# Assessing population sustainability and response to fishing in terms of aggregation structure for greenlip abalone (*Haliotis laevigata*) fishery management

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**Abstract:** The greenlip abalone (*Haliotis laevigata*) population in Waterloo Bay, South Australia, has undergone collapse and fishery closure twice since 1978. A rich data set, including survey measures of degree of spatial aggregation, has been gathered over that time and provides a unique opportunity to identify factors accounting for persistence or collapse, an issue that is of significance to abalone fisheries worldwide. Statistical analyses of fishery and survey data were undertaken to infer functional relationships between catch, effort, recruitment, adult density, and extent of aggregation. Catch rates were hyperstable, an observation consistent with the targeting of large aggregations. Statistical analysis of recruitment showed a significant year effect, implying an environmental signal, and suggested that aggregation size impacts fertilization success. Aggregation size grew under closure, suggesting an impact of fishing on this demographic feature. Aggregative behaviour appears to be critical for subpopulation sustainability. Fishery collapse may be triggered by depletion of larger abalone aggregations by heavy fishing, resulting in declines in fertilized egg production. When heavy fishing coincides with unfavourable environmental conditions, recruitment may be insufficient to sustain the subpopulation. If aggregation is similarly critical for other subpopulations, management strategies could be adapted according to the extent of aggregation in each subpopulation.

**Résumé :** La population de l'ormeau *Haliotis laevigata* de la baie de Waterloo en Australie du Sud a subi un effondrement et, à deux reprises depuis 1978, la pêche commerciale en a été interdite. Pendant cette période, cependant, se sont accumulées d'importantes banques de données, en particulier des mesures d'inventaire du degré de contagion spatiale; c'est là une occasion unique d'identifier les facteurs qui expliquent la persistance ou l'effondrement de la population, une question d'importance pour les pêches commerciales d'ormeaux partout dans le monde. Des analyses statistiques des données de pêche et d'inventaire ont permis de mettre en évidence des relations fonctionnelles entre les captures, les efforts de pêche, le recrutement, la densité des adultes et le degré de contagion. Les taux de captures sont hyperstables, ce qui s'explique par le ciblage des grands regroupements. Les analyses statistiques du recrutement révèlent un effet significatif de l'année, ce qui laisse croire qu'il existe un signal de l'environnement et que la taille des regroupements affecte le succès de la fertilisation. La taille des regroupements augmente lorsque la pêche est interdite, indiquant que la pêche affecte cette caractéristique démographique. Le comportement de regroupement semble jouer un rôle essentiel dans le maintien des sous-populations. L'effondrement du stock semble être déclenché par l'élimination des grands rassemblements à cause d'une pêche intensive qui entraîne un déclin dans la production d'oeufs fécondés. Lorsque la pêche intensive coïncide avec des conditions environnementales défavorables, le recrutement peut ne pas suffire à maintenir la sous-population. Si les rassemblements sont aussi essentiels chez d'autres sous-populations, les stratégies de gestions peuvent être adaptées selon les niveaux de contagion de chacune des sous-populations.

[Traduit par la Rédaction]

## Introduction

The greenlip abalone (*Haliotis laevigata*) is extensively harvested in South Australia for export to Asia. The stock consists of approximately 300 subpopulations, three of which (Waterloo Bay, Backstairs Passage, and Avoid Bay) have experienced population collapse (Shepherd and Rodda 2000). A subpopulation is defined as a group of abalone occurring in clusters on patches of loosely connected habitat that together form a local population whose spatial dimensions are of the

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scale over which the habitat is continuous (usually tens to hundreds of metres). Local populations are then grouped into metapopulations whose spatial dimension is of the scale of larval dispersal and mixing (Shepherd and Brown 1993). To date, the causes of collapse in these subpopulations have not been formally investigated. However, McShane (1995), Shepherd and Partington (1995), and Shepherd and Brown (1993) suggested that the situation is more complex than one of simple overfishing and that a dynamic understanding of fishing intensity, factors affecting recruitment, and the importance of aggregations (Gorfine et al. 1998) is required before the factors responsible for collapses may begin to be identified.

As in most fisheries, abalone management strategies are generally implemented on a broad spatial scale. Specifically, the *H. laevigata* stock for the state of South Australia is divided into three management units, each on the order of hundreds of kilometres of coastline: the southern, central, and western zones (Keesing and Baker 1998). However, collapses have occurred at the subpopulation level (e.g., reefs or bays). The persistence under exploitation of subpopulations managed identically but with different egg production and recruitment characteristics has been highly variable (Shepherd and Baker 1998). This suggests that management regulations should be tailored to individual subpopulations, notably those for which indicators suggest declining abundance (Prince and Shepherd 1992; Shepherd and Brown 1993; McShane 1995).

In this study, we investigated the greenlip subpopulation in Waterloo Bay (Elliston, South Australia), which has experienced two collapses (1979 and 1987). Subsequent to each collapse, the bay was closed to fishing (from 1982 to 1986 and from 1995 to the present), with the exception of two controlled "fish-downs" in 1998 and 1999. Annual research surveys have been conducted in the bay since 1978 (Shepherd and Partington 1995), and a spatially resolved catch–effort database has been maintained since 1967. Of particular value are a semiregular time series of survey measures of the degree of abalone aggregation. Thus, there exists for this subpopulation a detailed data history spanning two fishery collapses and closures. The population is thought to be largely or entirely self-propagating (Shepherd and Brown 1993; Shepherd and Partington 1995).

Our objective was to infer the functional relationships between catch, effort, recruitment, adult density, and level of aggregation. These data are examined using generalized linear modelling to find the predictor variables accounting for annual variation in catch and recruitment and thus provide insight into the factors that are most important for abalone population sustainability. Temporal trends in egg-to-recruit survival and reevaluations of Shepherd and Partington's (1995) stock–recruitment relationship and temporal aggregation data are considered in the context of the results of the statistical models. Our goal was to identify key factors accounting for population persistence or collapse in Waterloo Bay and thus formulate a basis for improved management and fishery models.

## Methods

### Data

The fishery-dependent and -independent variables used in the analyses are defined in Table 1. Data were available from Waterloo Bay from 1975 to 1999. During this time, the following events are noteworthy: (*i*) the bay was closed to fishing between 1982 and 1986 and from 1995 to 1998 and (*ii*) in 1998 and 1999, the bay was opened for 2 weeks to limited quota fishing within a size slot of 125–145 mm total length (the longest section of the shell).

Fishery-independent surveys were undertaken immediately before and after the size-slot fishing in 1998 and 1999. In 1998, surveys consisted of random swims and trials of a line transect method. Details of each method can be found in Appendix A. The prefishing (April) data were obtained from 57 random swims and 11 line transects (2089 individual abalone counted), and the postfishing (May) data were obtained from 46 random swims and eight line transects (1217 individuals counted). In 1999, April data were obtained from 65 random swims and 74 line transects (4797 individuals counted) and May data from 68 random swims and 81 line transects (4829 individuals counted). Aggregation data were combined across both types of surveys. It should be noted that the catch and effort data from these two years were not used in the statistical catch models or analyses because the values are affected by the imposition of a quota.

Data on aggregation patterns were obtained from surveys of aggregation size distributions from 1982, 1984, 1986, and 1988 (published as fig. 7 in Shepherd and Partington 1995) and from 1998 and 1999 (before and after fish-down). Data from 1982 to 1988 were combined across the three geographical relief categories ("low", "medium", and "high") used by Shepherd and Partington (1995). Aggregations binned by Shepherd and Partington (1995) in the aggregation size class ">26" were conservatively assigned the aggregation size range of 26–30 individuals. In the 1998 and 1999 surveys, the size of each aggregation encountered was explicitly recorded. Following Shepherd and Partington (1995), the size of an aggregation was defined as the number of abalone greater than 120 mm total length less than 1 m from the nearest neighbour. A distance of 1 m was chosen because modal nearest-neighbour distances are 20–30 cm (Shepherd and Partington 1995) but also because individuals greater than 1 m apart show a dramatic decline in fertilization success with increasing distance from their nearest neighbour (Babcock and Keesing 1999). For the line transect surveys, only aggregations whose size could be fully viewed from the line were recorded. For larger aggregations that extended beyond the transect edge, divers left the transect line to count the individuals.

To summarize changes in aggregation patterns over time, the mean aggregation size was then calculated for each year as follows:

$$(1) \qquad \bar{i} = \sum_{i=1}^{n} (iP_i)$$

where $i$ is aggregation size and $P_i$ is the proportion of individuals found in aggregation size $i$.

### Exploratory statistical analysis

To investigate the critical factors affecting the population sustainability, three response variables were investigated: catch, recruitment, and aggregation structure.

**Table 1.** Primary data and secondary data for Waterloo Bay from 1976–1997.

| Time series | Symbol | Source | Years available | Description |
|---|---|---|---|---|
| **Primary data** | | | | |
| Catch | $C$ | Monthly commercial catch logs: South Australian Reasearch and Development Institute (SARDI) records | 1975–1999 | Kilograms meat weight harvested by commercial divers. Meat weight assumed to be one third of the total weight |
| Fishing effort | $E$ | Monthly commercial catch logs: SARDI records | 1975–1999 | Total hours spent underwater by commercial divers |
| Recruitment | $R$ | Research dive surveys conducted by S.A. Shepherd | 1976–1990, 1994, 1996–1999 | Numbers per 100 m² for the 2-year-old age class ("cohort") determined using modal separation of length–frequency distributions (Shepherd and Partington 1995) |
| Mean adult stock density | $D$ | Research dive surveys conducted by S.A. Shepherd | 1976–1990, 1994, 1996–1999 | Numbers per square metre for individuals ≥4 years of age determined using modal separation of length–frequency distributions (Shepherd and Partington 1995) |
| Aggregation frequency distributions | Not applicable | Shepherd and Partington 1995; research dive surveys conducted by S.A. Shepherd and N.A. Dowling | 1982, 1984, 1986, 1988, 1998, 1999 | Frequency distributions of individuals in aggregation size categories. Aggregations defined as the number of individuals >120 mm total length found <1 m from their nearest neighbour (Shepherd and Partington 1995) |
| **Secondary data** | | | | |
| Index of fertile gamete production | IFGP | Shepherd and Partington 1995 | 1976–1990 | An index of biomass weighted for the degree of aggregation calculated as the product of the aggregated spawning biomass (a linear function of adult density) and the fertilization success factor $F$, where $F = \sum_{i=1}^{n} P_i E_i$, $P_i$ is the proportion of individuals, and $E_i$ is the proportion of eggs fertilized in aggregations of the $i$th size) (Shepherd and Partington 1995) |
| Survival of an average egg to age 2 | $R/\text{IFGP}$ | Derived | 1976–1990 | Recruitment (density of 2-year-old age class) divided by the IFGP giving an index for the survival of an average egg to age 2 |
| Fishery index | FISH | Monthly commercial catch logs: SARDI records | 1975–1999 | Binary index indicating whether the fishery was open in a given year. This index removed any effect of the fishery status from the year factor in statistical models. Any resulting effect attributed to year was thus independent of that resulting from the status of the fishery |

**Fig. 1.** Surveyed estimates of adult density (squares and shaded line) and recruitment (2-year-olds, lagged by 2 years to correspond to year of spawning) (circles and solid line) versus year obtained using the timed random swim technique.
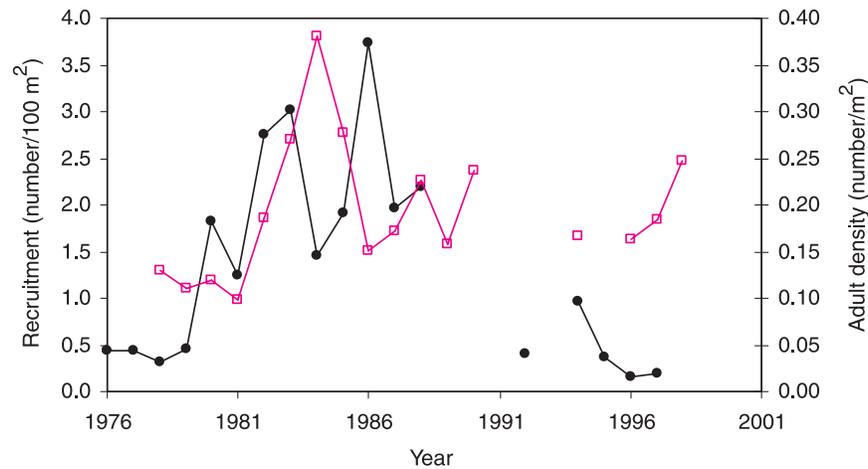


Combinations of annual catch, effort, catch-per-unit-effort (CPUE), and adult biomass were plotted and their regression coefficients compared in an attempt to identify systematic bivariate relationships and potentially important predictor variables for catch. Auto- and cross-correlation were used to test for periodic trends in time series and time lags in correlations between recruitment (of 2-year-olds) and adult biomass, recruitment and the index of fertile gamete production (IFGP) (see Table 1), and survival to age 2 and adult biomass. The cross-correlation function, $r_{xy}(k)$, measures the degree of correlation between variables $x_t$ and $y_{t+k}$, where $k$ is the lag number (Chatfield 1975).

Recruitment values were lagged by 2 years to associate the recruitment density, defined as the density of 2-year-old abalone (Table 1), with the year of spawning. A generalized Deriso equation gave a better fit to the data, in terms of both least squares and overall shape, than the Ricker stock–recruitment relationship presented by Shepherd and Partington (1995). The equation, modified to include an $x$-intercept, as described by Chen et al. (2002), is of the form

$$(2) \qquad R = \alpha(\text{IFGP} + c)[1 - \beta(\text{IFGP} + c)/\Gamma]^\Gamma$$

where $R$ is recruitment, IFGP is the index of fertile gamete production (Table 1), and $\alpha$, $\beta$, $\Gamma$, and $c$ are fitted parameters.

Catch and recruitment were more formally investigated using generalized linear models. The advantage of such models is that they allow explanatory variables to be collectively examined to determine the relative contribution of each to the variation in the response. Each yields single linear coefficients associated with each predictor. Residual and quantile–quantile plots were used to assess model fit. As such, recruitment was modelled assuming a Gamma error distribution and a log link function, whereas catch and effort were square root transformed and the square root catch was modelled assuming a Gaussian error distribution and an identity link function to relate the mean of the behavioural parameter to its linear predictors (Crawley 1993).

The minimum adequate model for each response variable (catch and recruitment) was determined by sequential deletion of terms from a full model. Significant changes in deviance associated with the deletion or change of an explanatory

variable from the model, as determined by $F$ test, implied that the explanatory variable had a significant influence on catch or recruitment. Model fits were assessed using residual, fitted value and quantile–quantile plots.

The full catch and recruitment linear models tested were

$$(3) \qquad \sqrt{C} = \alpha_1\sqrt{E} + \alpha_2 D + \alpha_3(\text{YR}) + \varepsilon$$

$$(4) \qquad R = \beta_1 D + \beta_2(\text{IFGP}) + \beta_3(\text{YR}) + \beta_4(\text{FISH}) + \varepsilon$$

where $C$ and $R$ are the response variables catch and recruitment, $E$, $D$, and IFGP are the numeric explanatory variables effort, adult density, and index of fertile gamete production, YR and FISH are the explanatory variables year and fishery status index (open or closed), treated as factors, $\alpha_i$ and $\beta_i$ are single linear coefficients, and $\varepsilon$ is an error term.

To investigate aggregation structure, mean aggregation size was plotted against year, and cluster analysis was performed on the frequency distributions for 1982–1988 and 1998–1999. This indicated the degree of relatedness between distributions from different years and, for 1998 and 1999, those observed before and after fish-down events. For the 1998 and 1999 data, the $\chi^2$ test was employed to determine whether the frequency distributions before and after fishing in each year differed significantly.
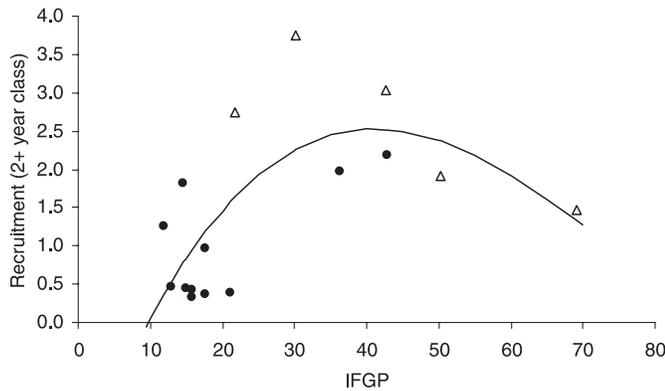
## Results

### Recruitment analyses

Peaks in recruitment lagged those in adult density by 2 years (Fig. 1), and the cross-correlation function for adult density versus recruitment was maximized at a lag number of two ($r_{xy}(2) = 0.724$). That is, recruitment was most positively (and significantly ($r_{df=8,\alpha=0.05} = 0.632$, $P < 0.05$)) correlated with adult density 2 years subsequently. Recalling that recruitment equates to the density of 2-year-old abalone, shifted back 2 years to correspond to the year of spawning, the density of 2-year-old abalone was strongly positively correlated with the density of adults in the same year.

Similarly, the cross-correlation function was maximized at a lag number of 2 for both combinations of IFGP versus recruitment and adult density versus survival to age 2 (R/IFGP)

**Fig. 2.** Generalized Deriso stock–recruitment equation (curved line) fitted to 16 data points representing annual estimates of recruitment and IFGP (index of fertile gamete production, an index of biomass weighted for the degree of aggregation). Circles, surveyed recruitment during years of fishing; triangles, surveyed recruitment during closure years. Adapted from Shepherd and Partington (1995).



**Fig. 3.** Time series plot for an index of the survival of an average egg to age 2 calculated as $R$/IFGP (recruitment divided by the index of fertile gamete production). The plot indicates an oscillatory trend with peaks in 1980–1982 and 1986.



($r_{xy}(2) = 0.789$ and $r_{xy}(2) = 0.801$, respectively). Both cross-correlation coefficients were statistically significant ($r_{df=8,\alpha=0.05} = 0.632$, $P < 0.05$). That is, the density of 2-year-old abalone was positively correlated with the index of biomass weighted by the degree of aggregation (IFGP) (Table 1), and survival to age 2 was positively correlated with adult density in the year in which the recruits turn 2 years old.

Cross-correlations for recruitment versus adult density and recruitment versus IFGP did not show a strongly positive cross-correlation function at any lag number (for lag number = 0, $r_{xy}(0) = 0.242$ ($r_{df=10,\alpha=0.05} = 0.576$, $P > 0.05$) and $r_{xy}(0) = 0.288$ ($r_{df=10,\alpha=0.05} = 0.576$, $P > 0.05$), respectively). Thus, recruitment success was not positively correlated with the adult abundance in the year of spawning.

The cross-correlation function for survival to age 2 ($R$/IFGP) versus adult density was negative for all lag numbers but was highest in magnitude at lag number 0 ($r_{xy}(0) = -0.433$). Although this correlation coefficient is not statistically significant ($r_{df=10,\alpha=0.05} = 0.576$, $P > 0.05$), it suggests that a high adult density resulted in a low survival rate to age 2 for abalone spawned in the same year.
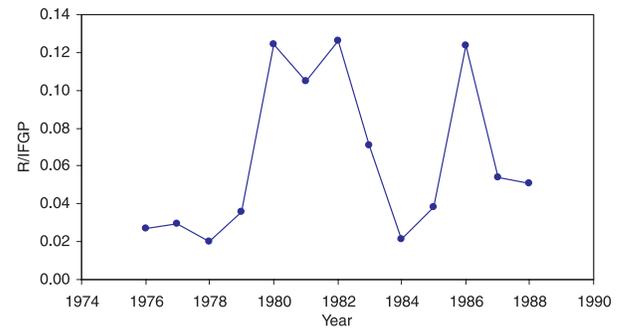
The relationship between stock, expressed as IFGP (the index of biomass weighted by the degree of aggregation), and recruitment was best described by the following Deriso equation, which was fitted to 16 data points (Fig. 2):

$$(5) \qquad R = 0.176(\text{IFGP} - 9.696)$$
$$\times [1 - 0.020(\text{IFGP} - 9.696)/1.665]^{1.665}$$

Maximum recruitment occurs at IFGP = 42, which corresponds to an adult density of ~0.22 adults·m$^{-2}$ (significant linear regression between adult density and IFGP ($r^2 = 0.92$)). Three of the four data points to the right of this maximum (including the highest two IFGP values) are from the years in which the bay was closed to fishing.

A time series plot of survival to age 2 (calculated as $R$/IFGP) (Fig. 3) exhibited an oscillatory trend with peaks in 1980–1982 and 1986. Indeed, autocorrelation analysis yielded a maximum, although not statistically significant, autocorrela-

tion coefficient at a lag of $k = 6$ years for $R$/IFGP ($r_6 = 0.224$, $r_{0.05(2),6} = 0.707$, $P > 0.05$).

Recruitment patterns were most adequately described by a linear model of IFGP (adult biomass weighted for aggregation) and year:

$$(6) \qquad R = -19.05(\text{IFGP}) - 0.3446(\text{YR})$$
$$- 0.0096(\text{IFGP} \times \text{YR}) + 683.83$$

where IFGP × YR is the interaction between IFGP and YR (Table 2).

This model reduced the null deviance by 72.8% for a loss of 3 degrees of freedom compared with the null model (Table 2). There was a significant interaction between year and IFGP (Table 3). Both IFGP and adult density, $D$, were used as indices of biomass in the models, but IFGP was a significantly better predictor in terms of residual deviance (Table 3), albeit at the cost of 2 degrees of freedom (Table 2). Importantly, the effect of fishing was treated as a separate factor, and so the significant year effect was not due to the status of the fishery.

**Catch analyses**

Catch showed a strong positive-linear relationship with effort ($r^2 = 0.98$) (Fig. 4a) that was highly significant (regression ANOVA: $F = 1462.91$, df = 1, 27, $P = 0$) but no significant relationship to adult density ($r^2 = 0.37$) (Fig. 4b) (regression ANOVA: $F = 4.15$, df = 1, 7, $P = 0.08$). This implies that catch is independent of abundance but is a strong linear function of effort. Further, adult density showed no significant relationship with respect to CPUE ($r^2 = 0.20$) (Fig. 4c) (regression ANOVA: $F = 1.76$, df = 1, 7, $P = 0.23$). This suggests that CPUE is not proportional to greenlip abalone abundance in Waterloo Bay.

Linear models also indicated that effort accounted for the majority of variation in catch. There was also a significant interaction effect between effort and year, whereby effort decreased over time. The minimum adequate model was

$$(7) \qquad \sqrt{C} = 3.898\sqrt{E} + 17.301D - 5.293\sqrt{E} \times D - 4.776$$

where $E \times D$ is the interaction between effort and adult density. This model reduced the null deviance by 98.3% (see Table 4 for analyses of deviance).

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**Table 2.** Analysis of deviance tables for linear models predicting recruitment.

| Number | Model | Null deviance | Null df | Residual deviance | Residual df |
|---|---|---|---|---|---|
| 1 | $R \sim$ IFGP + CALYR + $D$ + FISH | 7.0630 | 12 | 2.3910 | 8 |
| 2 | $R \sim$ IFGP + CALYR + FISH | 7.0630 | 12 | 3.1708 | 9 |
| 3 | $R \sim$ IFGP + FISH | 7.0630 | 12 | 6.2369 | 10 |
| 4 | $R \sim$ CALYR + FISH | 12.5763 | 16 | 12.3192 | 14 |
| 5 | $R \sim$ IFGP + CALYR | 7.0630 | 12 | 4.2629 | 10 |
| 6 | $R \sim$ IFGP + CALYR + IFGP × CALYR[a] | 7.0630 | 12 | 1.9227 | 9 |
| 7 | $R \sim$ IFGP | 7.0630 | 12 | 6.3289 | 11 |
| 8 | $R \sim$ CALYR | 12.5763 | 16 | 12.5200 | 15 |
| 9 | $R \sim D$ + CALYR | 10.1899 | 14 | 9.4843 | 12 |
| 10 | R $\sim D$ + CALYR + FISH | 10.1899 | 14 | 8.9077 | 11 |

**Note:** The null degrees of freedom vary because of variations in the number of available data points for the response variables included in each model. ~, modelled as a function of; CALYR, calendar year; IFGP × CALYR, interaction term for IFGP and CALYR.

[a]Minimum adequate model.

**Table 3.** Results from ANOVAs comparing the recruitment linear models.

| Models compared | Variable tested | Change in deviance | $F$ | $P(F)$ |
|---|---|---|---|---|
| 2 vs. 3 | YR | 3.0661 | 8.5063 | 0.0171275* |
| 2 vs. 4 | IFGP | 9.1484 | 5.0762 | 0.017334* |
| 2 vs. 5 | FISH | 1.0921 | 3.0300 | 0.1157253 ns |
| 5 vs. 6 | IFGP and YR interaction term | 2.3403 | 10.8510 | 0.0093175** |
| 5 vs. 9 | $D$ as compared with IFGP | 5.2213 | 6.2680 | 0.0172038* |
| 4 vs. 10 | $D$ | 3.4114 | 1.6466 | 0.2353892 ns |

**Note:** *, Significant at the 5% level; **, significant at 1% level; ns, not significant at the 5% level.

Consistent with Figs. 1–3, catch was not related to adult density and year but was highly linearly dependent on effort. The interaction effect between adult density and effort was weaker when the 1986 data point was excluded (Table 5). In 1986, the fishery was reopened after the 4-year closure and experienced a greater increase in effort relative to the corresponding increase in adult density that had taken place, resulting in the two variables becoming aliased.

**Aggregation data**

After the closure of the fishery in 1982, individuals showed a progressive trend towards larger ($\geq$20) aggregation sizes (Figs. 5a–5c). After the reopening of the fishery in 1986, fewer individuals were found in larger aggregations by 1988 (Fig. 5d). However, this reduction of larger aggregation sizes did not approach the 1982 distribution observed before closure, possibly because of the newly imposed larger size limit of 145 mm total length as opposed to 130 mm (Shepherd and Partington 1995). Mean cluster size, a parameter sensitive to the intensity of aggregation (Shepherd and Partington 1995), showed a similar trend between 1982 and 1988 (Fig. 6); its magnitude increased from approximately 5 to 11 after the fishery closure and declined to below 9 in 1988 (recall that the maximum aggregation size had been conservatively set at 30 individuals).

Cluster analysis of the 1982–1988 distributions yielded results consistent with Figs. 5 and 6. A Bray–Curtis similarity dendrogram (Fig. 7) showed that the distributions for 1984 and 1986 were more closely related to one another than to the 1988 distribution and that the 1982 distribution showed the least degree of relatedness to any of the other distributions.

Unlike the 1982–1988 data, for which aggregations over the size of five had been binned, the specific sizes of each aggregation were recorded in 1998 and 1999. The April 1998 aggregation frequency distribution (Fig. 8a) reflects the population aggregation structure after 3.5 years of closure to fishing. The maximum aggregation size surveyed was 190 individuals, and 30% of surveyed abalone occurred in aggregations $\geq$20. Three aggregations larger than 80 individuals were recorded. After the 1998 fish-down, where licensees were permitted a 50-kg (meat weight) quota, only one aggregation >80 was observed during surveys (Fig. 8a), and the proportion of individuals in aggregations of 20 or more individuals had dropped to 18%.

After the 1998 fish-down, the population was unfished until April 1999. The survey immediately before the commencement of the 1999 fish-down showed the population collecting into larger aggregation sizes (Fig. 8b), with 25% of surveyed individuals in aggregations of 20 or more. Four aggregations of more than 80 individuals were recorded; however, the proportion of individuals in aggregations of more than 80 did not approach that of April 1998 (Fig. 8a). Licensees each removed 150 kg (meat weight), and after fishing, the population again contracted towards smaller aggregation sizes (Fig. 8b), with only 15% of individuals found in aggregations $\geq$20. Only one aggregation >80 was observed. In both 1998 and 1999, the proportion of individuals in aggregations of two to four increased by 24% and 29% respectively.

Mean aggregation size showed a decrease from 37 to 19 after the 1998 fish-down, an increase to 22 over the next 11 months, and a decline to 14 after the 1999 fish-down (Fig. 9). Cluster analysis of the 1998 and 1999 distributions indicated that between-year

**Fig. 4.** Scatterplots of (*a*) financial year catch versus effort (underwater), (*b*) financial year catch versus surveyed adult density, and (*c*) financial year CPUE versus adult density, each with fitted regression lines.
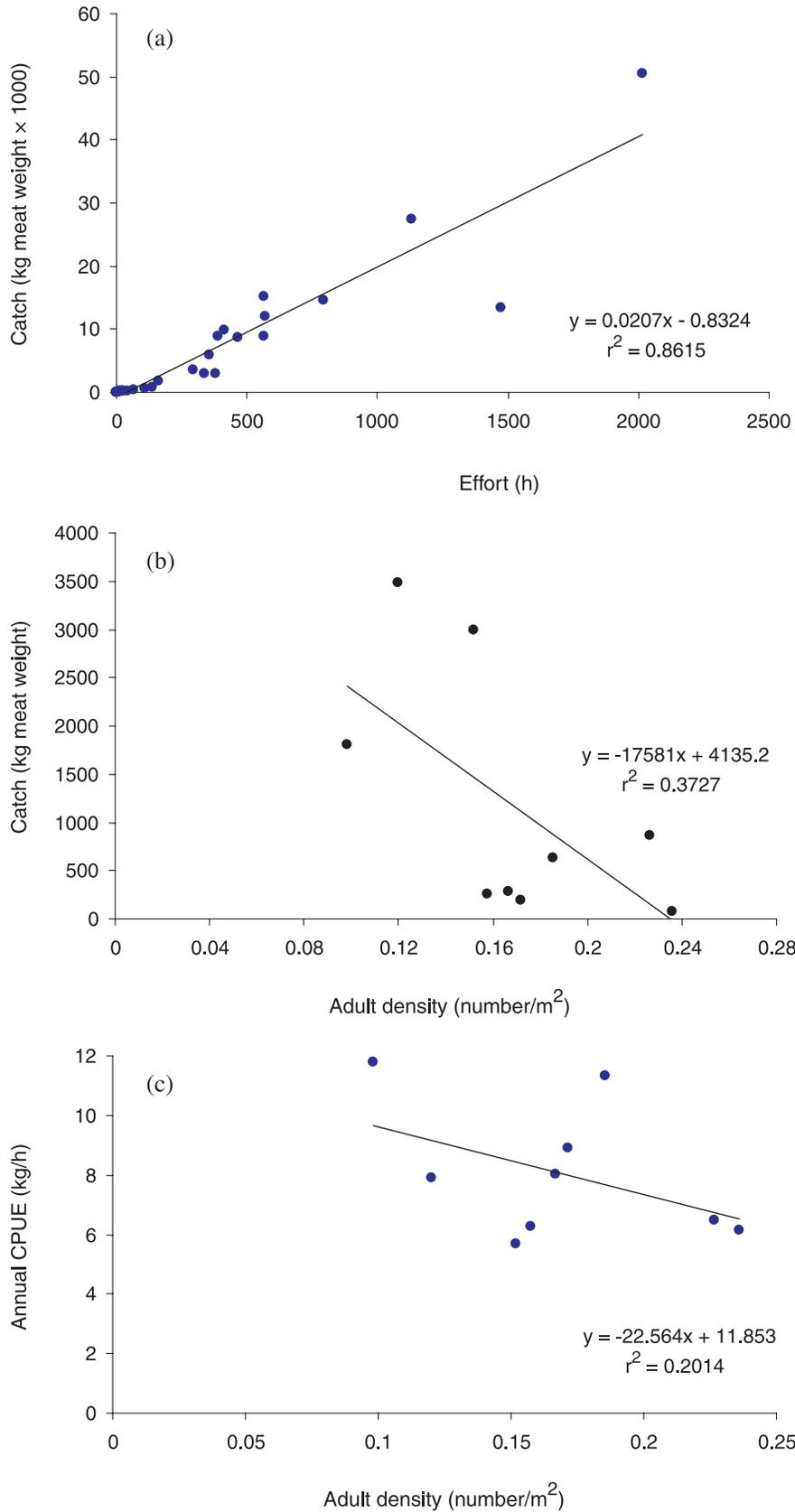
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**Table 4.** Analysis of deviance tables for linear models predicting catch.

| Number | Model | Null deviance | Null df | Residual deviance | Residual df |
|---|---|---|---|---|---|
| 1 | $C \sim E + D + \text{CALYR}$ | 6883.085 | 14 | 160.005 | 11 |
| 2 | $C \sim E + \text{CALYR}$ | 6893.589 | 18 | 185.704 | 16 |
| 3 | $C \sim D + \text{CALYR}$ | 6883.085 | 14 | 3248.432 | 12 |
| 4 | $C \sim E + D$ | 6883.085 | 14 | 160.009 | 12 |
| 5 | $C \sim E$ | 6893.589 | 18 | 186.328 | 17 |
| 6 | $C \sim D$ | 6883.085 | 14 | 4719.080 | 13 |
| 7 | $C \sim E + D + E \times D^a$ | 6883.085 | 14 | 118.719 | 11 |
| 8 | $C \sim E + D$ with 1986 data point excluded | 5301.836 | 13 | 156.220 | 11 |
| 9 | $C \sim E + D + E \times D$ with 1986 data point excluded | 5301.836 | 13 | 118.073 | 10 |

**Note:** ~ modelled as a function of; $E \times D$, interaction term for E and $D$.
[a]Minimum adequate model.

**Table 5.** Results from ANOVAs comparing the catch linear models.

| Models compared | Variable tested | Change in deviance | $F$ | $P(F)$ |
|---|---|---|---|---|
| 1 vs. 2 | $D$ | 25.6988 | 0.3533 | 0.8697 ns |
| 1 vs. 3 | $E$ | 3088.4270 | 212.3225 | $1.54586 \times 10^{-8}$** |
| 1 vs. 4 | CALYR | 0.0040 | 0.0003 | 0.9871 ns |
| 4 vs. 7 | $D \times E$ | 41.2898 | 3.8257 | 0.0763 ns |
| 8 vs. 9 | $D \times E$ excluding 1986 data | 38.1471 | 3.2308 | 0.1025 ns |

**Note:** *, Significant at the 5% level; **, significant at the 1% level; ns, not significant at the 5% level.

**Fig. 5.** Frequency distributions of the proportion of individuals in each aggregation size for (*a*) 1982, (*b*) 1984, (*c*) 1986, and (*d*) 1988 (adapted from Shepherd and Partington 1995). Aggregations greater then 5 were binned by 5 up to the "plus" class of ≥26. The final category was conservatively truncated at an aggregation size of 30.
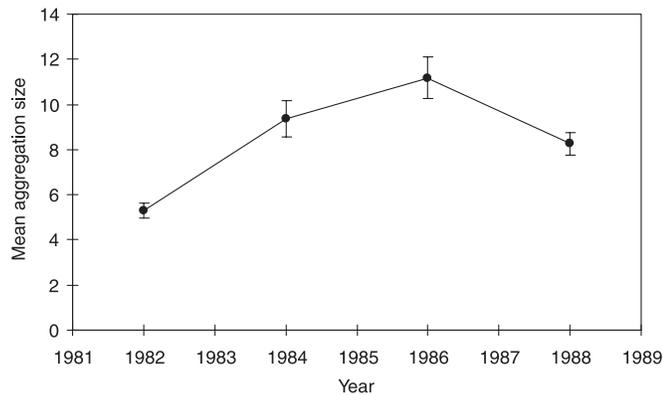


Aggregation size (beyond aggregation size of 5, bin width = 5)
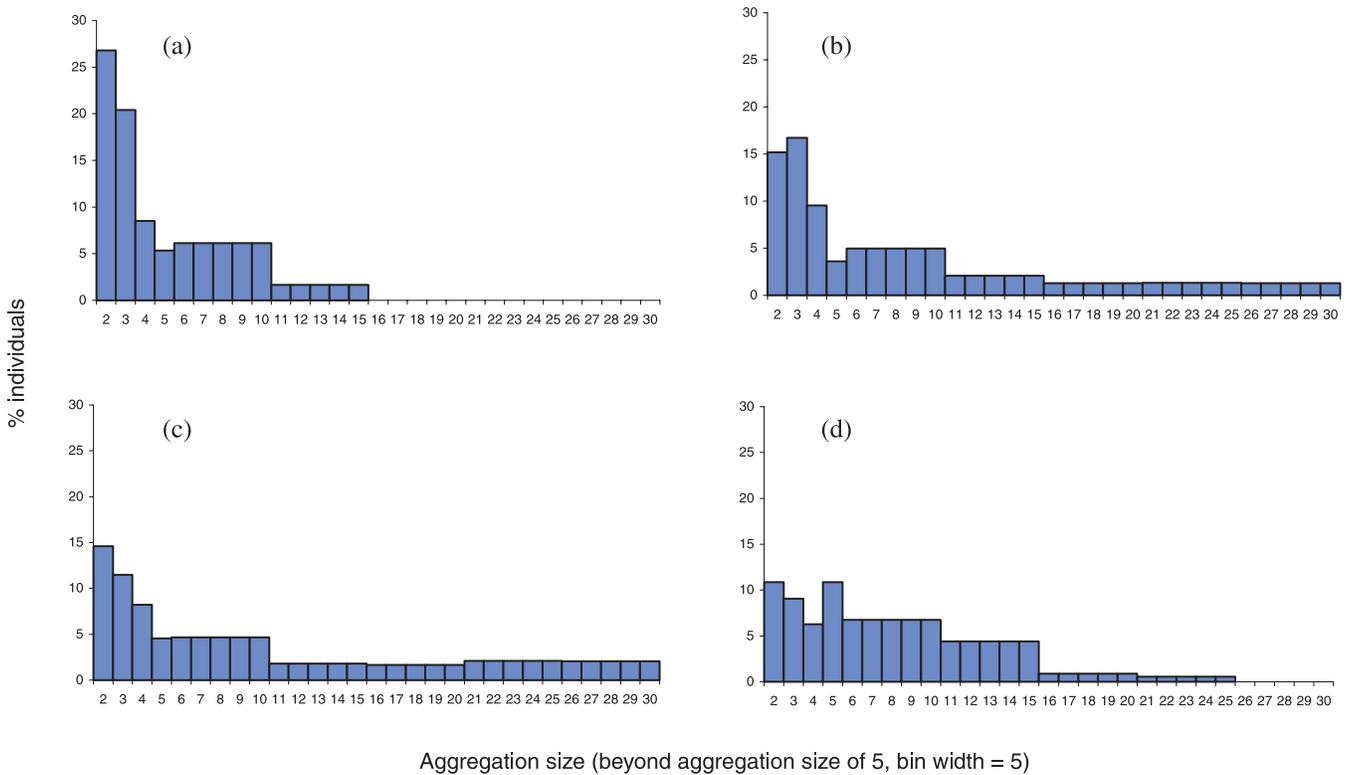
variability was greater than the within-year variability induced by fishing (Fig. 10). However, $\chi^2$ analyses indicated a significant difference between the pre- and post-fishing distributions for both the 1998 data ($\chi^2_{df=15, \alpha=0.05} = 172.8$, $P = 0$) and 1999 data ($\chi^2_{df=20, \alpha=0.05} = 648.6$, $P = 0$).

## Discussion

### Recruitment

The fitted Deriso stock–recruitment equation, together with the negative correlation between survival to age 2 and adult

**Fig. 6.** Mean aggregation size versus year for 1982–1988 data. Error bars are ±1 SE.



**Fig. 7.** Bray–Curtis similarity dendrogram from cluster analysis illustrating the degree of relatedness for aggregation size–frequency distributions for 1982–1988.



density, shows that density dependence occurs. Shepherd and Partington (1995) suggested that the IFGP corresponding to the recruitment maximum on the stock–recruitment curve is a threshold value above which density dependence takes place and below which the subpopulation is vulnerable to over-exploitation. That three of the data points in the "density-dependent" regime of the curve (i.e., to the right of the fitted recruitment maximum) correspond to the years of fishery closure supports this notion. The likely mechanism responsible for density dependence is limitation in appropriately sized crevices to shelter the juveniles, which are then vulnerable to predation.

Attempts to derive stock–recruitment relationships for other South Australian greenlip abalone populations such as Avoid Bay and Cape Jervis resulted in an apparently random scatter of stock–recruitment data (Shepherd and Rodda 2000). The ability to define an underlying stock–recruitment relationship for fisheries that typically have high fecundity and high larval dispersal has been disputed (Underwood and Fairweather 1989; Koslow 1992) because small changes in prerecruit natural mortality lead to large changes in survivorship (Koslow 1992). As the Waterloo Bay subpopulation is isolated with no external larval sources (Shepherd and Brown 1993), it is reasonable to consider stock–recruitment dynamics within the subpopulation. Indeed, Prince et al. (1988) showed a strong relationship between local population breeding stock density and recruitment (albeit on a scale of metres) in blacklip abalone (*Haliotis rubra*).

Although a threshold IFGP for overexploitation may be a reasonable concept, it is not explicit with respect to the mechanisms responsible for recruitment failure, since IFGP is a variable constructed from three variables: adult stock density, fertilized egg production, and degree of aggregation. Using linear modelling, both IFGP and a year effect were shown to significantly affect recruitment. As the status of the fishery had no significant effect on recruitment, the year effect was attributed to an environmental signal. The latter may also have been responsible for the oscillating time series for survival of an average egg to age 2 ($R$/IFGP). The nature of this signal has not been identified. However, the CPUE for sand crabs in Coffin Bay, Eyre Peninsula, also shows a 6-year periodic oscillation such as that found for survival to age in Waterloo Bay greenlip abalone (Jones 1995; Jones and Deakin 1997). Additionally, Venus Bay prawns and west coast rock lobster CPUEs follow the same 6-year oscillation
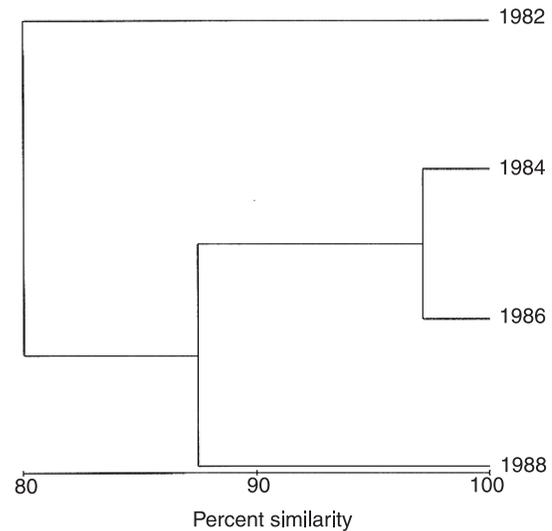
as the sand crab CPUE (G.K. Jones, SARDI Aquatic Sciences, P.O. Box 120, Henley Beach, South Australia 5022, Australia, personal communication). This may suggest a large-scale environmental signal affecting invertebrate fisheries on the west coast of South Australia.

Linear modelling showed that IFGP (an index of biomass weighted by the degree of aggregation) was a better predictor of recruitment than adult density. This suggests that aggregation size has a significant impact on recruitment, most likely in terms of fertilization success. Abalone are broadcast spawners, and it has been shown experimentally (Babcock and Keesing 1999) that fertilization success is a negative-exponential function of near-neighbour distance for greenlip abalone. As larger aggregations have a lowered average near-neighbour distance and a higher local density, their probability of fertilization success for broadcast gametes increases. Group size (4 individuals versus 16 individuals) and degree of aggregation (0.25 individual·m$^{-2}$ versus 4 individuals·m$^{-2}$) were shown to significantly affect fertilization success in sea urchins (Levitan et al. 1992). Indeed, it is on this assumption that Shepherd and Partington (1995) calculated the IFGP parameter. The proportion of eggs $E_i$ fertilized in each aggregation $i$ was derived from the results of Levitan (1991) and Levitan et al. (1992) for sea urchins.

**Validity of recruitment**

Cross-correlation analyses showed that the density of 2-year-old abalone was strongly positively correlated with the adult abundance (adult density or IFGP) in the same year. That is, if adult density is high in a given year's survey, so is the density of 2-year-olds. Survival to age 2, calculated as $R$/IFGP, was also strongly positively correlated with the adult density surveyed in the same year as the recruitment density.

This suggests that recruitment estimates may be biased by overall abundance. The small size of 2-year-old abalone (40–80 mm) makes them difficult to detect in surveys, and as such, recruitment estimates are based on very small observed numbers. For example, of the 2612 abalone measured in May 1999, only 26 fell into the length category for 2-year-

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**Fig. 8.** Frequency distributions of the proportion of individuals in each aggregation size for April (prefishing, solid bars) and May (postfishing, open bars) in (*a*) 1998 and (*b*) 1999. Note that the maximum aggregation size is 190 for 1998 and 120 for 1999.
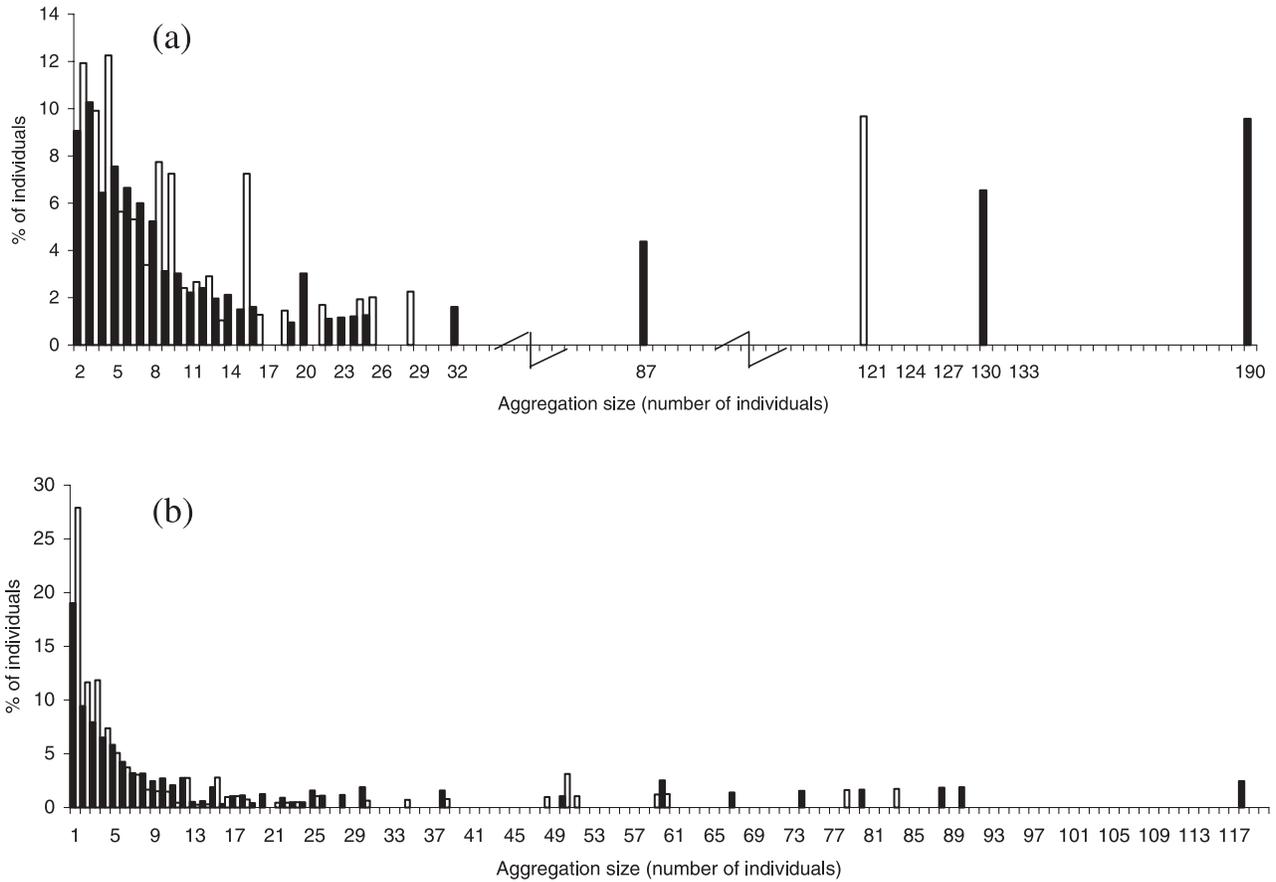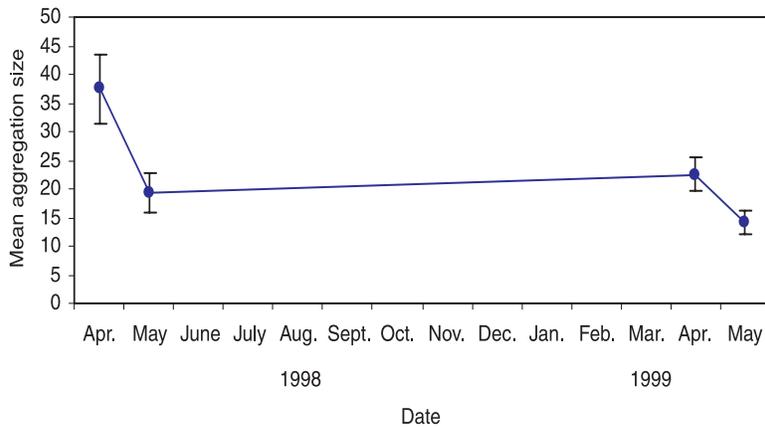


**Fig. 9.** Mean aggregation size versus time for 1998 and 1999 data. Error bars are ±1 SE.



old individuals. It may be that when overall abalone abundance is high, the observer spends more time looking closely at the bottom and thereby is more likely to notice smaller abalone. Whatever the case, the cross-correlation results indicate that recruitment densities should be used with caution.
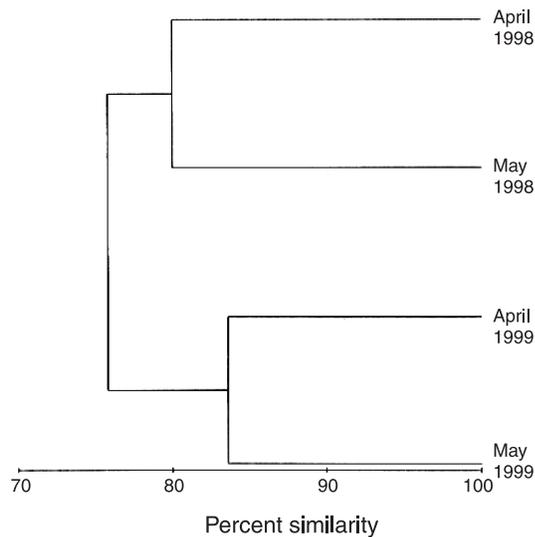
**Catch**

Catch in Waterloo Bay was linearly proportional to effort and independent of density and year, whereas CPUE also showed no relationship with adult density. The bivariate

relationships between catch or CPUE and adult density were not positive-linear; indeed, both relationships showed negative associations. This supports Prince's (1992) conclusion that catch or CPUE should not be used as an index of abundance for abalone. It also implies that the traditional catch equation (Schaefer 1954)

$$(8) \qquad C = qEB$$

where $C$ is catch, $q$ is the catchability coefficient, $E$ is effort, and $B$ is biomass, does not apply to this fishery because annual

**Fig. 10.** Bray–Curtis similarity dendrogram from cluster analysis illustrating the degree of relatedness for aggregation size–frequency distributions for April and May in 1998 and 1999.



catch was shown to be solely a function of effort (confounded by year). Biomass is more likely to influence catch in terms of a discrete threshold level below which fishers give up searching. However, this "cutoff" situation has not been observed for Waterloo Bay.

These results are consistent with the concept that abalone actively aggregate (Shepherd 1986; Prince 1992; Gorfine et al. 1998) and abalone divers target the aggregations. The implication is that the abalone subpopulation behaves similarly to a pelagic fishery in that the prey (abalone) continually reaggregate and the fishers hunt the aggregations (Hilborn and Walters 1992). If divers spend little time randomly searching for abalone, checking the condition of known "abalone beds" by looking at the state of an abalone bed's aggregations before deciding whether to dive in that location, catch tends to remain proportional to the time spent diving (Prince 1989; Prince et al. 1998). As such, catch is a linear function of effort and is not sensitive to the depletion of the surrounding biomass that replenishes the aggregations. Potentially, the ultimate situation under continued effort is one of hyperdepletion and fishery collapse (Hilborn and Walters 1992).

### Aggregation

The correlation of trends in aggregation with the status of the fishery, whereby larger aggregations are formed in the absence of fishing and are reduced to smaller aggregations when fishing takes place, suggests that fishing has a significant effect on aggregation frequency distributions. The increase in the proportion of individuals in larger clusters after fishery closure is consistent with the implication of the results for catch that fishing targets and depletes large aggregations. It must be emphasized that the above analyses do not show conclusively that commercial abalone divers target large aggregations. This issue is addressed in Dowling et al. (2004). However, when the above results are considered in the context of that of Babcock and Keesing (1999) that fertilization success is a function of near-neighbour distance, it may be concluded

that the depletion of larger aggregations has serious implications for reproductive success.

### Hypotheses for population sustainability

The analyses conducted suggest two hypotheses. The first is that cyclic environmental factors impact the Waterloo Bay subpopulation to reduce the recruitment success of an average egg on a 6-year period. At this stage, the environmental factor has not been conclusively identified. The second hypothesis is that aggregative behaviour has a critical role with respect to subpopulation sustainability. Although this has been suggested indirectly by Prince (1992), McShane (1995), and Shepherd and Partington (1995), these results provide the first statistical evidence to support this hypothesis. It appears that exploitation targets aggregations, which are believed to have the greatest contribution to reproductive success (Babcock and Keesing 1999), so that the most significant contributors to fertilized egg production are those that are the most vulnerable to exploitation. Aggregation level appears to drive the population dynamics to a greater extent than does absolute biomass. Therefore, rather than proposing an IFGP level below which the subpopulation is vulnerable to overfishing (Shepherd and Partington 1995), it may be preferable to consider a critical aggregation frequency for adequate fertilization success and to define the degree of vulnerability to fishing in terms of aggregation structure. A more simple management strategy may be to designate areas known to contain large aggregations as reserves, although enforcement would be difficult.

It is tentatively hypothesized that fishery collapse in the Waterloo Bay greenlip abalone subpopulation is due to overfishing resulting in the depletion of larger aggregation sizes, which in turn implies a decline in fertilized egg production. When this is combined with unfavourable environmental conditions, recruitment may be insufficient to sustain the subpopulation.

The issues of hyperstability and recruitment overfishing, resulting in the rejection of CPUE as a valid index of abundance, have implications for spatially heterogeneous fisheries in general. How fish are distributed and how fishers allocate their fishing effort in space are essential ingredients in understanding how a fishery develops and the relationship between catch rate and abundance (Hilborn and Walters 1987). In this context, the findings are applicable to schooling pelagic stocks where CPUE is a poor index of abundance, such that schooling leads to a strong depensatory effect (Clark 1974). The purse-seine fishery, where floating attraction devices are used to aggregate tuna species, is an example of such a fishery, as is the northern cod fishery. Incorporating aggregation structure in a model of the latter explained how cod vulnerability to fishing could increase with declining stock biomass (Hutchings 1996).

Waterloo Bay is perceived by fishers and fishery managers to be a "unique" subpopulation that is not representative of abalone population dynamics and responses to fishing because of its history of heavy fishing and closure. Although management strategies should account for subpopulation variability, it is important to ensure that the factors affecting Waterloo Bay subpopulation sustainability are reflective of the population dynamics for the species. To validate these conclusions in a broader context, if aggregation can be shown

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to be a critical factor for population sustainability for other subpopulations with different histories of sustainability, then there may be a basis for generalization across subpopulations. If this is the case, management strategies may be adapted given the extent of aggregation in each subpopulation.

## Acknowledgments

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## Appendix A. Description of random swim and line transect methods

In both years, an experienced five- or six-member research team conducted dive surveys in Waterloo Bay in the week immediately preceding and in the week after the opening period. The spatial grid from previous years was used to subdivide the bay into 20 survey blocks (Fig. A1). The ma-

jority of these were surveyed in each year, but swell and visibility restricted access to some blocks. Four days of diving was required to complete each set of surveys. Diving was not necessarily conducted on consecutive days, as inclement weather sometimes prohibited surveying. However, a complete survey did not take longer than 7 days to complete.

In 1998 and 1999, the blocks were surveyed using the timed random swim technique (Shepherd 1985). Divers swam in a random direction for 10 min, during which time they measured in situ the length of all greenlip abalone encountered, with the exception of aggregations greater than four individuals, in which case they measured four abalone. This was the existing survey protocol designed to maximize the area surveyed by limiting the time spent measuring. The size of each aggregation encountered was also recorded. Following Shepherd and Partington (1995), the size of an aggregation was defined as the number of abalone greater than 120 mm standard length less than 1 m from the nearest neighbour. A distance of 1 m was chosen because modal nearest-neighbour distances are 20–30 cm (Shepherd and Partington 1995) but also as a functional definition based on reproductive success; individuals greater than 1 m apart show a dramatic decline in fertilization success with increasing distance from their nearest neighbour (Babcock and Keesing 1999).

A line transect technique was also used to survey the greenlip population in 1998 and 1999. The line transect technique is a form of distance sampling that has been used extensively for terrestrial ecological surveys (Buckland et al. 1993). It has also been used for censuses of commercial reef fishes (Kulbicki 1998) but was trialed for abalone for the first time during the 1998 survey periods and incorporated into the survey protocol in 1999 to estimate abundance.

The line transect technique involved swimming in a straight line for 50 m using a reel with a line, marked at 50-m intervals, attached to a stable object on the bottom. The number of abalone in each aggregation as seen from the line was recorded, together with an approximation of the perpendicular distance of the centre of the aggregation to the line to the nearest half-metre. As it is an assumption of the technique that every individual located directly about the line was detected, divers examined the area under the line thoroughly, moving aside algae and checking under rock overhangs. Having completed a 50-m transect, the diver would swim laterally for a distance of approximately 20 m and conduct a replicate 50-m transect by reeling in the line while swimming along this second radius back to the anchor point. This

**Fig. A1.** Map of Waterloo Bay illustrating the survey block subdivisions.
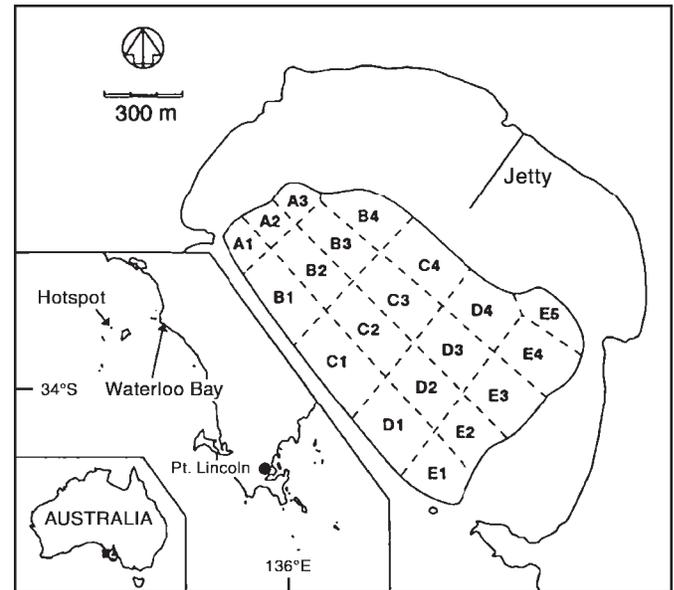


procedure would then be repeated in the opposite direction so that four replicate 50-m transects would ideally be obtained in a single dive. The locations for transects were randomly determined, were not stratified, and were not revisited identically on subsequent surveys.

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