



Interpreting evidence of dispersal by *Haliotis midae* juveniles seeded in the wild

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Abstract

Recovery rates of hatchery-raised juvenile abalone seeded in the wild are a result of both survivorship, and dispersal in the time between seeding and sampling. Seeding experiments with juvenile *Haliotis midae* were conducted at two localities in South Africa to determine recovery rates, which were high at one of the sites (McDougall's Bay) and low at the other (Gouriqua). This difference may reflect the influence of habitat suitability on survivorship, but cannot be interpreted as such without a knowledge of dispersal rates because high dispersal may hinder detection of surviving juvenile abalone. We hypothesized that significant active dispersal by the abalone took place at Gouriqua, where they were seeded in a shallow habitat in which wave and surf activity had a direct impact. Conversely, at McDougall's Bay, a wave-sheltered site, where the juvenile abalone were seeded at slightly greater depth, there was little or no active dispersal by juvenile abalone. We argue that dispersal at Gouriqua took place in response to the effects of wave and surf action, which could be dampened by seeding the abalone at greater depths. Adverse water conditions limit the time and scale of foraging that juvenile abalone can undertake, effectively limiting the number of juveniles that can be accommodated. Within this context, water depth and exposure to adverse ocean conditions must be among the attributes that need to be considered when identifying seeding sites, and interpreting recovery data, since an increase in dispersal makes it more difficult to detect seeded juveniles and therefore will diminish recovery rates without necessarily altering survivorship.

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1. Introduction

Research into technology to optimize ranching of *Haliotis midae* in South Africa (Sweijid et al., 1998; de Waal and Cook, 2001a,b; de Waal, 2002; de Waal et al., in preparation) has resulted in a series of seeding experiments being conducted both east and west of Cape Agulhas. Two of the areas where experiments have been conducted were McDougall's Bay, near Port Nolloth on the north–west Namaqualand coast, and Gouriqua on the south coast (Fig. 1). To date, the main objectives of seeding research have been to determine the ecological and habitat requirements that are vital for juvenile abalone and to analyze the conditions that optimise survival of seeded juveniles, so that appropriate seeding sites can be identified. Recovery rates, i.e., the number of seeded juveniles found by researchers in searches at the end of an experimental period, have been used to measure effectiveness of selected sites and judge the criteria used to select viable sites. The question, however, is what exactly does a specific recovery rate mean? Does a low recovery rate mean a site is unsuitable, and all or most of the juveniles would have died before reaching a harvestable size? Or does it indicate that although the site is capable of providing adequate refuge and foraging habitat for juvenile abalone, there are factors that lead to a high rate of dispersal and, hence, low recovery rates? Dispersal cannot, however, be assumed without evidence. Although it is difficult to measure dispersal of wild juvenile abalone, movements of seeded juvenile abalone can be monitored more easily because they can be differentiated visually from coexisting wild juveniles. Such observations can shed light on the relative densities and patterns of dispersal of abalone in different habitats.

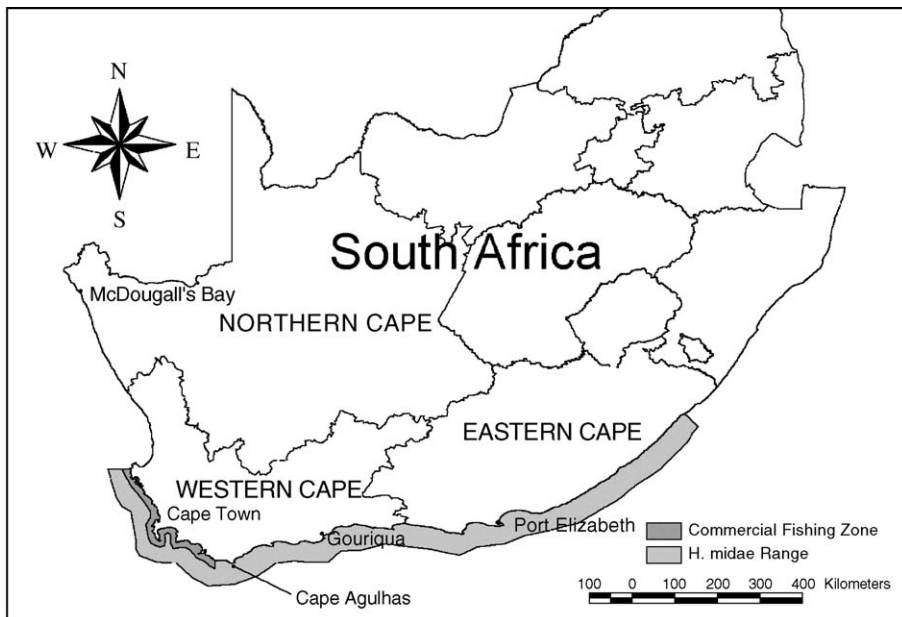


Fig. 1. The experimental areas and natural range of *H. midae* along the South African coast. Cape Agulhas is regarded as the point of distinction between east coast and west coast *H. midae* stocks.

These are important ecological questions that affect management decisions regarding methods of seed release and the relative suitability of seeding sites. With this in mind, experiments are crucial in determining and examining generalizations that can be used to develop the science of stock enhancement and ranching of *H. midae*. In this paper, the results from two sets of seeding experiments—at respectively McDougall's Bay and Gouriqua—are interpreted in the context of direct measurements of dispersal that were made at the time that recovery rates were determined.

Gouriqua, which is situated on the South Coast of South Africa within the natural range of *H. midae*, is ecologically substantially different from McDougall's Bay, which lies on the Namaqualand coast. Namaqualand is outside the natural range of *H. midae*, and falls in the Benguela Current ecosystem, a nutrient-enriched upwelling system that has produced a seaweed flora quite distinct from that at Gouriqua, east of Cape Agulhas (Bolton and Levitt, 1987; Branch et al., 1987). The kelps *Ecklonia maxima* and *Laminaria pallida* are abundant on the west and south–west coasts, where they form the major source of nutrition for *H. midae* (Barkai and Griffiths, 1986; Tarr, 2000). These species are of little importance at Gouriqua on the south coast, where the predominant vegetation consists of smaller algae and algal biomass and cover are lower than on the west coast (Baird et al., 1986; Wood and Buxton, 1996).

Variations in inshore temperatures in the Benguela region are relatively small; a 10-year mean shows a difference of between 2 and 4 °C between the coldest and warmest months. In contrast, temperatures on the south coast are on average higher and annual temperature variations of up to 7 °C have been recorded there (Shannon, 1989). Although the physical substrata on which the seeding experiments at Gouriqua and McDougall's Bay were conducted were visually similar, the average water depth in which seeding took place at Gouriqua was relatively shallow (≈ 0.6 m) than at McDougall's Bay (≈ 2 m).

The objectives of this research were to test the hypothesis that significantly more dispersal took place at Gouriqua than at McDougall's Bay, to offer a hypothesis explaining the reason for active dispersal at Gouriqua, and to develop generalizations that can be used to interpret recovery data from seeding experiments.

2. Methods

2.1. Site attributes

Although the two sets of seeding experiments were conducted in areas that differ with respect to a range of environmental factors, the seeding sites were all selected to provide shelter in the form of under-boulder habitat (Table 1; de Waal, 2002; de Waal et al. in preparation). In both sets of experiments abalone in the size range 12–25 mm were released at the same density from the same type of release module. Additional dispersal data were collected for 45-mm abalone released by hand in McDougall's Bay (de Waal, 2002). The structure of the release modules is described in Sweijd et al. (1998), de Waal and Cook (2001a) and de Waal (2002) but, in brief it comprised 40-cm lengths of PVC piping of three different diameters, cut longitudinally in half and mounted in concentric layers on steel plates (Fig. 2). Habitat assessments and experimental protocol were

Table 1
Physical attributes of the seeding sites at McDougall’s Bay and Gouriqua, and mean recovery rates of seeded juvenile abalone

Site attributes	Average % cover		
	McDougall’s Bay	Gouriqua	<i>p</i> -value
Boulders of diameter			
>50 cm	56	35	0.2
30–50 cm	15	27	0.7
<30 cm	9	25	0.03*
Total under-boulder habitat	27	29	0.65
Exposed habitat	20	12	1
Average depth (m)	2	0.6	0.0001*
Size class of abalone	Average recovery rate (%)		
14-mm	24	5	
26-mm	59	8	

Physical attributes of the seeding sites at McDougall’s Bay and Gouriqua, and mean recovery rates of seeded juvenile abalone; *p*-values were derived from Mann–Whitney *U*-tests, and asterisks indicate significant differences between sites. Exposed habitat is habitat in which no suitable shelter exists for juvenile abalone. Under-boulder habitat is considered to be the inverse of exposed habitat, comprising cracks, crevices or under-boulder habitat.

standard between sites. Physical habitat was quantified according to the attributes listed in Table 1. Average attribute values were compared between the two experimental areas using a Mann–Whitney *U*-test. Wave and surf action at the seeding sites were not quantified, but visual observations of their magnitude were made over the experimental period.

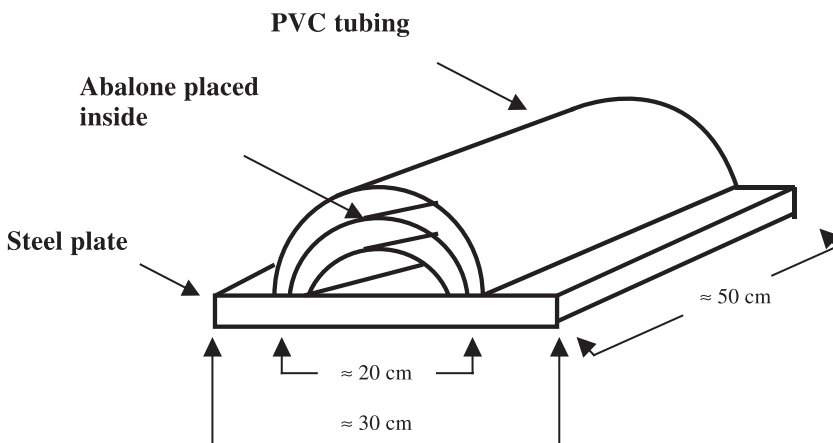


Fig. 2. A line diagram of the type of release module used in the seeding experiments, both on the Namaqualand coast and at Gouriqua.

2.2. Dispersal activity

In the series of experiments conducted with the two smaller size classes of abalone (12 and 25 mm), the experimental procedure prior to the abalone being placed in the release module, during transport (in the release modules), and during release, was standardised as far as possible. In all the experiments, both size classes of abalone were released from the same modules, at the same time. The procedure was as follows:

1. In all cases the abalone used in the seeding experiments were bred and reared on abalone farms. The abalone were transferred to the release modules from holding tanks in which they had been kept prior to the seeding experiments. To achieve this, the release modules were placed in the holding tanks in which the juvenile abalone were being kept. Without the use of any anaesthetic, 100 animals of each size class were placed in the release module, and the modules were closed on each end with a piece of thin, stiff plastic with a number of holes to allow free passage of water. A rubber band was used to keep the plastic covers in place. The modules were totally submerged throughout the loading procedure.
2. The release modules were then left in the holding tanks for approximately 30 min, allowing the abalone to settle and most of the mucus that had been exuded by the abalone to wash away (the loading process takes approximately 5–10 min for each 100 abalone).
3. The modules were then lifted out of the holding tanks, drained of excess water, and placed in sealed styrofoam containers that were transported to the release sites by vehicle. Once there, the modules were taken out of the styrofoam containers and placed in the shallows, completely submerged by the sea water. The modules were then carried underwater to the sites selected for release, where they were placed on a stable area of substratum, and opened. The period between the modules being removed from the holding tanks to the time that they were submerged in the shallows took approximately 15–20 min at Gouriqua. In the McDougall's Bay experiments, this period was approximately 25–35 min. (De Waal, 2002).
4. At both McDougall's Bay and Gouriqua, there were eight seeding modules. At Gouriqua, the area around the first four were sampled after 32 days, and the last four after 62 days (de Waal, 2002). At McDougall's Bay the first four were sampled after 33 days and the last four after 56 days.

In the seeding trial with the larger 45-mm abalone released in McDougall's Bay, no anaesthetic was used. However, in this case the abalone were seeded by hand from a nylon netting bag. The juvenile abalone were placed in the bag, which was kept submerged in the holding tank for approximately 30 min, drained of excess free water and placed in a sealed styrofoam container. The transport time was again between 25 and 35 min, after which the bag was removed from the styrofoam box and placed in the shallows, completely submerged. The bag was then carried underwater by a diver (with SCUBA) to a series of eight pre-selected sites, where 25 abalone were placed by hand per site. At each site the abalone were placed under boulders within a circle of radius approximately 50 cm. The diver placed the abalone individually, holding the abalone

with the foot on the substratum until it was obvious that it had fastened itself securely. The first four sites were sampled after 30 days and the last four after 60 days.

Destructive searches, in which all loose boulders were lifted or rolled, and all cracks and crevices were searched, were conducted around each release module, and the numbers of abalone from each of the size-classes (14 and 24 mm at Gouriqua; 14, 25 and 45 mm at McDougall's Bay) were counted in three distance-categories (1, 2 and >2 m radius from the module). A chi-square analysis (Everitt, 1977) was performed on the data and the adjusted residuals for the contingency tables calculated. Absolute adjusted residuals with a positive value indicate over-representation by individuals in a distance category, while negative values indicate under-representation. Adjusted residuals were considered significant at $p=0.05$ if ≥ 1.96 .

The evenness of adjusted residuals from the different distance categories gives an indication of dispersal activity. If these values are not significantly different, it would indicate that the seeded abalone have merely moved short distances, to position themselves randomly within suitable habitat. If however, adjusted residuals were over-represented in the distances further from the release modules, it would indicate that active dispersal has taken place. Thus, the pattern of dispersal would be shown by the under or over-representation of juvenile abalone in the different distance-categories. At the scale at which the experiments were done, it is not safe to go beyond attempting to test for significant evidence of active dispersal or its absence.

Two separate analyses were undertaken, the first to compare dispersal by the three size classes of seeded abalone (45, 26 and 14 mm) within McDougall's Bay, and the second to compare dispersal by the two smaller size classes between Gouriqua and McDougall's Bay.

3. Results

3.1. Site attributes

The two experimental areas showed little difference with respect to boulder cover and exposed area, with mean percentage boulder cover spanning 27–29%, and exposed habitat being between 12% and 20%. Mann–Whitney *U*-tests failed to detect significant differences between the attributes of the two sites in most cases (Table 1). The only significant difference between the two areas was the percentage cover by boulders <30 cm in diameter, the habitat at Gouriqua comprising an average of 25% boulders <30 cm, and that at McDougall's Bay area 9%. The average depth of the Gouriqua seeding sites (0.6 m) was also significantly lower from that at McDougall's Bay (2 m).

An unquantified effect of depth and exposure differences between the two experimental areas was the relative impact by direct wave and surf action on the seeding habitat. Nevertheless, visual observations and diving conditions made it clear that the seeding habitat in McDougall's Bay was protected from direct wave action and relatively sheltered when compared to the shallower and exposed seeding sites at Gouriqua (de Waal, 2002).

3.2. Recovery rates

Recovery of seeded abalone differed both among size classes and between the two sites. At McDougall's Bay, recovery was greatest for 45-mm animals, and at both sites it was greater for 25-mm abalone than for 14-mm individuals. For both the latter size classes, recovery was significantly greater at McDougall's Bay than at Gouriqua (Table 1). At both sites, extensive searches showed that none of the seeded abalone were ever found >5 m away from the release modules.

3.3. Comparing dispersal activity by 14-, 25- and 45-mm abalone seeded in McDougall's Bay

Barring the 14-mm abalone, which were significantly over-represented in the 2-m distance category, differences in the relative abundance of abalone in the three size classes in McDougall's Bay were not significant (Fig. 3). These results can be interpreted to indicate that the abalone were spread out evenly and were not in a process of active movement out of the seeding area. The results also show that (with the exception of the 14-mm animals at 2 m), there were no significant differences in dispersal between the size classes.

3.4. Dispersal activity in McDougall's Bay compared to Gouriqua

Analyses of the two smaller size classes of seeded abalone from both Gouriqua and Port Nolloth yielded significant departures from expected frequencies (Chi-square = 168.5, $p = 0.0001$). The adjusted residual analyses showed that with respect to 25-mm abalone the pattern of dispersal in McDougall's Bay was the opposite of that at Gouriqua, with all six residual values being significant (Fig. 4a). The McDougall's Bay abalone were over-

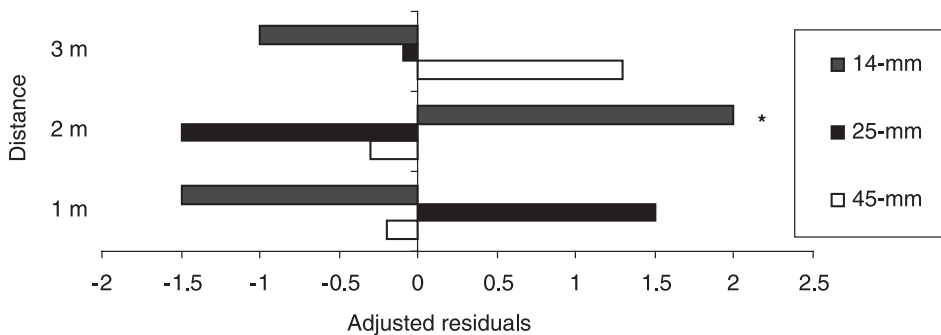


Fig. 3. Adjusted residual analyses of dispersal patterns from McDougall's Bay for 14, 25 and 45 mm seeded abalone over the 1, 2 and 3 m distance categories. A positive adjusted residual value indicates over-representation by individuals in the distance category, and a negative value indicates under-representation. An asterisk indicates significance of absolute adjusted residuals (≥ 1.96 at $p = 0.05$).

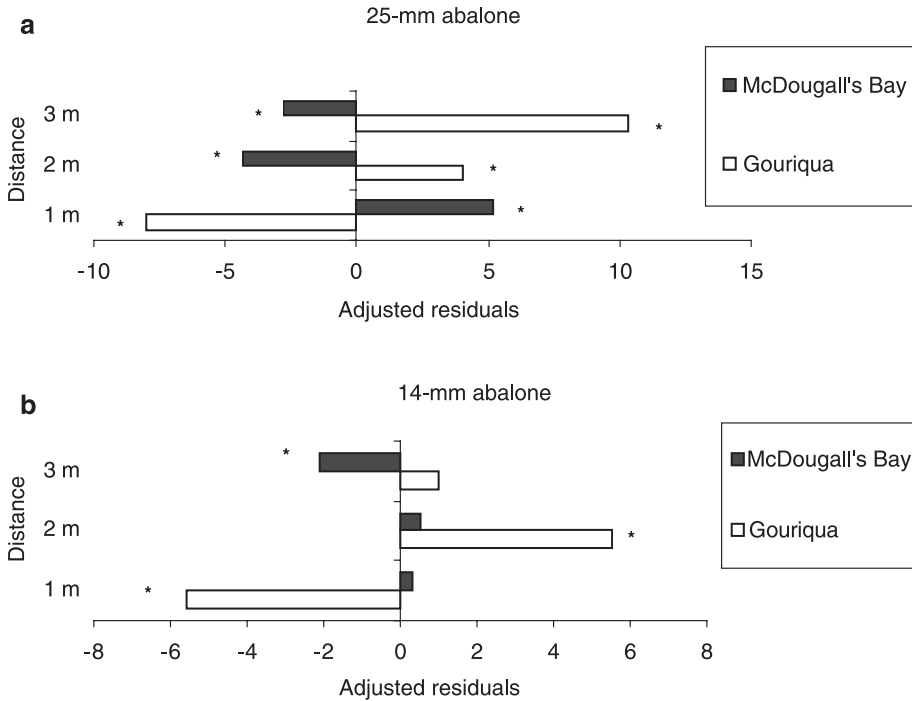


Fig. 4. Adjusted residual analyses of dispersal patterns for (a) 25 mm and (b) 14 mm seeded abalone in the 1, 2 and 3 m distance categories from McDougall's Bay and Gouriqua. A positive adjusted residual value indicates over-representation by individuals in the distance category, and a negative value indicates under-representation. An asterisk indicates significance of absolute adjusted residuals (≥ 1.96 at $p=0.05$).

represented in the 1-m category and under-represented in the 2 and >2 m categories, whereas the Gouriqua abalone exhibited the opposite pattern (Fig. 4a).

In terms of the 14-mm individuals, McDougall's Bay abalone were over-represented in the 1-m category while the Gouriqua abalone were significantly under-represented (Fig. 4b). Conversely, the McDougall's Bay abalone were significantly under-represented in the >2-m category while the Gouriqua abalone were over-represented.

Overall, the McDougall's Bay abalone were under-represented in the 1-m category, while the Gouriqua abalone were generally over-represented >2 m away from the release module. This indicates that the abalone seeded at Gouriqua were actively dispersing, whereas at McDougall's Bay, active dispersal was not taking place.

4. Discussion

All field experiments suffer from the fact that not all variables can be held constant, and there are several ecological and environmental differences between the two experimental areas that need to be recognized when interpreting the results. In particular, these differences must be considered at a scale that is relevant to that at which abalone utilise

habitat (de Waal et al., in preparation). In general, there are three factors that are important when considering areas for seeding or ranching experiments:

1. The abundance and composition of algal species that are the primary sources of nutrition for *H. midae*.
2. Biological interactions between abalone and other species, including predation, competition and commensalism.
3. Physical refuge or shelter from predation and adverse environmental factors that is offered by the habitat.

As outlined in the introduction, differences in floral composition do exist between the two sites, and must be recognized. The nature and abundance of predators at the two sites were not quantified, but differences between the sites are likely. In terms of commensalism, the sea urchin *Parechinus angulosus* has been shown to be extremely important for the survival of juvenile *H. midae* in the Western Cape, providing shelter against predators and capturing drift kelp that subsidises the diet of juvenile abalone concealed under the urchins (Day and Branch, 2000, 2002). Both Gouriqua and McDougall's Bay support populations of *P. angulosus* that are sufficient to have provided shelter for the seeded abalone, although most of the abalone were recovered beneath boulders, and few hid beneath urchins.

In some respects, there are therefore differences in biological conditions between the two sites. We cannot assess the potential influence of these on the patterns of recovery and dispersal described, but their existence needs to be acknowledged. Both sites are, however capable of supporting abalone: natural populations occur at Gouriqua, and survivorship of introduced abalone has been shown to be high at McDougall's Bay (Sweijd et al., 1998). Thus, at a broad geographic level, both sites can be considered suitable as seeding sites.

However, the microhabitat scale at which abalone survive, measured in cm to 10's of m, is the scale at which physical refuge and potential biological interactions become important (de Waal et al., in prep). It is also on this level that selection of seeding sites is important and must be made. Within this context, the most important attribute in seeding site selection determined to date is the potential amount of shelter that can be provided by boulders and reef, with under-boulder habitat being the most important, and cracks and crevices playing a less important role (de Waal, 2002; de Waal et al., in preparation). The physical composition of the substrata differed little between the two sites, offering similar amounts of physical shelter to the seeded abalone (Table 1).

Abalone are sedentary animals that, during the juvenile stage, almost exclusively graze both micro-algae and crustose coralline algae. If juveniles compete for food, which induces movement and dispersal from areas of high density, movement out of shelter means exposure to predation and adverse sea conditions. Adverse sea conditions, such as direct wave action and strong currents dislodge sedentary species, influencing the extent to which routine movement is restricted or limited. Increased water depth has a dampening effect on the strength of wave action and may, as a result, have a direct effect on movement and survival of juvenile abalone. Although wave action was not measured at the two sites, it was clearly greater at Gouriqua than at McDougall's Bay, partly because of the existence

of a protective reef that sheltered McDougall's Bay, but also because the release modules were placed deeper there than at Gouriqua.

Differences in recovery rates of seeded abalone existed both among size classes and between sites (Table 1). As the differences in dispersal among size classes were minor at McDougall's Bay, recovery rates probably reflect the relative rates of survivorship of the different size classes. Had there been substantial differences in dispersal, recovery might not have been related to survivorship but rather to the decreased chance of detecting individuals that disperse widely. This leads to the clear conclusion that recovery and survivorship increases with the size of the seeded abalone. The gains of greater recovery then need to be balanced against the economic costs of seeding abalone of different sizes (de Waal, 2002; de Waal and Cook, 2001a,b).

However, recovery rates or densities need to be interpreted within the context of specific habitats and patterns of dispersal. Dispersal could also be a simple reflection of unsuitable seeding sites, with juvenile abalone actively moving and seeking more suitable habitat in localities where conditions are unfavorable. Regardless of the reason for dispersal, however, it cannot be assumed without evidence.

The interpretation of experimental recovery data of seeded juvenile abalone is an issue of importance to a range of authors (Tegner and Butler, 1985; Rogers-Bennet and Pearse, 1998; Shepherd et al., 2000; Tegner, 2000). Recovery rates are used as indicators of abalone density; as a result, the relationship between recovery rate and potential survivorship is directly affected by dispersal activity. If there is limited or no dispersal, most of the surviving abalone are likely to be detected when searches are made in the vicinity of the release modules. Under these conditions, recovery rate is probably a good reflection of potential survivorship. Conversely, a high rate of dispersal will diminish the detectability of seeded abalone, leading to low recovery rates and an apparently low survivorship. The recovery rates from the first scientific seeding experiments done in South Africa, also on the Namaqualand coast (Sweijd et al., 1998) were interpreted directly as minimum survival rates, without dispersal being factored into the relationship.

The experiments conducted in McDougall's Bay, yielded the highest recovery rates associated with evidence of limited dispersal, while those from Gouriqua yielded the lowest recovery rates coupled with evidence of significant active dispersal.

Habitat complexity and the associated availability of shelter (Caddy and Stamatopoulos, 1990) will affect densities of juvenile abalone that can be supported, and is an important factor in the identification of potential seeding sites. In this context, the relatively high recovery rates for abalone of all three size-classes at McDougall's Bay, coupled with evidence of limited dispersal, indicate that this site provided adequate under-boulder habitat. The same physical characteristics of substratum identification were used when choosing Gouriqua as a comparable experimental site for the release of seeded juvenile abalone. All the seeded abalone recovered there (together with wild juveniles) were utilising shallow under-boulder habitat exclusively as shelter (de Waal et al., in preparation). It is reasonable to assume that the physical boulder habitat plays a part in providing protection against both predation and adverse environmental factors (Shepherd, 1990). It is, however, difficult to determine to what extent small boulders provide refuge to juveniles when they are exposed to direct wave action, and to what extent exposure plays a role in determining densities of juvenile abalone.

Unless they are established over a long-term period, recovery rates do not necessarily reflect long-term suitability of a site. The Gouriqua abalone showed evidence of dispersal while at the same time showing active selection for the small boulders, albeit at lower relative densities, and survived there for a period of 60 days (de Waal, 2002). One hypothesis that may explain why active dispersal took place in Gouriqua is that high wave action restricts routine movement by foraging abalone. In this case, dispersal may be a product of abalone moving to place themselves in better sites within the under-boulder habitat. No measurement was made of dispersal direction. However, dispersal appeared random, with movement taking place in all directions. There were no indications that the juveniles were moving, for example, to deeper water.

Our results showed that higher rates of dispersal occurred at Gouriqua than at McDougall's Bay and the low recovery rates at Gouriqua are likely to be a reflection of this. We recognise that there are other differences between the two sites investigated, but the most likely explanation for the high rate of dispersal at Gouriqua is the more intense wave action experienced there. Further work that isolates this factor will be needed to confirm this.

5. Conclusion

On a practical level, low rates of recovery—whether associated with low detectability due to dispersal or due to high mortality—do mean that yields from seeding will be low. Based on present evidence, positioning release modules at sites with high wave action or in too shallow water is unlikely to produce favorable yields, unless the shallow sites are very sheltered from direct wave action.

Water depth affects the impact of wave action on juvenile habitat, and therefore should be considered in the identification of seeding habitat and in interpreting experimental data from seeding experiments.

To develop the science of ranching, seeding experiments must be conducted based on sound ecological principles and they must be interpreted within this context. Because ranching is a commercial venture, it should be based on the selection of ecological conditions that enhance yields.

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