated tank supplied with 20 µm-filtered flowing seawater, and 40 to 70 10-40 mm-long juvenile H. rubra were placed on the plates. The grazing activity of these juveniles then allowed second-phase algae (principally Myrionema species) to establish on the plates within two weeks. The plates were then ready for use.

The study was conducted on the northern side of George III Rock (146°58'E, 43°31'S) in southern Tasmania (Fig. 2), where the reproductive condition of H. rubra had been monitored monthly for three years.

The collectors were deployed at ~7 m depth, arrayed over a distance of ~4 m, and replaced at two-weekly intervals. This interval was the most frequent practicable; moreover, experience in commercial abalone hatcheries has shown typical post-larval mortality 14 days after settlement of ~50%. The study took place between June 1991 and June 1992.

Larval collector plates were transported in sealed plastic containers with a small amount of seawater to the laboratory for sorting. After immersion in a 1% solution of Benzocaine to anaesthetize the post-larvae, the plates were lightly brushed to ensure

that all abalone were dislodged. All material washed off the plates was then sieved through a 125-μm mesh and organisms retained on the mesh were stained with a 0.5% Alizarin Red S solution and preserved in 90% ethanol. The stain is taken up by organic tissue; empty shells are not stained. In a small number of samples, post-larvae were separated prior to staining; the samples were then stained and re-sorted. A significant number of post-larvae were found in re-sorted samples. Re-sorting of these samples before staining did not increase the counts, illustrating the importance of staining to locate all post-larvae. The zinc chloride flotation method of Sellmer (1956) was used to separate organic material such as H. rubra juveniles in samples containing large amounts of sediment. The low-density organic matter was decanted from the surface of the zinc chloride solution and washed prior to sorting.

All small abalone found were counted and measured. When the number of post-larvae collected was large, a random subsample of 200 post-larvae per collector was measured. H. rubra is the only haliotid species living in southern Tasmania and so cannot be confused with other congeners. In addition 75 species of other gastropods were found to have settled on the collectors. These were photographed for a reference collection and used to avoid confusion with small H. rubra.

The four-plate collector design was used to provide surfaces with different water movement strengths and different microhabitats, and to allow us to test for larval preference for particular plates. From 19 August to 2 September, 1991 (three sampling periods) the four plates from each collector were placed individually in separate containers upon retrieval, and preserved; post-larvae were removed and sorted as previously described.

Samples of 60 sexually mature H. rubra were sampled from the reef near the collectors at monthly intervals throughout this study to measure seasonal variation in reproductive condition and to measure the relationship between this and post-larval

recruitment rates. Reproductive condition was measured by the gonad bulk index (Newman 1967), measured at the base of the conical appendage. This index is linearly related to fecundity (Nash et al. 1994). Results of these reproductive studies will be published fully elsewhere.

A suction sampler (McShane and Smith 1988) was used to sample the substratum for juvenile H. rubra on 28 August 1991, nine days after the collectors were retrieved with exceptionally large numbers of H. rubra post-larvae. Three sites were sampled on George III Rock, one in the immediate vicinity of the collectors. Coralline algal surfaces were selectively sampled because McShane and Smith (1988) found few or no juvenile H. rubra on other surfaces. An estimated 1 m^2 of substratum (usually comprising several non-contiguous coralline algal patches because of the small size of individual patches) was sampled at each site.

Results

The succession of diatoms on the plates was similar to that described by Suzuki et al (1987): a thick film of diatoms, principally Nitzschia and Navicula species (the first-phase algae), developed within two weeks from immersion and the second-phase algae (principally Myrionema species) within a further three weeks. The major difference from the results of Suzuki et al. (1987) was that species of Cocconeis were the predominant second-phase algae in their study.

Settlement of H. rubra larvae on the larval collectors occurred for most of the year during the study, with peaks in July-August and October 1991 and in the following June (i.e., during winter and spring) (Fig. 3). Settlement rates were low between December 1991 and May 1992. A maximum mean post-larval settlement rate of 1281 post-larvae per collector (2135 post-larvae m^{-2}) was recorded in mid-August 1991, with a maximum of 1408 post-larvae per collector (2347 post-larvae m^{-2}). The major

settlement peak in August 1991 corresponded with the first decline in the gonad index (Fig. 3). Subsequent settlement peaks until December were matched by a continuing decline in the gonad index.

The larval shell, which is clearly distinguishable from the post-larval shell, has a length of ~290 μm. The post-larval size compositions for the five sampling periods of highest post-larval abundances are shown in Fig. 4. The unimodal size frequency distributions for the 17 July 1991, 19 August 1991 and 17 October 1991 samples suggest single pulses of settlement on the collectors. The 1 August 1991 sample has several modes, the most prominent at 300 μm, indicating that settlement of these larvae occurred only one or two days before retrieval of the collectors. Other modes in this sample, at ~380, 430 and 500 μm, suggest that several settlement episodes may have occurred within the two-week sampling period. Two, possibly three, modes are visible in the 2 September 1991 sample, at ~350, 470 and 540 μm. The daily growth of 540-μm post-larvae must have been at least 18 μm if settlement occurred on the first day the collectors were deployed, and faster if settlement occurred later.

Larval settlement rate vs plate position

When the results for the three collectors were combined, the mean number of post-larvae was highest on the top plates, least on the bottom plates, and intermediate on the two middle plates (Table 1); however, the differences were not statistically significant (1-way ANOVA; $P>0.1$).

The heavy settlement of larvae in August coincided with a strong flow of freshwater northwards across George III Rock from the rivers entering Recherche Bay (Fig. 2) forming a freshwater lens 2-3 m deep on the surface.

Suction samples

A maximum of six small (<1.5 mm) juveniles were found in any of the three samples obtained by the suction method in 40 minutes of searching each sample. The samples were not searched completely because it was apparent that the numbers of post-larvae were very low at each site.

Discussion

The very high post-larval recruitment rates achieved in this study, and the concordance between recruitment and indices of reproductive condition, demonstrate that conditioned collector plates may be used to examine temporal and spatial patterns of larval settlement to natural abalone populations.

The high densities of juvenile H. rubra immediately after settlement recorded by McShane and Smith (1991) (as high as 12 456 m^{-2}) in eastern Victoria in 1988 demonstrate that the heavy settlement (2135 post-larvae m^{-2}) observed in mid-August 1991 in this study is not exceptional for this species. Similar densities were recorded for H. discus hannai by Tanaka et al. (1986) and Sasaki and Shepherd (1995).

The low number of small juvenile H. rubra obtained by suction sampling the substrata in the vicinity of the collectors within three weeks of the heavy larval settlement in August 1991 was not expected, and may have been caused by one of the following: (i) high post-settlement mortality; (ii) movement after settlement to crevices and sub-boulder spaces inaccessible to the suction sampler; (iii) low attractiveness of the sampled substrata to the larvae; (iv) inefficiency of the suction sampling method; or (v) higher settlement rates on the larval collectors than the surrounding substrata. It is very difficult to distinguish between the first two possibilities, although McShane (1991) has attributed similar observations on H. rubra in Victoria to mortality, and concluded that post-settlement mortality is density-dependent. The third factor is unlikely because McShane and Smith (1988) found larval settlement was highest on

coralline algal surfaces, consistent with laboratory and other field studies (Morse et al. 1980). The fourth factor cannot be discounted: the capture efficiency of a suction sampler is greatly affected by the roughness of the coralline algal surface (P. McShane, personal communication). Similarly, capture efficiency may decline to as little as 1% using a worn brush (P. McShane, personal communication), although this is unlikely in this study because the brush was new. The fifth factor may be important if the attractiveness of the larval collectors is high and that of the surrounding substrata is low (Nash 1992), because low substratum attractiveness will mean that the larvae are in the water column for longer, and therefore more likely to encounter the larval collectors.

Whatever the cause, the low counts obtained in this study within three weeks of a heavy larval settlement highlight the importance of sampling very soon after larval settlement if settlement alone is to be measured. Density-dependent mortality is unlikely to have occurred immediately after settlement, even at a density of 2500 post-larvae m^{-2}, because each larva has, on average, more than 1000 times its own area to graze in. Larval clumping or aggregation to preferred microhabitat may reduce the available area per larva to some extent but it is unlikely that juvenile density affects survival until a larger size.

The large settlement in August 1991 may have been the result of either a large spawning or a patch of larvae happening to encounter the collectors at this time. The latter is unlikely because the conditions that exist at the study site do not favour retention of the larvae or concentration of the larvae into a dense patch: the tidal current through the area at mid-tide is quite strong and the site is not on the downcurrent side of the reef where eddies might form. Deployment of collectors at several spatial scales would reveal the extent and synchrony of settlement.

Sorting abalone post-larvae from the other material on the collector plates is very time-consuming. The use of a dye to stain invertebrates in the samples increases searching efficiency (McShane and Smith 1988), and the zinc chloride separation method reduces sorting time substantially (McShane and Smith 1991). Sorting effort may be further reduced by reducing both the size and number of plates per collector; there is no evidence from this study that middle or bottom plates receive or retain more larvae than top plates.

A number of methods are now in use to measure abalone larval or post-larval abundance. First, there are the studies that sample the plankton quantitatively (Tanaka et al. 1986; Sasaki and Shepherd 1995); second, there are the studies that measure post-larval recruitment strength on artificial collectors (this study; Keesing et al. 1995); and third, there are those that measure the density of post-larval recruits. These include anaesthetic sampling (Prince and Ford 1985), visual searching with underwater magnifying lens (Shepherd and Turner 1985) and suction sampling (McShane and Smith 1988). The efficiency, advantages and drawbacks of these methods for measuring abundance of larvae and post-larvae are summarised in Table 2. Effort required to sort abalone post-larvae from other material is an important problem for all methods, particularly for the suction sampling and larval collector methods. This is a lesser problem for the plankton sampling method. Sorting effort can be reduced for the suction sampling method by selectively sampling bare coralline algal substrata, but this is often difficult in practice because the crevices and holes almost invariably contain sediment. Similarly, sediment settlement rates to larval collectors may be reduced by deploying them over hard substrata away from sandy areas, although sediment entrained during rough weather is transported to these sites as well. The suction sampling method would be unsuitable for species (such as H. laevigata) inhabiting sandy areas; sediment levels in the samples would make searching for juveniles impossibly time-consuming.

Rates of larval settlement may be most accurately inferred with the larval collector method because sampling is continuous; it is not necessary to know when spawning and settlement occur. Suction sampling may measure settlement rates if done immediately after settlement (McShane and Smith 1991) but high mortality rates or movement of post-larvae to inaccessible positions shortly after settlement will otherwise obscure settlement rate patterns (McShane 1991; this study). Post-settlement mortality may be measured by sequential retrieval of collectors at several intervals after deployment (Keesing et al. 1995). Plankton sampling may measure larval abalone abundance if done shortly after spawning; as with suction sampling, it must therefore be carried out repeatedly around the time of spawning (judged by gonad analysis) unless the spawning cues are known (Sasaki and Shepherd 1995).

The importance of substratum conditioning for settlement of H. rubra larvae needs further evaluation. Higher settlement rates of H. discus hannai (Seki and Kan-no 1981) and H. rufescens (Slattery 1992) larvae were achieved on surfaces conditioned with diatoms and the mucous secretions of grazing conspecifics than on unconditioned surfaces. Nevertheless, reasonably high settlement rates of haliotid larvae to collector plates have been achieved with only primary conditioning (Keesing et al. 1995), or even with no conditioning at all (J. Keesing, personal communication). Larval settlement rates may also be affected by both colour and reflectance of the settlement surface: Horiguchi et al. (1984) found deep purplish red plates of low reflectance yielded highest settlement rates. Colourless plates (as used in this study) attracted relatively low rates of settlement. Presence of an algal film on the plates, which obscure the surface, would reduce the importance of these properties, however. Settlement rate patterns to unconditioned or primary-conditioned surfaces may be misleading unless they are the same as those to plates with secondary conditioning. This has not been confirmed in any study so far.

Slattery (1992) also found that survival rates between settlement and three days post-settlement were highest on diatoms + mucus, least on diatoms + GABA and intermediate on diatoms alone. It is apparent from Fig. 2 of Slattery (1992) that survival rates after day 3 were similar between the substrata, and that the effect of mucus on survival lasts no longer than three days after secretion of mucous trails ceases. From this it may be concluded that, if Slattery's results are applicable to H. rubra, larval survival rates on our collectors that were in the sea for two weeks will depend on how soon after deployment of the collectors settlement occurs. The settlement rates shown in Fig. 3 will therefore be confounded by variable survival effects. Nevertheless, the high spatfall in August 1991 occurred an estimated 7.5 to 10 days before retrieval of the collectors, which was at least eight days after the collectors were deployed. If presence of conspecific mucus does affect larval survival after settlement, it was insufficient to mask this strong settlement.

Post-settlement survival is also affected by intensity of grazing on the Myrionema, whether by abalone post-larvae or other organisms. The filaments that grow from Myrionema, if insufficiently grazed, can entangle H. rubra post-larvae and cause death by exhaustion or starvation (A. Cuthbertson, personal communication).

Unless immediate post-settlement mortality is minor (and the evidence suggests that this is strongly substratum-dependent: Slattery 1992), the numbers of juveniles found on the collectors will be the result of both post-settlement mortality and settlement strength. This problem is unavoidable because sampling at more frequent intervals than fortnightly is rarely feasible logistically. Hatchery observations of entanglement and death of H. rubra post-larvae by filaments of Myrionema several days after grazing has ceased (A. Cuthbertson, personal communication) imply that survival rates on the collectors will depend on how soon after deployment of the collectors larval settlement occurs and on the intensity of grazing by other invertebrates that settle onto the plates.

If the proximate spawning stimulus (or stimuli) for H. rubra could be identified, sampling effort could be reduced to periods shortly after spawning, thereby substantially reducing research effort. It is therefore desirable to identify the proximate spawning stimuli for H. rubra. Unusually heavy rainfall and river flows (the fourth highest in 25 years: Tasmanian Land and Water Resources Division river flow data for the Esperance River) occurred shortly before the heavy larval settlement in August 1991; although this may have been causally related to the heavy larval settlement, settlement rate and environmental data for more than one year are needed to establish a pattern. The only known observations of in situ spawning by both female and male H. rubra in Tasmania were on the south-east coast in a strong south-east (i.e., onshore) swell on two separate occasions (G. Cleaver, personal communication). These observations more closely resemble those of Sasaki and Shepherd (1995) (spawning during typhoons) than those of Breen and Adkins (1980) and Steckoll and Shirley (1993), who described observations of in situ spawning by H. kamtschatkana on warm, calm days. Shepherd (cited in Sasaki and Shepherd 1995) observed spawning by H. rubra in South Australia in calm conditions. In situ observations of spawning are less likely during typhoons or other rough weather because diving is less common at this time.

It seems likely that, apart from haphazard observations of spawning, identification of spawning stimuli in natural conditions is most likely to come from detailed monitoring of environmental factors (water temperature, sea condition, water current direction and strength, salinity and nutrient levels), reproductive condition and larval or post-larval abundance.

Although studies of the distribution and abundance of planktonic larvae and larval settlement may elucidate the early life history of abalone, they will not be useful for fishery management unless settlement rate variation is reflected in rates of

recruitment to the fishery. If post-settlement survival rates were strongly density-dependent, as Shepherd (1990) and McShane (1991) suggest, this would not be so. (For a discussion of the relative importance of larval and benthic stages to the dynamics of marine invertebrate populations see Grosberg and Levitan (1992) and references therein.) From a fishery management perspective it is therefore important to determine the earliest age at which abundance is an index of future recruitment to the fishery before undertaking a major study of larval or early post-larval abundance. The 2+ year class of H. laevigata is such an index (Shepherd 1990). Earlier (0+ and 1+) age classes become increasingly difficult to find because of their cryptic behaviour and small size, and are therefore less useful as an index of future recruitment to the fishery except in small-boulder substrata that can be overturned. Modal progression analysis of size-frequency distributions (Oba et al. 1968; Shepherd 1990) can be used to determine whether fluctuations in early juvenile strength (at ~10 mm shell length) carry through to legal size. Such a study should precede (or at least accompany) larval settlement studies if fishery assessment and management are the objectives.

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References

Booth, J. D., and Tarring, S. C. (1986). Settlement of the red rock lobster, Jasus edwardsii, near Gisborne, New Zealand. New Zealand Journal of Marine and Freshwater Research 20, 291-7.

Breen, P. A. (1986). Management of the British Columbia fishery for northern abalone (Haliotis kamtschatkana). Canadian Special Publication of Fisheries and Aquatic Sciences 92, 300-12.

Breen, P. A., and Adkins, B. E. (1980). Spawning in a British Columbia population of northern abalone, Haliotis kamtschatkana. Veliger 23, 177-9.

Grosberg, R. K., and Levitan, D. R. (1992). For adults only? Supply-side ecology and the history of larval biology. Trends in Ecology and Evolution 7, 130-3.

Horiguchi, Y., Noda, H., and Amano, H. (1984). Settlement behavior of young abalone to chromatic and achromatic plates made of methacrylate resin. Bulletin of the Faculty of Fisheries, Mie University 11, 219-26.

Keesing, J. K., Grove-Jones, R., and Tagg, P. (1995). Measuring settlement intensity of abalone: a pilot study. Australian Journal of Marine and Freshwater Research Vol, ppp-ppp. [This issue]

McShane, P. E. (1991). Density-dependent mortality of recruits of the abalone Haliotis rubra (Mollusca: Gastropoda). Marine Biology 110, 385-9.

McShane, P. E. (1992). Exploitation models and catch statistics of the Victorian fishery for abalone Haliotis rubra. Fishery Bulletin 90, 139-46.

McShane, P. E. (1993). Evidence for localized recruitment failure in the New Zealand abalone Haliotis iris (Mollusca: Gastropoda). In 'Proceedings of the Second International Temperate Reef Symposium'. (Eds C. N. Battershill, D. R. Schiel, G .P. Jones, R. G. Creese and A. B. MacDiarmid.) pp. 145-50. (NIWA Marine: Wellington, New Zealand.)

McShane, P. E., Black, K. P., and Smith, M. G. (1988). Recruitment processes in Haliotis rubra (Mollusca: Gastropoda) and regional hydrodynamics in southeastern Australia imply localized dispersal of larvae. Journal of Experimental Marine Biology and Ecology 124, 175-203.

McShane, P. E., and Smith, M. G. (1988). Measuring recruitment of Haliotis rubra Leach (Gastropoda: Haliotidae) – comparison of a novel method with two other methods. Australian Journal of Marine and Freshwater Research 39, 331-6.

McShane, P. E., and Smith, M. G. (1991). Recruitment variation in sympatric populations of Haliotis rubra (Mollusca: Gastropoda) in southeast Australian waters. Marine Ecology Progress Series 73, 203-10.

Morse, D. E., Tegner, M., Duncan, H., Hooker, N., Trevelyan, G., and Cameron, A. (1980). Induction of settling and metamorphosis of planktonic molluscan (Haliotis) larvae. III: Signaling by metabolites of intact algae is dependent on contact. In 'Chemical Signals in Vertebrate and Aquatic Animals'. (Eds D. Muller-Schwarze and R. M. Silverstein.) pp. 67-86. (Plenum Press: New York.)

Nash, W. J. (1991). Recruitment rate variation complicates abalone management. Fishing Today 3(6), 25-7.

Nash, W. J. (1992). What do abalone spat settlement studies measure? The effects of substrate attractiveness on abalone larval settlement rate to artificial surfaces. In 'Australian Society for Fish Biology Workshop on Recruitment Processes'. (Ed. D. A. Hancock.) pp. 26-32. Bureau of Rural Resources. Proceedings No. 16. (Australian Govt Publishing Service: Canberra.)

Nash, W. J., Sellers, T. L., 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 Furneaux group of islands. Tasmanian Sea Fisheries Division Technical Report 48, 1-69.

Newman, G. G. (1967). Reproduction of the South African abalone Haliotis midae. Investigational Report, Division of Sea Fisheries, Republic of South Africa 64, 1-24.

Oba, T., Sato, H., Tanaka, K., and Toyama, T. (1968). Studies on the propagation of an abalone, Haliotis diversicolor supertexta—III. On the size of the one-year-old specimen. Bulletin of the Japanese Society of Scientific Fisheries 34, 457-61.

Prince, J. D., and Ford, W. B. (1985). Use of anaesthetic to standardize efficiency in sampling abalone populations (genus Haliotis; Mollusca: Gastropoda). Australian Journal of Marine and Freshwater Research 36, 701-6.

Sainsbury, K. J . (1982). Population dynamics and fishery management of the paua, Haliotis iris. I. Population structure, growth, reproduction and mortality. New Zealand Journal of Marine and Freshwater Research 16, 147-61.

Sasaki, R., and Shepherd, S. A. (1995). Larval dispersal and recruitment processes of Haliotis discus hannai and Tegula spp. in Kesennuma Bay, Japan. Australian Journal of Marine and Freshwater Research Vol, ppp-ppp. [This issue]

Seki, T., and Kan-no, H. (1981). Induced settlement of the Japanese abalone, Haliotis discus hannai, veliger by the mucous trails of the juvenile and adult abalones. Bulletin of the Tohoku Regional Fisheries Research Laboratory 43, 29-36.

Sellmer, G. P. (1956). A method for the separation of small bivalve molluscs from sediments. Ecology 37, 206.

Shepherd, S. A. (1990). Studies on Southern Australian abalone (Genus Haliotis). XII. Long-term recruitment and mortality dynamics of an unfished population. Australian Journal of Marine and Freshwater Research 41, 475-92.

Shepherd, S. A., Lowe, D., and Partington, D. (1992). Studies on southern Australian abalone (genus Haliotis). XIII: Larval dispersal and recruitment. Journal of Experimental Marine Biology and Ecology 164, 247-60.

Shepherd, S. A., and Partington, D. (1995). Studies on southern Australian abalone (genus Haliotis). XVI. Recruitment, habitat and stock relations. Australian Journal of Marine and Freshwater Research Vol, ppp-ppp. [This issue]

Shepherd, S. A., and Turner, J. A. (1985). Studies on southern Australian abalone (genus Haliotis). VI: Habitat preference and abundance and predators of juveniles. Journal of Experimental Marine Biology and Ecology 93, 285-98.

Slattery, M. (1992). Larval settlement and juvenile survival in the red abalone (Haliotis rufescens): an examination of inductive cues and substrate selection. Aquaculture 102, 143-53.

Stekoll, M. S., and Shirley, T. C. (1993). In situ spawning behaviour of an Alaskan population of pinto abalone, Haliotis kamtschatkana Jonas, 1845. Veliger 36, 95-7.

Suzuki, H., Ioriya, T., Seki, T., and Aruga, Y. (1987). Changes of algal community on the plastic plates used for rearing the abalone Haliotis discus hannai. Nippon Suisan Gakkaishi 53, 2163-7.

Tanaka, K., Tanaka, T., Ishida O., and Ohba, T. (1986). On the distribution of swimming and deposited larvae of nursery ground of abalone at the southern coast of Chiba Prefecture. Bulletin of the Japanese Society for Scientific Fisheries 52, 1525-32.

Tegner, M. J., Breen, P. A., and Lennert, C. E. (1989). Population biology of red abalones, Haliotis rufescens, in southern California and management of the red and pink, H. corrugata, abalone fisheries. Fishery Bulletin, 87, 313–39.

Table 1. Numbers of Haliotis rubra post-larvae in relation to position of collector plate within a collector. n = number of larval collectors.

Plate position	Mean	s.d.	n
Top	18.00	5.57	3
Upper middle	11.33	9.45	3
Lower middle	14.00	2.65	3
Bottom	10.00	9.64	3

Table 2. Advantages and disadvantages of several methods to sample abalone larvae and juveniles.

Method	Advantages	Disadvantages
Plankton sampling[1,2]	Less sorting effort than larval collectors or suction sampling. Non-destructive sampling.	Moderate-high sorting time. Timing is critical: sampling must be within a few days of spawning.
Larval collectors[3,4]	Standardised collector surface, allowing spatial and temporal patterns to be studied. Non-destructive sampling.	High sorting time. Not suitable for deployment in sandy habitat.
Suction sampling[5-7]	Suitable for sampling caves, crevices and cliff faces.	Very high sorting time. Timing is critical: sampling must be shortly after spawning. Capture efficiency dependent on roughness of the coralline algal surface and newness of brush. Shallow-water sampling difficult. Not suitable for species living in sandy habitat. Not suitable for boulder habitat because too much sediment is entrained.
Anaesthetic sampling[7,8]	Accuracy high (limited by efficiency of sorting).	High sorting time. Suitable only in small-boulder habitat. Destructive sampling.
Underwater magnifier[7,9]	Accuracy potentially high. Useful for measuring post-settlement survival rates. No sorting effort. Behaviour and habitat of animals observable.	High diving effort (to 1 h m^{-2} of substratum). Only manipulable boulders can be effectively searched. Inefficient at animal sizes <1 mm.

[1]McShane et al. (1988); [2]Sasaki and Shepherd (1995); [3]This study; [4]Keesing et al. (1995); [5]McShane and Smith (1988); [6]P. McShane (personal communication); [7]Shepherd et al. (1992); [8]Prince and Ford (1985); [9]Shepherd and Turner (1985).

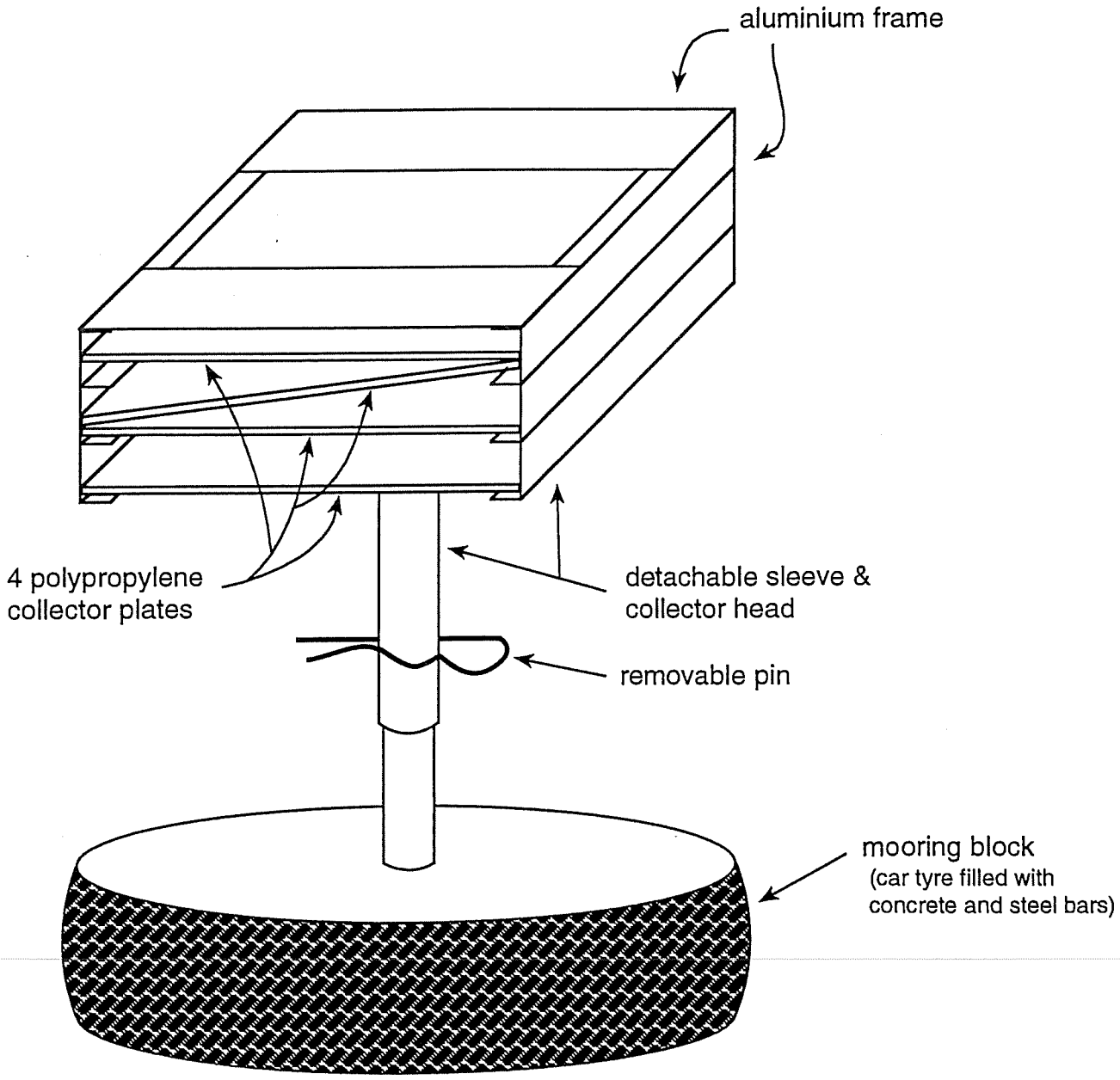
Figure captions

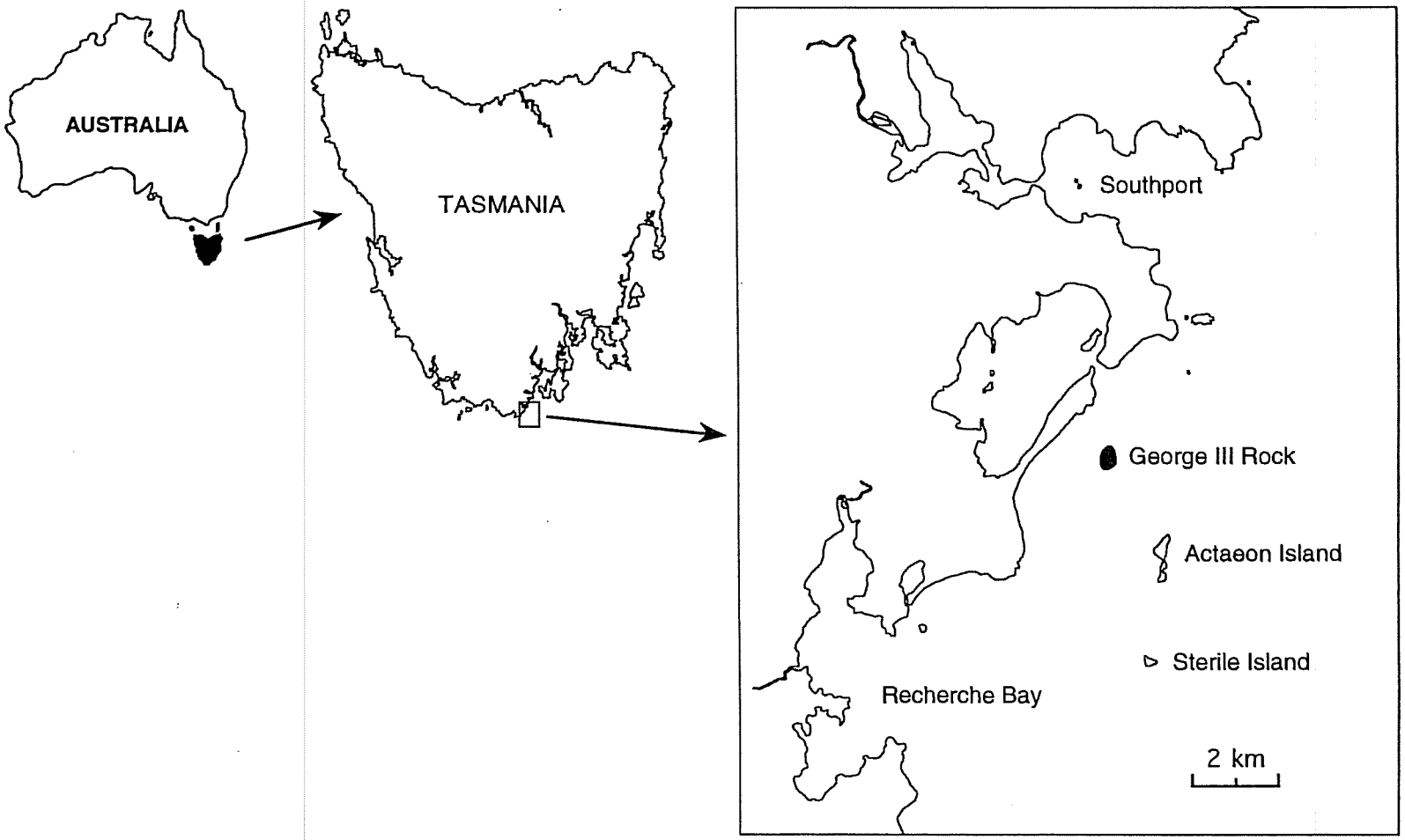
Figure 1 The four-plate larval collector used in this study.

Figure 2 Map of south-eastern Tasmania showing the study site.

Figure 3 Abundance of Haliotis rubra post-larvae on the larval collectors for each of the sampling periods (bar graph), and the gonad index (line graph) for the same period. Periods when collectors were deployed but no post-larvae were collected are shown with an asterisk. Error bars are 95% confidence intervals.

Figure 4 Post-larval size distribution for five of the sampling periods. Bar width: 20 μm.


aluminium frame
4 polypropylene
collector plates
detachable sleeve &
collector head
removable pin
mooring block
(car tyre filled with
concrete and steel bars)


AUSTRALIA
TASMANIA
Southport
George III Rock
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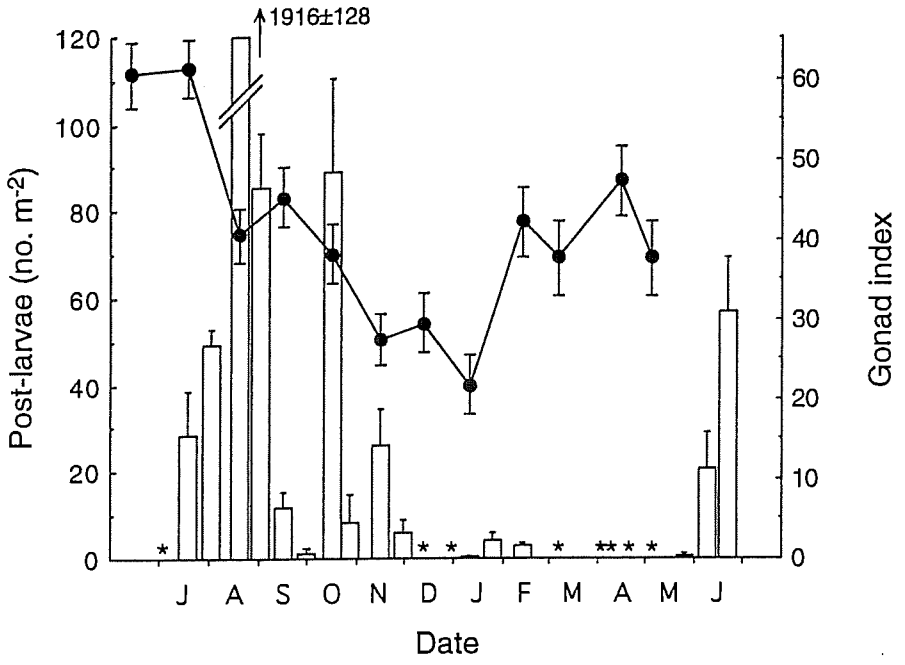
Sterile Island
Recherche Bay
2 km


1916±128
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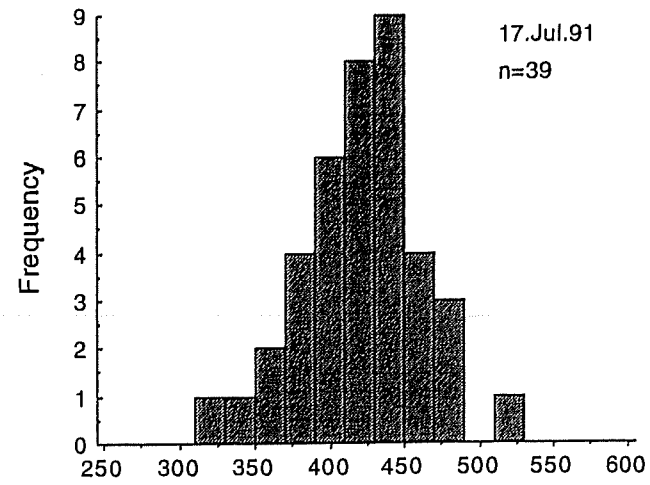
100
80
60
40
20
0
60
50
40
30
20
10
0
Post-larvae (no. m-2)
Gonad index
J A S O N D J F M A M J
Date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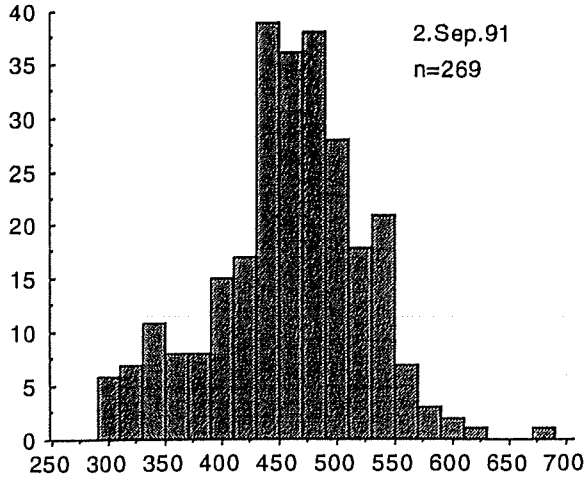
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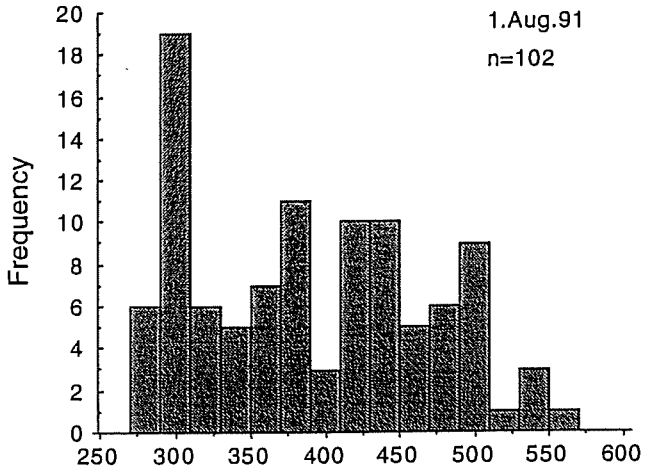
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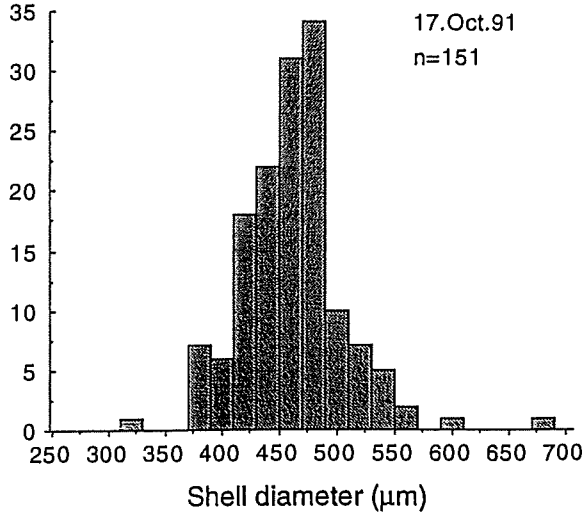
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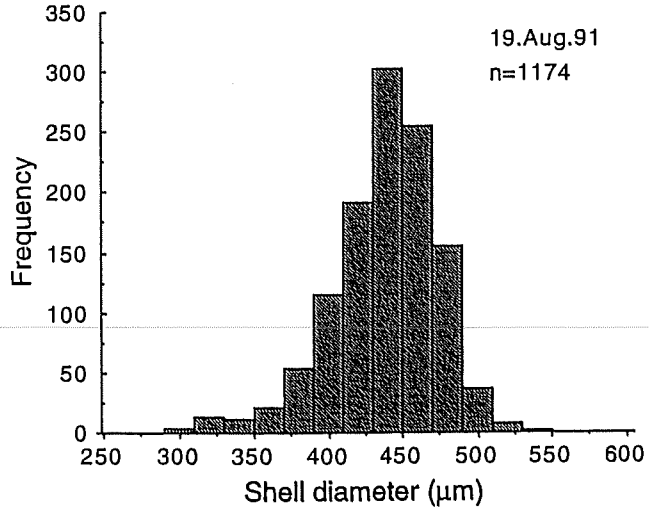
Shell diameter (µm)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Frequency
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250 300 350 400 450 500 550 600
Shell diameter (µm)

SECTION 4.: SEXUAL REPRODUCTION OF BLACKLIP ABALONE (*HALIOTIS RUBRA*) IN SOUTHERN TASMANIA

WARWICK J. NASH, DAVID WIKELEY, SIMON R. TALBOT AND ANDREW CAWTHORN

4 Sexual reproduction of blacklip abalone (*Haliotis rubra*) in southern Tasmania

Warwick J. Nash, David Wikeley, Simon R. Talbot and Andrew Cawthorn

Progress toward completion of this section is as follows:

- All histological sections have been processed, all sections have been staged, and all of the data are on computer.
- Preliminary analyses of the data have been conducted.

A thorough analysis of the data has not been done, and notes and manuscripts of the topic are in draft form only.

SECTION 5.: GROWTH AND AGEING OF BLACKLIP ABALONE (*HALIOTIS RUBRA*) IN SOUTHERN TASMANIA

WARWICK J. NASH, J. CRAIG SANDERSON, SIMON R. TALBOT, ANDREW CAWTHORN AND DAVID WIKELEY

5 Growth and ageing of blacklip abalone (*Haliotis rubra*) in southern Tasmania

Warwick J. Nash, J. Craig Sanderson, Simon R. Talbot, Andrew Cawthorn and David Wikeley

INTRODUCTION

The primary reason for tagging abalone in this study was to estimate survival, probability of capture and movement by multiple mark-recapture methods (as described in Sections 1 and 2). Multiple measurements of tagged abalone also allow growth rates and age-length relationships to be estimated. This information may be used to estimate recruitment ('birth') rates to the targeted population (≥80 mm) since the previous tagging survey, and to help distinguish 'births' from other sources of untagged abalone (immigration, emergence from the sub-boulder habitat, and presence of abalone that were emergent within the study site at the time of tagging but were overlooked). The measurement of growth was largely incidental to the objectives of this study. Consequently, the results are not presented comprehensively here. A growth and ageing paper is being prepared for publication in the *Australian Journal of Marine and Freshwater Research*.

METHODS

Abalone were tagged with the rivet tags described by Prince (1991), and the tag number and maximum shell diameter (measured to ±1 mm) at time of tagging was recorded. On the final survey of each site, the recaptured abalone were re-measured. Few size measurements were made during the intervening surveys because disturbance (removal of the abalone from the bottom to measure them) may have affected their movement patterns; since the primary aim of the study was to measure catchability using the movement results, disturbance or re-sighted abalone was avoided as much as possible.

Growth increment analysis

Growth increment data were fitted to the von Bertalanffy growth function (VBGF) using, firstly, Manzer-Taylor plots; that is, by plotting growth increment between successive periods of measurement (converted to growth increment per year) against size at first capture. The x-intercept of the regression line fitted through the data points is an estimate of L_∞ (*i.e.*, when growth rate is zero), and the slope (b) of the regression line $= e^{-K} - 1$, from which the Brody growth coefficient $K = -\log_e(b + 1)$.

This plot is linear if growth is according to the VBGF – *i.e.*, if absolute growth rate decreases monotonically from age 0 in linear fashion. If the relationship between age and length is sigmoid, as would be the case if absolute growth rate were maximal at some age >0, this will be detectable from the Manzer-Taylor plot. The VBGF was then fitted only to those data for abalone as large as or larger than size at which annual growth rate was maximal.

The mark-recapture data were fitted to the following difference form of the VBGF:

$$\delta s = (L_\infty - L_t) \cdot (1 - \exp(-K \cdot \delta t))$$

using non-linear regression methods using the statistical program Systat, where δs is the growth increment between tag and recapture (or between successive recaptures), L_t is the size at first capture and δt is the time interval between tag and recapture (or between successive recaptures). Estimation was carried out using the Simplex algorithm, and the values of L_∞ and K calculated from the Manzer-Taylor plots were used as a check that the non-linear estimation method did not converge to a local minimum least squares rather than the true (global) minimum least squares. Parameter estimates obtained by the Manzer-Taylor and non-linear regression methods were always similar; however, the non-linear estimates were used.

Growth ring ageing analysis

Approximately 60 sexually mature abalone (generally larger than 100 mm) were collected from each of the three study sites each month for reproductive analysis. The shells of these abalone were retained for ageing analysis.

Growth layers in the shell were exposed for counting by cutting a small rectangular section from the top of the shell using a lapidary saw. One edge of the section was through the apex of the shell, ensuring that the earliest layers of the shell could be visualised. The apex of the shell was cut at a constant position so that the same stage of the shell was examined on all shells, regardless of shell size and position of the growing edge of the shell relative to the apical whorls. The shell layers, which are alternating calcite and aragonite, differ in their density and texture; these differences allow the layers to be readily distinguished by eye. This difference between the layers was enhanced by sanding the exposed section with very fine sandpaper glued to a rotary turntable, then acid etching and staining the cut edge of the shell using the method of Dickson (1965), which imparts a deep red colour to the calcite layer, leaving the aragonite layer relatively unstained.

This method of sectioning the shell was used instead of grinding down the apex of the shell as described by Prince *et al.* (1988) because (i) it was found that the layers were easier to interpret; (ii) one or more inner layers may be lost when grinding down the apex of the shell if grinding does not cease as soon as a small hole appears (the layers are still present but they cannot be seen by examining the ground section from above); and (iii) the relatively large outer surface of the shell that has to be removed by grinding before the inner shell layers are exposed—particularly on the older, thicker shells—may cause complete obliteration of one or more outer layers.

Shell layers were counted in three positions (left, right and centre) on each shell. Each shell was assigned a 'clarity' rating which was based on the ease of distinguishing growth lines, which in turn is affected by the degree of shell erosion and boring. This is an advantage of counting rings from vertical sections: the outer shell surface next to the section can be inspected for erosion. Although we counted rings at three places on the shell section, the counts from the right side of the section were used in the ageing analyses. Although this is not the youngest part of the shell (the left side is) shell layers were generally more regularly spaced, and therefore easier to interpret, in this position. The number of rings in this position was generally one less than the count at the top or right-hand side of the section. It is often possible to follow rings around to the top of the shell and determine the number that have been eroded.

A large sample of the shells were ring-counted by three people to examine the errors associated with this method. The degree of concordance was estimated and the effect of ring-count variability on estimation of the VBGF parameters was evaluated.

From a study of growth and ageing of *H. rubra* at George III Reef, Prince *et al.* (1988) concluded that shell layers are deposited in the shell annually. In order to confirm this rate of shell deposition in the three study populations, marginal increment analysis was carried out: the thickness and identity (whether calcite or aragonite) of the inner shell layer (in process of deposition when the animal was killed) were recorded for each of the abalone collected each month for reproductive analysis. If there is synchrony of layer deposition (*e.g.*, with all members of the population commencing deposition of the calcite layer in early summer), then the mean thickness of the inner layer in the population sample will show a gradual increase as the layer thickens, followed by a sudden decrease as the deposition of the next layer begins. The number of cycles of shell layer deposition per year will indicate the rate at which layers are deposited; direct conversion of layer counts to age for individual abalone may then be possible.

Various indices of shell deposition may be used for marginal increment analysis, but the index adopted in this study was the width of the aragonite layer, measured at the right-hand end of the shell section. The calcite layer was not measured because this exhibited marked variation in thickness between animals; also, consecutive layers of the calcite layer in individual animals exhibited irregular variation in thickness; this was not so for the aragonite layer.

RESULTS

Growth increment analysis

Growth rate patterns at each of the sites are shown as Manzer-Taylor plots in Fig. 1. Exclusion of recapture data for cases where the time interval between mark and recapture was less than 300 days substantially reduced the spread of data points on these plots because seasonal variation in growth rate was removed. Seasonal variation in growth is not presented here. The VBGF parameter estimates are shown in Table 1. The shell length and time interval restrictions applied to the data are given in Table 2. Negative growth (caused by error in measurement) was recorded for a small number of animals. These were not excluded from the analysis prior to analysis because similar (but positive) errors in measurement were likely to have occurred. Since these cannot be distinguished from true size increases, they cannot be excluded in the way that negative growth cases can. Exclusion of cases of negative growth may therefore result in measured mean growth being positively biased. These were not excluded from the analysis because exclusion or inclusion of these made little difference to the growth parameter estimates. This is because nearly all cases of negative growth (once time intervals <300 days were excluded) are of large animals for which the error in length measurement is similar to the growth increment; since these are very close to the fitted regression line, they have little leverage (influence) on the position of the regression line through the data points.

The regression lines are fitted, in each case, to those animals for which time interval between mark and recapture (or successive recaptures) was ≥300 days, and with animals smaller than those with peak annual growth rates excluded. Size at peak growth rate was determined for each population by calculating the mean growth rate in 10-mm size classes. As shown in Fig. 1 (lower graphs), growth rates were maximal at a size >0 mm at all sites. Regression lines were fitted to the Manzer-Taylor plots with size at first capture less than 70, 60 and 80 mm for the shallow George III Rock , Stinking Bay and Shag Rock Bay sites, respectively, excluded from the analysis. No

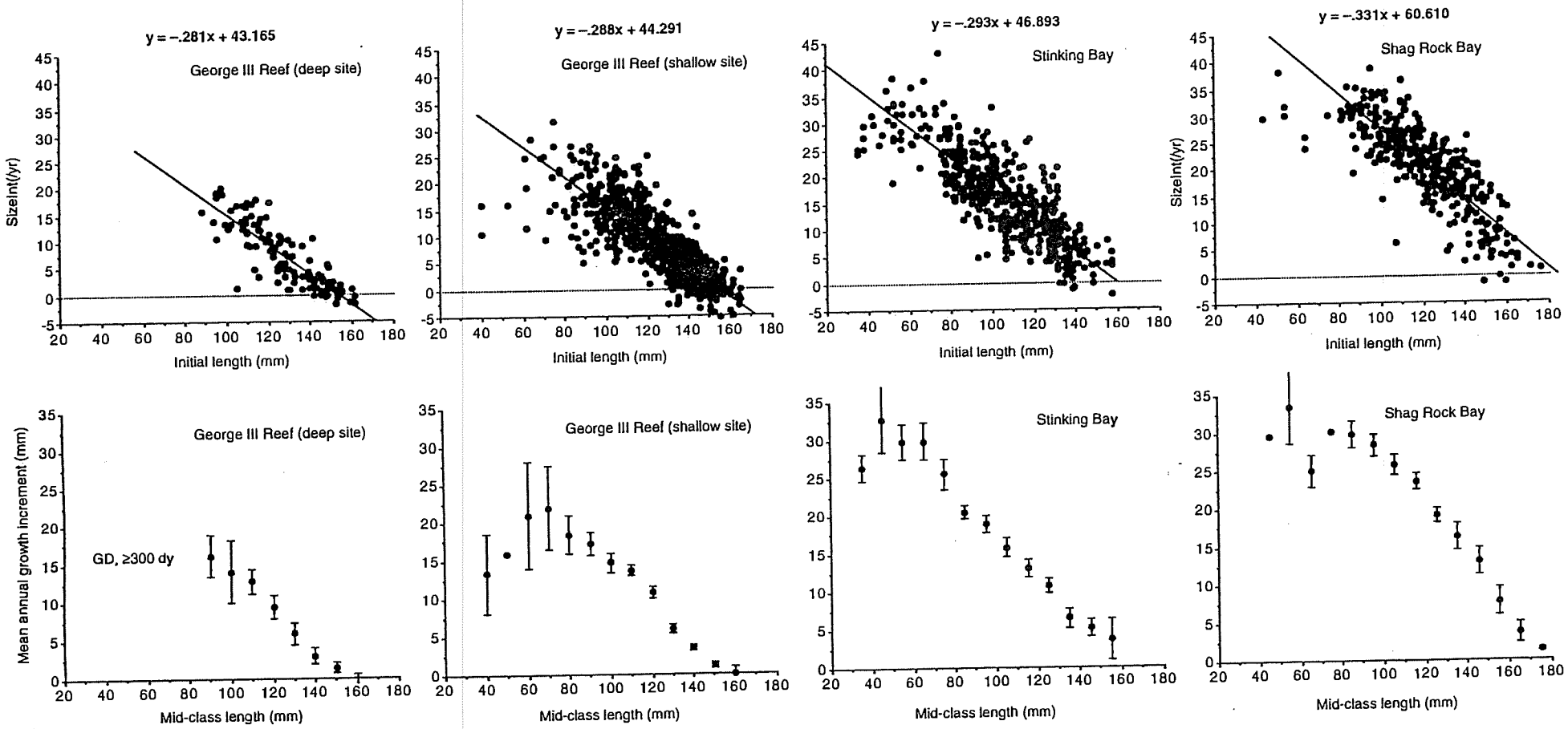

Figure 1. Growth increment results for *Haliotis rubra* at the four study sites. Graphs in the lower row show mean growth per 10-mm size class. Error bars are 95 percent confidence intervals. The lower plots are of abalone at large for ≥300 dy between mark and recapture. The data points in the upper plots are of all abalone at large for ≥300 dy, but the regression lines in the upper plots are of abalone at large for ≥300 dy *and* larger than size at maximal annual growth rate.

Table 1. Estimates of the von Bertalanffy growth parameters L_∞ and K at the four study sites, measured from growth increment data obtained from recaptures of tagged animals. L_t is $0.95*L_\infty$; r^2 = coefficient of variation; n = sample size; A.S.E. = asymptotic standard error. Data range restrictions for these data are shown in Table 2.

							95% C.L. (L_∞)			95% C.L. (K)			Age at L_t
Site	Sex	L_∞	K	r^2	n	A.S.E. (L_∞)	lower	upper	A.S.E. (K)	lower	upper	L_t	(yr)
George III Rock	all	153.2	0.460	0.783	126	1.520	150.2	156.3	0.040	0.381	0.540	145.93	9.1
(deep site)	F	150.5	0.625	0.822	26	3.243	143.8	157.2	0.154	0.308	0.942	142.87	8.0
	M	155.5	0.451	0.763	32	3.526	147.8	162.2	0.090	0.268	0.634	149.68	10.2
George III Rock	all	153.9	0.413	0.781	874	0.604	152.7	155.1	0.012	0.390	0.436	146.10	8.8
(shallow site)	F	152.2	0.466	0.819	69	2.417	147.3	157.0	0.058	0.350	0.583	148.38	9.4
	M	151.7	0.389	0.821	64	1.565	148.2	154.5	0.032	0.324	0.453	142.46	8.9
Stinking Bay	all	159.7	0.356	0.675	491	1.767	156.3	163.2	0.014	0.328	0.384	152.04	8.6
	F	166.5	0.322	0.683	35	7.150	151.9	181.0	0.049	0.222	0.421	154.12	9.1
	M	159.6	0.387	0.816	33	4.922	149.5	169.6	0.043	0.299	0.474	148.80	7.5
Shag Rock Bay	all	182.2	0.439	0.765	336	2.155	178.0	186.5	0.020	0.399	0.479	173.96	7.5
	F	182.7	0.460	0.783	128	3.500	175.7	189.6	0.036	0.388	0.532	176.26	7.4
	M	178.5	0.480	0.756	144	2.939	172.7	184.5	0.034	0.412	0.548	170.79	7.0

data were excluded for the deep George III Rock population since the smallest size at first capture was 88 mm – larger than the size at maximal absolute growth rate.

Table 2. Range restrictions on the mark-recapture data used to estimate the von Bertalanffy growth parameters in Table 1. Time interval is the period between tagging and recapture.

Site	Time interval (days)	Length at first capture (mm)
George III Rock (deep)	≥300	≥80
George III Rock (shallow)	≥300	≥70
Port Arthur	≥300	≥60
Shag Rock Bay	≥300	≥80

If growth had been according to the VBGF since birth, growth rate should have been maximal at age 0. The fact that peak growth rate occurs at age >0 indicates that the relationship between age and size is sigmoid.

Shell ageing analysis

The relationship between shell diameter and number of shell growth rings for the Shag Rock Bay site is shown in Fig. 2. When fitted to the VBGF $L_t = L_\infty(1-e^{-K(t-t_0)})$ there were no significant differences in the parameter estimates between the two shell agers. Note that, in all plots, there is dome-shaped distribution: abalone with the largest number of growth rings are not the largest animals. Possible reasons for this are discussed below.

Marginal increment analysis

The temporal change in width of the inner aragonite layer at the Shag Rock Bay site (Fig. 3) provides strong evidence that shell layers are deposited at the rate of one per year, as found by Prince *et al* (1988) in other sites in southern Tasmania. The data for the George III Rock and Stinking Bay sites have yet to be completely analysed.

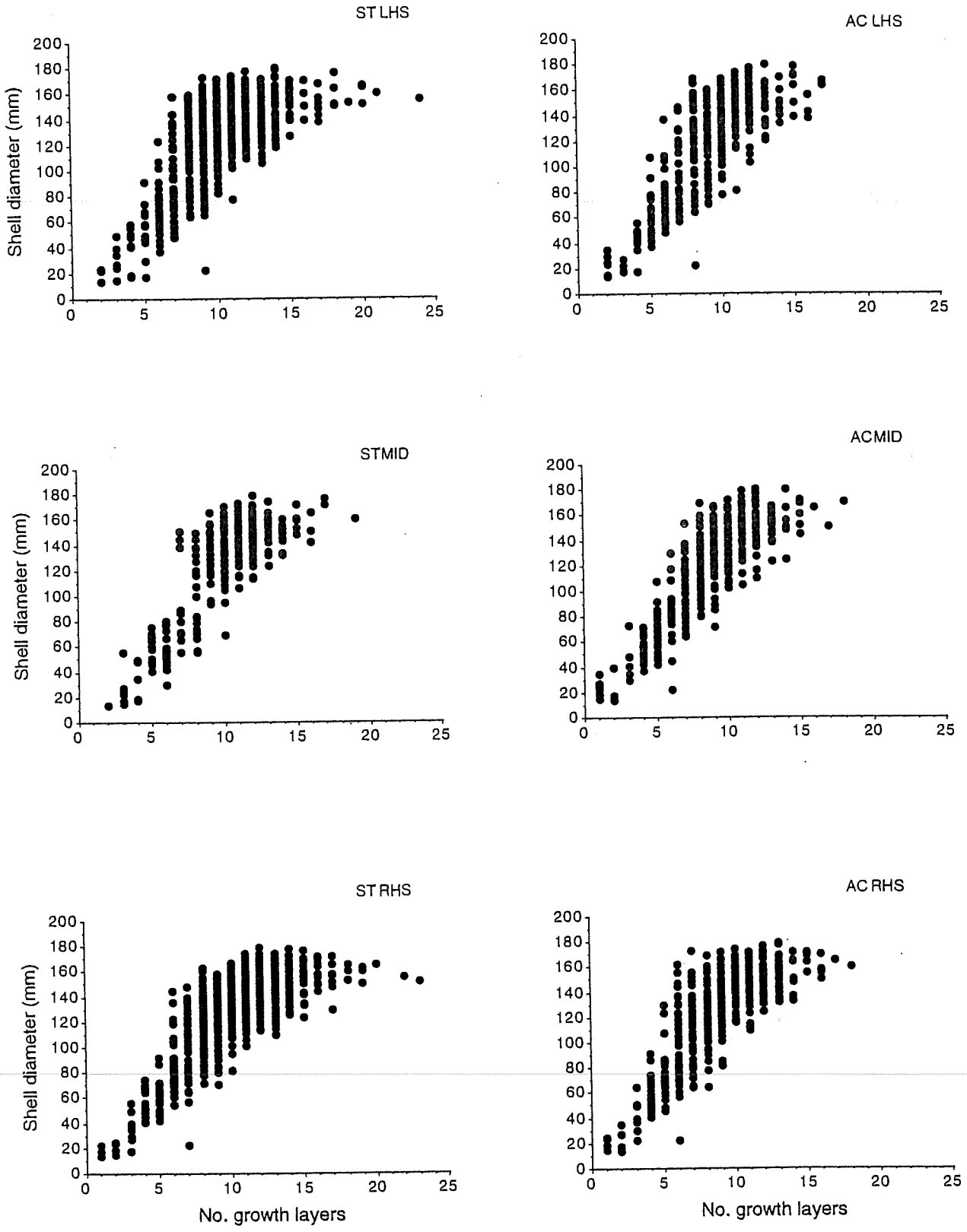

Figure 2. Relationship between shell diameter and number of growth layers in the shell of *Haliotis rubra* from Shag Rock Bay, as measured by two personnel (ST and AC) at three positions on the section through the shell spire: left side (LHS), middle (MID) and right side (RHS).

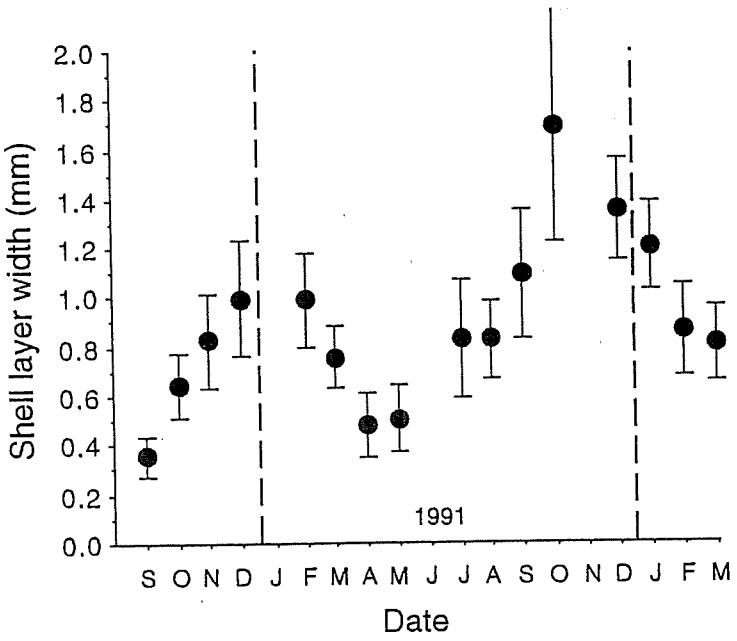

Figure 3. Change in mean width of the inner aragonite layer in blacklip abalone (*Haliotis rubra*) sampled monthly from the Shag Rock Bay site.

DISCUSSION

The Manzer-Taylor plots of the mark-recapture data (Fig. 1) show that growth rate (in absolute terms) is maximal at an age and size greater than 0, indicating that growth rate (plotted as size against age) is sigmoid. Fitting of the VBGF to the growth data therefore is valid only for sizes greater than or equal to the size at which growth rate is maximal.

The Manzer-Taylor plot for the Shag Rock Bay population shows a pronounced departure from the von Bertalanffy growth pattern by abalone larger than approximately 140 mm: almost all of these larger abalone fall below the regression line (Fig. 1). This means that these larger abalone are growing more slowly than would be predicted from the growth rates of abalone <140 mm. This may be an example of Lee's phenomenon (Jones 1958; Ricker 1969)—that is, selection against fast-growing individuals: fast-growing individuals enter the fishery at a younger age than slow growers, and so are likely to be caught at a younger age. Thus, slow-growing individuals, which enter the fishery at an older age, are likely to live longer than fast growers, with the result that growth rates of older age classes measured from a fished population are likely to be less than those from an unfished population.

In contrast with the Shag Rock Bay population, the George III Reef population, which has been unfished since 1984 (except for a single pulse of fishing in July 1987; Prince 1989), shows no deviation from von Bertalanffy growth in older age classes (Fig. 1). The Stinking Bay population also shows no departure from linearity (Fig. 1), despite the fact that, until closure of the area to fishing for the purposes of this study, it was regularly fished. It is suggested that the Stinking Bay data do not show the departure from linearity shown by the Shag Rock Bay data because abalone at Stinking Bay grow more slowly and to a smaller maximum size (Fig. 1, Table 1); they are therefore subject to less intense genetic selection against rapid growth. A non-genetic cause for the observed growth rate patterns at these two sites is difficult to see.

Genetic selection against fast-growing abalone would be greatest in intensely fished populations. Because abalone at both Shag Rock Bay and Port Arthur live for several years after reaching fishable size (as deduced from both the growth increment and shell ring analyses), fishing pressure appears not to be very high. Since onset of sexual maturity in *Haliotis rubra* appears to be primarily age-related (Nash 1990), the proportion of the population egg production that is contained in abalone below the legal minimum size limit is less in the faster-growing Shag Rock Bay population than in the slower-growing Port Arthur population. Thus, selection against fast growers will be higher at Shag Rock Bay. The impact of this on the genetic structure of the

population will depend on the size at which the minimum legal length limit is set relative to the size at onset of sexual maturity. Size at 50 percent maturity for a population sample taken from O'Hara Bluff (adjacent the Shag Rock Bay study site) is 106 mm (unpublished results). If onset of sexual maturity at this site is age-related, as the evidence from *Haliotis rubra* populations elsewhere in Tasmania suggests (Nash 1990), then fast-growing abalone will become vulnerable to fishing before making a significant reproductive contribution to the population. If growth rate variation has a large genetic component (as opposed to an environmental one) then genetic selection against rapid growth is possible.

The marginal increment analysis provides strong evidence that shell layers are deposited at the rate of one per year, at least in abalone in the size range (≥80 mm) examined in this study. Studies of growth and ageing of juvenile *Haliotis rubra* in southern Tasmania strongly suggest that one shell layer is deposited in juveniles also (unpublished work in progress). A strong cohort was sampled at two intervals 12 months apart and the shells from the two periods ring-counted. The difference in mean number of rings was 1.

The evidence of these two studies in southern Tasmania provide strong evidence that the conclusion of McShane and Smith (1992) that shell growth rings are unreliable indicators of age in *Haliotis rubra* is not true generally.

REFERENCES

Dickson, J.A.D. (1965). A modified staining technique for carbonates in thin section. *Nature* 4971: 587.

Jones, R. (1958). Lee's phenomenon of "apparent change in growth rate" with particular reference to haddock and plaice. pp. 229-242 in *International Commission for the Northwest Atlantic Fisheries, Special Publication 1*. Halifax, Canada.

McShane, P.E. and M.G. Smith (1992). Shell growth checks are unreliable indicators of age of the abalone *Haliotis rubra* (Mollusca: Gastropoda). *Australian Journal of Marine and Freshwater Research* 43: 1215-1219.

Nash, W.J. (1990). Abalone mature with age not size. *Fishing Today* 3(2): 38-39.

Prince, J.D. (1989). The fisheries biology of the Tasmanian stocks of *Haliotis rubra*. *Unpublished Ph.D. thesis, University of Tasmania*: Hobart.

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

Prince, J.D., T.L. Sellers, W.B. Ford and S.R. Talbot (1988). A method for ageing the abalone *Haliotis rubra* (Mollusca: Gastropoda). *Australian Journal of Marine and Freshwater Research* 39: 167–175.

Ricker, W.E. (1969). Effects of size-selective mortality and sampling bias on estimates of growth, mortality, production and yield. *Journal of the Fisheries Research Board of Canada* 26: 479-541.

SECTION 6: POPULATION STUDIES OF BLACKLIP ABALONE (*HALIOTIS RUBRA*) IN SOUTH AUSTRUALIA

WARWICK J. NASH, SIMON R. TALBOT, ANDREW CAWTHORN AND JAMES BRIDLEY

6 Population studies of blacklip abalone (*Haliotis rubra*) in South Australia

Warwick J. Nash, Simon R. Talbot, Andrew Cawthorn and James Bridley

As outlined in the Executive Statement, the South Australian component of this study was unable to achieve its objectives because of bad weather and lack of a suitable site. Nevertheless, the following work was done:

- 468 blacklip abalone (*Haliotis rubra*) were tagged and released at Sherbet Reef in Rivoli Bay. Twenty-one of these were recovered in early 1995, five years after tagging. This will be used by the South Australian Research and Development Institute in their program to elucidate the relationship between nimber of shell growth rings and age.

- Radial transects surveyed around three emergent reefs in Rivoli Bay demonstrated a clear pattern of abundance and distribution with respect to the prevailing swell. Small (young) abalone were in highest abndances on the lee side without exception. This work has given rise to various hypotheses about the factors determining abalone abundance and distribution, and about the dispersal capacity of *Haliotis rubra* larvae under the conditions prevailing in Rivoli Bay.

SECTION 7.: POPULATION STUDIES OF BLACKLIP ABALONE (*HALIOTIS RUBRA*) IN NEW SOUTH WALES

WARWICK J. NASH, SIMON R. TALBOT, ANDREW CAWTHORN AND STEWART DICKSON

7 Population studies of blacklip abalone (*Haliotis rubra*) in New South Wales

Warwick J. Nash, Simon R. Talbot, Andrew Cawthorn and Stewart Dickson

Introduction

As with the South Australian component of this study, the New South Wales objectives could not be met because of limited time and lack of suitable isolated reefs with adequate numbers of abalone. Nevertheless, the surveys conducted there were important because they provided an initial assessment of the impact of fishing on the stock. Length-frequency and abundance surveys were conducted at a number of sites along the southern NSW coast. In addition, size-at-maturity analysis was conducted on samples of the fished population, suggesting that the minimum size limit is reasonably protective of the stock.

All data and field notes from this survey have been given to Dr Neil Andrews, scientist in charge of abalone research and assessment at the NSW Fisheries Research Institute.

The following notes are in draft form only.

Size, growth, maturation and fishing: interactions between these and implications for fishery management

Optimal allocation models of growth and reproduction show that the two most important determinants of size/age at onset of sexual maturity (OSM) are food availability and mortality (Kozlowski, 1992). The discussion in this note relate primarily to mortality.

If fitness is defined as the number of offspring left by an individual that survive to reproductive age, then the size at which fitness will be maximised depends on the mortality rate. If population mortality rate is low, the expectation that an animal will survive to old age is high. Since larger individuals of a species can have larger gonads, and therefore higher reproductive output, than small individuals, a selective advantage is conferred on those animals which delay OSM until they have reached a large size. Delaying OSM until a large body size is attained is not selectively advantageous if the expectation of living long beyond the age at OSM is low – that is, if the population mortality rate is high. In this case, an animal which matures at a

young age (and small size) is more likely to have greater fitness (produce more offspring) than an animal which defers OSM until a larger body size is attained.

This trade-off between growth and maturation is likely to be reflected in variation in the pattern of maturation by size and age between populations of a species, which in turn is determined by spatial variation in mortality rates.

Temporal variation in mortality rates is also likely, as causes of mortality (predation, environmental factors) fluctuate in both the short and long term.

For a species which is fished, such as abalone, one of the major causes of mortality is fishing; the expectation of surviving to an old age, relative to that prior to fishing, is substantially reduced. Selective pressures will therefore operate to favour OSM at a younger age (and therefore smaller size). Animals that mature early will not grow as large as late maturers, since much (most?) of the available energy (remaining after metabolic demands are met) that would otherwise be invested in somatic growth is no longer available; it has been spent of reproductive development. Thus, intensive fishing will promote early maturation, with a consequent decline in production rates from the population. Although there is little doubt that this is occurring, it is difficult to say at the moment whether this is a strong selective factor. In many areas of Tasmania this seems unlikely, since large abalone are still relatively common. (But perhaps the variation in growth rate reflects variation in fishing intensity rather than (or as well as) variation in food availability. The large abalone on the west coast may therefore be under less selective pressure to reproduce at a smaller size than those in the east and south-east.

There is one place, however, where decline in age and size at OSM may be happening: New South Wales. In a survey of the abalone stocks there in September 1991, knife-edge selection was the prevailing situation: fishing pressure is so intense that few abalone survive to grow more than a few millimetres larger than the size limit, even though the maximum size attainable in many areas is/was much larger than this. The size composition of the sample taken at Gary Hamer's Mowarry Point site shows a clear reduction in maximum size compared to Gary's sample taken about 10 years earlier. The NSW divers said on a number of occasions that fishing in some areas along the south coast (those producing the largest quantities of abalone) was so intense that individual abalone that were not quite legal size were probably removed, measured and replaced on the bottom more than once a day. It is difficult to imagine fishing pressure much greater than this; it amounts to very high levels of fishing mortality. The importance of fishing as a mechanism/force for increasing maturation

at small size can therefore hardly be questioned. It would be instructive to find out whether Gary Hamer did any size-at-OSM sampling at any NSW sites. If so, it would be worthwhile going to the same place(s) and re-sampling the population(s), and comparing the results. If the above decline in age/size at OSM, anticipated above, did occur, it should be detectable.

It was noteworthy that several NSW divers told me that abalone no longer grow as large as they used to. A couple suggested weather as the cause (unusually warm for the past few years – this may have affected the abundance and nutrient content of the algae upon which the abalone feed). If this is so, then the second cause of early maturation (food availability) may have been operating in concert with fishing pressure to reduce the age/size at OSM, and hence growth rate and maximum size. Water temperature records should confirm whether this has in fact occurred; also algal surveys (species composition, abundance, distribution and/or nutrient content), if they have been carried out.

I was initially surprised that a couple of the NSW divers I spoke to, and whose opinion I had come to respect, had suggested that the size limit should be *reduced*, rather than raised. If the size at OSM has in fact decreased over time, this would not be hazardous, since a substantial proportion of the egg production would still be conserved. But it would place even further pressure on the stocks and, if possible, drive the age/size at OSM down even further, thereby reducing the productivity of the populations to an even lower level (if the species or population has the inherent genetic capacity to continue to respond). So lowering the size limit would not be a wise move.

The decline in age/size at OSM, and therefore of productivity, described above have important implications for management of abalone and other species that are managed by a size limit regulation. Elsewhere (refs) I have argued that, in principle at least, it is possible to manage a fishery by minimum size limit alone: if the size limit is high enough to protect an adequate proportion of the population egg production for recruitment rates to be sustained, then assigning a TAC is unimportant since the fishery and population will be sustained by egg production by animals smaller than the size limit, even if all legal-sized animals are taken. If fishing pressure on the legal-sized animals is vary high, however, then selective forces are likely to drive the size at OSM downward, and the numbers and proportion of the population growing to legal size will decline. A reasonable return from the fishery may then be achieved by lowering the size limit (a short-term solution) or reducing fishing pressure (a long-term solution). It would therefore seem that management by size limit alone, in the

absence of controls on the proportion of the legal-sized fraction of the population taken, is inadvisable; rapid growth and late OSM (ingredients for a productive fishery) within a population can only be maintained if fishing pressure is sufficiently light that a substantial proportion of the population survives to grow substantially larger than the minimum size limit. **[Refer here to Parma and Deriso (1990)]**

Reduction in size at OSM in NSW, but not across the border in Victoria, could only be considered a possibility for a species with limited larval dispersal. Abalone satisfies this condition, although the dispersal capacity is uncertain.

How might the importance of mortality and food availability to the decline in size of NSW blacklip abalone be assessed (or if a decline has in fact occurred)? There are at least four ways:

(i) Check with Gary Hamer to see if size at OSM was measured for any populations in the past. If so, a comparison made with size-at-OSM measurements taken now should show whether or not there has been a change in size at OSM at all.

(ii) Set aside an abalone sanctuary within the NSW abalone fishing grounds, in an area where the present size limit is now considered to be too high. Assuming the sanctuary is not fished, then, if there has been no decline in age/size at OSM, monitoring of growth (of animals that are tagged for the purpose) should show growth to a size similar to that recorded 10 to 20 years ago.

(iii) Transplant abalone from a very heavily fished site in NSW to a site (over the border in Victoria?) where abalone still grow to a fairly large size (*e.g.*, near the wreck of the *Iron Prince*). If the cause of the stunting is genetic, then the pattern of growth and maturation of these transplanted abalone should resemble that of the parental population from which they were derived. If the cause is environmental/physiological (food availability, high temperatures), then the transplanted abalone should exhibit growth and maturation patterns similar to those of abalone in the area to which the NSW abalone have been transplanted. The experiment could best be done using immature abalone; abalone which are sexually mature may not have the capacity to show a desired response (increase in growth rate) since they may be committed to allocating their energy to reproduction. (I doubt this would the case, actually, since the reason that growth slows once an animal matures (when it has an environmental, not genetic, basis) is that it is not possible *under the prevailing conditions* to allocate energy to somatic growth. If transplanted to an area of better environmental conditions,

however (more or better food, or more suitable temperatures), then the abalone may then be able to allocate more energy to reproduction as well as to growth. The results obtained from a transplantation of sexually mature abalone may be different from those obtained for immature abalone, but they may still yield an answer to the question of whether slow growth in NSW is due to environmental reasons (limited food or suboptimal temperatures) or genetic reasons (high mortality).

The question that would most directly answer the genetics/environment question is: *Does the pattern of age/size at OSM change when abalone are transplanted from a small-abalone area (NSW) to a large-abalone area?* This question can only be answered explicitly by transplanting immature abalone and comparing the rate of OSM of these transplanted abalone with that of (i) abalone in the area of origin, and (ii) abalone at the transplant site. A comprehensive experiment would require both controls and reciprocal transplants.

(iv) Genetic studies on other animals have shown that fast-growing individuals are heterozygous at a greater proportion of gene loci than slow-growing individuals. If growth has in fact slowed in NSW abalone (as appears to be the case), then a genetic analysis of NSW and Victorian abalone populations may show a difference (higher levels of heterozygosity in Victoria). This result may not be achieved if the mechanism causing slower growth of predominantly homozygous individuals of other species are not somehow causally related to OSM at an earlier age.

(v) Find out if records have been kept in NSW of water temperatures (and perhaps algal abundance and algal nutrient content). An increase in temperature and decline in algal abundance or quality would indicate that decline in age/size at OSM (if it is in fact occurring) is related to food availability rather than mortality. (But these two factors may be intimately – perhaps inextricably – linked, because animals that are short of food may also die sooner.

A relevant paper to read is the one by a Chinese author and Carl Walters on the shift of a fish species living in the South China Sea from a large, fast-growing, late-maturing life history to a small, slow-growing, early-maturing life cycle. Check to see if this fishery became less productive as a result. It is possible that, even though individuals became slower growing, the habitat may have been able to support more of them (since they were smaller and required, individually, less food but, as a population, the same amount of food as before).

A conclusion from the arguments presented here is that if a minimum size limit is imposed when a fishery commences (or soon afterwards), and if the size limit is conservative of its protection of egg production (say 40 percent or more), it will be almost impossible to collapse the stock: growth overfishing will not be followed by recruitment overfishing because the animals will become sexually mature at progressively smaller sizes, and a progressively greater proportion of the egg production will be occurring in animals smaller than the size limit. Whether or not the *total* egg production will increase as size at OSM declines will depend on whether the decrease in fecundity per individual (due to the smaller average size of sexually mature animals) is compensated for by increase in abundance of sexually mature animals below the size limit.

Another point: Andrew pointed out that abalone that mature at a smaller size are covered in coralline algae by the time they reach the size limit. They are therefore less conspicuous, and less catchable, than abalone that emerge, as they mature, at a size larger than the size limit. This will be an additional pressure selecting against fast growers/large maturers.

More thoughts on mortality, growth and reproduction

If mortality rates are high in small abalone and low in large abalone, there will be selective pressure to grow fast through small sizes, then grow big before OSM. If mortality rates are high for large abalone (or for abalone of all sizes), selection will favour maturation at a small size (which will therefore not grow so big). The existence of populations of big abalone therefore suggests that most of the mortality takes place in the young age classes. Therefore, population regulation (factors determining the stock-recruitment relationship) is probably occurring during the early life stages. The stock-recruitment relationship may therefore be expected to be looser for these populations. In general, the more evenly spread the mortality is over the life stages/ages, the closer the stock-recruitment relationship is likely to be (but it still may not (cannot?) be very close, since abalone are such high-fecundity animals).

References

Kozlowski, J. Optimal allocation of resources to growth and reproduction: implications for age and size at maturity. *Trends in Ecology and Evolution* 7: 15-19.

Parma, A. M. and R. B. Deriso, 190. Dynamics of age and size composition in a population subject to size-selective mortality: effects of phenotypic variability in growth. *Canadian Journal of Fisheries and Aquatic Sciences* **47:** 274-289.

SECTION 8.: AN APPRAISAL OF THE USEFULNESS OF STOCK-RECRUITMENT RELATIONSHIPS FOR ASSESSING AND MANAGING ABALONE FISHERIES

WARWICK J. NASH

8 An appraisal of the usefulness of stock-recruitment relationships for assessing and managing abalone fisheries

Warwick J. Nash

A major objective of this study was to estimate how accurately blacklip abalone abundance can be estimated. As set out in the original application to FIRDC, it was proposed that these findings would then be used to monitor the abundance of a spawning stock and of recruits to that stock. Time series of these data would then be used to define the stock-recruitment relationship (SRR) and to determine the spawning stock density at which recruitment rate above replacement levels is maximal. Management could then aim to maintain stocks at this optimal density.

In the following discussion it is argued that the SRR is unlikely to be useful for managing abalone fisheries because of (i) the fine spatial scale over which the relationship between stock and recruitment is likely to vary, and the inability to manage a fishery at this spatial resolution; (ii) the high fecundity of abalone; (iii) some evidence of recruitment failure in north-east Tasmania from catch statistics (catch, effort *and* CPUE going down) despite high levels of conserved egg production in this area (Nash 1992).

Recruitment rate variation

Population surveys conducted in north-east Tasmania have shown that two blacklip abalone populations separated by about 10 km are almost identical in their rates of growth, survival and fecundity, yet differ markedly in abundance of immediate pre-recruits (Nash 1990). The most likely explanation is that these two populations differ in recruitment rates; that is, in the proportion of spawned larvae that survive to enter the fishery at the legal minimum size limit. If this is so, then an important [corollary] is that the levels of egg production required to enable these populations to sustain equal levels of fishing will also vary. Management measures used to conserve abalone fisheries in Australia (legal minimum size limits and a total allowable quota) would be impossible to implement at as fine a spatial scale as recruitment rate variation is likely to occur.

Population surveys conducted elsewhere in Tasmania indicate that the above example is not exceptional. Marked differences in size, growth rate and abundance between blacklip abalone populations inhabiting bays and exposed headlands lead to the same conclusion (unpublished data).

Shepherd (1990) and McShane (1991) presented evidence that post-settlement survival rates of blacklip abalone (*Haliotis rubra*) and greenlip abalone (*H. laevigata*), respectively, are strongly density-dependent. If this is so, little or no relationship between spawning stock and recruitment would exist except at high and low stock abundances.

Fecundity and the stock-recruitment relationship

[Mention Shepherd's recent work on greenlips. I think he suggests a Ricker-type relationship.]

Evidence from catch-effort statistics

[NE blocks: decline in catch, effort and CPUE suggests (but is not conclusive evidence of) a decline in recruitment rate. Yet EPR analysis suggests ?? to ?? percent of the virgin stock egg production was being conserved [in 1989], which should be more than adequate to sustain a high-fecundity species like *Haliotis rubra*. Similarly, Shepherd (1990) reported levels of egg production required to sustain greenlip abalone fisheries varied considerably between localities.

It is concluded that, unless abalone fisheries can be managed at spatial scales similar to those over which recruitment rates (and therefore stock-recruitment relationships) vary, abalone fishery management must steer a middle course between being over-conservative (all stocks adequately protected) and risky (few stocks protected). Perhaps the most effective means of doing this is to set the legal minimum size limit at a level that neither excludes most stocks from the fishery nor exposes a large proportion of the stocks to the dangers of overfishing.