ZOOGEOGRAPHY AND CHANGES IN MACROINVERTEBRATE COMMUNITY DIVERSITY OF ROCKY INTERTIDAL HABITATS ON THE MAINE COAST

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Abstract

Epibenthic macroinvertebrate communities were examined at six rocky intertidal locations along the Maine shore. Sampled locations were distributed across nearly the entire coast of Maine from Kittery to Perry (43º 5' 3" N, 70º 39' 30" W to 44º 58' 28" N, 67º 02' 04" W) and were situated roughly equidistant from each other. All field sites were registered Critical Invertebrate Areas designated with this status in the 1970s by the Maine State Planning Office Critical Areas Program (1970-1987). Sampling of epibenthic macroinvertebrates was conducted by recording species observed on the substratum surface and under rocks during a random walk through the intertidal zone. Intertidal areas ranged from 6 to 12 acres and both sampling time and frequency of rock flipping were accordingly proportionate. Numbers of species (S) decreased south to north from 71 to 42. A geographic trend in β-diversity was discovered. Specifically, species assemblages south of Penobscot Bay clustered together and were significantly different from communities sampled north of the bay which also formed a distinct cluster. Distinct clusters emerged also according to gross regional geographic scale (south versus north of Penobscot Bay) from 2- and 3-multidimensional ordination of the six sample sites. Change in diversity was measured with average taxonomic distinctness (AvTD) as a metric. The sampled species assemblage from each location was compared statistically to a historical master species list compiled nearly 30 years previous by the Maine Critical Areas Program. Intertidal epibenthic macroinvertebrate diversity has changed significantly according to AvTD at Sea Point and Bailey Island. Comparisons made with original site descriptions and photographs did not show any detectable disturbances that could account for changes in AvTD at the two southern-most locations. While the causes for the measured changes are probably multifaceted, a trend of increasing sea water temperature may be a clue.

Introduction

Most of the shoreline of the Gulf of Maine is formed by the 8,690 km coast of the state of Maine, not including the shores of the 3,500 islands that lie off the Maine coast. The complex convoluted shoreline is largely the result of glaciations that have occurred at least five times (Knott and Hoskins 1968). The last glaciation produced great changes in sea level which strongly influenced regional climate and the distribution of littoral invertebrates (Bousfield and Thomas 1975; Campbell 1986; Belknap et al. 1987). These were largely the result of changes in coastal oceanography which were linked to the Gulf of Maine, a semi-enclosed macrotidal sea which itself is influenced by both continental and marine factors (Hertzman 1992).

The coast of Maine is perhaps best known for its rocky intertidal zone, although marshes, mudflats, eel grass beds, and sandy beaches share this coastline to different extents. Sand beaches and salt marsh predominate in southern Maine and are present as pockets and fringes in northerly locations. As these habitats become less frequent in the north, the intertidal becomes rocky with mud and coarse grain flats (Kelley et al. 1989). The differential distribution of habitats is largely the result of geological history (Caldwell 1998).

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The present distribution of shallow water invertebrates along the Gulf of Maine is mainly the result of coastal geology and sea water temperature. Zoogeographic patterns in β diversity of intertidal invertebrates along coastal Maine have been attributed to surface sea water temperatures (Bousfield and Laubitz 1972; Larsen 1985; Larsen and Doggett 1985; Watling 1979). These patterns persist apparently across various habitats with one exception, i.e., mudflats (Larsen and Doggett 1991). Causes for the regimes in sea water temperature recorded along the coast result from physical oceanography of the Gulf of Maine, with oceanic fronts and upwelling implicated as a cause (Larsen and Dogett 1985).

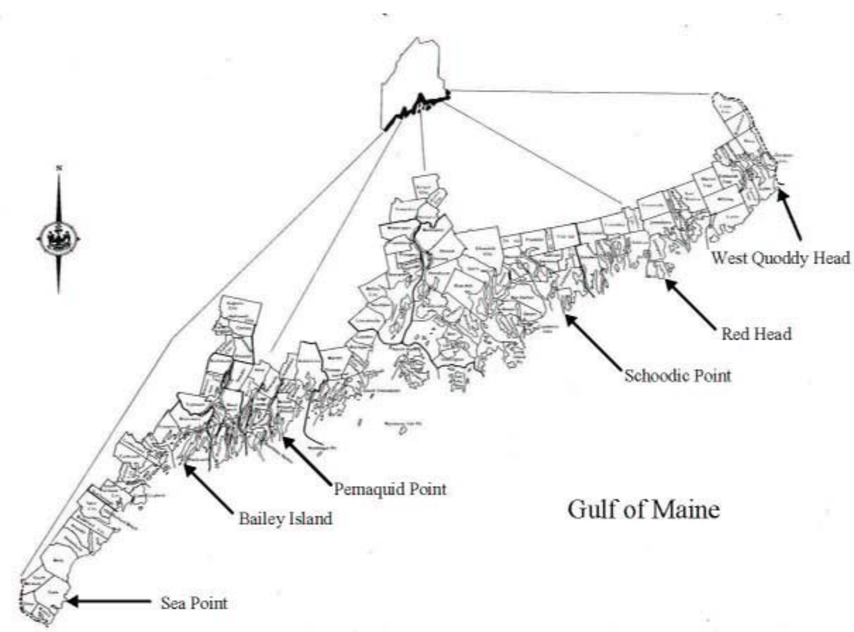
This study examined the intertidal distribution of macroinvertebrates along the coast of Maine by revisiting special areas where baselines were generated by the Maine State Planning Office Critical Areas Program (1970–1987). This program recognized the high diversity of intertidal communities by establishing Critical Invertebrate Areas distributed along the entire seaboard of Maine from Kittery to Cobscook Bay. Only rocky intertidal habitats were chosen for study. They were examined for zoogeographic patterns in β diversity (between habitat diversity) and changes in α diversity (local diversity).

Methods

Field Site Selection

Sample locations were chosen according to a preliminary study of 22 Critical Marine Invertebrate Areas conducted in the summer of 2004 (Trott, unpublished). Criteria used for selecting these field sites were similarity in habitats and well documented species assemblages with high species diversity. The distribution of field sites spanned nearly the entire Maine coastline making possible an examination of latitudinal trends in biodiversity (Figure 1). No sample locations were in the Penobscot Bay area since no Critical Marine Invertebrate Areas were established there. North and south of the bay, sampling locations were approximately equidistant from each other.

Figure 1. Map of coastal Maine showing locations of Critical Invertebrate Area sample sites



General Field Site Descriptions

Sea Point Marine Invertebrate Area. This exposed granite headland faces southeast and is bordered by sandy beaches. The high intertidal area is steep and banked with granite and igneous rock. Much of the mid-intertidal area of Sea Point is cobble with boulder (Figure 2A). There are pockets of gravel and sand. Bedrock outcrops are present in the low intertidal. Tide pools are scattered throughout the area. On a 0.64 ft (19 cm) tide, the intertidal area slopes approximately 1.4° away from mean high water to just beyond 747.5 ft (230 metres) (Figure 3). The first species list for this area is dated 1959.

Bailey Island Marine Invertebrate Area. This partially exposed, bedrock formation faces southwest and is part of a highly corrugated coastline. The intertidal contains areas of bedrock, boulder and cobble (Fig. 2B). The high intertidal is steep (60° - 80°). It grades into the lower intertidal that has a more gradual, 2.3° slope (Figure 3). Patches of gravel and sand are found between the finger-like projections of bedrock that create an irregular shape to the shore. Tide pools of various sizes and depths are located throughout the area but concentrated mostly in the eastern section. The species list is dated 1983.

Pemaquid Point Marine Invertebrate Area. This exposed bedrock headland projects seaward, south-southeast. The intertidal zone is narrow and nearly flat bedrock forming a shelf ending in deep open water (Figure 2C). Above it is a steep bedrock wall of approximately 90° that grades into the gradually, 2.4° sloping intertidal (Figure 3). Tide pools, few in number but large in size, are distributed mainly along the bedrock shelf. The species list is dated 1977.

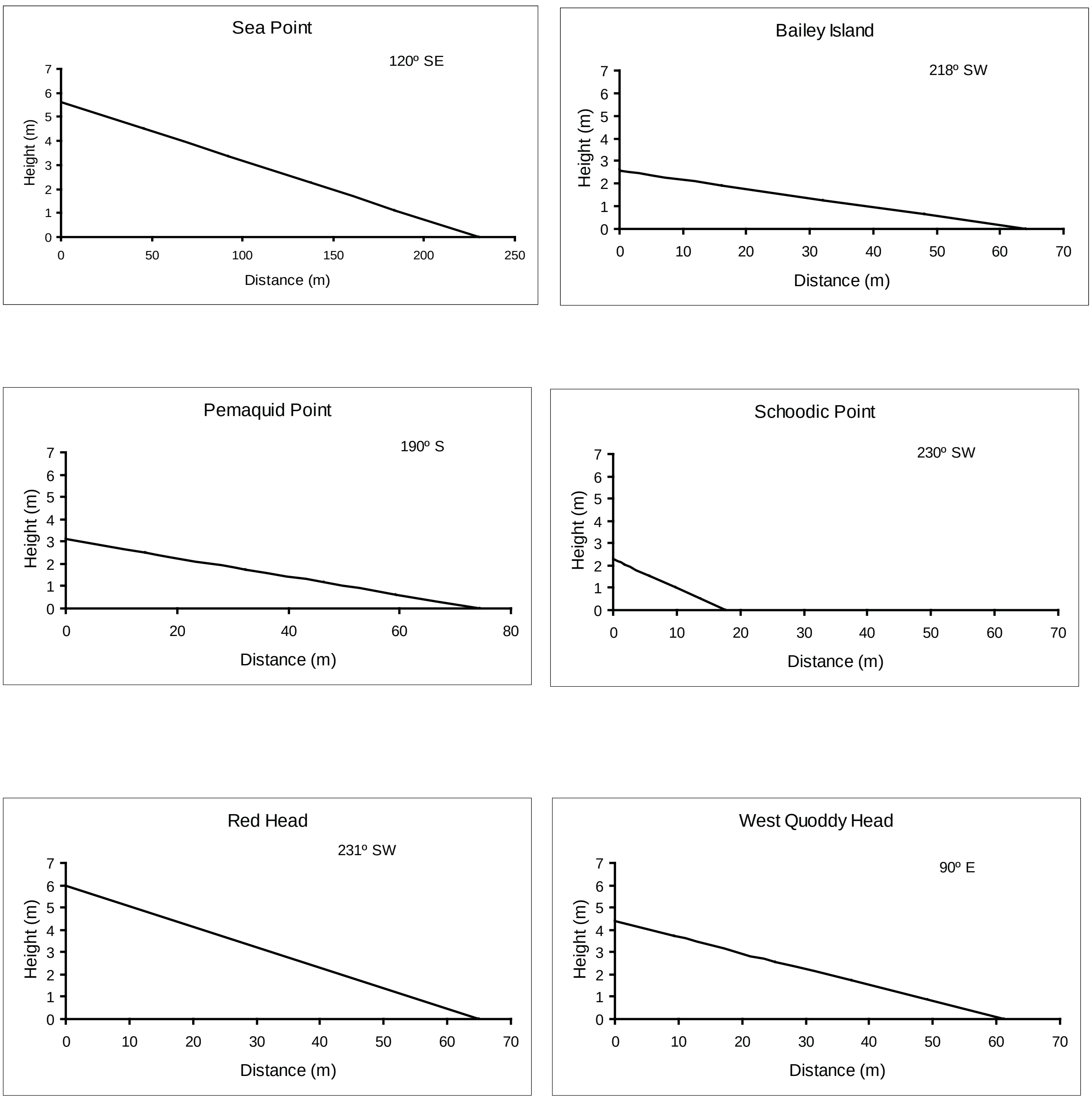
Schoodic Point Marine Invertebrate Area. This exposed pink granite headland is located on the western shore of the Schoodic Point peninsula. Most of the area has a granite escarpment cut by gullies making the topography complex in some places. While the ledge is the dominant feature, cobble and boulder prevail in some locations (Figure 2D). The escarpment is pitched at an angle of roughly 7° (Figure 3), although the slope is quite variable and can reach 90° on cliff faces. Numerous tide pools of various sizes are scattered throughout the high and low intertidal. The species list is dated 1977.

Red Head Marine Invertebrate Area. This exposed headland faces southwest and is primarily red granite. The head is formed by massive, very high and steep bluffs (Figure 2E). There are many deep grottos which are nearly inaccessible because of the steep, rockweed covered cliff faces that surround them. Wave surge can be extreme. Cobble and boulder are minor components of the substratum. The complex topography of the head is steep (Figure 3). Slopes range from 10 to 90° along this convoluted shoreline. The species list is dated 1977.

West Quoddy Head Invertebrate Area. This exposed, largely basalt headland faces east (Figure 2F). Steep, 75 ft (22.5 m) - 125 ft (37.5 m), irregular cliffs with 20° - 90° slopes border the intertidal zone. Cobble beaches lie at both the northern and southern boundaries of the area. Most of the intertidal zone is a mix of boulder, cobble and bedrock, although the latter predominates (Figure 2F). There are patches of gravel and sand. Numerous tide pools of various sizes are scattered throughout the high and low intertidal. The intertidal zone has a shallow 4° slope (Figure 3) and is influenced by 20 ft (6 m)tides.

Figure 2. Critical Invertebrate Area sample sites. A, Sea Point; B, Bailey Island; C, Pemaquid Point; D, Schoodic Point; E, Red Head; F, West Quoddy Head

Figure 3. Simple profiles of field locations indicating general slope of intertidal zone measured from high tide mark to low tide mark at a single position within each area. Note that distance scale differs for Sea Point. Seaward direction given in degrees.



Qualitative Faunal Evaluations for Taxonomic Distinctness

Faunal composition at all sites was documented by recording species of macroinvertebrates living on or near the substratum surface. Macroinvertebrates included animals ≥ 1mm. This is an operational definition based on the ability to identify animals of this size in the field. Intertidal areas were sampled continuously four hours each day along a random walk with random boulder turning. During sampling, the discovery of each new species encountered was recorded with a digital voice recorder. Organisms were identified to species either on site or if unknown, collected and identified later that day.

Sampling effort was proportional to the size of the critical area and lasted 3 to 9 days (Table 1). Day to day, start and end points of sample paths were recorded three ways: WASS GPS, landmarks, and photographs. Sampling effort differed from site evaluations of the Critical Areas Program which usually lasted one low tide (Peter Larsen, personal communication). Effects from differences in the spatial areas of each habitat type can be accommodated by spending proportionately similar sampling times in each of the different habitats (Somerfield, personal communication). The amount of time spent in each habitat was based on their estimated species richness. For example, more time was spent in mixed coarse and fine (cobble and/or gravel with sand/shell hash) habitats than sand, since the latter will not have boulders to turn over and few species of epifauna live on the sand surface.

Table 1. Description of field sites along coastal Maine by location, area, and sampling effort

Critical Invertebrate Area	Location	Heading	Area (acres)	* Days
Sea Point	N 43° 05' 03"; W 70° 39' 30"	120° SE	10	8
Baily Island	N 43° 43' 03"; W 70° 00' 16" N 43° 43' 15"; W 70° 00' 25"	218° SW	5.79	4
Pemaquid Point	N 45° 50' 15"; W 69° 30' 15" N 43° 50' 08"; W 69° 30' 27"	190° S	2.2	3
Schoodic Point	N 44° 21' 10"; W 68° 05' 26" N 44° 21' 09"; W 68° 04' 31"	230° SW	12.4	9
Red Head	N 44° 27' 05"; W 67° 34' 30" N 44° 27' 01"; W 67° 34' 53"	231° SW	3.27	4
West Quoddy Head	N 44° 48' 50"; W 66° 56' 55" N 44° 49' 17"; W 66° 57' 12"	90° E	7	4

*Field sites were sampled four hours each day

Data Analysis

Patterns in diversity related to latitude were investigated by comparing species assemblages at different sites using PRIMER 6 (Plymouth Routines in Multivariate Ecological Research) and its various subroutines. Two methods were used, the first examined similarity among sample sites by simple matching of species between locations with cluster analysis and multidimensional scaling. Another procedure developed by Izsak and Price (2001) was used to evaluate β-diversity, i.e., differences in diversity between sample sites. Their dissimilarity coefficient Γ+ (upper case Greek gamma) takes into account the taxonomic relatedness of species of the compared species assemblages. Among the types of patterns that can be revealed using this method are gradients in biodiversity across latitude, e.g., increasing or decreasing β-diversity with increasing latitude.

Changes in α diversity of species assemblages were evaluated with PRIMER 6 using a univariate approach. The species assemblage of each sample site was described with average taxonomic distinctness (AvTD) and variation in taxonomic distinction (VarTD). These two metrics describe diversity, i.e. AvTD, and evenness, i.e. VarTD, of species assemblages according to their taxonomic structure (Clarke and Warwick 1998a, b). Sites south of Penobscot Bay were treated separately from sites north of Penobscot Bay since these groups were found to form distinctly different assemblages. Two master species lists were assembled from species lists collected by the Critical Areas Program for sample sites north and south of Penobscot Bay. They were used to calculate expected taxonomic spread of these two sample groups by creating funnel graphs of predicted 95 per cent confidence intervals for predicted AvTDs. Change in α-diversity was evaluated by superimposing on the funnel graph values of actual AvTD calculated for each location from sample species lists. Species assemblages significantly different from their expected AvTD would have AvTD plots outside the 95 per cent probability of expected taxonomic spread. A similar method was used to calculate predicted taxonomic evenness with the two master species lists. They were used to calculate expected variation in taxonomic distinctness for locations north and south of Penobscot Bay by creating funnel graphs of predicted 95% confidence intervals for predicted VarTDs. Species assemblages significantly different from their expected VarTD had observed VarTD plots outside the 95% probability of expected taxonomic spread.

Results

Species Composition and Community Structure

More species were encountered at all locations during the present investigation than during original critical area evaluations except Sea Point and West Quoddy Head (Figures 4, 5). This difference held for higher taxa as well, excluding West Quoddy Head that differed by only one phylum, Platyhelminthes. There were trends in dominant phyla consistent among all sample sites. Molluscs dominated in number of species present at all locations, a feature consistent with the original critical area evaluations. Arthropods were the next most common taxon found both historically and in this study, except in the original site evaluations for Red Head and West Quoddy Head where there were more species of Annelida and Echinodermata, respectively. These two phyla were the next most frequently encountered taxa in this study followed by cnidarians. Poriferans, plathyhelminths, nemerteans, ectoprocts, and chordates comprised minor portions of species assemblages at all locations.

Species richness decreased from south to north, with the greatest numbers of species found at Sea Point where habitats were most heterogeneous, i.e. bedrock, boulder, cobble, gravel, and sand (Table 2). Average phylogenetic diversity (AvPD) increased and total phylogenetic diversity (PD) decreased south to north. No latitudinal trends were observed in either AvTD or VarTD.

Latitudinal Trends in Diversity

Similarity of species found among sample sites was related to their location (Figure 6A). When sample sites were compared by simple matching of species found, two significantly distinct clusters formed north and south of Penobscot Bay (Simprof Test; $P < 0.05$). The geographic pattern of species similarity among sample sites is preserved when species assemblages were examined with multidimensional scaling. MDS maps show

Figure 4. Community composition of sampled critical invertebrate areas south of Penobscot Bay. Each area is represented by data from the current study paired with those from area evaluations conducted by the Critical Area Program, ca. 1977. Numbers in parentheses indicate the number of species in each phylum. The total number of species found at each location is represented by S.

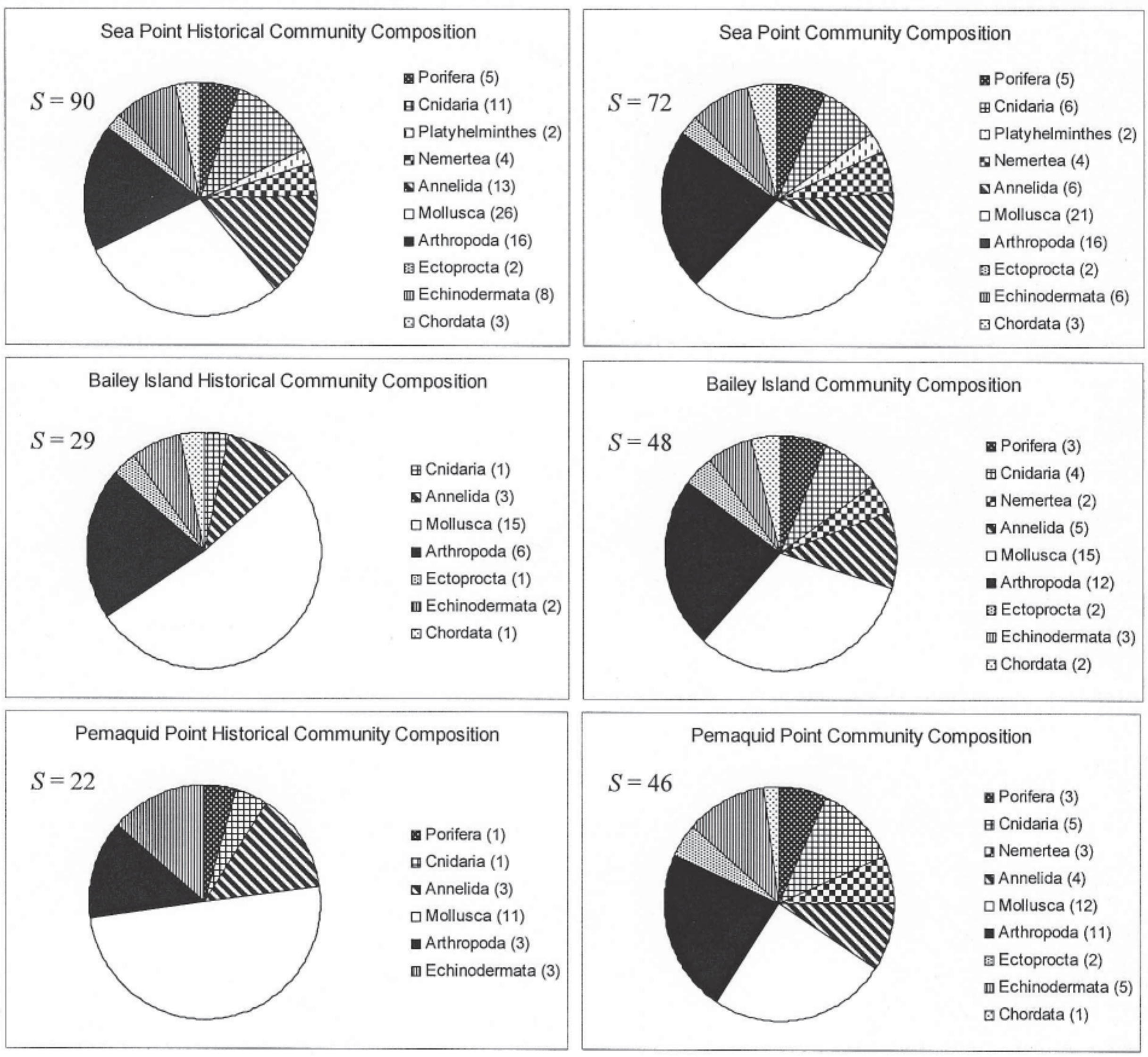


Figure 5. Community composition of sampled critical invertebrate areas north of Penobscot Bay. Each area is represented by data from the current study paired with those from area evaluations conducted by the Critical Area Program, ca. 1977. Numbers in parentheses indicate the number of species in each phylum. The total number of species found at each location is represented by S.

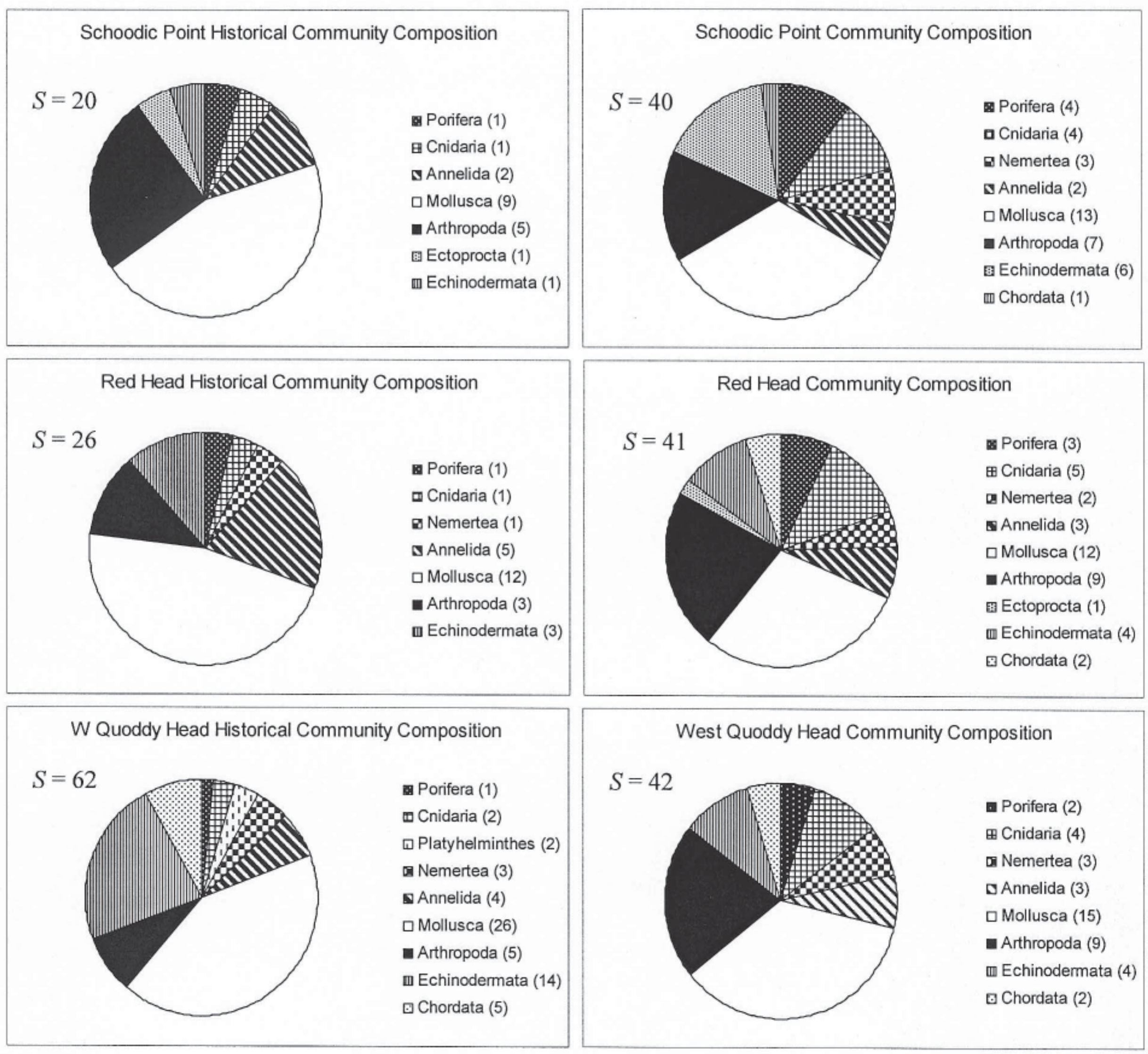
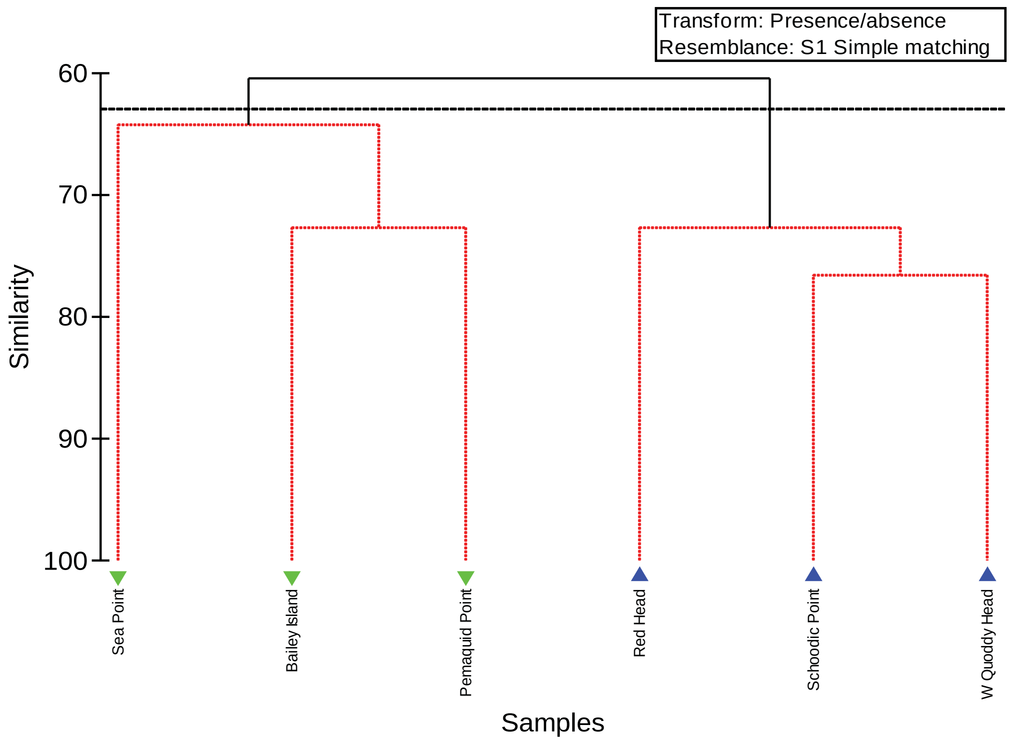


Figure 6. Dendrograms from cluster analysis of all six critical areas sampled based on (A) simple matching and (B) taxonomic dissimilarity (β-diversity). (A) Slice (dotted line) in is at 63 per cent similarity. Red dotted lines indicate clusters not significantly different from each other. Solid black lines indicate clusters significantly different from each other. (B) Slice (dotted line) is at 18 per cent dissimilarity. ▲ represents locations north of Penobscot Bay. ▼ represents locations south of Penobscot Bay.



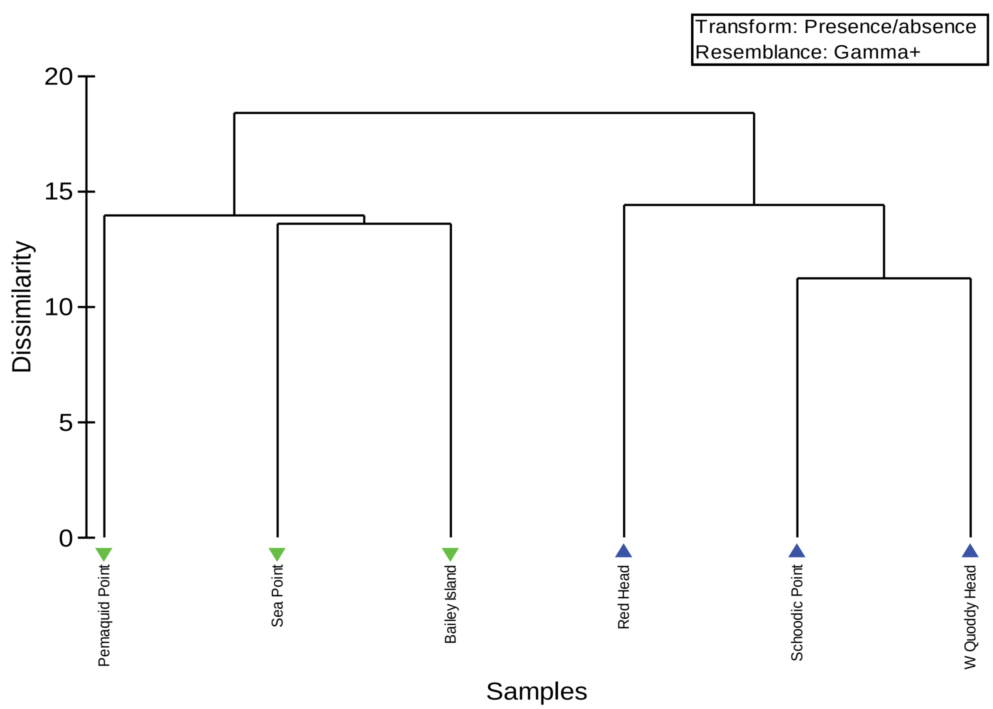


Table 2. Characterization of field sites located along Maine coast according to various indices of biodiversity

Critical Invertebrate Area	Diversity Index				
	S	AvTD	VarTD	AvPD	PD
Seal Point	72	91.8	396.1	39.7	2855.0
Bailey Island	48	91.1	423.4	45.5	2183.0
Pemaquid Point	46	92.3	376.7	46.7	2149.8
Schoodic Point	40	91.7	399.4	47.7	1909.7
Red Head	41	92.5	365.3	48.9	2003.2
West Quoddy Head	42	91.2	401.3	49.0	2058.0

significant structure amongst sample sites with Stress = 0 for 2-dimensional and 3-dimensional plots (Figures 7A, B). The separation of sample locations into two groups north and south of Penobscot Bay supports the idea that Penobscot Bay represents a faunal break point.

The taxonomic structure of communities sampled along the coast of Maine, measured as β-diversity, also differs north and south of Penobscot Bay. Taxonomic dissimilarity or β-diversity of intertidal communities revealed a clear clustering of locations south and north of Penobscot Bay (Figure 6B). A geographic pattern of dissimilarity among sample sites is evident from analysis of sample locations with multidimensional scaling. MDS maps show significant structure amongst sample site β-diversity with Stress = 0.01 for 2-dimensional and 3-dimensional plots (Figures 8A, B). Distinct groups of locations north and south of Penobscot Bay based on β-diversity parallel the groupings of similarity of shared species among sample locations.

Community Change

Changes in community structure were detected by superimposing measured values of average taxonomic distinctness (Table 2) for each location onto a funnel plot created from a historical species list. Significantly reduced taxonomic distinctness was measured at Sea Point and Bailey Island (Figure 9A). None of the species assemblages at sample locations north of Penobscot Bay had changed significantly (9B). This change in taxonomic structure of species assemblages represents a shift to assemblages with more closely related species, i.e., more belonging to fewer higher taxa. Variation in taxonomic diversity of species assemblages had not changed significantly (Figures 10A, B).

Discussion

Coastal Maine rocky intertidal communities sampled along the Sea Point to West Quoddy Head transect are dichotomous, separated at Penobscot Bay into two distinct, north and south species assemblages. Similar patterns in β diversity along the Maine coast were reported by previous investigators with temperature given as the principal cause (Bousfield and Laubitz 1972; Watling 1979; Larsen and Doggett 1990). Temperature is a determinant of the spatial distribution of species limited by their physiological ecology, specifically through thermal tolerances and reproductive requirements. Sea water temperature delineates the New England shore north of Cape Cod into two zoogeographic subregions (Bousfield and Laubitz 1972) or provinces (Watling 1979) with a faunistic break occurring in the vicinity of Penobscot Bay. Another division was described by Larsen and Doggett (1990) who reported sand beach macrofauna assemblages are separated by two sharp discontinuities resulting from

Figure 7. A. Two-dimensional ordination plot from multidimensional scaling analysis of the six critical areas sampled examining species similarity among locations. Slice shown in Figure 6 is superimposed upon plot (black line). B. Three-dimensional ordination plot from multidimensional scaling analysis of the six critical areas sampled examining species similarity among locations. ▼ represents sites south of Penobscot Bay. ▲ represents sites north of Penobscot Bay.

A

B

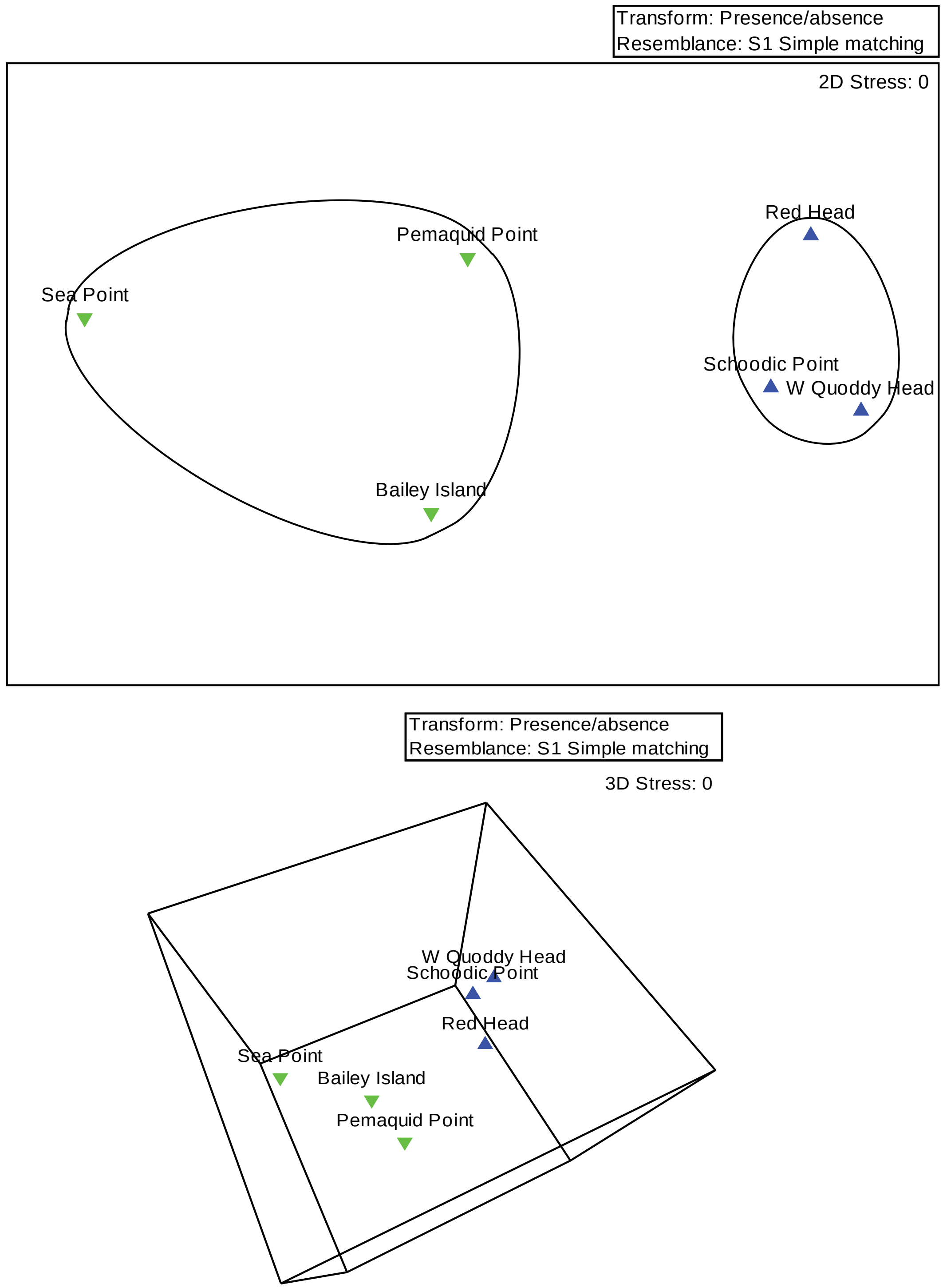


Figure 8. A. Two-dimensional ordination plot from multidimensional scaling analysis of taxonomic dissimilarity (β-diversity) among the six critical areas sampled. Slice shown in Figure 8 is superimposed upon plot (black line). B. Three-dimensional ordination plot from multidimensional scaling analysis of the six critical areas sampled examining taxonomic dissimilarity (β-diversity) among locations. ▼ represents sites south of Penobscot Bay. ▲ represents sites north of Penobscot Bay.

A

B

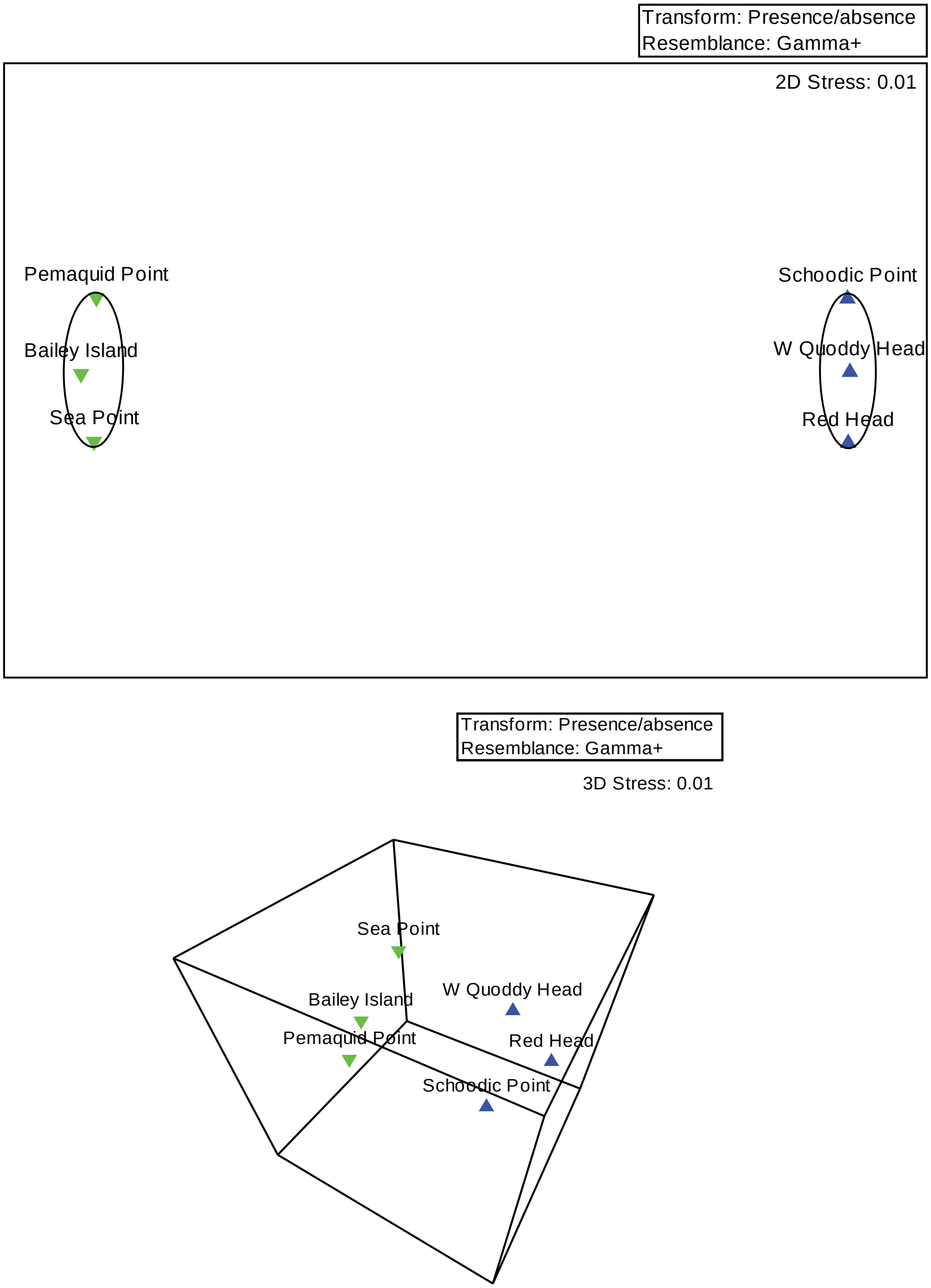
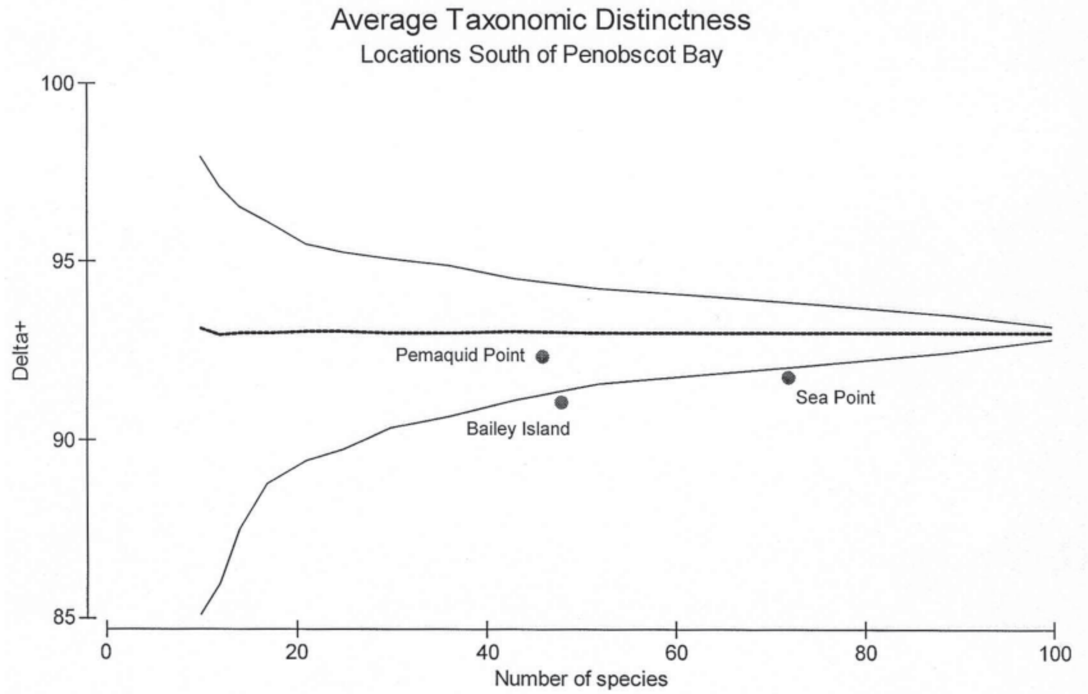


Figure 9. Average taxonomic distinctness (AvTD) for the locations south (A) and north (B) of Penobscot Bay plotted against their species list size. Lines forming the funnel represent the 95 per cent confidence intervals of AvTD simulated from historical species lists. The dotted line represents the average value of AvTD from the historical species lists.

A



B

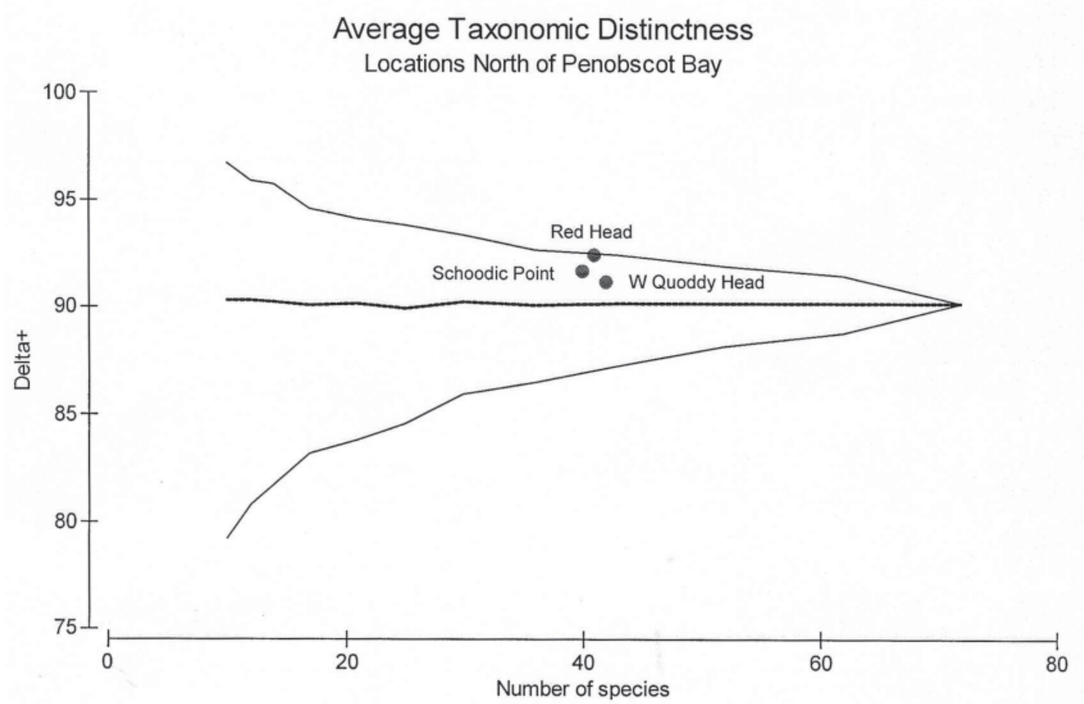
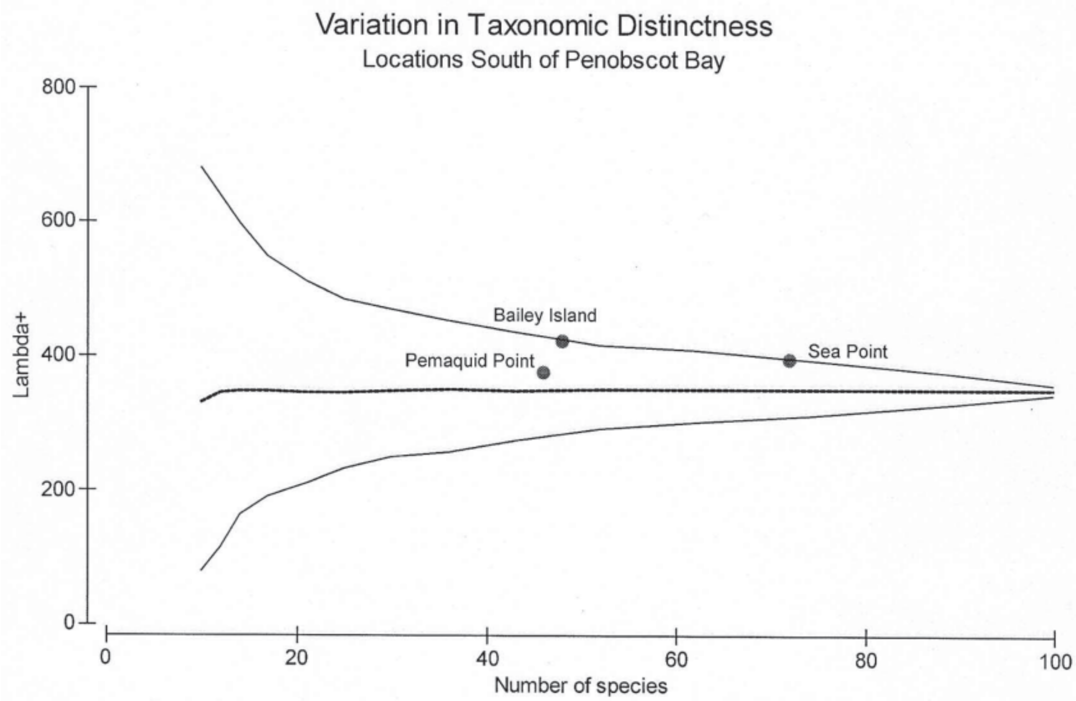
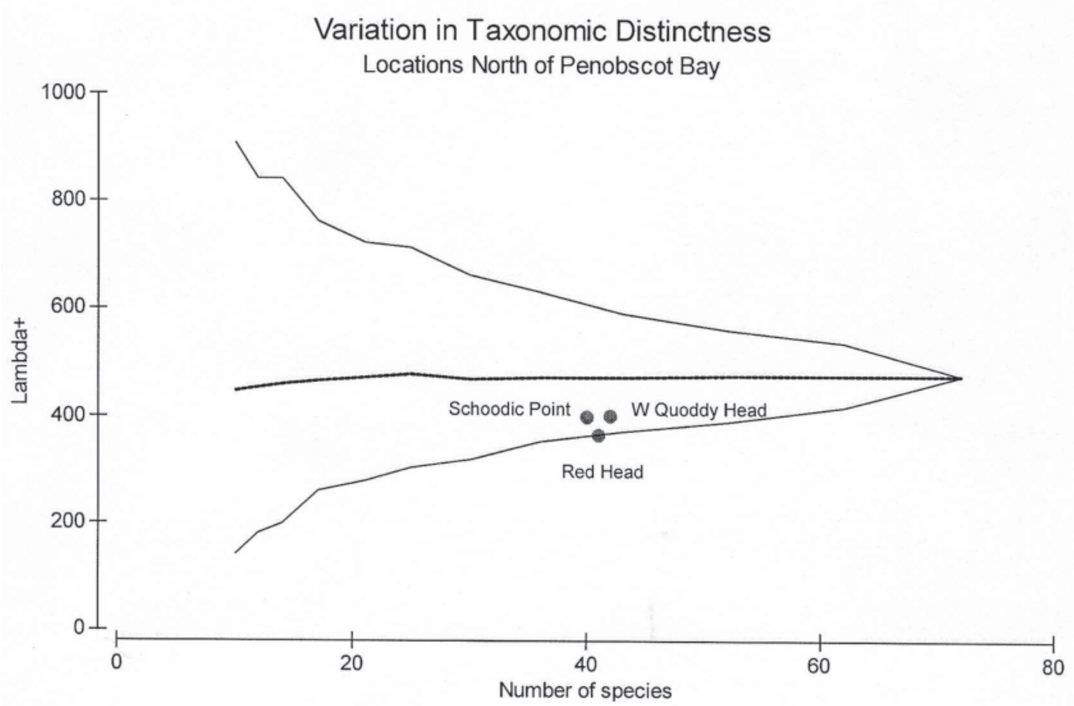


Figure 10. Variation in taxonomic distinctness (VarTD) for locations south (A) and north (B) of Penobscot Bay plotted against their species list size. Lines forming the funnel represent the 95 per cent confidence intervals of VarTD simulated form historical species lists. The dotted line represents the average value of VarTD from the historical species lists.

A



B



steep temperature gradients. These create a third faunistic group in the Penobscot Bay region delineated by southern and northern boundaries in the vicinity of the Sheepscot River and Mount Desert/Jonesport area, respectively (Larsen and Doggett 1990).

The zoogeographic dichotomy of coastal Maine rocky intertidal species assemblages coincides with the two principal branches of the Gulf of Maine Coastal Current (Lynch et al. 1997; Pettigrew et al. 2005). These are the Eastern Maine Coastal Current (EMCC) that flows along eastern Maine to Penobscot Bay where it is deflected to a variable degree offshore and the Western Maine Coastal Current (WMCC) that flows westward from Penobscot Bay to Massachusetts Bay. The extent of separation between these branches is variable; its strength dependent on how much of the EMCC veers offshore (Pettigrew et al. 2005). The two currents differ in temperature, speed and structure which contribute additionally to their distinctness, most defined in the spring and summer (Lynch et al. 1997). The EMCC is a colder, faster current well mixed out to 50 m depth while the WMCC is warmer, slow surface current consisting primarily of a trapped plume of fresh water flowing from the Kennebec River (Hetland and Signell 2005; Pettigrew et al. 2005).

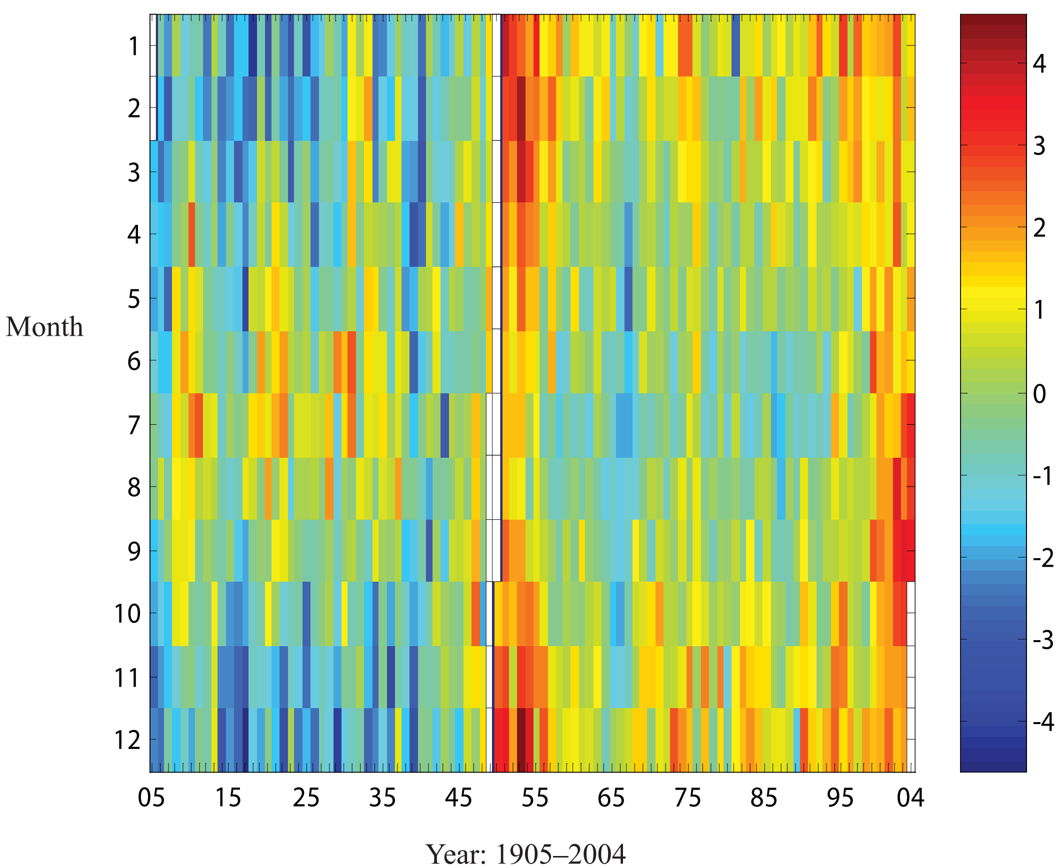
The region where the EMCC and WMCC diverge could represent a variable oceanographic barrier which, in addition to the speed, structure, and temperature differences of the currents, account for the faunistic break observed at Penobscot Bay. Geological differences between the eastern and western coastlines which influence habitat types also may reinforce the discontinuity (Caldwell 1998). Nearshore processes structuring communities of species that have life histories with larval dispersal are connected to offshore physical oceanography of the Gulf of Maine (Brooks and Townsend 1989). Transport of phytoplankton and larvae, and the resulting distribution of blooms and settlement along the coast of Maine, have been linked to the split between the EMCC and WMCC (Incze and Naime 2000; Townsend et al. 2005). Ultimately, the final transport of larvae to benthic habitats is strongly influenced by very nearshore coastal oceanography, and fronts created by nearshore flow patterns affect recruitment in the intertidal zone (Shanks et al. 2003; McCulloch and Shanks 2003). Because the strength of divergence between the two coastal currents is variable, the strength of an oceanographic barrier would vary likewise, and could account for the southern extension of some coldwater species as far south as Long Island and beyond (Bousfield and Laubitz 1972). In this region, patterns of distribution along the southern Maine coast must also be influenced by wind-driven coastal upwelling and its cooling affects on surface sea water temperature (Yentsch and Garfield 1981).

Differences in average and total phylogenetic diversity paralleled closely the number of species (S) found at each site (Table 2) and demonstrates how both of these metrics of diversity are dependent on S in their calculation. In contrast, average taxonomic distinctness was not related to differences in habitat or number of species. For example, the mostly bedrock Schoodic Point and boulder/cobble Sea Point are roughly similar in AvTD (Table 2). The independence of AvTD from S (Clarke and Warwick 1998a) is evident from comparing Schoodic Point and Sea Point (Table 2). The number of species found was very different yet these locations have roughly similar AvTD. Variation in taxonomic distinctness is also independent from sampling effort.

The causes of reduced average taxonomic distinctness at Sea Point and Bailey Island can be many and all are speculative. Anthropogenic disturbance can decrease species diversity, sometimes through salient affects. Sediment redistribution from harvesting commercial species has been implicated as the cause for a qualitative faunal shift from hard bottom to soft bottom species over a span of 30 years (Trott 2004). Environmental degradation decreases average taxonomic distinctness by creating communities with more closely related species (Clarke and Warwick 2001). For example, organic enrichment from salmon mariculture can result in decreased diversity with some closely related taxa, *Nucula proxima* and *N. delphinodonta*, increasing in abundance (Pohle et al. 2001). The possibility that anthropogenic disturbance could have caused the change at Sea Point and Bailey Island was investigated by comparing archived field evaluations and photographs with those made during this study. Neither of the critical areas appeared to have changed in a way that was noticeable. Natural disturbance from large storms and heavy sea ice could result in shifts of community composition and taxonomic distinctness. Since community structure is being compared across only two points in time separated by 28 years, identifying responsible disturbances is not possible.

Attributing a single cause for change in the taxonomic structure of the species assemblages may not be realistic, but temperature variability stands out for reasons previously discussed as a likely candidate that acted alone or in combination with other factors. Surface sea water temperatures at Boothbay Harbor, Maine recorded by the Department of Marine Resources have increased since 1952, particularly during the winter months (Figure 11). If this warming trend has occurred further south, community composition may have changed as cold water species were lost. While more species were found during the present study at most sample sites, greater sampling

Figure 11. Boothbay Harbor (43.84º N, 69.64º W) Monthly surface sea water temperature anomaly 1905 – 2004. Anomaly °C is the deviation from 20th century mean, 1905-1999. Data after September 2004 not plotted and other missing data (1950-51), both in white. Note the trends of warmer summers in first half of time-series, warm throughout the year in early 1950s and again beginning 2000. Then from the early 1970s to late 1990s, the warming trend was expressed mostly during winter months. (Figure courtesy of Lew Incze)



effort is the likely cause for greater species richness than evidence countering the temperature hypothesis for change in taxonomic distinctness. Community composition examined at taxonomic levels lower than phyla may better reveal changes caused by a warming trend. Only one cold water species in the echinoderm genus *Psolus* was documented in 1959 at Sea Point but not in 1960, 1962, 1964, 1971–73, and the present study. Since no other documented cold water species are absent from either Sea Point or Bailey Island assemblages, the idea that warming temperatures restructured taxonomic relationships of intertidal species is speculative.

General Conclusions

1. A faunistic break occurs in the vicinity of Penobscot Bay, creating a zoogeographic dichotomy with southern intertidal communities significantly different from those to the north. This conclusion is supported both by similarities of species composition and taxonomic dissimilarity.
2. Diversity measured as average taxonomic distinctness, a measure of diversity based on the structure of the classification of species in a community, was determined for six intertidal locations distributed across the length of the Maine coast.
3. Average taxonomic distinctness at Sea Point and Bailey Island has changed significantly from baselines established approximately 30 years ago.
4. Variation in taxonomic distinctness, a metric for the taxonomic evenness of a community, has not changed significantly for all locations from baselines established approximately 30 years ago.
5. The causes for changes in diversity are probably multifaceted, interactive, biotic and abiotic factors, making a simple overarching explanation unlikely. However, warming sea water temperature could be one cause which acting alone or in combination with others influenced a change in species assemblages at the two most southern Maine sample sites.

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