

Status and habitat associations of the threatened northern abalone: importance of kelp and coralline algae

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ABSTRACT

1. Northern abalone (*Haliotis kamtschatkana kamtschatkana*) is a federally listed species of concern.
 2. The status of northern abalone and the characteristics of the habitats they associate with were determined showing that northern abalone have declined dramatically in Washington State with present day abundances <10% of those found in 1979.
 3. Northern abalone inhabited kelp beds (*Nereocystis luetkeana*), more than red sea urchin beds (*Strongylocentrotus franciscanus*) ($X^2 = 16$, d.f. = 1, $P < 0.01$) or habitats with both kelp and sea urchins ($X^2 = 13.2$, d.f. = 1, $P < 0.01$). Sites with *Nereocystis* kelp canopy had twice the percentage cover of encrusting coralline algae compared with sea urchin sites.
 4. No juvenile abalone (<75 mm) were found in any of the habitat types raising concerns about recruitment failure.
 5. Abalone co-occurred with other molluscs including limpets and scallops. Kelp holdfast microhabitats had significantly higher species richness ($t = 2.2$, d.f. = 6, $P < 0.05$), twice the effective number of species and 5x more individuals than sea urchin spine microhabitats.
 6. In laboratory choice experiments, juvenile abalone (20 mm) preferred coralline rocks to kelp holdfasts or sea urchin spine canopy. The small snail, *Amphissa* spp. (5–15 mm) was more abundant inside kelp holdfasts than under sea urchins or in rock cobble, suggesting this may be an important microhabitat.
 7. It is recommended that kelp beds with abundant coralline substrate be used for restoration including stocking juveniles and adult aggregations as this biogenic habitat may enhance northern abalone restoration actions.
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INTRODUCTION

Marine systems are often defined by their engineering or foundation species such as kelp forests (Carr, 1989; Estes and Duggins, 1995; Graham, 2004), coral reefs (Reaka-Kudla, 1997; Idjadi and Edmunds, 2006), or mussel beds (Suchanek, 1978, 1986). Kelp and sea urchin beds (Rogers-Bennett *et al.*, 1995; Hartney and Grorud, 2002) are structuring components in nearshore subtidal ecosystems along the west coast of North America from northern California to Alaska and often

co-occur. Engineering species directly or indirectly modulate the flow of food and shelter resources within communities (Jones *et al.*, 1994). Despite the recognition of ecosystem engineers (Jones *et al.*, 1994, 1997) or foundation species (Dayton, 1972) few studies have examined whether they support species richness, species diversity (evenness) or rare species.

Species diversity in kelp forest communities may function to maintain stability and resilience (Steneck *et al.*, 2002). Fishing within kelp forests, however (Tegner and Dayton, 2000), and

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specifically the fishing of ecosystem engineers such as red sea urchins, can have negative impacts on diversity, rare species, and ecosystem structure (Coleman and Williams, 2002; Rogers-Bennett, 2007a). The fished status of a site and whether it is a marine protected area (MPA) may be an important factor in promoting local richness, diversity and rarity (Halpern and Warner, 2002; Parnell *et al.*, 2006). Northern abalone (*Haliotis kamtschatkana kamtschatkana*) is in low abundance in southern British Columbia except in front of a heavily guarded prison, which serves as a 'de facto' MPA (Wallace, 1999).

Northern abalone, once a dominant member of subtidal communities along the west coast of North America, is now rare (Jamieson, 2001). Rarity has three components; geographic range, local population size and habitat specificity. While northern abalone have a wide geographic distribution from Mexico to Alaska (O'Clair and O'Clair, 1998; Geiger, 1999), with the threaded abalone subspecies dominating from Point Conception into Mexico, their populations have declined precipitously throughout the range. Northern abalone appear to be habitat specific, occurring in shallow rocky subtidal habitats with low to medium exposure, some boulders, and kelp canopy (Tomascik and Holmes, 2003; Lessard and Campbell, 2007). Specific habitat requirements for abalone in the Puget Sound, Washington State need to be assessed to better define the status of the population, discern the role of ecosystem engineers, and make recommendations for restoration.

Conservation of northern abalone began with the closure of the fisheries in Alaska (1995), British Columbia (1990), Washington State (1994) and California (2000). NOAA fisheries in the USA in 2004 listed northern abalone as a federal species of concern (M. Neuman pers. comm.). In Canada, northern abalone are listed as 'threatened' under the Species at Risk Act (in force 2003) and the Committee on the Status of Endangered Wildlife has recommended uplisting to 'endangered'. Despite the closure of the fisheries there is still illegal fishing and populations are declining (Rothaus *et al.*, 2008) prompting the formation of the Transboundary Abalone Recovery Group. In the southern portion of the range, populations have declined over a period when sea surface temperatures have risen (Rogers-Bennett, 2007b) suggesting ocean warming may be an additional threat to recovery. Furthermore, the genus is also susceptible to Allee effects (Allee *et al.*, 1949) with reduced reproductive capacity at low population densities (Shepherd and Brown, 1993; Hobday *et al.*, 2001). Recovery measures for northern abalone in Washington State will be aided by information about population status, microhabitat utilization patterns and community structure (Campbell, 2000; Sloan, 2004).

In this study, the habitat specificity of northern abalone was examined within habitats structured by *Nereocystis*, red sea urchins, and both species. Abalone abundances today were compared with those of similar surveys from 1979. It was determined whether northern abalone were associated with other molluscs on natural rock reefs and which habitats had higher species richness and diversity indexes. The microhabitat preferences of small molluscs (surrogates for juvenile abalone) were examined by looking at the macroinvertebrate community found in kelp holdfasts, on coralline covered rocks and under sea urchin spine canopies. Abalone abundances are compared between MPA and fished sites. Finally, microhabitat preferences

of hatchery reared juvenile northern abalone were determined in the laboratory. The implications of the relationship between northern abalone and biogenic structure as it relates to critical habitat and the development of recovery strategies for the species is discussed using an ecosystem based approach.

METHODS

Abalone surveys

Ten locations in the San Juan Archipelago were selected as survey sites in the summer of 2005 (Figure 1). All sites were located within or adjacent to the San Juan Channel, a passage that includes a commercial closure to sea urchin and sea cucumber fishing. Sites were selected based on information from previous surveys or local knowledge suggesting they had northern abalone. Sites were divided into habitat types based on the availability of *Nereocystis* kelp and *Strongylocentrotus franciscanus* sea urchins; two habitat engineering species. Three sites had only *Nereocystis* kelp and another three had only *S. franciscanus* sea urchins. Four sites had both *Nereocystis* kelp and *S. franciscanus* sea urchins. Half of the sites were located within a reserve that prohibited sea urchin and sea cucumber fishing and half were located outside this closed area.

Timed swim surveys were conducted on scuba at each of the 10 sites. During the timed swims, divers sought appropriate abalone habitat, typically rocky reefs with little silt at 5 to 12 m depth. All the abalone observed were counted and measured. Abalone exposure was recorded as either cryptic or emerged as well as their location on the habitat (reef, boulder, and crevice). To examine associations between northern abalone and other molluscs as well as brachiopods, divers also enumerated sea scallops *Hinnetes giganteus* and the pink scallop *Chlamys species*, keyhole limpets *Diodora aspera*, white cap limpets, *Acmaea mitra*, and leafy hornmouth snails, *Ceratostoma foliatum* and brachiopods, recorded as *Terebratalia transversa*. Note that brachiopod species identification *in situ* was difficult and other species may have been observed. Divers recorded the depth and estimated substrate composition and algal cover at the beginning, middle, and end of each timed swim survey. Two divers conducted two timed swims, averaging 35 min each at each site. All divers were experienced in searching for northern abalone. The time spent ascending, descending and quantifying habitat was not included in the abalone search time.

Sea surface temperatures were examined from Race Rocks (48°180' N, 123° 320' W) located in the eastern entrance of the Strait of Juan de Fuca, midway between the cities of Victoria on Vancouver Island in British Columbia and Port Angeles on the Olympic Peninsula of Washington State, USA. Data on sea surface temperature have been collected at this lighthouse daily since 1921 by collecting a bucket sample of water and measuring the temperature 1 h before high tide. The station became automated in 1997. Monthly averages were calculated to yield yearly averages and then compared with the mean of yearly averages from 1969 to 2006. (<http://www.racerocks.com/racerock/abiotic/temperature/seatemperature.htm>).

Multivariate analyses

The timed swim data resulted in 18 samples, two from each of nine sites. One of the original 10 sites that had both kelp and sea urchins was eliminated from the final analysis owing to



Figure 1. Map of northern abalone study sites from 2005 in the San Juan Islands, Washington State.

missing data on white cap limpets. Mollusc counts (six species) from the 18 samples were log transformed, and relationships among species were examined using exploratory graphics. The relationship of the mollusc species among sites (variables) was then examined using a principal component analysis (PCA). A matrix was generated to summarize the variance among the variables over space (sites). The matrix contained columns ($N=6$) which represented the molluscs, and rows that were the sites ($N=18$). PCA examines patterns of covariance (or correlation) among variables in the matrix and reduces multivariate data into a few uncorrelated (orthogonal) indices, or principal components (Chatfield and Collins, 1980).

A scree plot was examined to show the amount of variance explained by each of the components. Plots of factor scores were constructed showing the relationships among the sites with respect to each principal component. These plots indicate the degree to which habitat type (kelp, urchin and both) distinguished between sites with high or low abundances of molluscs. A second set of plots was used to determine if MPA status distinguished between sites with high or low abundances of molluscs. All statistical analyses were performed using S-PLUS.

Microhabitat collections

Collections of invertebrates and small fishes were made in microhabitats within or adjacent to each of the 10 survey sites. The microhabitats of interest were inside *Nereocystis* kelp holdfasts, coralline covered rocks, and under the spine canopy

of red sea urchins, *S. franciscanus*. *Nereocystis* kelp holdfast samples were collected by cutting off the stipe and blades and then detaching the holdfast from the substrate. Holdfasts were placed immediately in zip-lock plastic bags *in situ*. Coralline covered rocks less than 10 cm in diameter were collected and placed in zip-lock plastic bags. Sea urchin spine canopy samples were collected by airlift suction first removing the urchin and collecting the animal community under the canopy using the suction sampler into sample bags at the end of the airlift.

In total, 10 collections of either kelp holdfast or sea urchin canopy or coralline rocks were made at each site in an area approximately 1000 cm². Kelp occurred at seven of the 10 sites; the three kelp sites and the four kelp and urchin sites. Likewise, sea urchins occurred at seven of the 10 sites; the three sea urchin sites and the four kelp and urchin sites. *Nereocystis* kelp holdfasts and sea urchin spine canopy samples were collected at all seven sites where they occurred. Samples of crustose coralline covered rocks at each site were collected using the airlift from an area approximately 1000 cm² at each site. All samples were transported to the laboratory for identification and cataloguing of the invertebrate and fish community. The size distribution of *Amphissa* snails found within the three microhabitat types was also examined.

Measures of species richness, species diversity, effective number of species, and total number of individuals were determined. Species richness and diversity were examined by microhabitat type. The species diversity measure used was the Shannon Index. This index accounts for both abundance and

evenness (Shannon, 1948). The proportion of species i relative to the total number of species (p_i) is calculated, and then multiplied by the natural logarithm of this proportion ($\ln p_i$). The resulting product is summed across species, and multiplied by -1 :

n_i = number of individuals in species i
 N = total number of all individuals

$$p_i = \frac{n_i}{N}$$

Shannon Index

$$H' = - \sum_{i=1}^s p_i \ln p_i$$

where S = number of species = species richness, and p_i = the relative abundance of each species calculated as the proportion of individuals of a given species to the total number of individuals in the sample.

Effective number of species can be examined for each of the microhabitat types using

$$\text{effective number of species} = e^{\text{Shannon species index}}$$

Effective number of species is the number of equally common species needed to reach a given diversity index value (for example an index value of 3.0 would have an effective number of species of 20). This is also known as the diversity of the community in units of numbers of species (Jost, 2006). Significant differences in species richness and diversity values between the three microhabitat types (kelp holdfast, coralline rocks, and sea urchin spine canopy) was tested using a two tailed t -test.

Microhabitat preference trials

At the University of Washington's, Friday Harbor Laboratories, six seawater tables 7 feet long by 48 inches wide and 24 inches deep were set up in two stacks of three. The gravity-feed, re-circulating seawater system was maintained at 11 ° C with a flow-rate of 2.58 L min⁻¹. Water changes of 30 gallons occurred every 12 h. Each table was divided into thirds of equal area. Within each of the thirds one of three different microhabitats was randomly assigned and established: (1) *Nereocystis* kelp holdfasts; (2) live red sea urchins *S. franciscanus*; and (3) coralline algae encrusted rock cobble. This created six replicates for each trial in the seawater tables. Large red sea urchins, each with a test diameter of 145 mm, offering a spine canopy area of approximately 315 cm² were used in the sea urchin microhabitat. Three of these sea urchins were used in the urchin section of the seawater table creating a total spine canopy area of approximately 945 cm². All red sea urchins were observed feeding and actively moving during the experiments. Coralline rock cobble and kelp holdfasts were then added to other sections of the seawater table to offer an equivalent microhabitat area of 945 cm², typically three or four holdfasts or rocks.

Juvenile northern abalone were purchased from Huu-Ay-Aht Community Abalone Project in Bamfield, Canada and transported to the Friday Harbor Labs where they were active (at times swinging the whole shell) and vigorously feeding on kelp. The broodstock used to spawn these

juveniles was outer coast stock. Juvenile abalone reared in the hatchery were used in the microhabitat preference trials after a 2 week acclimation period. To start each trial, 30 juvenile abalone (mean length 19.5 mm) were released into each section of the seawater tables with six replicate tanks for each trial. Since juvenile northern abalone are thought to be active at various times of the day the trials were conducted during the day and night. All trials lasted for 12 h and at the termination of the trial the locations of the juvenile abalone were recorded to ascertain microhabitat preference.

Crab predators were used in a second set of trials to stimulate the juvenile abalone to take cover in one of the microhabitat options. Two rock crabs common in the shallow subtidal habitats in the region were used, the helmet crab, *Telmessus cheiragonus* and the red rock crab, *Cancer productus* in the microhabitat preference trials. Crabs were collected 36 h before their use in the trials. Crab chelipeds were banded to prevent predation and to assess the effect of predator stress on microhabitat preference. Two banded crabs were introduced per tank in these trials. During the final trial, five *Cancer productus* were introduced per tank without banded chelipeds to allow predation. The mean carapace length of the rock crabs was 103 mm. Six replicates of this final predator trial were conducted. These active predator trials ran for less than 12 h (7 h average) as many of the abalone were eaten during this time.

In a third set of trials, the small snail *Amphissa versicolor* was used in microhabitat preference experiments as an alternative to juvenile abalone smaller than (19 mm): the size available from the hatchery. In each of the trials, 20 wild caught *Amphissa* were added to the tank.

The microhabitat selection experiments are summarized as follows:

1. Abalone, Night, No Crabs – 3 trials with 6 replicates each ($N=18$)
2. Abalone, Day, No Crabs – 2 trials with 6 replicates ($N=12$)
3. Abalone, Day, Crab claws bound – 2 trials 6 replicates each ($N=12$)
4. Abalone, Day, Crab claws free – 1 trial 6 replicates ($N=6$)
5. *Amphissa*, Day, No Crabs – 1 trial 6 replicates ($N=6$)
6. *Amphissa*, Night, No Crabs – 1 trial 6 replicates ($N=6$)

Significant preferences for one microhabitat type over another was tested using a non-parametric chi square test.

RESULTS

Abalone surveys

Few northern abalone were observed during the surveys at the 10 sites in 2005. Only 17 abalone were found and of these 16 were in the sites with *Nereocystis* only (Tables 1 and 2). The remaining abalone was found at a site with both kelp canopy and sea urchin habitat. Abalone found during the timed swims ranged in size from 75 to 142 mm with an average size of 107 mm (Table 1). The majority of abalone found were exposed, with the exception of the two 75 mm animals and one other animal (120 mm) that were cryptic. Abalone were

Table 1. The abundance of adult northern abalone found during Washington Department of Fish and Wildlife surveys in 1979 ($N=8$ sites) and 2005 ($N=10$ sites) in the San Juan Channel

| Year | Search time (min) | Number of abalone (Abs h^{-1}) | Size range (mm) (mean size) |
|---------------------------|-------------------|-----------------------------------|-----------------------------|
| 1979 | 480 | 224 (28^{-1}) | 57–139 (101) |
| WDFW 2005 (this study) | 694 | 17 ($1.5h^{-1}$) | 75–142 (107) |

Table 2. The abundance of adult northern abalone found at sites within the San Juan Channel in the summer of 2005 with (1) *Nereocystis* kelp canopy cover only, $N=3$ sites; (2) red sea urchin spine cover only, $N=3$ sites; and (3) a combination of both *Nereocystis* kelp canopy and red sea urchin spine canopy cover, $N=4$ sites

| Habitat type | Number of sites | Number of abalone |
|------------------|-----------------|-------------------|
| Kelp | 3 | 16 |
| Urchins and Kelp | 4 | 1 |
| Urchins | 3 | 0 |

generally on reef habitat although one was on a boulder and another in a rock crevice.

The number of abalone observed in 2005 was dramatically less than those found during similar timed swim surveys conducted in 1979 by the WDFW (unpubl. data). During the 1979 surveys 224 abalone were found at eight sites despite less search time in 1979 (Table 1). In 1979, juvenile northern abalone were observed as small as 57 mm with a mean SL of 101 mm and more of an even size distribution indicating that recruitment was ongoing. In 1979 the abalone were reported to occur in a narrow depth range, in the 2005 survey the abalone were all found within a narrow depth band from 6–7 m.

The kelp sites had relatively high percentages of *Nereocystis* canopy cover from 80–100%, with one exception. These sites also had mean algal cover percentages of subcanopy (35%) and foliose algae (75%), but low percentages of turf (11%). In contrast, the sea urchin dominated sites had low mean percentages of canopy, subcanopy and foliose (52%) but turf algal cover (38%) was greater than at the kelp canopy dominated sites. Red sea urchin dominated sites had half the amount of encrusting algae (31%) compared with the kelp canopy sites (64%). Encrusting algae were made up of primarily pink corallines such as *Lithothamnion* spp. and *Pseudolithothamnium* spp. as well as a small percentage of *Ralfsia* and fleshy *Hildenbrandia* spp. Kelp and urchin sites were similar with respect to substrate type having similar percentages of cobble, boulder, and reef (65–75%).

White cap limpet counts were correlated with abalone counts. Those sites with many limpets ($N=210$ per site) were also sites with the most northern abalone, kelp, and coralline cover while sites with both kelp and urchin had intermediate numbers of limpets ($N=57$ per site) and sea urchin dominated sites had the least limpets ($N=8$ per site).

Multivariate analysis

Adult northern abalone abundance was correlated with the abundance of white cap limpets, rock and pink scallops but, not brachiopods or keyhole limpets. The scree plot indicated

that 88% of the variation was explained by the first three principal components. The factor loadings indicate PC1 (47% variance) reflects a general association among the mollusc species with the exception of keyhole limpets and brachiopods. Whereas, PC2 (24%) reflects an association of keyhole limpets with white cap limpets among the sites. PC3 reflects an association between abalone and white cap limpets which explains less of the total variation (17%).

PC1 successfully separated the factor scores in multivariate space across habitat types with those from the kelp and coralline habitats clustering to the right with high PC1 scores, those clustering on the left from the urchin habitat with low PC1 scores, and those from habitats with both kelp and urchin in the middle (Figure 2). PC1 was unsuccessful at separating the factor scores in multivariate space based on MPA status (Figure 3) indicating mollusc abundance was not related to the protected status of the site.

Microhabitat collections

The coralline rock microhabitat had higher species richness than the sea urchin spine canopy microhabitat (Table 3). The difference in species richness between the two microhabitats was significant using a two tailed *t*-test (t stat = 3.0, d.f. = 12, $P < 0.01$). The difference in the average diversity values between the two microhabitats was significant using a two

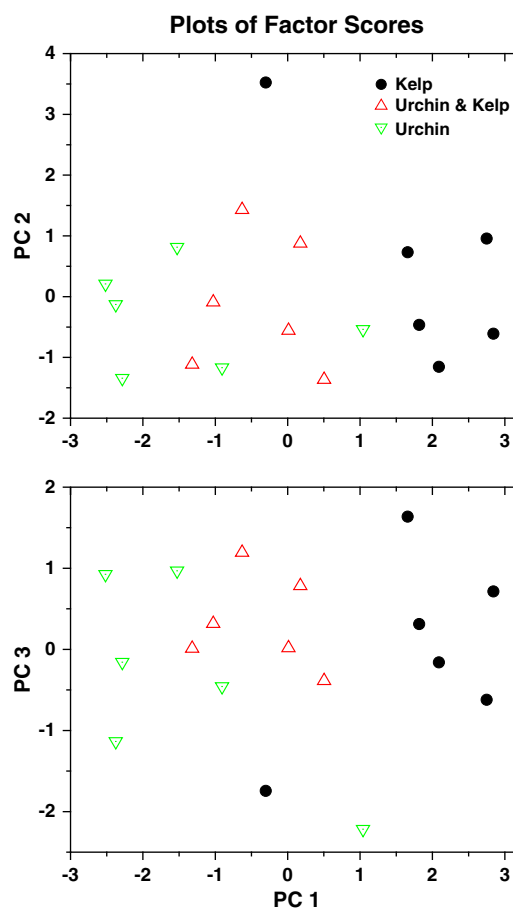


Figure 2. Plot of factor scores in multivariate space showing factor scores from samples at different habitat types with Principal Component 1 along the X axis and PC2 on the Y axis (A top plot) and PC3 on the Y axis (B bottom plot).

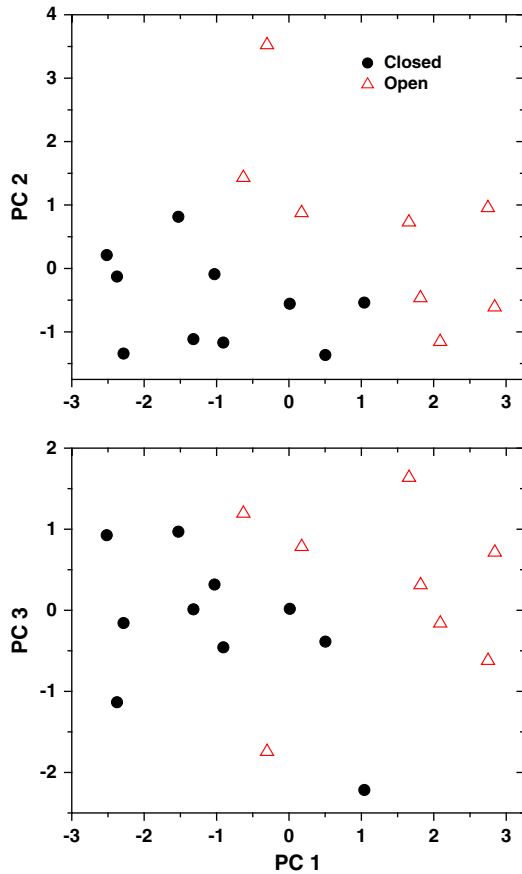


Figure 3. Plot of factor scores in multivariate space showing factor scores from samples at reserve and fished sites with principal component 1 along the X axis and PC2 on the Y axis (B bottom plot) and PC3 on the Y axis (A top plot).

tailed *t* test (t stat = 3.76, d.f.15, $P < 0.001$). Coralline rock and kelp holdfast both had high species richness but kelp holdfast had more than twice the number of individuals compared with coralline rocks, suggesting this microhabitat provided the best refuge. Coralline rock and kelp holdfasts also had five times more individuals than samples from under the spine canopy of red sea urchins.

The smaller size classes of *Amphissa* (<10 mm) were found more often within kelp holdfasts than within the sea urchin spine canopy and coralline rock microhabitats. Larger *Amphissa* (20–30 mm) no longer used kelp holdfast microhabitat primarily (Figure 4) but occurred in all microhabitat types.

Microhabitat preference trials

In the laboratory microhabitat preference trials, juvenile northern abalone (19 mm) preferred to be in the section of the tank with coralline covered rocks rather than with the sea

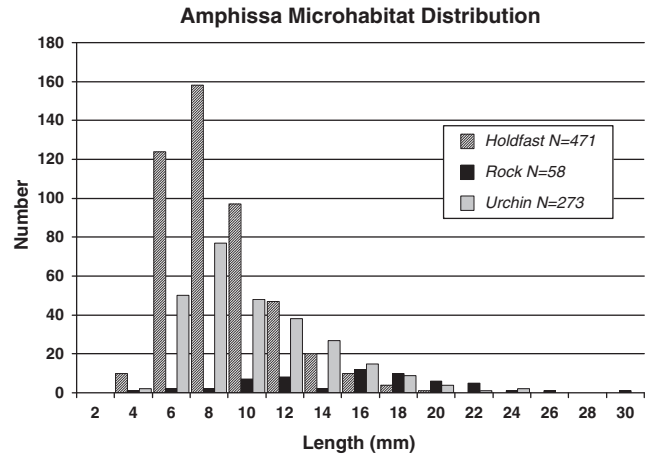


Figure 4. Microhabitat preference of *Amphissa* snails across a range of snail sizes (1–30 mm). Microhabitats investigated were *Nereocystis* holdfasts, sea urchin spine canopy and coralline rock microhabitats in the San Juan Islands.

urchins or in the kelp holdfasts. This preference appeared in both day ($X^2 = 33$, d.f. = 2, $P < 0.001$) and night ($X^2 = 108$, d.f. = 2, $P < 0.001$) as well as in crab trials with bound claws ($X^2 = 62$, d.f. = 2, $P < 0.001$) and with unbound claws ($X^2 = 59$, d.f. = 2, $P < 0.001$). In the final trial, when the bands on the crabs were removed and juvenile abalone were eaten, juvenile abalone still preferred to be in the rock section of the tank. Those juvenile abalone that did go into the section of the tank with red sea urchins were almost always found under the spine canopy suggesting this is a suitable cryptic microhabitat for juvenile northern abalone but that it is not preferred.

There were no significant differences in the section of the tank occupied by the small snail *Amphissa* in the day ($X^2 = 4$, d.f. = 2, $P > 0.1$) or night trials ($X^2 = 1$, d.f. = 2, $P > 0.1$). *Amphissa* occurred in the kelp, sea urchin and coralline rock sections equally during all the trials.

Sea surface temperatures

There was a general warming trend in the yearly mean of sea surface temperatures measured at Race Rocks, in southern Vancouver Island (Figure 5). Temperatures appear to have increased more than 1 °C over the 35 year time record. The two warmest years in the record were the 1983 and 1998 El Niño years. No anomalously cool years appear in the temperature record in the past 20 years.

DISCUSSION

Ecosystem engineers

Adult northern abalone were most abundant in habitats structured by *Nereocystis* with coralline present (Table 2).

Table 3. Average species richness (variance), Shannon species diversity index (variance), effective number of species and number of organisms found within three microhabitats types: *Nereocystis* kelp bed ($N = 7$ sites); coralline rock ($N = 10$ sites); and sea urchin beds ($N = 7$ sites)

| Microhabitat | Richness (var) | Diversity (var) | Effective Spp. | Number of individuals |
|----------------|----------------|-----------------|----------------|-----------------------|
| Kelp holdfast | 20 (39) | 1.98 (0.33) | 7.2 | 2274 |
| Coralline rock | 22 (170) | 2.36 (0.39) | 10.6 | 909 |
| Urchin canopy | 9 (19) | 1.35 (0.23) | 3.9 | 441 |

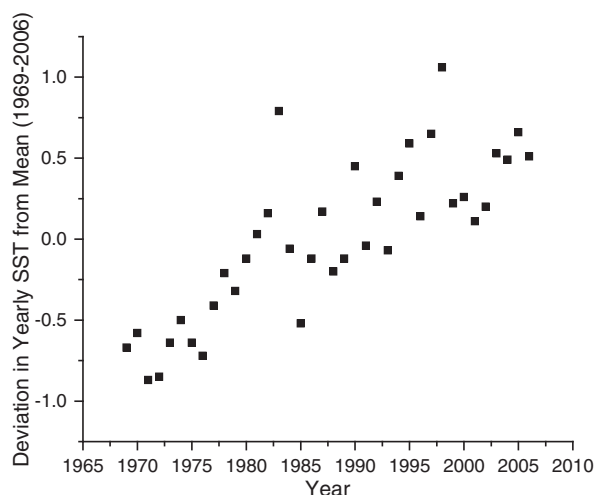


Figure 5. Deviations of the yearly means from the long-term mean (1969–2006) in sea surface temperature (Celsius) at Race Rocks, southern Vancouver Island, Canada. The two warmest years in the time series are the 1983 and 1998 El Niño years.

Nereocystis may provide abalone a suite of features critical to survival including food, shelter, and protection from water currents. Kelp holdfast microhabitats were species rich compared with habitats structured by sea urchin spine canopy alone (Table 3). Subcanopy, foliose, and encrusting coralline algae were all abundant in the *Nereocystis* habitats, indicating that shading by kelp canopy did not negatively impact these algae. Some corallines such as *Lithothamnium phymatodeum* are known to survive and grow well in shaded conditions (Dethier and Steneck, 2001). Sea urchins co-occurred with *Nereocystis* at some sites in this study as they did in a previous study (Carter *et al.*, 2007) indicating that overgrazing of algae by sea urchins is not occurring. Northern abalone were associated with other mollusc species such as white cap limpets, rock and pink scallops (Figure 2) suggesting these easy to survey species could be used as indicators of suitable northern abalone habitat for restoration. Mathematical models of ecosystem engineers show that population dynamics could be affected by the presence or absence of engineers (Gurney and Lawton, 1996).

Juvenile abalone (<75 mm) were absent from all habitat types as would occur with recruitment failure. Few juvenile northern abalone have been found inside artificial recruitment modules in the San Juan Islands (Bouma, 2007) and in northern California (Rogers-Bennett *et al.*, 2004). In contrast, juvenile northern abalone have been recruiting regularly in the Queen Charlotte Islands, British Columbia (DeFreitas, 2003). Recruitment failure in the San Juan Islands indicates a need for restoration actions as natural rebuilding may not be occurring. Similarly, active enhancement measures have also been recommended in the recovery plan for the endangered white abalone, *H. sorenseni* (NMFS, 2008) to overcome recruitment failure.

In laboratory experiments hatchery reared juvenile northern abalone (19 mm) showed preference for coralline covered rocks over kelp holdfasts and sea urchin spine microhabitats. All juveniles in the section of the tank with sea urchins were found in close association with the spine canopy suggesting this too is suitable microhabitat but not preferred. In the wild, juvenile (<45 mm) northern abalone have been observed under the

spine canopy of red sea urchins (7% found under sea urchins) off the west coast of Vancouver Island (Tomascik and Holmes, 2003). Elsewhere in the world, juvenile abalone also utilize sea urchin spine canopy microhabitats (Kojima, 1981; Mayfield and Branch, 2000; Rogers-Bennett and Pearse, 2001).

The risk of predation on juvenile northern abalone has been shown to be significantly higher for very small juveniles <13 mm (Griffiths and Gosselin, 2008) compared with large juveniles (>20 mm). Field data from the small snail *Amphissa* (1–15 mm) in this study, showed a clear preference for kelp holdfasts while the larger *Amphissa* utilized all microhabitat types. *Nereocystis* could provide not only food but also cryptic microhabitat for small molluscs (<12 mm) (Figure 4), while the larger juveniles were associated with coralline algae covered rocks. In this study, corallines were twice as abundant in kelp sites and encrusting corallines have been shown to be cues for larval settlement and metamorphosis for abalone and other marine invertebrates (Morse *et al.*, 1979; Sloan and Breen, 1988; Hahn, 1989). We found lower percentages of encrusting coralline cover in sites with sea urchins perhaps as a result of grazing as has been found in Kenyan coral reefs (O'Leary and McClanahan, 2010). In other regions, corallines are positively associated with grazers which can eat competing fleshy algae (Guidetti, 2006). An understanding of these types of direct and indirect effects (trophic cascade) of engineering species will be critical to restoration planning.

Critical habitat and ocean warming

Recovery planning for threatened and endangered species may involve the decision to list critical habitat, as is being done for the endangered black abalone (M. Neuman pers. comm.). Here it is shown that *Nereocystis* and corallines are critical habitat components for northern abalone and they are associated with increased species richness (Tables 3 and 4). Stocking very small (<12 mm) juvenile northern abalone may be more successful in sites with kelp holdfasts and coralline cover. Designating shallow nearshore kelp beds as critical northern abalone habitat should be considered, as extant adults were found in a very narrow depth band (6–7 m) and this rocky habitat is limited.

The communities and species associated with kelp and corallines may be affected by warm water (Blight and Thompson, 2008) as has been found elsewhere (Tegner and Dayton, 1987). *Nereocystis* may be more sensitive to increased sea surface temperatures than *Macrocystis* since during the 1998 El Niño event *Nereocystis* populations suffered a 75% decrease compared with an 8% decrease for *Macrocystis* beds (Berry *et al.*, 2001). Corallines may also decrease growth when temperatures rise above 15°C (Adey,

Table 4. Laboratory results of microhabitat preference trials for juvenile northern abalone and the snail *Amphissa*

| Species | Treatment | N | Microhabitat | | |
|-----------------|---------------------|----|--------------|--------|----------|
| | | | Rock | Urchin | Holdfast |
| Abalone | Day | 12 | 168 | 94 | 97 |
| Abalone | Night | 18 | 262 | 174 | 94 |
| Abalone | Day – with predator | 18 | 273 | 140 | 109 |
| <i>Amphissa</i> | Day | 6 | 36 | 33 | 35 |
| <i>Amphissa</i> | Night | 6 | 44 | 27 | 40 |

2008). Sea surface temperatures at Race Rocks, near the study sites, indicate that the 1998 El Niño was the warmest year on record for the 90 year time series. Warm water can have multiple negative impacts on abalone including affecting reproduction (Vilchis *et al.*, 2005; Rogers-Bennett *et al.*, 2010), growth (Haaker *et al.*, 1995) and mortality (Vilchis *et al.*, 2005). Warm water may also act synergistically with other sources of mortality such as fishing to negatively affect abalone (Harley and Rogers-Bennett, 2004). The past 35 years have been a period of increasing sea surface temperatures in the region (Figure 5) and the link between warm water and abalone declines in Washington State and the southern portion of their range (Rogers-Bennett, 2007b) needs to be examined further.

Species diversity

In some regions, habitats with ecosystem engineers have been shown to have three times the species richness of habitats without ecosystem engineers (Bracken *et al.*, 2007). There is now a growing body of evidence for marine systems that species-diverse ecosystems have a positive effect on ecosystem function including enhanced fishery yields and greater resilience to perturbations (Tegner and Dayton, 2000; Worm *et al.*, 2006). Ecosystem engineers can be used to help restore and maintain marine ecosystem functions by ameliorating abiotic stresses (Byers *et al.*, 2006). Water motion in areas without kelp holdfast microhabitats could wash away small marine invertebrates. Many newly settled invertebrates including abalone also settle on and eat corallines during the early part of their life history. Therefore, it is concluded that in the Pacific North-west, restoration should take advantage of kelp bed with associated corallines to promote northern abalone recovery and conservation taking an ecosystem-based restoration approach.

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