

AN EXPERIMENTAL TRANSPLANT OF NORTHERN ABALONE, *HALIOTIS KAMTSCHATKANA*, IN BARKLEY SOUND, BRITISH COLUMBIA

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ABSTRACT

The biological and economic feasibilities of transplanting northern abalone, *Haliotis kamtschatkana* Jonas 1845, from exposed beds to two sites in sheltered, productive abalone habitat were investigated. After nine months, 39% and 72% of transplanted abalone were recovered at the two replicate sites. Recovery of tagged abalone at a control site, situated in the exposed source area, was 32%. Growth in shell length of transplanted abalone over the nine months averaged 7.8% whereas the average growth of non-transplanted controls was 3.7%, significantly less. There was little emigration of abalone from the transplant sites.

The study concludes that it is feasible to transplant 50–100 mm *H. kamtschatkana* in order to enhance growth. The economic feasibility of transplants is dependent on site-specific recovery rates and the costs of harvesting seed abalone. The population dynamics of abalone in exposed beds and the long-term potential for enhancing abalone settlement by introducing broodstock to depleted areas are two aspects which now require investigation.

The northern or pinto abalone, *Haliotis kamtschatkana* Jonas 1845, ranges from San Diego, CA to Sitka, AK (Mottet 1978); is most abundant in British Columbia and southeast Alaska; and is the only species of abalone found in British Columbia. Although present in the low intertidal zone in the northern part of its range, northern abalone are normally found subtidally to depths of 15 m (Cox 1962). In British Columbia the species is common in rocky habitats associated with surface kelps (*Macrocystis integrifolia* and *Nereocystis luetkeana*) at depths of 3–7 m.

In 1976 a market for Canadian abalone developed in Japan, and annual landings increased from less than 50 t (Farlinger and Bates 1985) to 425 t by 1978 (Breen 1980). Attempts were made to reduce the catch through effort control and the imposition of annual catch quotas. Despite these harvest restrictions, the northern abalone population in British Columbia has been extensively depleted and recruitment of legal-sized (>100 mm) abalone to the fishery is low (Breen 1980; Boutillier et al. 1984, 1985).

Although unharvested beds of legal size northern abalone are now uncommon, sublegal size abalone are often abundant in exposed habitats adjacent to once-productive commercial grounds. These smaller

northern abalone are referred to as "surf" abalone by fishermen. They most often occur in beds of *Pterygophora californica* or under *Laminaria setchellii* cover. Breen (1980) estimated mean population densities of 9.5 abalone m⁻² in seven beds of *Pterygophora* and 1.1 abalone m⁻² in 20 beds of canopy-forming *Macrocystis*. However, only 3% of the abalone in the *Pterygophora* habitat were of legal size as compared with 46% in *Macrocystis* habitat. In exposed areas, northern abalone may be slow-growing and never reach legal size because of food limitation. Alternatively, these northern abalone may grow at normal rates but experience high rates of mortality, or emigrate to other habitats.

Breen (1986) transplanted 617 sublegal size *H. kamtschatkana* from exposed habitat in the Queen Charlotte Islands to a more sheltered *Macrocystis* community. Recovery after one year was 10%, and the author concluded that growth of these "surf" abalone was enhanced when transplanted to more favorable habitat. The present study examines the feasibility of transplanting large numbers of sublegal size northern abalone from an exposed area to more sheltered habitats. Specific goals were 1) to determine the growth of transplanted individuals relative to nontransplanted controls, 2) to monitor the recovery of northern abalone in transplant and control areas after approximately one year, and 3) to assess the economic feasibility of transplanting sublegal size northern abalone for subsequent commercial harvest.

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MATERIALS AND METHODS

Study Sites

Study sites were located in Barkley Sound on the west coast of Vancouver Island (Fig. 1). Sublegal size northern abalone were removed from 5 km of exposed shoreline at the entrance to Barkley Sound (source area), and these abalone were transplanted to site A on Fleming Island and site B on Tzartus Island, 10–12 km towards the head of Barkley Sound from the source area. For the purposes of this study, sublegal size northern abalone are defined as 50–99 mm in length. These individuals should recruit to the fishery within 0–3 years, given suitable habitat.

An exposed rocky pinnacle (site C) within the source area was designated as a control site to measure growth and recovery of nontransplanted northern abalone. The three study sites were isolated by natural features (e.g., sand) from nearby abalone habitat to minimize immigration or emigration.

The source area consisted of a series of rocky headlands and bays. The habitat of the headlands and control site was typical of exposed rocky outcrops on the west coast of Vancouver Island. At the control site, a 2 m band of vegetation (*Lessoniopsis littoralis* and *Laminaria groenlandica*) formed the lower intertidal zone, and northern abalone and sea urchins, *Strongylocentrotus franciscanus*, occurred

below this zone on a rocky reef dominated by encrusting coralline algae. Bays in the source area were sloped less steeply and contained beds of *Nereocystis luetkeana* and *Pterygophora californica*. Transplanted northern abalone were collected from both headland and bay habitats in the source area.

Both transplant sites were located in and directly below beds of *Macrocystis integrifolia* situated on isolated rocky reefs. Sites were defined by marking 60 m wide × 8 m deep sections of these beds with a weighted line at each lateral boundary. The *Macrocystis* bed at site A was 2–5 m wide, bordered by a deeper 3 m wide band of brown algae, *Desmarestia ligulata*. The substrate at this site was steeply sloped bedrock. Large boulders, covered by *P. californica* and encrusting coralline algae, occurred at the base of the bedrock slope. Sea urchins (*S. franciscanus* and *S. purpuratus*) occurred below the vegetation zone to a depth of 8 m. At deeper depths the bottom was composed of sand, isolated cobbles, and boulders.

At site B, the *Macrocystis* zone was 6–8 m wide and bounded at the lower edge by kelps (*Laminaria saccharina*, *P. californica*, and *Agarum fimbriatum*). *Desmarestia ligulata*, although present, did not form a distinct zone as at site A. The bedrock substrate was sloped less steeply than at site A and was overlain with loose cobbles. At deeper depths, sand was the primary substrate. As at site A, sea urchins were present below the vegetation zone.

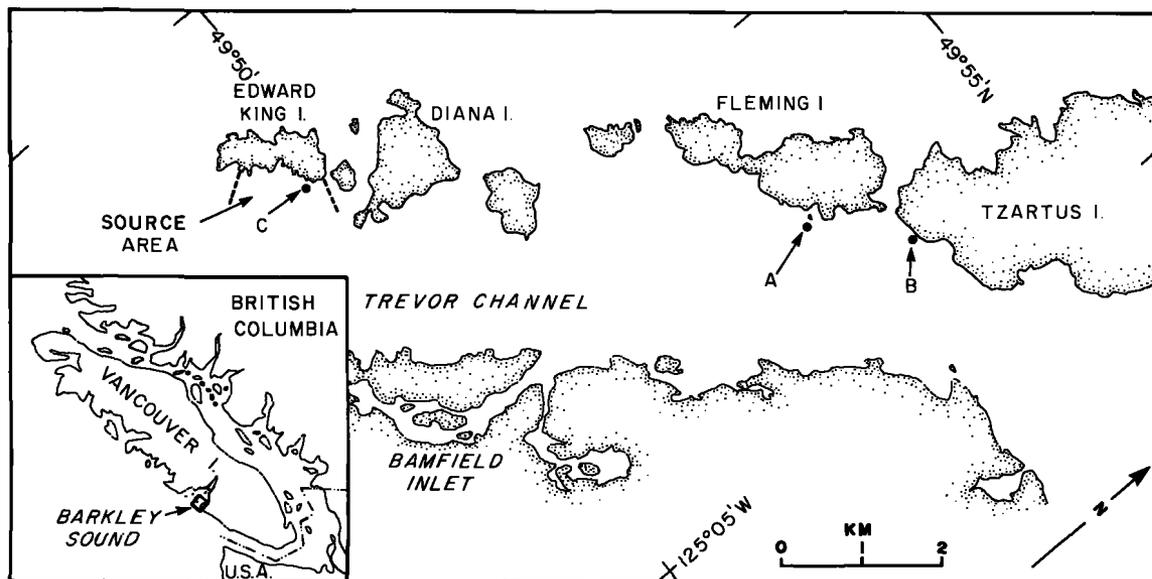


FIGURE 1.—Location of the study sites in Barkley Sound on the west coast of Vancouver Island.

Removal, Tagging, and Transplanting

Prior to transplanting any northern abalone, divers searched for and removed indigenous abalone from the transplant sites. The divers then collected the abalone from the source area using a dull knife or the arm of the sea star, *Pycnopodia helianthoides*. The arms elicit an escape response, which allows the abalone to be hand-picked without damaging the foot. Tagging and transplanting were conducted from mid-June to July 1984. Approximately 20% of the northern abalone, selected haphazardly, were tagged with individually numbered, stainless steel washers immediately after capture. A loop of stainless steel wire was inserted through the last two respiratory pores of the abalone shell, a washer tag was added to one end of the loop, and the wire was then twisted with a pair of pliers to anchor the tag against the abalone shell. Length, width, and sex of all tagged northern abalone were recorded. Shell lengths of a subsample (10%) of untagged abalone were measured for comparison with the tagged samples. Tagged abalone were placed between layers of moist kelp so that the tag wires did not damage overlying abalone. Abalone were then transported to transplant sites within 3–4 hours of harvest and placed by divers in or immediately below the *Macrocystis* zone, the preferred habitat for adult abalone in sheltered locations (Breen 1986). A total of 502 tagged abalone were placed at site A and 506 at site B. Abalone ($n = 438$) were also removed from the control site (C), tagged and replaced onto the site within 2–3 hours.

Divers searched the transplant sites within 48 hours of completing the transplant, and monthly from August 1984 to February 1985. All tagged and untagged abalone shells found in the study sites were collected.

Recovery of Transplanted Abalone

In March 1985, divers harvested tagged and untagged northern abalone at the transplant sites and tagged abalone at the control site. To maximize recovery, divers divided each site into a series of 5 m sections using cinder blocks and cord. The area of each section was measured and divers then searched repetitively for abalone within each section. Harvesting was terminated when repetitive searches in each area recovered less than 5% of the abalone harvested in the initial search. Divers also searched areas adjacent to the study site for tagged abalone to establish the magnitude and distance of emigration. Length, width, and sex of recovered,

tagged abalone were recorded, along with the lengths of all tagged abalone.

RESULTS

Abalone Transplants

A total of 2,737 northern abalone were transplanted to site A and 2,677 abalone were transplanted to site B (Table 1). The mean length of tagged abalone transplanted to site A was 88.7 mm and to site B, 90.2 mm. The mean length of abalone tagged at the control site (site C) was 78.7 mm. The differences in mean length between sites were all significant ($P < 0.05$). The mean length (\pm SD) of subsamples of untagged abalone transplanted to sites A and B were 84.6 ± 12.8 mm ($n = 204$) and 8.8 ± 11.5 mm ($n = 257$), respectively.

TABLE 1.—Summary of number and mean length of abalone at each site. Density for site C is estimated from random quadrat surveys conducted prior to tagging (\pm SD).

Site	Study area (m ²)	Number transplanted	Density (abalone m ⁻²)	Tagged abalone		
				n	\bar{x} (mm)	SD (mm)
A (transplant)	550	2,737	4.98	502	88.7	11.5
B (transplant)	590	2,677	4.54	509	90.2	9.8
C (control)	1,800	—	0.56 ± 0.91	438	78.7	11.0

Although divers carefully placed each transplanted northern abalone foot down in suitable rock crevices or loose rock within the study areas, many abalone subsequently moved outside the lower boundary of the sites to depths of 7–10 m. This movement made the effective area of the transplant sites about three times larger than the original 60 m \times 8 m dimensions. Little lateral movement of northern abalone beyond the boundaries of the study sites was observed.

At sites B and C, the recovery of tagged shells by monthly diving inspections was highest in August, one month after the transplant (Fig. 2). Recovery of both tagged and untagged shells at all sites in early July suggests that mortality one week after transplanting was less than 2%. The relatively high recovery of tagged shells in March 1985 was probably a consequence of the more intensive searching effort during the final harvest. Cumulative recoveries of tagged shells were 10.5% at site A, 18.0% at

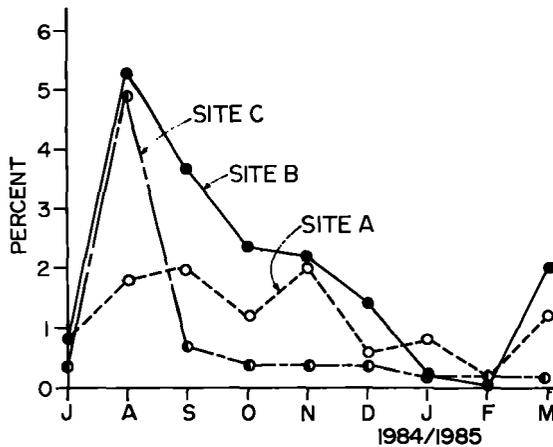


FIGURE 2.—Monthly recovery of tagged shells and tagged shell fragments from dead abalone. Results expressed as the percentage of the original number of tagged abalone.

site B, and 7.2% at site C (expressed as a percentage of the original tagged number).

Predation and Seasonal Variation in Habitat

Shells recovered during monthly inspections were categorized by the nature of breakage. Shells present on the sites prior to the transplant were not categorized. These older shells were identifiable by degree of shell deterioration and epiphytization. Most shells were recovered whole: 68% at site A, 51% at site B, and 79% at site C.

Recoveries of loose tags owing to tag loss or predation ranged from 0% of the initial tagged population at site C to 1.3% at site B. The relative proportion of loose tags recovered at each site corresponded to the proportion of broken shells at each site, suggesting that shell breakage due to predation may be the main cause of loose tags.

One to three octopus dens were present at each site. Abalone shells found outside the dens were unbroken and not drilled. Over the course of this study, four octopuses were removed from site A, two from site B, and one from site C. Dens were often reoccupied three to four months after removal. Red rock crab, *Cancer productus*, were also a numerically important prey item of octopus at the study sites.

In July and August, the sunflower star, *Pycnopodia helianthoides*, preyed intensively on abalone at the transplant sites. This species was seen to prey on weakened or stressed abalone, and starfish were

observed actively feeding on abalone immediately following the transplant. As with octopus, shells of abalone eaten by *P. helianthoides* were always recovered unbroken, either under actively feeding stars or entirely within the stomach.

In contrast, broken or chipped shells were presumed to be due to predation by red rock crabs, wolfeels (*Anarrhichthys ocellatus*), or cabezons (*Scorpaenichthys marmoratus*). Red rock crabs were abundant during the spring and summer at all sites except site C, but were rarer in the fall and winter. A few abalone shells were recovered outside a wolfeel den at site A, and one or two cabezon were observed at all sites throughout the study period.

Considerable seasonal variation in the marine plant community at the transplant sites was observed. Annuals, such as *Desmarestia ligulata*, died back in October and were completely gone by November. The *Macrocystis* canopy was also reduced in fall and winter as a result of storm damage. Plants at site A were stripped of most fronds over the winter while losses were lower at site B, the more sheltered of the two transplant sites. Holdfasts remained intact and growth was renewed by March.

Recovery of Abalone

After nine months, 72% of the transplanted northern abalone were recovered from site A, and 39% from site B (Table 2). When shells from dead northern abalone collected during the 9-mo period were included, 88% of abalone at site A and 55% of abalone at site B could be accounted for. At the control site (C), 31% of the tagged abalone were recovered live and 40% of the original tagged abalone could be accounted for by including tagged shells recovered over the study period. The difference in percent recovery between the two transplant sites suggests that either abalone survival, abalone movement, or the ability of divers to find abalone differed between the sites.

The recovery of tagged northern abalone was 6% less than recovery of untagged abalone at both transplant sites (Table 2), and the ratio of tagged to untagged abalone at recovery (0.20) was less than the initial ratio of 0.23. This difference is not significant (χ^2 analysis, $P < 0.05$), indicating that losses due to the tagging procedure were minimal.

The number of tagged shells recovered by divers over the 9-mo study allowed estimation of minimal instantaneous natural mortality (M_{\min}) (Ricker 1975). This calculation assumes that divers recov-

TABLE 2.—Recovery of live abalone in March 1985, recovery of abalone shells over the study period, and estimation of M_{\min} (from tagged shell recovery) and M_{\max} (from live tagged abalone recovery). Number recovered was after 9 months, so $M = -\ln \left(\frac{\# \text{ tagged survivors}}{\# \text{ initially tagged}} \right) \cdot \frac{12}{9}$.

Site	Initial number		Recovery				% live recovery			M	
	tagged	untagged	tagged		untagged		tagged	untagged	Total	M_{\min}	M_{\max}
			shells	live	shells	live					
A (transplant)	502	2,235	53	330	396	1,628	66	73	72	0.15	0.56
B (transplant)	509	2,168	92	175	353	861	34	40	39	0.27	1.42
C (control)	438	—	33	141	—	—	31	—	31	0.10	1.51

ered the shells of all tagged northern abalone that had died. The recovery of live tagged abalone allows estimation of maximal instantaneous natural mortality (M_{\max}), assuming that divers recovered all the living abalone. Values for M_{\min} ranged from 0.10 to 0.27 for the three study sites; M_{\max} ranged from 0.56 to 1.51 (Table 2).

The movement of northern abalone from the lower edge of the *Macrocystis* bed to deeper (5–11 m) water shortly after the transplant (described above) effectively increased the area of each transplant site by threefold. Approximately 30% of recovered northern abalone were found below the vegetation zone at both transplant sites. This movement, coupled with abalone losses, resulted in final abalone densities of 1.27 m⁻² at site A and 0.73 m⁻² at site B.

Prior to final harvesting, divers searched beyond the expanded boundaries of the sites for tagged northern abalone. Little lateral movement of northern abalone along the shoreline had occurred. At site A, 11 tagged abalone (2.2% of the original tagged number) were found outside the study area. Maximum distance from the site was 37 m, and one tagged abalone was found at a depth of 18 m. At site B, three tagged abalone were found outside the site area, all in deeper water. The most extensive movement was recorded at the control site. Ten tagged abalone (2.2% of the tagged population) were recovered outside the site boundaries; one abalone had moved 125 m; and three abalone had crossed a 50 m wide sandy channel.

At sites B and C, a considerable proportion of the transplanted or tagged population could not be accounted for. The low recovery of tagged abalone outside the boundaries of the sites suggests that emigration is not the sole explanation. However, searches conducted outside the site boundaries were less intensive than those conducted within.

Growth

Figure 3 gives the length frequencies of tagged northern abalone at each site at the initiation of the study in June 1984 and upon recovery in March 1985. Differences between mean initial and final lengths at each site were, in all cases, significantly different (paired *t*-test, $P < 0.05$). The mean growth of tagged northern abalone after 9 months was 7.1 mm at site A, 7.2 mm at site B, and 2.9 mm at site C, the control site. Mean growth of untagged northern abalone was 9.4 mm at site A and 9.9 mm at site B.

Growth rates of northern abalone were analyzed by Walford plots, in which the initial length of individual tagged abalone (l_0) are plotted against the length of the same individual at recovery in March 1985, 9 months later (l_1). The numbers of data pairs were 306, 167, and 126 at sites A, B, and C, respectively. Table 3 summarizes parameters of the regression lines of Walford plots for each site as well as the annual Brody coefficient and asymptotic length calculated from these regression parameters (Ricker 1975). The annual Brody coefficient varied from 0.178 to 0.440, and was lowest at the control site. Values for asymptotic length varied from 104 to 112 mm, also being lowest at the control site.

TABLE 3.—Parameters for linear regression, annual Brody coefficient (K), and asymptotic length (l_{∞}) as calculated from Walford plots.

Site	N	Linear regression			K	l_{∞} (mm)
		a	b	r ²		
A (transplant)	306	30.8	0.719	0.64	0.440	110
B (transplant)	167	24.8	0.779	0.76	0.333	112
C (control)	126	13.0	0.875	0.87	0.178	104

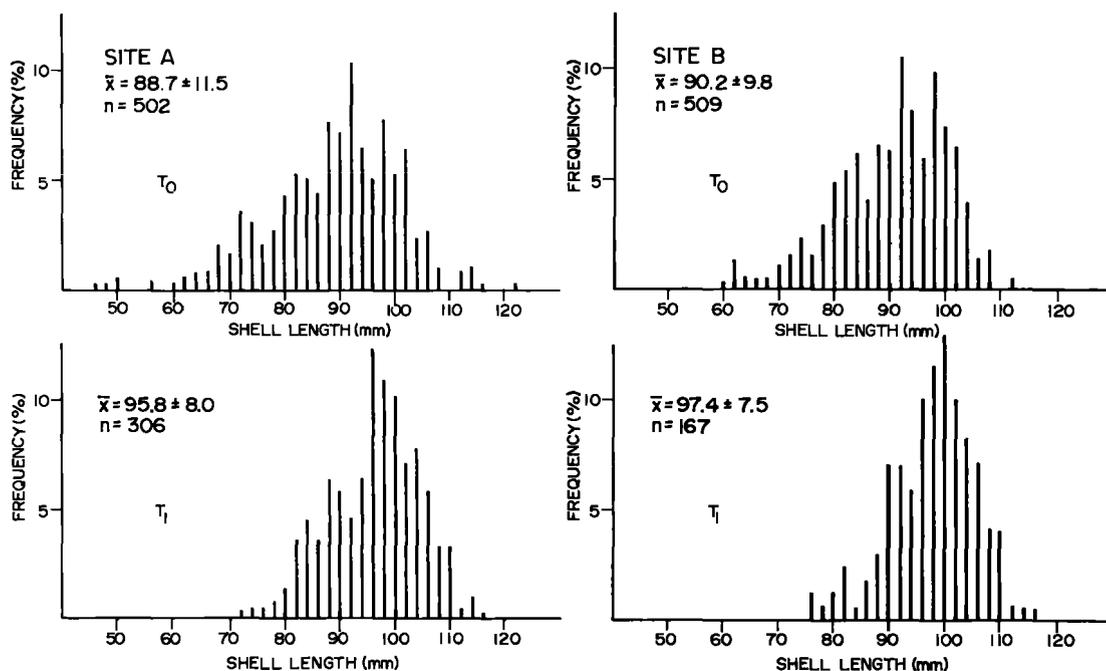


FIGURE 3.—Length frequencies of tagged abalone at each site at the beginning (June 1984 - T_0) and at end

Growth of northern abalone at the transplant and control sites was compared by using the Walford regression to estimate final lengths and associated confidence intervals for abalone of initial lengths equal to the lower (75 mm) and upper (100 mm) size range of abalone placed at the two transplant sites (Table 4). As confidence intervals are narrowest at the mean value of l_0 , between site comparisons using these more extreme values are more rigorous than using l_0 values which fall between 75 and 100 mm. The hypothesis that predicted l_1 values at $l_0 = 75$ and 100 mm for transplanted northern abalone are greater than the corresponding l_1 value for control abalone was then tested (one tailed t -test). All differences were significant at $P < 0.05$ (Table 4), indicating that northern abalone growth was significantly greater for abalone transplanted to sites A and B as compared with nontransplanted abalone at the control site.

Economic Feasibility

The economic feasibility of transplanting wild northern abalone seed for subsequent commercial harvest depends primarily on three factors: 1) the cost to collect and transplant stock, 2) the rate of recovery of legal-sized abalone after a suitable grow-

TABLE 4.—Estimates of growth calculated from Walford plots for abalone for the lower (75 mm) and upper (100 mm) size range of transplanted abalone. Values are expressed \pm 95% confidence interval. l_0 = length at initiation of study, l_1 = length after nine months. Values in parentheses are t - statistic and degrees of freedom comparing the l_1 values at each transplant site with the corresponding l_1 values at the control site. $P < 0.05$ in all cases.

Site	Length after 9 months t_1 (l_1)	
	$l_0 = 75$ mm	$l_0 = 100$ mm
A	84.7 \pm 0.7	102.7 \pm 0.5
(transplant)	(16.22, 305)	(7.97, 305)
B	83.3 \pm 0.9	102.8 \pm 0.5
(transplant)	(10.02, 166)	(8.85, 166)
C	78.6 \pm 0.4	100.5 \pm 1.0
(control)		

ing period, and 3) the price of abalone. The first factor depends on abalone density in the source area and the distance to the transplant sites. The present study shows that the second factor (recovery rate) can vary greatly between sites.

In this study 6 diver-days were required to collect 5,000 sublegal-sized northern abalone at the source area and move them to the transplant sites. This variable cost was estimated to be \$1,500, at a rate of \$250 diver-day⁻¹ for wages and fuel costs.

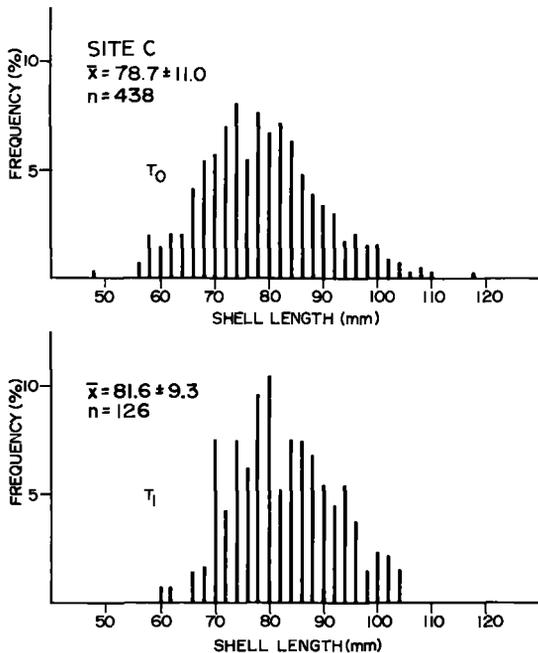


FIGURE 3.—Continued—(March 1985 - T_1) of the study.

Harvest costs were similarly estimated at \$1,575. Fixed costs were not included and were assumed to be zero. This information is used in the following simple economic model which examines the rate of economic return as a function of M_{\max} (instantaneous natural mortality estimated from recovery of live abalone).

Assuming that 5,000, 80 mm abalone are transplanted, they reach legal size (100 mm and 340 g) in two years, and can be sold at a price of \$11 kg^{-1} . Then

$$\text{gross return} = \$11 \text{ kg}^{-1} \times 0.34 \text{ kg abalone}^{-1} \times 5,000 \text{ abalone} \times e^{-tM}, \text{ where } t = 2, M = M_{\max}$$

$$\text{net return} = \text{gross return} - \text{harvest costs, where harvest costs} = \$1,575$$

$$\text{profit} = \text{net return} - \text{initial costs, where initial costs} = \$1,500$$

$$\text{discounted profit} = \text{net return} \left(\frac{1}{1+d} \right)^t - \text{initial costs, where } d = \text{discount rate} = 10\%$$

$$\text{internal rate of return (IRR)} = e^{\text{return rate}} - 1.0, \text{ where return rate} = (\ln(\text{net return}/\text{initial costs}))/t.$$

Table 5 summarizes these economic parameters for values of M_{\max} ranging from 0.10 to 1.00. These data indicate that a reasonable value for the internal rate of return (i.e., >20%) would be obtained at M_{\max} values of 0.80 or less. Transplants to site A but not site B would show a reasonable rate of return.

This model can be generalized to estimate economic returns for variable abalone seed costs in the case of transplanting hatchery-reared seed to the wild. Figure 4 summarizes internal rates of return for 20 mm hatchery seed of variable cost, a 4.5 yr growth period, planting costs of \$0.20 per abalone, and harvest costs of \$0.40 per kg. All other assumptions are the same as the model given above. Under these price assumptions, M_{\max} values must be less than 0.6 to show a reasonable rate of return if seed costs are \leq \$0.10 per abalone. At M_{\max} values greater than 0.8, transplanted abalone seed will not yield a reasonable rate of return unless seed costs are extremely low ($<$ \$0.02 per abalone).

TABLE 5.—Summary of economic returns from transplanting abalone, assuming 2 years to recovery. Calculated from the economic model given in text. IRR = Internal rate of return; t = 2 years.

M_{\max}	Profit	Discounted profit	IRR ($\times 100\%$)
0.10	\$12,235	\$9,865	203
0.20	9,460	7,553	171
0.40	5,328	4,139	113
0.60	2,557	1,851	64.8
0.80	700	318	21.4
0.90	16	-250	0.8
1.00	-544	-710	—

DISCUSSION

In this study northern abalone transplanted from exposed areas to more sheltered habitat grew faster than nontransplanted controls. These results corroborate the observations of Breen (1986) that "surf" abalone retain the potential to grow well when placed in more productive habitat. These observations suggest that abalone are, to some degree, food limited in exposed habitats which have little to no canopy-forming algae.

Because northern abalone varied in size in different sections of the source area, the initial size of nontransplanted abalone at the control site was significantly less than that of the transplanted abalone (Fig. 3). This bias would be expected to reduce the difference in growth rate between the abalone at

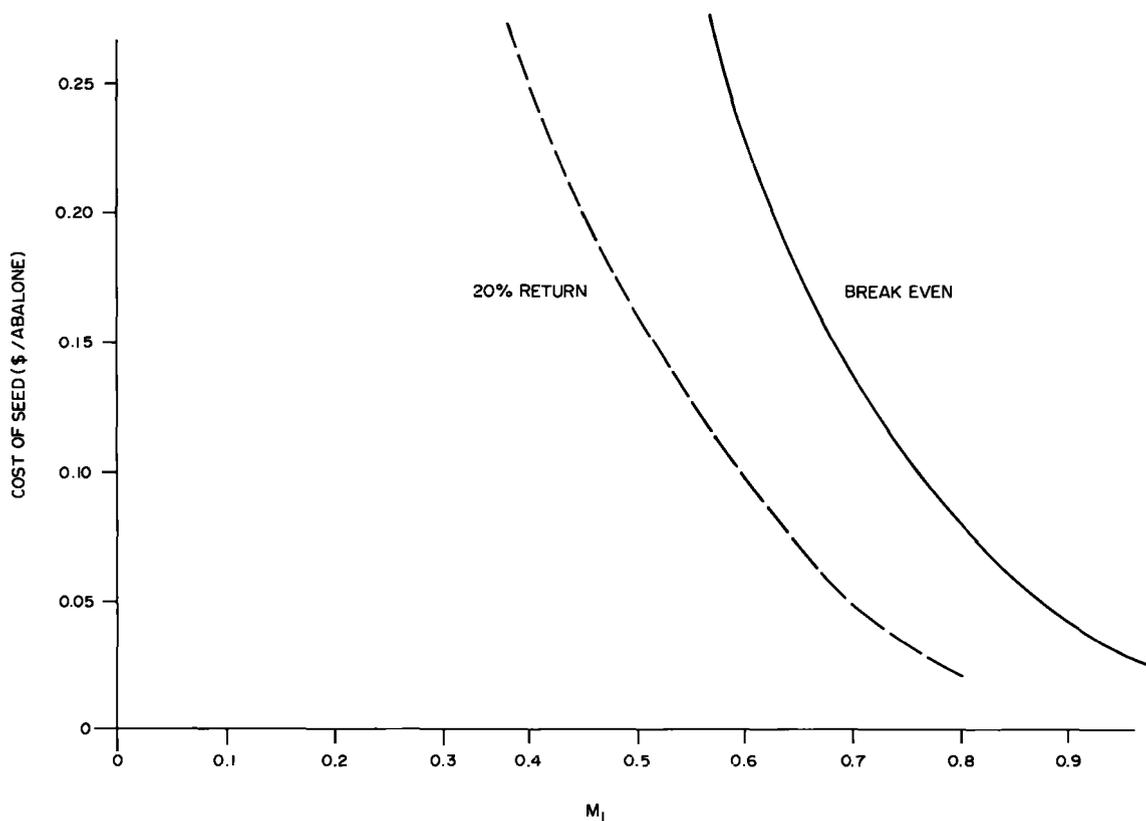


FIGURE 4.—Isoprofit lines drawn from internal rates of return calculated at varying seed cost and natural mortality values. Solid line = breakeven point, dotted line = 20% internal rate of return.

the control and transplant sites, because growth rate is inversely related to body size. Therefore the growth rate differences observed in this study are likely smaller than would have been observed if the mean length of transplanted abalone had been equal to the mean length of the control group at the initiation of the study. Analyzing growth rates by Walford plots diminishes this bias because the analysis compares the length of individual abalone at the beginning and end of the study period and does not use pooled data to compare growth rates among sites.

In most transplant experiments, recovery following transplanting depends on both abalone size and source and is greatest with larger abalone collected from the wild. In the present study wild-harvested northern abalone of 50–100 mm length were transplanted, and recovery was 72% and 39% at the two sites 9 months after the transplant. Saito (1984) reported 18% recovery 9 months after transplanting 25 mm hatchery-reared *Haliotis discus hannai*

in Japan. The author also stated that commercial recapture rates are 5–10% for hatchery-reared seed and 20–25% for wild seed. Recovery of 45–71 mm, hatchery-reared *Haliotis rufescens* in California was less than 1% one year after transplanting (Tegner and Butler 1985). Inoue (1976) reported increased survival with increasing seed size up to 70 mm. Tegner (pers. commun.)² estimated an annual mortality rate of 9.1% for mature, native green abalone, *Haliotis fulgens*, one year after being transplanted in California. The use of large, wild-harvested northern abalone likely contributed to the relatively high recovery rates observed in the present study.

The markedly different rates of recovery between the two transplant sites seemed independent of handling, tagging, and transplant procedures. Shells collected within two weeks of release indicated that immediate posthandling mortality was similar (<2%)

²M. J. Tegner, Scripps Institution of Oceanography, La Jolla, CA 92092, pers. commun. January 1987.

at all sites. The similar ratio of tagged to untagged northern abalone at the initiation and end of the study demonstrated that both tagged and untagged animals had similar survival rates.

Breen (1986) calculated M , from population size structure and growth rate estimates, to be 0.05–0.24 for *H. kamtschatkana* at eight sites in British Columbia. These values are consistent with estimates of M , derived from a variety of techniques, of 0.05–0.40 for abalone populations in Australia and New Zealand (Shepherd et al. 1982; Sainsbury 1982). In California, estimates of M (partly based on dead shell recovery) are higher, ranging from 0.36 to ∞ for four native species of *Haliotis* (Tutshulte 1976; Hines and Pearse 1982). The highest estimates are from areas that experience sea otter, *Enhydra lutris*, predation. Estimates of M calculated from data given by Tegner and Butler (1985) are 0.40 and 0.55 for two transplanted populations of red abalone, *H. rufescens*.

In the present study, estimates of M based on recovered, tagged shells (M_{\min}) are similar to values determined for abalone populations from similar latitudes in British Columbia (Breen 1986) and southern Australia (Shepherd et al. 1982). Values of M determined from the recovery rate of live abalone (M_{\max}) are higher than most values of M reported in the literature. It is likely that M_{\max} estimates of instantaneous natural mortality are high because some abalone probably emigrated or remained hidden within the sites. However, while unrecovered abalone would still be able to contribute to population reproduction, they would not likely be available for harvest; the after-harvest population density would be too low to encourage the return of fishermen, and the animals might remain well hidden. Effectively, these abalone can be considered removed from the harvestable biomass, and since there are only two categories, available and unavailable animals, in most cost-benefit and/or exploitation models, unrecoverable abalone should be considered unavailable abalone. For this reason M_{\max} is an appropriate term for use in models assessing the economic feasibility of abalone transplants and in other situations where animals are established in an area for the purpose of future exploitation.

A considerable proportion of tagged and/or transplanted northern abalone were unaccounted for at sites B and C. The difference in percent recovery of live abalone at the two transplant sites (72% versus 39%) was due primarily to these abalone, as approximately the same number of shells were collected at each site. There are several explanations: 1) difficulty in locating abalone due to complex bot-

tom topography, 2) physical removal of abalone from the site by mobile predators such as octopus and sea stars, 3) the destruction of shells by predators such as crabs, 4) emigration, and 5) transport of shells from the site by waves or currents.

In California, Tegner and Butler (1985) attributed abalone loss during transplant experiments to both predation and emigration, citing the recovery of shells in all directions outside the study site as evidence of random dispersal of live animals. In the present study, searches outside the sites at the termination of the study suggested little emigration of tagged abalone, except at the control site. Although no studies have been done on the natural movement of *Haliotis kamtschatkana*, the mean distance moved in a year by tagged ormers (*Haliotis tuberculata*) in France was only 6.7 m for the 68% of the population that showed any evidence of movement (Clavier and Richard 1984). That study also showed that smaller abalone tended to be less mobile. Hines and Pearse (1982) reported that marked abalone shells drifted 2–3 m in three months. The degree of shell drift due to wind or current action is obviously site specific and probably only occurred at the more exposed control site in the present study.

Three fundamental questions concerning the feasibility and benefit of transplanting abalone from exposed areas remain: 1) the number and extent of abalone in exposed coastal areas has not been established, 2) the population dynamics and the reproductive contribution from such populations to the total coastal stock remain unknown, and 3) the potential of transplanted abalone to enhance population reproduction and ultimately recruitment at specific transplant sites has to be determined on a site-by-site basis.

ACKNOWLEDGMENTS

This study was carried out in conjunction with the West Coast Abalone Harvesters Association (W.C.A.H.A.). Eric Wickham, Bob Harrington, and Guy Whyte of the W.C.A.H.A. and Thomas Shields of Archipelago Marine Research were responsible for much of the initial planning of this project. We thank Dave Johnstone and Mark Bath of the W.C.A.H.A. for their participation in all phases of the field work; their experience as abalone divers and their firsthand knowledge of the study area made the field program run smoothly and efficiently. Paul Breen of the New Zealand Minister of Agriculture and Fisheries offered many useful comments throughout the study and provided the equations for the economic feasibility model. Howard

McElderry provided advice on data analysis. Valuable comments on the manuscript were provided by three anonymous reviewers. This project was financially supported by the Department of Fisheries and Oceans unsolicited proposal program, D.S.S. Contract No. 08SB.FP 597-4-0145.

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