

DESCRIBING NORTHERN ABALONE, *HALIOTIS KAMTSCHATKANA*, HABITAT: FOCUSING REBUILDING EFFORTS IN BRITISH COLUMBIA, CANADA

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ABSTRACT The northern abalone is listed as *threatened* under the Canadian Species at Risk Act. Northern abalone occur in a wide range of habitats from fairly sheltered bays to exposed coastlines. However, not all habitats are likely to support high abalone densities with large northern abalone that have high fecundity. Therefore, habitats that can support dense concentrations of large abalone would be better suited for aggregation rebuilding projects. Several experimental rebuilding projects are currently underway; the experimental sites were, in general, selected based on abalone presence and relative abundance. This study attempts to describe abalone habitat suitable for rebuilding efforts by using data from surveys completed at the start of the large decline of abalone densities observed in British Columbia (BC). Several areas were surveyed to determine abalone density on the southeast coast of the Queen Charlotte Islands and the north central mainland coast of BC between 1978 and 1980. Habitat data were recorded after each dive, including substrate types and dominant algae cover and species. Four categories of algal types were analyzed based on height and growth patterns: (1) canopy; (2) understory (large bottom cover); (3) turf (short bottom cover); and (4) encrusting. In addition, an index of wave exposure was also calculated for each site surveyed. Northern abalone density was inversely correlated to mean abalone shell lengths. The exposure index was correlated positively to abalone density but negatively to mean shell length. Regression tree classifications successfully separated habitats of high and low abalone densities, but these differed from habitats classified using mean shell length as the response variable. To optimize rebuilding efforts, a compromise between the two classification models, one with density as the response variable and the other with mean shell length, may have to be developed.

KEY WORDS: northern abalone, *Haliotis kamtschatkana*, population rebuilding, habitat description, species at risk

INTRODUCTION

Northern abalone, *Haliotis kamtschatkana* (Jonas 1845), in British Columbia (BC) is listed as *threatened* under the Canadian Species at Risk Act. Highly prized for harvesting, the stocks have continued to decline since the complete closure of the fishery in 1990 (Atkins et al. 2004). Poaching and low recruitment, caused by low spawner densities, are considered the most significant threats hindering the recovery of the species in BC (Abalone Recovery Team 2002). To increase recruitment, a few pilot rebuilding projects, mainly through aggregation of adult abalone, are underway.

Northern abalone occur from Turtle Bay, Baja California, to Yakutat, AK (McLean 1966, O'Clair & O'Clair 1998), in a wide range of habitats from fairly sheltered bays to exposed coastlines on rocky substrates from the low intertidal zone to shallow sub tidal depth, with most adults found <10 m depth (Abalone Recovery Team 2002). This is considered a broad definition of habitat, because not all habitats support high abalone densities. In BC, habitat is not considered limiting for abalone. However, the resources available to recover northern abalone are limited and rebuilding efforts should focus in areas with a good chance of recovery. A more detailed definition of optimal northern abalone habitat is needed to aid rebuilding efforts.

Breen & Adkins (1979) first described relationships between some habitat types and the size and number of northern abalone. From surveyed sites, they qualitatively classified abalone habitat into eight communities and calculated mean abalone density and shell length (SL in mm), for each community. Canopy-forming kelp, namely *Macrocystis integrifolia* and *Nereocystis luetkeana*, and two genera of understory kelp, *Pterygophora californica* and *Laminaria* spp., were used to

define these communities. Abalone densities were low in *Macrocystis* forests and highest in *Pterygophora* forests without surface canopy; densities in *Nereocystis* forest were between these two extremes. The relationship was reversed for abalone size. The classification was considered rough because no formal classification method was used and, because only a few sites were surveyed, it was unknown if the habitat definitions could be applied to other areas (Breen & Adkins 1979). However, little has been done on northern abalone habitat classification to date. Tomascik & Holmes (2003) examined several northern abalone habitat attributes in relation to abalone and red sea urchin densities and sizes in the Broken Group Islands, west coast of Vancouver Island, but did not classify or define habitats. In addition, the relationships explored were for micro-habitats because they were based on quadrat (1 m²) data. Because abalone have the ability to move, it is unknown if some of these relationships can be used to determine appropriateness of sites selected for rebuilding efforts. Jamieson et al. (2004) created a model to determine areas of suitability for abalone habitat, but the model was based on available mapped data only (i.e., not on surveyed abalone habitats).

If possible, sites chosen for rebuilding efforts should have the capacity to contain dense concentrations of large abalone. Spawning aggregations are believed to enhance reproductive success by increasing the chance of fertilization (Sloan & Breen 1988, Shepherd & Brown 1993, McShane 1995a, McShane 1995b, Shepherd & Partington 1995, Babcock & Keesing 1999). Because fertilization success depends on the aggregation density of abalone, concentrating mature abalone should increase larvae production (Campbell 2000). In addition, northern abalone fecundity increases with individual size and therefore for similar densities, large abalone have a potentially higher reproductive contribution than small abalone (Campbell et al. 2003). Shackell et al. (2005) recommended that only data

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derived prior to significant stock declines should be used to identify areas of high densities for species at risk because remaining distributions may not indicate core areas necessary for successful recovery. In six severely depleted fish stocks on the Scotian Shelf, Canada, areas occupied during periods of low abundance did not correspond to historical preferred core areas (Shackell et al. 2005). Habitat data collected from abalone surveys in recent years may or may not indicate best suitability for high densities of large northern abalone, because their densities have declined by more than 75% in 25 y and some areas that had supported abalone populations in the past are now devoid of abalone (e.g., Cumsheewa Inlet, QCI [Atkins et al. 2004]). Therefore, abalone habitats suitable as rebuilding sites should be able to support high densities of large abalone and their definition should be based on survey data collected prior to the intensive phase of the commercial fishery, which peaked in late 1970s. In addition, the definition should be fairly straightforward to use because many local community groups are involved in the northern abalone rebuilding efforts.

The main objective of this study is to define northern abalone habitat suitable for rebuilding efforts with variables that could be easily measured and/or collected in the field. To do this, we used survey data collected at the initiation, or shortly thereafter, of the intense commercial fishery of northern abalone.

METHODS

Habitat definition analysis was based on historical surveys conducted at the initiation of the intense commercial fishery during 1978 to 1980. Northern abalone stocks have been assessed through surveys of index sites in the north central mainland coast (CC) of BC and southeast Queen Charlotte Islands or Haida Gwaii (QCI) (Fig. 1) using a standard survey design since 1978 (Breen & Adkins 1979). Much of the commercial fishery for northern abalone was carried out in

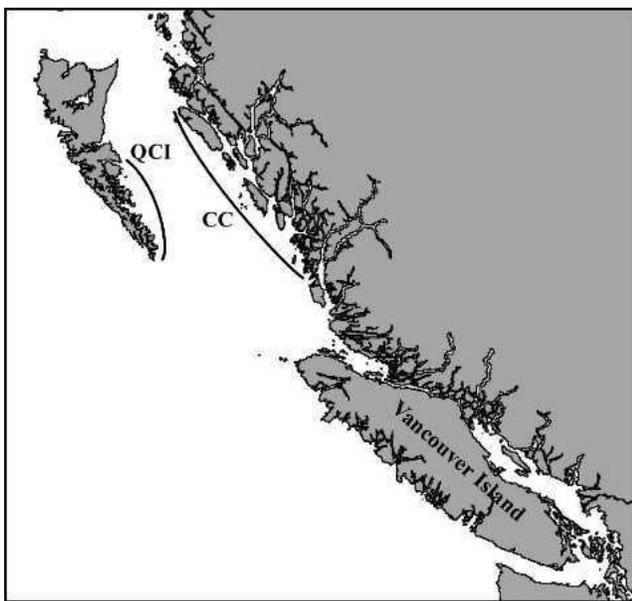


Figure 1. Map of British Columbia showing the historical survey areas (QCI, Queen Charlotte Islands; CC, Central Coast) included in the analyses.

these areas during 1977 to 1990 (Harbo 1997). The survey design and data collected are described below.

Historical Surveys

The surveys used for the northern abalone habitat definition were completed as follows: (1) QCI August 1978 (108 sites); (2) CC November 1978 (12 sites); (3) CC April 1979 (14 sites); (4) QCI July 1979 (10 sites); (5) CC April 1980 (4 sites); (6) CC June 1980 (4 sites); and (7) CC July 1980 (11 sites) (Adkins & Stefanson 1979, Breen & Adkins 1979, 1980, 1981, 1982, Breen et al. 1982). The surveyed sites were known to be suitable good habitat for northern abalone, based on observations from the surface and from swim over dives, with the help of experienced harvesters and/or harvest records. Some sites had been harvested, whereas others were within areas closed to commercial fishing.

Because abalone density was used as a response variable to classify habitat (see below for habitat analysis), only sites where the same sampling design had been applied were used. All sites were surveyed using the method described by Breen & Adkins (1979). Once each site was located, divers placed a 1-m² quadrat at the top of the abalone habitat zone and then systematically sampled 16 quadrats within a 7 m × 16 m area (4 rows of 4 quadrats). Mean densities were calculated for each site as the number/m² for total number of abalone counted. At most sites (all of CC and about half of QCI sites), all emergent northern abalone found within the quadrats were brought up at the surface where each SL was measured to the nearest millimeter. Mean SL was also calculated for each site where abalone were measured. After each dive, divers would record a habitat description. Habitat data, therefore, represented the site as divers remembered. There was no systematic habitat data collection while underwater, but a standard habitat description form was used for most sites surveyed.

Habitat Data

Habitat data were reconstructed from original field notes as well as from published description of the sites (Adkins & Stefanson 1979, Breen & Adkins 1979, 1980, 1981, 1982, Breen et al. 1982). A summary list of variables and their values is shown in Table 1.

If no value could be determined for a given habitat variable, it was given a null value and the site was excluded from the analysis when that variable was included. Therefore the number of sites given in the results, tables, and figures will change depending on the number of unknown values and the variables included.

Wave Exposure

The method to calculate the index of exposure was based on Ekeboom et al. (2002). Sites coordinates were imported into ESRI ArcView 3.2 GIS software. The basemap was a seamless coastline and depth contours from amalgamated digital Canadian Hydrographic Survey charts. Some of the points were moved to ensure they were in the water portion and not on the land portion, of the basemap. From each point, a full circle of 120 radiating lines, 200 km each, were created using an ArcView script from Jenness (2001). These lines were then cut if they overlaid the land portion of the basemap shoreline using the “erase” function of XTools (Oregon Department of Forestry

TABLE 1.

Response and predictor variables used for northern abalone habitat classification. See Table 2 for explanation of algal acronyms.

| Variable Name | Variable Description | Values or Range |
|---------------------|---|--|
| Response Variables | | |
| Density | Mean site abalone density | 0–9.5 abalone/m ² |
| Mean SL | Mean shell length of all abalone measured at a site | 34.1–114.1 mm |
| Predictor variables | | |
| Exposure | Calculated wave exposure index | 9.7×10^4 – 1.0×10^7 |
| Substrate | Substrate category | 1, 2, 3, 4 (see 'Methods' for codes) |
| Slope | Slope in degrees | 0–70° |
| Canopy% | Canopy forming algae % cover | 0–100% |
| CanopySp | Dominant canopy algal species | MA, MANT, NO, NT |
| Understorey% | Large algae % cover | 0–100% |
| UnderstoreySp1 | Dominant understorey algal species | AG, AL, CF, CO, CY, DB, DE, EG, GI, HE, LA, LS, LT, NO, PH, PT, UL |
| UnderstoreySp2 | 2nd dominant understorey algal species | AG, AL, CF, CO, CS, CY, DB, DE, EG, GI, HE, LA, LE, LT, MA, NO, PH, PL, PT, RB |
| Turf% | Short algae % cover | 0–95% |
| TurfSp | Dominant turf algal species | AC, NO, RB, UL |
| Encrusting% | Encrusting algae % cover | 10–100% |
| Urchin | Relative sea urchins abundance | 1, 2, 3, 4 (see "Methods" for codes) |
| UrchinSp | Sea urchin species | D*, F*, FD* |

* Urchin species codes are F, *S. franciscanus*; D, *S. droebrachiensis*; FD: both species with *S. franciscanus* as dominant.

2003) and each resulting line intersecting a site point was selected. For each site, the lengths (in meters) of all the lines were summed and the result was the exposure index. Therefore the maximum value for the exposure index was 2.4×10^7 m.

These steps were integrated, and made easier to use, using an ArcView extension created by Ian Murfitt (DFO, Nanaimo, BC, pers. comm.). There were two main modifications of the method described by Ekebom et al. (2002) (i.e., the number and length of the lines). The length of each radiating line was determined as the maximum distance between the Queen Charlotte Islands and the mainland coastlines of BC; between Cape St James, southern tip of QCI, and the north-western tip of Calvert Island. This distance ensured that all sites were comparable within BC. As well, the exposure index was computed several times using different numbers of lines to determine the minimum number of lines that could be used with the most consistent results. Because the BC coastline has many islands, and considering the length (200 km) of a radiating line, the difference between a line intercepting an island close by and just missing it can change the resulting value of the exposure index and therefore its relative importance.

This exposure index was not a perfect measure of wave energy because factors such as depth, slope, offshore reefs, wave refraction, and wind direction were not taken into account. However, the exposure index was easy to calculate, did not require expensive engineering software, and had the advantage it could be calculated as part of the preparation of future field work. Consequently, sections of coastline can potentially be eliminated if the exposure index is clearly too high or low.

Substrate

Substrate was categorized into 5 groups: (1) mostly bedrock (smooth or with crevices); (2) complex hard (mostly boulders [rocks > 30 cm]; may be with bedrock, cobbles, or shell); (3) cobble (rocks <30 cm and >7–9 cm); (4) mixed soft/hard (soft

substrate [gravel, sand, shell] on top of hard substrate); and (5) mainly soft (gravel, sand, shell, mud) providing little or no attachment to kelp.

The historical sites were mainly composed of substrate categories 1 or 2 (52 and 93 sites, respectively); few (16) sites had other values for substrate. Not surprisingly, there was no site with a substrate category 5.

Slope

Slope, in degrees, was visually estimated from drawings of depth profile if no estimate was expressively given in either the field notes or the published site descriptions.

Algae

Algal information was recorded under four categories based on height and growth patterns: (1) canopy forming algae; (2) understorey (large bottom cover; 15 cm–2 m); (3) turf (short bottom cover, <15 cm); and (4) encrusting. A maximum of two algae were recorded for each category, except for encrusting, which consisted of percent cover only. Algae were recorded to species whenever possible (see Table 2 for list of algal species and their acronyms used in this study). The absence of algae was coded as NO for species and 0%. In the case where percent cover was not explicitly written, 5% was entered if species were written without % cover for the three categories of erect algae; 50% was entered for "encrusting" if hard substrate was present and the absence of encrusting algae was not noted.

Canopy forming algae in BC were comprised mainly of two species: *Macrocystis integrifolia* and *Nereocystis luetkeana* (as there is only one species for each genus present in BC, they are referred to by their genus name only). Other species can sometimes reach the surface (e.g., *Pterygophora californica*, *Egria menziesii*), but for the purpose of the habitat definition presented here, only *Macrocystis* and *Nereocystis* were considered

TABLE 2.
Algal species list from the site descriptions and acronyms used in the analysis.

| |
|---|
| AC = articulated coralline algae |
| AG = <i>Agarum</i> sp (Bory de Saint-Vincent, 1826) |
| AL = <i>Alaria</i> sp (Greville, 1830) |
| CF = <i>Codium fragile</i> ([Suringar] Hariot, 1889) |
| CO = <i>Costaria costata</i> ([Agardh] Saunders, 1895) |
| CS = <i>Codium setchellii</i> (Setchell & Gardner, 1903) |
| CY = <i>Cymathere triplicata</i> ([Postels & Ruprecht] Agardh, 1867) |
| DB = <i>Dictyota binghamiae</i> (Agardh, 1894) |
| DE = <i>Desmarestia</i> sp (Lamouroux, 1813) |
| EG = <i>Egregia menziesii</i> ([Turner] Areschoug, 1876) |
| GI = <i>Gigartina</i> sp (Stackhouse, 1809) |
| HE = <i>Hedophyllum sessile</i> ([Agardh] Setchell, 1901) |
| LA = <i>Laminaria</i> sp (Lamouroux, 1813) |
| LE = <i>Leathesia difformis</i> ([Linnaeus] Areschoug, 1847) |
| LS = <i>Laminaria saccharina</i> ([Linnaeus] Lamouroux, 1813) |
| LT = <i>Laminaria setchellii</i> (Silva, 1957) |
| MA = <i>Macrocystis integrifolia</i> (Bory, 1826) |
| MANT = mix of MA and NT |
| NO = no algae |
| NT = <i>Nereocystis luetkeana</i> ([Mortens] Postels & Ruprecht, 1840) |
| PH = <i>Phyllospadix</i> sp (Hooker, 1838) |
| PL = <i>Pleurophyucus gardneri</i> (Setchell & Saunders <i>ex</i> Tilden, 1900) |
| PT = <i>Pterygophora californica</i> (Ruprecht, 1852) |
| RB = branched red algae |
| UL = <i>Ulva</i> sp (Linnaeus 1753) |

as CanopySp. For the analysis, the canopy species were combined into one code if both species were present.

The understory algal species were numerous and sometimes difficult to determine which species listed in the field notes was dominant. Although it may have been possible to include percent cover for each algae species encountered, this seemed impractical as only two species were usually recorded for “understorey” and other species might have been present but were not recorded therefore biasing the analysis.

The turf category consisted mainly of articulated corallines (e.g., *Corallina* spp. [Linnaeus 1759]) and profusely branched red algae (e.g., *Microcladia* spp. [Greville 1830]). Because determining articulated coralline and many branched red algae to species was difficult, the codes for the turf category were for generic algae only (e.g., RB for red branched algae).

Sea Urchins

The historical field sheets noted visual estimates of abundance of urchins (urchins were not counted or measured). These estimates were transformed into 4 categories: (1) none; (2) few (estimate <2 urchins/m² or “sparse”); (3) many (estimate 2–5 urchins/m² or urchins starting deeper and/or patchy at 5–10 urchins/m²); (4) abundant (estimate >5 urchins/m² throughout or “very abundant”). The relative urchin abundance encompassed the red sea urchin, *Strongylocentrotus franciscanus* (Agassiz 1863) as well as the green sea urchin, *S. droebrachiensis* (O. F. Müller 1776). Purple sea urchins, *S. purpuratus* (Stimpson 1857) were sometimes mentioned, but their numbers were always low and therefore were not included in the relative abundance.

Sea urchins were present at most sites surveyed; only eight sites had no urchins. *S. franciscanus* was the most abundant species of sea urchins at most sites; 11 sites (out of 154) had *S. droebrachiensis* as the dominant sea urchins species.

Habitat Classification

For habitat definition, three historical data sets were considered: (1) QCI alone, which was considered the most accurate because all sites descriptions were recorded on a standard form; (2) CC alone, to evaluate if the habitat definition could be applied to other areas; and (3) QCI and CC combined, to increase the number of sites. The latter was expected to give the best definition for rebuilding efforts throughout BC. Initially, relationships between habitat variables and abalone density or mean SL were explored through simple correlations. This was particularly important for the relationship between the exposure index and abalone density or mean SL if the exposure index was to be used to exclude sites before future field work would be initiated. ANOVA were performed to look at differences in mean SL and exposure between the two areas, and a non-parametric Mann-Whitney test was used for abalone density because this variable is usually not normally distributed.

Multiple linear regression did not produce satisfactory results; the results were not easily transferable in the field and several variables were left out because either the number of variables was too great (percent cover for algal species encountered) or the variables were categorical and regression made little sense (e.g., substrate). These problems were also encountered with other types of classification methods. Regression tree analysis has been used successfully to predict productivity of fish habitat in the Great Lakes, Canada (Randall et al. 2004), as well as for determining habitat preference of sea cucumber in the Cook Islands (Džeroski & Drumm 2003). For the latter, the classification produced by regression trees was superior to linear regression. Thus, regression tree analysis was chosen to define abalone habitats because it is nonparametric and as a result numerical and text variables can be used at the same time to classify habitats. Using text variables has the added advantage that no recoding is necessary before or after the analysis.

Regression tree analysis does not assume a linear relationship between the predictor variables and the response variables (SYSTAT 2000). For regression tree analysis, a least squares loss function was used to estimate the PRE statistic (Proportional Reduction in Error) attributable to the predictive model. The PRE value is considered a goodness of fit statistic equivalent to the multiple R² in regression models (SYSTAT 2000). The analysis produced graphical trees beginning with one group (entire sample) and branching (splitting) to two or more terminal groups, each with similar habitat attributes. Each split was determined by one habitat predictor (variable), which divided the nodes using a split value (e.g., Group 1 Turf % ≥30%; Group 2 Turf % <30). At the end of each branch was a terminal group box showing the average and SD of the response variable and the number of observations (in this study, the number of sites) for that group. Branches stopped when the PRE achieved for that split was less than 0.05 and/or the minimum number of observations for the terminal groups was less than five. Abalone density and mean SL were used as response variables; all other habitat variables, as described above, were used as predictor variables (Table 1). For each

dataset (QCI or CC or combined), two sets of predictor variables were used: (1) all habitat variables; and (2) all, excluding Understorey Sp 2, Canopy %, Understorey %, and Encrusting %, which were considered the least reliable (estimated most often from field notes). Excluding some variables also increased sample size. Turf% was kept in the second set of variables because it was determined to be a predictor variable in the first set of analyses; the assumption was that when Turf% was not given in the field notes, but species were listed, it was considered important in terms of quantity, and the assigned value was 5%.

Terminal group numbers were assigned to the data and differences in mean densities or SL between groups were tested using ANOVA. If differences were detected at the 0.05 confidence level, a posthoc Bonferroni test was used for comparisons between groups.

One site was removed from all analyses because it was an outlier; the abalone density estimated at that site was almost twice that of the next highest estimate.

RESULTS

Site densities and mean SL were higher in CC than in the QCI, but were significantly different for site densities only ($U = 6.903$, $df = 1$, $P = 0.009$; F -ratio = 1.891, $df = 1$, $P = 0.172$). The results indicated that the commercial fishery may have progressed further in QCI than in CC. There was a significant correlation between abalone density and mean SL for the QCI dataset ($r = -0.446$; $P = 0.001$; $n = 53$), but not for CC ($r = -0.167$; $P > 0.2$; $n = 45$) (Fig. 2). The correlation was also significant when the data from both areas were combined ($r = -0.322$; $P = 0.001$; $n = 98$). For QCI, when abalone densities were high, generally abalone were smaller.

The mean exposure index estimates for the CC and QCI, respectively, were 37.4 ± 3.8 SE 10^5 m and 29.0 ± 2.0 SE 10^5 m. The relative exposure index was significantly higher for the CC data (F -ratio = 4.436; $df = 157$; $P = 0.037$) than for the QCI data. The exposure index was positively correlated with abalone density ($r = 0.237$, $P < 0.01$; $n = 117$) and mean SL ($r = 0.353$, $P < 0.02$; $n = 52$) in QCI. However, on the relationship between exposure and mean SL, two sites had small mean SL and

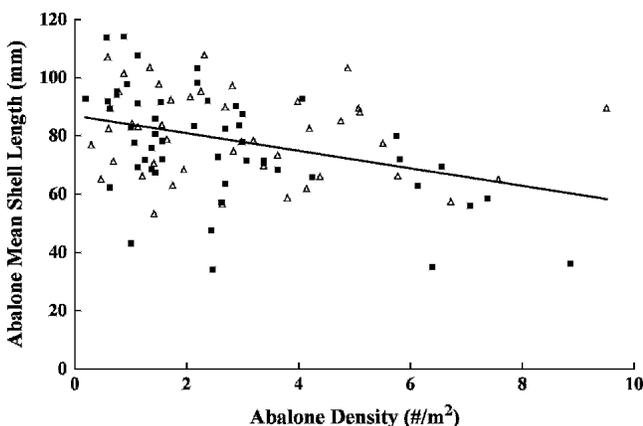


Figure 2. Plot showing the relationship between site densities and mean SL for QCI (closed squares) and CC (opened triangles) datasets. Regression line is for both datasets combined.

relatively large exposure index values ($>9.0 \times 10^6$), and when these values were removed, because they were isolated from the rest of the sites, the relationship was no longer significant ($r = 0.052$, $P > 0.7$; $n = 50$). For CC, there was no significant relationship between the exposure index and abalone densities ($r = 0.109$; $P > 0.5$; $n = 43$), but mean SL was negatively correlated to exposure ($r = -0.442$; $P < 0.005$; $n = 43$). When the datasets from both QCI and CC were combined, mean SL significantly decreased ($r = -0.399$; $P < 0.001$; $n = 95$) and density significantly increased ($r = 0.224$; $P < 0.005$; $n = 159$) as exposure intensified.

The results of the different regression tree analyses are summarized in Table 3 with two graphic examples (Fig. 3, Fig. 4) and ANOVA results (Table 4). All classifications produced terminal groups with significant differences between at least two groups (Table 3). In general, more terminal groups meant closer mean values, which did not differ from each other, except for the more extreme groups. As some of the values of biological variables were interpreted from written field notes (i.e., the original observer had not specified values), a regression tree classification using only physical data as predictor variables and density as response variable was tried. In addition to the very low PRE, the Bonferroni posthoc test showed significant differences between only 2 of the 3 groups, due primarily to large standard errors (equal or up to half of the mean values). For these reasons, tree analyses using only the physical variables were not repeated with other datasets.

The CC dataset produced results superior or equal to results from the larger QCI datasets. The combined datasets did not produce a classification model with higher PRE than for single area datasets, and, whereas the ANOVA showed significant differences, most of the groups were not different from each other using the Bonferroni posthoc test (Table 3). "All variables" produced the classification with the highest PRE, but using only the most reliable habitat variables, the PRE decreased slightly. The exception was for mean SL classification using the QCI dataset. Although the results using all variables with QCI dataset was the best for mean SL, six groups were produced with the middle groups having similar values, which were not significantly different from each other. The model also used two habitat variables (UnderstoreySp2 and Understorey%), which, for some sites, required more interpretation.

UnderstoreySp1 and CanopySp were the habitat variables used most often as predictors, especially for the split of the first or second level, which reduced the variability the most. Canopy species were always split with *Nereocystis* (NT) or no algae (NO) on one side and *Macrocystis* (MA) or a mix of *Macrocystis* and *Nereocystis* (MANT) on the other. Groups defined with MA, alone or mixed, had few abalone. In the QCI, the highest abalone densities were found in habitats with NT or no canopy, with *Alaria* sp, *Gigartina* sp, or *Desmarestia* sp. In the CC, the habitat group with the highest abalone densities was defined by having articulated corallines as TurfSp and *L. setchellii*, *Pleurophycus gardneri*, or *Costaria costata* as the second dominant understorey species. Abalone with the largest mean SL were found at sites with MA in the QCI. Few sites had MA in the CC dataset and CanopySp was not used as a predictor variable. In the CC, the habitats with abalone with the largest mean SL had an understorey mainly composed of *Laminaria* sp, *L. setchellii*, *Agarum* sp (probably *fimbriatum*), *Desmarestia* sp, *Pleurophycus gardneri*, *Codium fragile*, or no

TABLE 3.

Summary of regression tree classification of abalone densities or mean SL (response variables) using habitat attributes as predictors. Numbers in brackets are the level at which the given variable split the tree. PRE = proportional reduction in error.

| Response Variable | Dataset | Variables Included | N | Predictor Variables | PRE | Number of | | ANOVA | |
|-------------------|---------|--------------------|-----|--|-------|-----------|--------|---------|---------|
| | | | | | | Levels | Groups | F-ratio | P value |
| Density | QCI | Physical only | 117 | (1) Exposure (2) Exposure | 0.131 | 2 | 3 | 8.6 | 0.000 |
| | | All | 115 | (1) UnderstoreySp1 (2) CanopySp (3) UnderstoreySp1 (4) Turf% | 0.473 | 4 | 5 | 24.4 | 0.000 |
| | | Most reliable | 117 | (1) CanopySp (2) UnderstoreySp1 (3) Turf% | 0.426 | 3 | 4 | 28.0 | 0.000 |
| | CC | All | 40 | (1) TurfSp (2) UnderstoreySp2 (2) UnderstoreySp1 (3) UnderstoreySp1 | 0.576 | 3 | 5 | 13.1 | 0.000 |
| | | Most reliable | 40 | (1) TurfSp (2) UnderstoreySp1 (3) Slope | 0.509 | 3 | 5 | 9.3 | 0.000 |
| | | Both | 154 | (1) UnderstoreySp1 (2) CanopySp (3) Turf% | 0.292 | 3 | 4 | 22.0 | 0.000 |
| Mean SL | QCI | Most reliable | 162 | Same results as "All" | | | | | |
| | | All | 52 | (1) CanopySp (2) Understorey% (3) UnderstoreySp2 (3) UrchinSp (4) UnderstoreySp1 | 0.700 | 4 | 6 | 21.4 | 0.000 |
| | | Most reliable | 52 | (1) CanopySp (2) UnderstoreySp1 (3) Turf% (4) Turf% | 0.556 | 4 | 5 | 14.7 | 0.000 |
| | CC | All | 40 | (1) UnderstoreySp1 (2) Exposure (3) Turf% | 0.617 | 3 | 4 | 12.8 | 0.000 |
| | | Most reliable | 40 | Same results as 'All' | | | | | |
| | | Both | 92 | (1) UnderstoreySp1 (2) UnderstoreySp2 (2) Exposure (3) UnderstoreySp2 | 0.447 | 3 | 5 | 13.4 | 0.000 |
| | | Most reliable | 92 | (1) UnderstoreySp1 (2) Exposure (3) Slope | 0.419 | 3 | 5 | 15.1 | 0.000 |

algae; and the exposure index was low ($<1.6 \times 10^6$). Only Substrate, Canopy%, and Urchin were not used as predictor variables in one of the models produced.

DISCUSSION

Although many physical and biological factors may influence northern abalone abundance and size, this study only discusses the most relevant factors. For example, sea otter, *Enhydra lutris* (Linnaeus 1758), predation greatly affects abalone abundance and behavior (Watson 2000). However, sea otters were extirpated from the areas included in the analysis for several decades, and precisely because of their impact on abalone abundance, rebuilding efforts involving aggregation

or outplanting of larvae or juvenile will likely take place in areas currently unoccupied by reintroduced sea otters.

As northern abalone densities increased with relative exposure, mean SL decreased. Tomascik & Holmes (2003) also found a significant positive relationship between an exposure index and northern abalone densities in Barkley Sound. In BC, transplanting slow growing northern abalone from high wave exposure areas (referred as "surf abalone") to sheltered locations was shown to increase individual growth rates in both the QCI (Breen 1986) and in Barkley Sound (Emmett & Jamieson 1988). Several other studies have shown that fetch distance, as a measure of coastal exposure, can be a significant predictor of physical and biological habitat conditions (Chambers 1987, Harrold et al. 1988, Randall et al. 1998; 2004, Ekeboom et al. 2002).

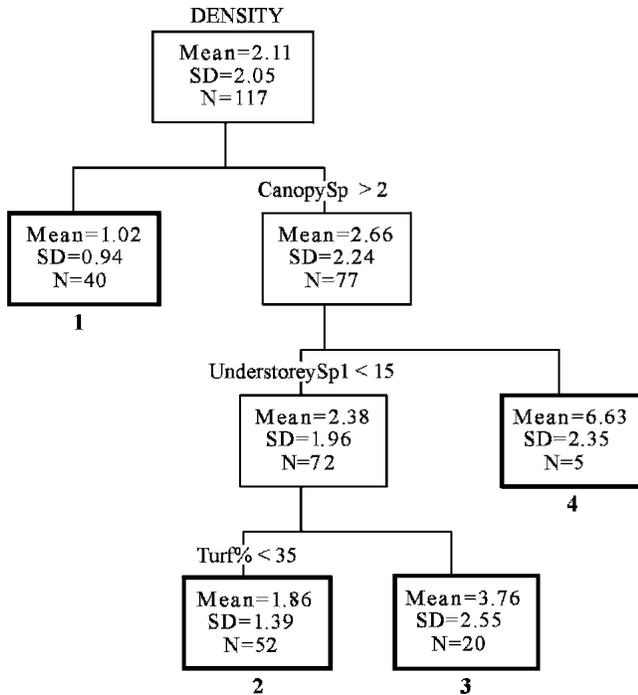


Figure 3. Regression tree classification results of abalone densities for the QCI dataset, excluding less reliable variables (Canopy%, Understorey%, UnderstoreySp2, Encrusting%). Terminal group numbers are below their respective boxes. Algae species included for, listed in order of increasing mean abalone density, CanopySp were MA, MANT, NO, NT; and UnderstoreySp1 were AG, CF, EG, LS, DB, CY, NO, LA, LT, PT, UL, PH, HE, CO, DE, AL, GI. See Table 2 for explanation of algal acronyms.

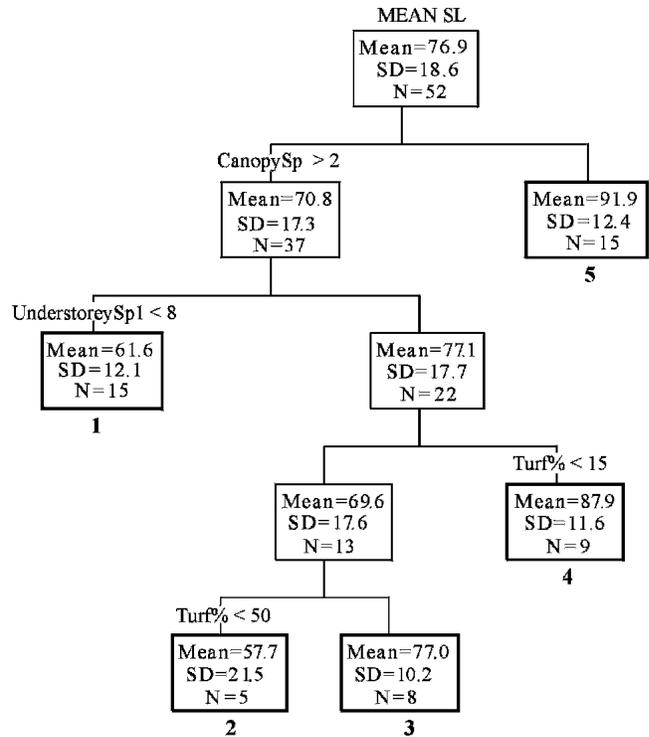


Figure 4. Regression tree classification results of abalone mean SL for the QCI dataset, excluding less reliable variables (Canopy%, Understorey%, UnderstoreySp2, Encrusting%). Algae species included for, listed in order of increasing mean abalone density, CanopySp were MA, MANT, NO, NT; and UnderstoreySp1 were DE, AL, GI, PH, CO, CF, NO, PT, DB, UL, LA, CY. See Table 2 for explanation of algal acronyms.

For QCI, the relationship between exposure index and abalone densities showed that perhaps two regression lines should exist (Fig. 5), but no habitat variables could create distinct groups of points that would separate the higher densities at low-medium exposure values and the lower densities with no apparent relationship with exposure. Even when the group numbers of the regression tree classification results were used, the higher densities did not form a separate cluster of points. These results indicated that another variable would be necessary to define the habitat present at the sites circled on Figure 5. These sites represent high abalone densities at low-medium

exposure, which, based on the exposure-mean SL relationship, could allow abalone to grow to a large size (i.e., they were not in the “surf” abalone range of the exposure index). Additionally, these sites would be more likely to be accessible for divers during surveys in varying weather conditions.

The exposure index, as calculated here, is an estimation of wave and swell energy (Randall et al. 1998, Ekebom et al. 2002), but

TABLE 4.

Posthoc Bonferroni test results comparing abalone densities or mean SL from terminal groups of regression tree classifications using QCI dataset and the most reliable habitat variables. Numbers represent *P* values; bold numbers indicate significant difference (*P* = 0.05).

| | Density | | | Mean SL | | | |
|---------|---------|---------|---------|---------|---------|---------|---------|
| | Group 1 | Group 2 | Group 3 | Group 1 | Group 2 | Group 3 | Group 4 |
| Group 2 | 0.080 | | | 1.000 | | | |
| Group 3 | 0.000 | 0.000 | | 0.091 | 0.120 | | |
| Group 4 | 0.000 | 0.000 | 0.002 | 0.000 | 0.001 | 0.865 | |
| Group 5 | | | | 0.000 | 0.000 | 0.112 | 1.000 |

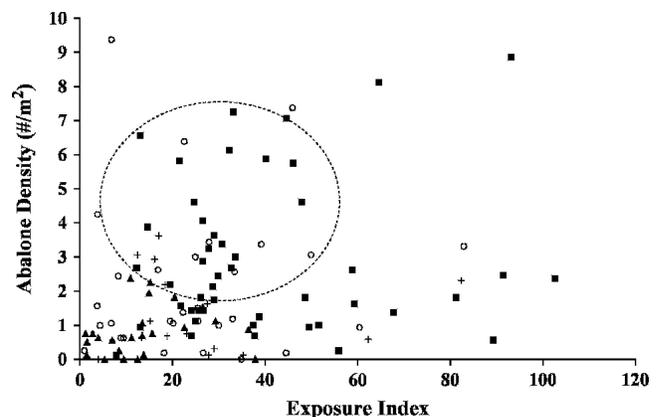


Figure 5. Plot showing the relationship between the exposure index ($\cdot 10^5$) and abalone densities for the QCI historical dataset by CanopySp: MA (closed triangles), NT (closed squares), NO (open circles) and MANT (crosses). The circled area shows the aggregation of points for which a habitat definition was sought.

does not reflect true water movement. The missing variable may be currents, but without long-term measurements or data intense oceanographic models, this variable would be difficult to estimate.

Regression tree analysis was helpful in defining northern abalone habitat. The use of two response variables, density, and mean SL was cumbersome. However, combining them resulted in classifications which were similar to those presented here, but less precise (lower PRE). Although all regression tree classifications significantly separated habitats with different abalone densities or mean SL, the definition based on the QCI dataset using the most reliable predictors gave the best results. The reasons for this choice, in addition to the larger sample size and easily identifiable attributes, are outlined below.

The CC data required considerable interpretation and were somewhat less diverse than the QCI data (e.g., there was only one site with MA and 4 sites with MANT as canopy, most sites had NT only). The CC dataset was included to see if there were differences in habitat definition between areas because there are rebuilding pilot sites on the CC. In areas where no historical surveys exist, there was a need to expand or ensure that the habitat definition from the QCI is transferable to other parts of BC. However, it was not possible to determine if the different habitat definitions resulting from the CC datasets were the result of the smaller sample size and the somewhat more homogenous dataset or reflected true habitat differences. The combined QCI and CC datasets did not produce better classifications (lower PRE, Table 3) and the results using density as response variable were similar to the QCI.

There were data problems with understory species and we considered that using the understory species as first level predictor variable was unwise (e.g., CC dataset with all variables and mean SL as response variable; Table 3). First, several species within a genus were often recorded with the genus name only. *Laminaria*, for example, included 3 species within abalone habitat from fairly sheltered to exposed habitats: *L. saccharina*, *L. bongardiana*, and *L. setchellii*. As algal species can be distributed along environmental gradients, particular species could indicate a habitat group. Second, because of how the site description data were collected, two sets of understory species variables were used in the regression tree analysis. Perhaps recording specific species instead of merely the two dominant ones should be noted in future surveys, which could provide additional determinant species for analyses. Third, some species were only recorded once or twice, and therefore the response variables had little or no variation for these species, which made it easy for the statistical software to place these sites into groups but may not have reflected the algal species true effect on abalone density or mean SL.

Little research has been conducted on marine algal communities and species along environmental gradients in BC (Lindstrom & Foreman 1978, Luning & Freshwater 1988, Druehl & Elliott 1996). Knowledge of algae species distribution along environmental gradients is needed to facilitate habitat classification, not only for abalone, but for most coastal sedentary species in general. Macroalgae are generally the dominant structural components on shallow temperate reefs and therefore the defining feature of habitat types is typically the species composition of algae (Shears et al. 2004). Algal species, which are distributed along environmental gradients are easier to see and measure than temperature, salinity, water movement, all of which vary in time and require long-term monitoring.

Whether areas with MA forests, capable of supporting large-sized northern abalone, could also support high abalone densities is unknown. Northern abalone recruitment may have been sporadic or occurred only before MA became the dominant kelp. MA habitats probably can support higher densities of northern abalone (e.g., a pilot rebuilding site in Barkley Sound, west of Vancouver Island, with MA had northern abalone densities increasing faster than other rebuilding sites without MA [J. Lessard, unpublished data]). However, until there is more evidence that MA forests can support relatively high abalone densities, rebuilding efforts should take place in NT forests, because they are easy to identify and from the analysis presented herein, can support important abalone densities.

The reasons for the inverse relationship between northern abalone densities and mean SL at sites surveyed in 1978 to 1980 were unclear. Factors involved could include differences in settlement abundance, postsettlement mortality, intra- and interspecies competition. Tomascik & Holmes (2003) found a positive significant relationship between encrusting algae and exposure. If northern abalone larvae settle on encrusting algae (Roberts 2003), this could explain why higher abalone densities were found in more exposed areas in our analyses. Balch & Scheibling (2000) found no significant differences in settlement of *S. droebranchiesis* between "kelp" and "barrens" habitats, but there were differences in recruitment between the two habitats, which probably reflected postsettlement mortality. They speculated that the small urchins were more preyed on in the kelp beds than in the barrens habitats. Schroeter et al. (1996) found no evidence that kelp forests reduced settlement in two sea urchin species. Connell (2003) found that physical abrasion by the canopy was sufficient to exclude all but a few individuals of invertebrates from successfully recruiting under canopy-forming algae. Duggins et al. (1990) on the other hand, showed that settlement within or outside kelp beds was dependent on species habitat preferences, and different sessile species settled in varying conditions depending on their life cycle requirements.

Small juvenile abalone are cryptic and rebuilding sites chosen should contain at least some cryptic habitat (Boutillier et al. 1985, Shepherd & Turner 1985, Cripps & Campbell 1998). Settlement is also believed to occur on encrusting coralline algae (Roberts 2003), which is usually present at sites where abalone are known to exist. The layer of encrusting algae may be maintained by sea urchins, and probably other herbivores although urchins are known for their intense grazing. Tomascik & Holmes (2003) found a significant positive relationship between urchin and abalone abundances, but a negative one between urchin abundance and abalone size. They also found a significant positive relationship between urchins and encrusting coralline algae and a negative relationship with macrophytes. Therefore the presence of sea urchins may benefit abalone through their maintenance of a habitat that is preferred by juvenile abalone (Steneck 1986, Tegner 2000, Tomascik & Holmes 2003).

In summary, rebuilding efforts should take place in areas of low-medium exposure with some boulders and a canopy of NT along with a cover of understory algae and articulated coralines. Although this is a broad definition, until more is known about northern abalone dispersal and how changes in habitat affect abalone growth and distribution, rebuilding efforts should at least attempt to produce larvae, some of which may recruit locally. Broad habitat definitions have been applied successfully in New Zealand (Shears et al. 2004). The objective

of these definitions was to quickly and efficiently classify habitats over large areas to detect changes and to calculate of abundances and productivity estimates based on habitat. Minns & Moore (2003) advocated that simple habitat classifications were efficient and gave the same results as data intense classifications. The advantage of standardized qualitative classification systems over purely quantitative descriptions for describing community structure is that they can be applied rapidly over large areas, and that ecological processes can be scaled by the area of habitat. In addition, these qualitative

habitat definitions can be used by different user groups that may not have the ability to conduct intense habitat surveys and do the ensuing analysis.

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