An Estuarine Habitat Classification for a Complex Fjordal Island Archipelago

G. Carl Schoch · David M. Albert · Colin S. Shanley

Abstract Spatial patterns of estuarine biota suggest that some nearshore ecosystems are functionally linked to interacting processes of the ocean, watershed, and coastal geomorphology. The classification of estuaries can therefore provide important information for distribution studies of nearshore biodiversity. However, many existing classifications are too coarse-scaled to resolve subtle environmental differences that may significantly alter biological structure. We developed an objective three-tier spatially nested classification, then conducted a case study in the Alexander Archipelago of Southeast Alaska, USA, and tested the statistical association of observed biota to changes in estuarine classes. At level 1, the coarsest scale (100–1000's km^2), we used patterns of sea surface temperature and salinity to identify marine domains. At level 2, within each marine domain, fjordal land masses were subdivided into coastal watersheds (10–100's km^2), and 17 estuary classes were identified based on similar marine exposure, river discharge, glacier volume, and snow accumulation. At level 3, the finest scale (1–10's km^2), homogeneous nearshore (depths <10 m) segments were characterized by one of 35 benthic habitat types of the ShoreZone mapping system. The aerial ShoreZone surveys and imagery also provided spatially comprehensive inventories of 19 benthic taxa. These were combined with six anadromous species for a relative measure of estuarine biodiversity. Results suggest that (1) estuaries with similar environmental attributes have similar biological communities, and (2) relative biodiversity increases predictably with increasing habitat complexity, marine exposure, and decreasing freshwater. These results have important implications for the management of ecologically sensitive estuaries.

Keywords Marine spatial planning · Conservation · Nearshore ecosystems

Introduction

The recent focus on marine spatial planning is a response to the general degradation of coastal ecosystems brought on by ocean margin development, overutilization of marine organisms, and the limited knowledge of coastal ecosystems and how to manage them at national (Crowder et al. 2006), and global scales (Halpern et al. 2008). In the politically charged arena of conservation ecology, there is general agreement about the importance of conserving biodiversity (Redford et al. 2003), knowing the biodiversity and spatial distribution of coastal ecosystems (Simenstad and Yanagi 2011), and how environmental changes influence their structure and function (Regan et al. 2005). Estuarine ecosystems in particular serve a number of ecological functions (Beck et al. 2001), and in order for conservation measures to be effective, we need to know what habitats exist, what biological communities are associated with them (Costello 2009), and the ecological status of each (Groves et al. 2002). The first goal of this study is to develop a spatially nested hierarchical classification that defines estuarine ecosystems based on physical factors at spatial scales ranging from meters to hundreds of kilometers and is compatible with (i.e., nests within) coarser-scale regional marine classifications of North America (e.g., Madden et al. 2009). We then applied the classification to the Alexander Archipelago of Southeast Alaska, USA, encompassing an ocean area of 30,721 km^2 (Fig. 1). To be useful as an ecosystem management tool, the

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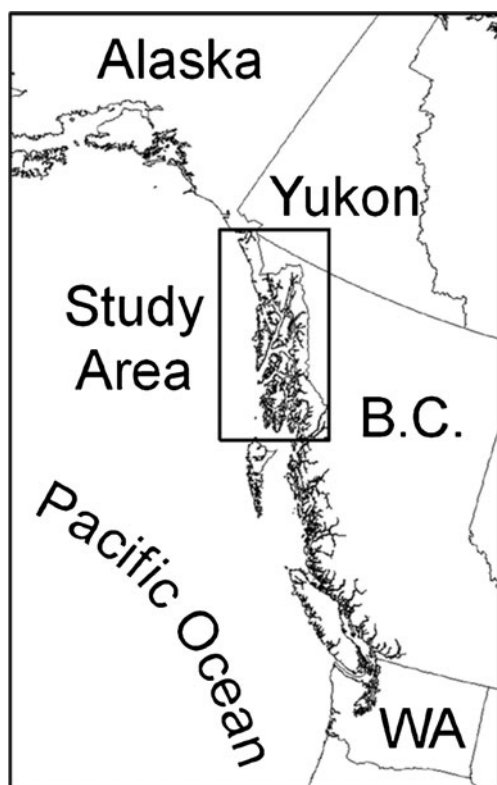Juneau, AK 99801, USA

Fig. 1 The Alexander Archipelago of Southeast Alaska, USA

estuarine classes should be biologically as well as physically distinct. Therefore, the second goal is to apply the classification and then test whether observed changes in biological communities are associated with changes in ecosystem classes.

The coastal Northeast Pacific biogeographic region is generally characterized by large volumes of precipitation on temperate rainforests (Mazza 2010), augmenting freshwater run-off from steep snow dominated watersheds (Hood et al. 2009), which contribute land-derived minerals and nutrients to the marine environment. Marine-derived nutrients can also be returned by anadromous fishes and recycled in estuaries and watersheds (Wipfli et al. 2003). Moreover, frequent storms and large semi-diurnal tides (up to 8 m) interact with complex fjord bathymetry and topography to influence flushing, mixing, and retention of nutrients, and their availability for biological assimilation. For the purposes of this study, estuaries are broadly defined by the confluence of watersheds with tidal shores and the concomitant mixing zone. The estuarine nearshore includes a complex mosaic of habitats, with spatial and temporal patchiness across many scales of observation. Nearshore benthic habitats (depths<10 m), from the shallow subtidal to the supratidal zone, are a net result of a suite of interacting environmental attributes such as substrate size and type, water temperature, salinity, water chemistry, silt loading, hydrology, and processes and patterns of coastal sediment

transport. These variables often act synergistically producing complex mechanisms operating across variable scales of space and time to influence the abundance, distribution, and diversity of benthic marine plants (Lindstrom 2009) and animals (O'Clair and O'Clair 1998).

Consideration of spatial pattern is essential to understanding how organisms interact with their environment since some physical–biological processes are coupled at small scales while others are coupled only at larger scales (Dethier and Schoch 2005). For example, physical factors contributing to spatial variation of benthic organism abundance, distribution, and diversity include wave exposure and associated forces of wave breaking (Denny et al. 2004), rock type (Raimondi 1988), desiccation (Williams and Dethier 2005), thermal stress (Helmuth et al. 2002), tidal range (Edgar and Barrett 2002), and disturbance from logs, ice, and sand scour (Dudgeon and Petraitis 2001). All of these factors may act in a patchy fashion, creating locally variable assemblages, because of meter- to kilometer-scale differences in rock aspect, local topography, slope, and wave exposure (Schoch and Dethier 1996). At larger scales, species composition is affected by oceanographic conditions such as current patterns (affecting dispersal and nutrient delivery), salinity, and water temperature (Connolly et al. 2001). Biogeographic provinces (very large-scale variations in species compositions) correlate well with marine climate boundaries, which integrate the above oceanographic conditions (Schoch et al. 2006). The environmental forcing of marine and estuarine biota varies temporally and the effect may be different at each spatial scale.

There has been much progress in the development and application of marine and estuarine ecosystem classifications, and many are reviewed by Dethier and Harper (2011), Pittman et al. (2011), and others in Wolanski and McLusky (2012). There is a growing awareness for the need to link habitats and ecosystems with biota (Llanso et al. 2002), especially through spatially nested hierarchical classifications (Hume et al. 2007), since many of our most pressing coastal management issues are at landscape scales but our best ecological understanding is at the scale of an organism. Raffaelli et al. (1994) noted that physical processes often operate in a hierarchy and drive biological heterogeneity across a complete range of spatio-temporal scales. Thus, any predictive model of community ecology should have simpler local-scale models nested within more complex larger-scale models (Guarinello et al. 2010). Hierarchy theory in landscape ecology states that complex systems can be divided into discreet sets of entities, with each level or unit characterized by a particular range of temporal and spatial scales (Allen and Starr 1982). A spatially nested hierarchy is one where the units at the apex of the system contain and are composed of all the lower units. While a unit in this case represents a homogeneous entity, what may be

homogeneous at a particular scale of observation may be considerably heterogeneous upon closer scrutiny (Kolasa and Rollo 1991), and Hurlbert (1984) noted that the degree of heterogeneity will affect the sensitivity to detect change. Therefore, we posit that a spatially nested hierarchical classification should, at a minimum, integrate external and internal environmental forces that potentially limit biological populations. Furthermore, to be ecologically meaningful for conservation planning, spatial changes in observed biota should be statistically detectable among ecosystem classes.

Classification Levels and Factors

We developed the following three-tier spatially nested hierarchical classification with large regional marine domains (100–1,000's km^2) at level 1, containing multiple estuarine mixing zones (10–100 km^2) at level 2, with a mosaic of nearshore habitats (100–1000 m^2) at level 3 (Fig. 2). The marine domains nest spatially within the marine ecoregions of the world (Spalding et al. 2007), marine priority conservation areas (Morgan et al. 2005), and national classifications (Madden et al. 2009), such as the Coastal and Marine Ecological Classification Standard.

Level 1: Marine Domains

The regional watersheds of the Alexander Archipelago include temperate rainforests and glaciers, and an extrapolation of data from 141 stream gauges provides an estimated 25,500 m^3 s^{-1} of freshwater flow; thus, the entire island complex represents a single or super estuarine water plume
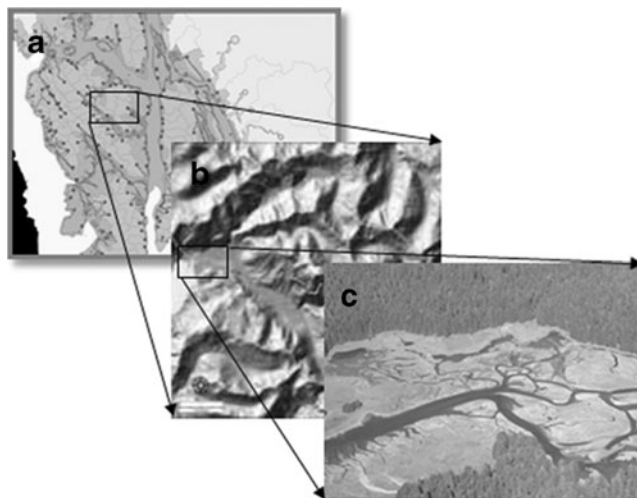

Fig. 2 A conceptual model for a spatially nested hierarchical classification of Southeast Alaska estuarine shorelines: **a** level 1 (1,000's km^2), ocean water properties define the extent of marine domains; **b** level 2 (10–100 km^2), marine exposure and watershed hydrographic attributes define estuarine classes; **c** level 3 (100–1,000 m^2), shoreline mapping defines nearshore benthic habitats as well as macro biotic assemblages

(Weingartner et al. 2009), with a cumulative annual discharge comparable to the Yukon or Columbia Rivers (Edwards et al. 2008). Oceanic temperature and salinity are both direct factors and indirect proxies for multiple benthic–pelagic coupling mechanisms at the scale of coastal and continental shelves. Landscape-scale differences in water temperature and salinity are often reflected in the composition of intertidal and nearshore benthic communities (Schoch et al. 2006; O'Connor et al. 2007). Spatial and temporal patterns of oceanic temperature and salinity indirectly affect the timing and abundance of primary production and the mechanisms of food and propagule delivery to nearshore habitats such as topographically generated fronts, internal waves, and upwelling (Broitman et al. 2008). Sea surface temperature and salinity are key tracers of oceanic water masses and are routinely used to define marine domains (Geiger et al. 2011).

Level 2: Estuarine Mixing Zones

Albert and Schoen (2007) inventoried over 12,000 intersections between individual streams and the shoreline in Southeast Alaska. Most of these are very small systems with watershed areas of <10 km^2. To spatially define estuaries, we applied the US Forest Service (USFS) system of value comparison units (VCU), modified to also include all non-USFS lands within the project area (Paustian et al. 1992). Generally, the VCU encapsulates the watershed, any adjoining embayment, or a 1–5 km seaward buffer in front of the stream mouth since a large number of streams flow directly into the ocean without a clearly defined estuarine enclosure. These criteria identified 719 estuarine systems typically ranging from 10 to 500 km^2, with some watersheds >5,000 km^2 for very large river systems. These estuaries are highly productive ecosystems that experience large salinity changes daily and seasonally. The timing, variability, and volume of freshwater into the estuaries of Southeast Alaska is largely controlled by glacier size, seasonal snow accumulation, and stream discharge characteristics (Edwards et al. 2008).

Wave energy affects community structure over short and long temporal periods. Denny (1995) discusses the direct effect of forces generated by waves on nearshore benthic organisms in terms of patch dynamics, one of the most important processes by which rocky intertidal communities are structured. Indirect effects of waves on community structure include estuarine water column mixing and the frequency of substrate movement. Unconsolidated substrates can be moved by the direct impact of waves, by wave run-up (i.e., wave swash), and by wave generated currents. On beaches with mobile substrates, the particles can be rolled or entrained continually, seasonally, or episodically in high wave energy environments. Mobile substrates typically harbor fewer organisms than stable substrates. For

example, high energy pebble and sand beaches are relatively depauperate of biota, while low energy stable substrates such as bedrock, large boulders, and angular pebble beaches are species rich (Jackson et al. 2002). The macrofloral community must adapt to the forces of the nearshore surf and swash zone and, in the absence of wave runup, must also tolerate long hours of desiccation (Gaylord et al. 2008). Exposure to wave energy is therefore fundamental to understanding the structure of estuarine communities.

Level 3: Nearshore Habitats

The regional mapping of Southeast Alaska shorelines was recently completed using the ShoreZone Mapping System first developed in British Columbia and now includes Oregon, Washington, and much of Alaska (Harney et al. 2008). This provides a qualitative and spatially comprehensive inventory of nearshore features (depths <10 m). We used shoreline partitions, mapped using the ShoreZone surveys, to represent physically homogenous alongshore segments. The term "alongshore segment" is used here as a spatial region that is relatively morphodynamically uniform as defined by a suite of environmental attributes. The ShoreZone habitat maps are partially based on spatially referenced, oblique low altitude aerial video, and digital still imagery of the coastal zone collected during the lowest daylight tides of the year (http://www.ShoreZone.org). Typically, these tides expose the shallow subtidal nearshore. A habitat shoretype class is assigned to delineated homogeneous alongshore segments based on aerial image interpretation and direct observations. Modifiers for each shoretype class describe details of the geomorphological form (e.g., lagoons, deltas, dunes, bars, spits, sea cliffs, reefs, wave-cut terraces, etc.), substrate material (e.g., boulders, pebbles, sand, biogenic silt, etc.) for vertical components of the nearshore zone (i.e., visible subtidal to supratidal). The ShoreZone data are catalogued using the ArcGIS mapping system (ESRI, Redlands, CA, USA) and a relational database.

Methods

Level 1: Marine Domains

The use of satellite imagery for mapping ocean color and temperature is now a routine. We used 1-km grid sea surface temperature estimates acquired by the advanced very high resolution radiometer on the polar operational environmental satellite. These data were processed by the Alaska Ocean Observing System and University of Alaska Geophysical Institute using the Multichannel sea surface temperature algorithm developed by McClain (1985). We combined

average monthly sea surface temperatures from 2006 to 2008 to provide a composite estimate of spatial variation across the Southeast Alaska region.

Similarly, NASA's Aquarius satellite has great potential to improve global ocean salinity mapping, but the resolution of the sensor is too coarse (150 km) to capture salinity structures that are typical of coastal and estuarine systems (Lagerloef et al. 2008). Until this technology improves, we used the best available composite of sea surface salinity from the World Ocean Atlas 2005 (Antonov et al. 2006). This atlas presents spatial climatologies and related statistical fields for salinity (and other parameters) on a one-degree latitude–longitude grid at standard depths from the surface. These climatologies use all available data regardless of year of observation. The World Ocean Atlas project uses spatial interpolation algorithms to fill data gaps and extend coverage to the coast (Boyer et al. 2002; Boyer et al. 2005).

The Iso Cluster tool in ArcGIS (ESRI Inc., Redlands, CA, USA) was used on the sea surface temperature and salinity data stack (Richards 1986). Stacked pixels were subsequently sampled on a 5-km grid and the data plotted to identify marine domains based on the combined sea surface temperature and salinity signature. One-way ANOVA was used to evaluate for differences among domains using S-Plus (Mathsoft Inc., Seattle, WA, USA).

Level 2: Estuarine Mixing Zones

Watershed flow volume estimates were derived from the precipitation–elevation regressions on independent slopes model (PRISM). PRISM is an analytical model that uses point data and a digital elevation model to generate gridded estimates of monthly and annual temperature and precipitation and incorporates a conceptual framework that addresses the spatial scale and pattern of orographic effects (Daly et al. 2002). The flow accumulation and flow direction tool in ArcGIS was used to estimate overland flow direction and stream discharge at the point it enters the ocean (Tarboton 1997). The monthly mean precipitation grids from PRISM (1961–1990) were summed for an estimate of annual precipitation. Each resulting grid cell was converted to cubic meters of precipitation by multiplying by the area of the cell. The volume values for each grid cell were then summed for the watershed and divided by the number of seconds in a year. An estimate of snow accumulation for each watershed was calculated by summing precipitation during each month when the mean monthly temperature was below 0ºC. Glacier size was obtained from a US Geological Survey Digital Line Graph file (Fegeas et al. 1983).

Marine exposure changes with the degree of protection from the full force of open ocean waves. Wave exposure is often quantified as a function of fetch, orientation, and nearshore bathymetry, or on maximum fetch and wind

forcing where wave exposure increases with increasing fetch distance and wind speed and duration (Lindegarth and Gamfeldt 2005). However, these estimates do not account for the cumulative effect of ocean swells including refracted, diffracted, and reflected waves. Estimates using fetch are only useful for estimating wave heights for protected embayments and inland shores subjected primarily to locally generated wind waves. We developed an estimate of marine exposure based on an index of the total area visible over water from shore, allowing for the penetration and effects of deep water waves. The marine exposure index was calculated as:

$$\ln \sum_{i=1}^{6} p_i r_i$$

where p=number of points visible at radius i, and r=distance in km of radius i. We first generated concentric buffers to seaward of the shoreline at distances of 1, 2, 5, 10, 20, and 100 km. These lines were then converted to points at 1-km intervals. We used the Viewshed tool in ArcGIS to identify the number of points at each radius visible from each segment along the shoreline. The distance-weighted index of marine exposure was calculated as the natural log of the sum of points visible at each radius multiplied by the radius distance and catagorized by area of exposure.

Watersheds were categorized based on hydrographic profile as per Edwards (2008): type I, rain-dominated, brown water; type II, snow-dominated, clear water; and type III, glacier/snowfield-dominated, turbid water. Type III watersheds with glaciers were further divided by glacier size. The precipitation regime was used to divide lower elevation rain dominated from higher elevation snow dominated watersheds. The discharge classes were categorized by flow volume.

The approaches to multivariate analysis methods developed by Clarke and Warwick (1994) and PRIMER software (Clarke and Gorley 2006) were used to group and test for differences among estuary types. The data matrix of watershed and ocean attributes was square-root transformed and normalized, and a Bray–Curtis similarity matrix was calculated from Euclidean distances. Nonmetric multidimensional scaling (MDS) was used to analyze relationships among groups of estuaries. One-way analyses of similarity (ANOSIM) tested the significance of any apparent differences among estuary classes (Clarke and Green 1988). Pearson's correlation coefficients (r) and the coefficient of determination (r^2) were calculated using the methods of McCune et al. (2002) to identify the hydrodynamic attributes that best explain the ordination patterns. The Pearson's correlation coefficient was calculated for each attribute along the axes that explained most of the variability. The resulting x and y coordinate was plotted, and a line was drawn connecting this plotted point to the ordination centroid. The length of the radiating line was calculated as the hypotenuse of the triangle created by the x and y distances from the ordination centroid. The attribute vectors were plotted, so that the angle and length of the radiating lines relate to the direction and relative magnitude of the Pearson's correlation (in two-dimensional ordination
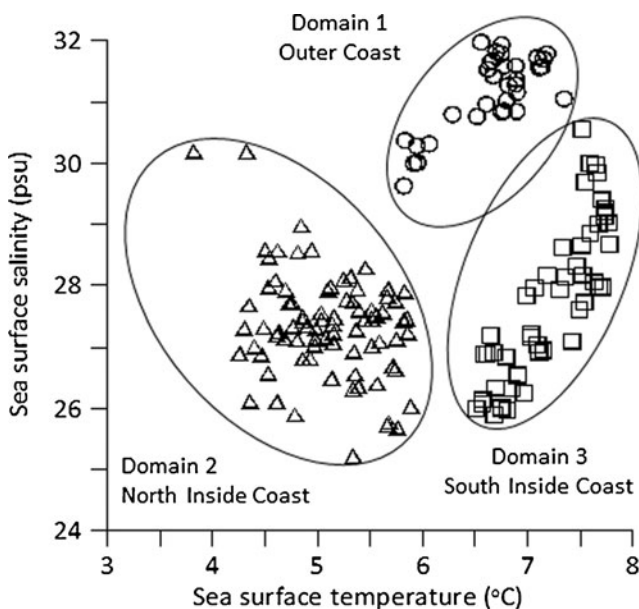

Fig. 3 Temperature–salinity plot for the marine domains of Southeast Alaska. Data were smoothed with a low pass filter and every sixth data point is shown for clarity. *Ellipses* delimit domain extents for illustrative purposes
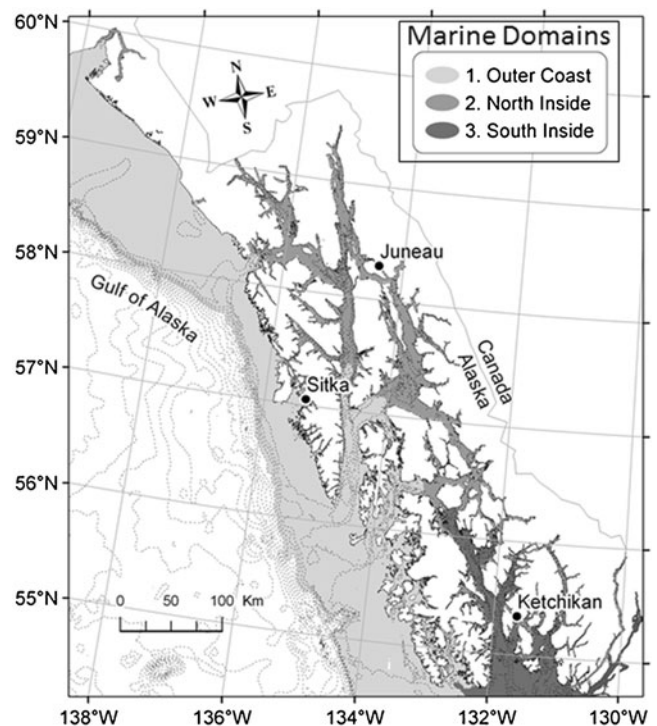

Fig. 4 The spatial extent for the marine domains of Southeast Alaska identified in this study. Locations for the largest communities are shown with *black circles*. *Dotted lines* are 200 m bathymetric contours
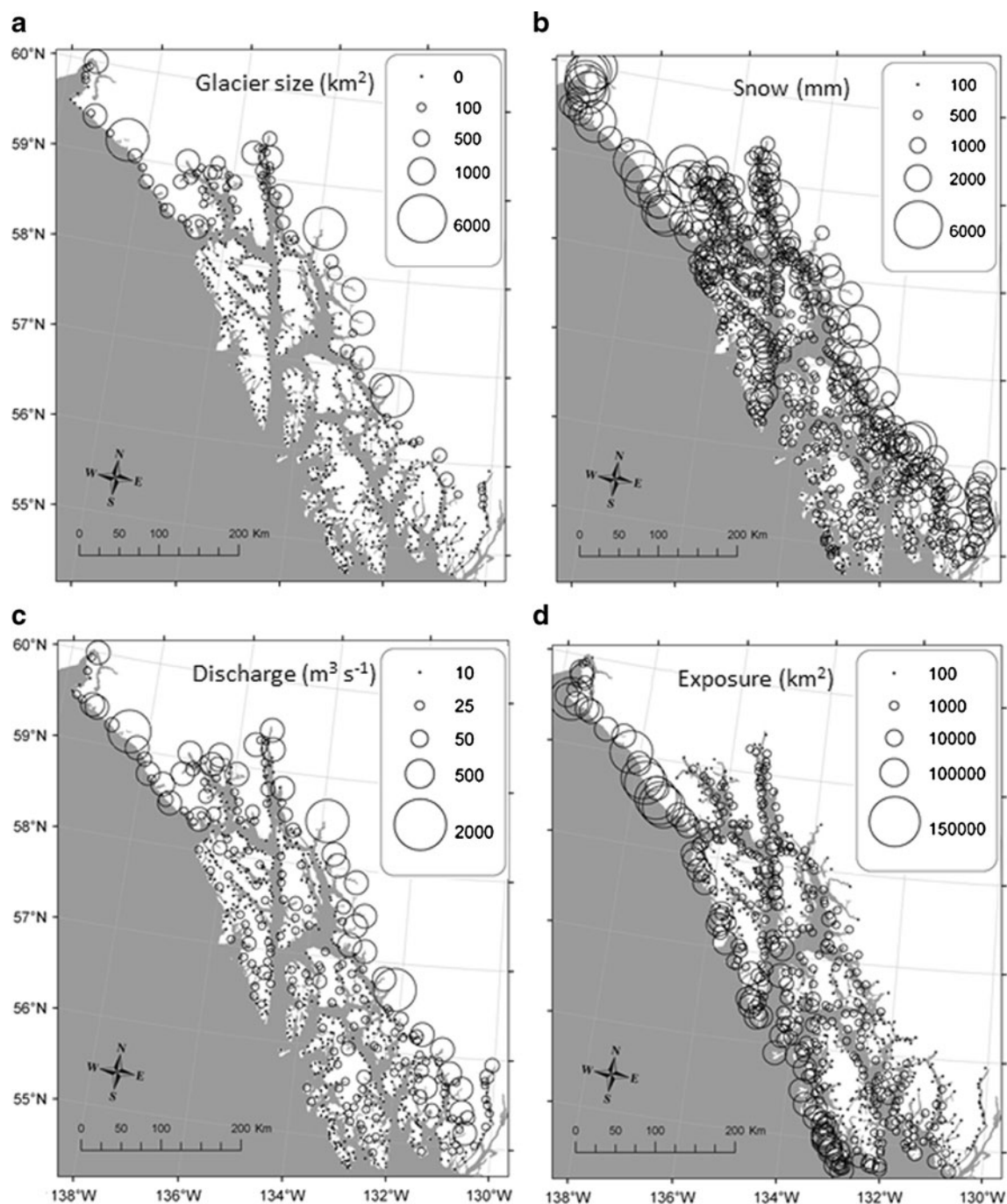
Fig. 5 The relative magnitudes of selected hydrodynamic attributes for Southeast Alaska estuaries where **a** shows glacier size for each watershed, **b** shows precipitation from the PRISM model, **c** is the calculated flow volume based on watershed area and accumulated precipitation, and **d** is an index of marine exposure. See text for details on each attribute

space). Joint plots were produced in PC-ORD to visualize these relationships (McCune et al. 2002). We examined multivariate dispersion as a measure of rank dissimilarity among replicates within estuary groups and evaluated the contribution of each environmental attribute to within group similarity using the similarity percentages module of PRIMER (Warwick and Clarke 1991).

Level 3: Nearshore Habitats

Alongshore segment attributes for 28,816 km of classified shoreline in the Alexander Archipelago were extracted from the ShoreZone database. Segments were grouped by level 2 estuary types in each of the marine domains, and the attributes were summarized and tabulated.
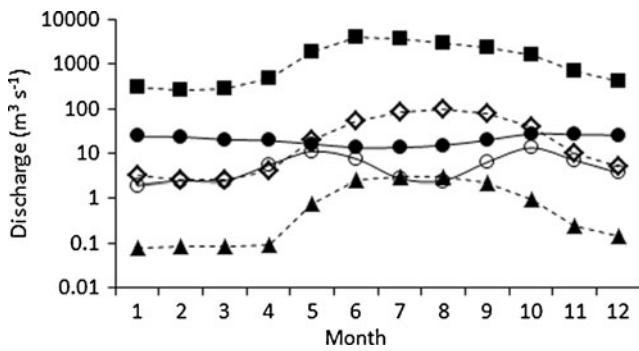
Fig. 6 Hydrographic profiles for selected streams of Southeast Alaska are shown to illustrate the relative differences of the annual hydrographic flow regime. Discharge is on a logarithmic scale. Glaciated type III streams are depicted as dashed lines with large (*square* Stikine), medium (*diamond* Mendenhall), and small (*triangle* Chilkoot) glaciers. Nonglaciated streams are illustrated as solid lines with type II snow dominated (*empty circle* Kadashan), and type I rain dominated (*filled circle* Hamilton)

Analysis of Ecological Patterns

The degree of environmental homogeneity captured by the ecosystem classification is critical to the desired sensitivity of the model to detect changing biological patterns (Schoch and Dethier 1996). For the classification to be ecologically meaningful, spatial changes in observed biota should be statistically detectable among ecosystem classes. Benthic plants and invertebrates from the ShoreZone bioband data were used for this analysis. Biobands are spatially distinct horizontal assemblages, with distinctive across-shore patterns of color and texture that are visible directly and in aerial imagery. Biobands are described for each across-shore zone, from the high supratidal to the shallow nearshore subtidal, within each alongshore segment. The biobands are periodically ground-truthed and named for the dominant taxa or taxa group that best represents the entire assemblage. Anadromous fish data for each watershed were compiled from the Alaska Department of Fish and Game stream surveys. All biotic data were transformed to presence/absence. Pearson's correlations were tabulated and examined for relationships between taxa and the two-dimensional structure of estuarine similarity represented by the MDS ordination plots. The null hypothesis is no relationship between estuarine classes and spatial patterns of biota. Joint plots were produced to visualize these relationships. Indicator values were calculated using the methods of Dufrene and Legendre (1997) to define the taxon or taxa group most characteristic of each estuary class. The biological data used do not qualify as an assessment of biodiversity per se and many organisms observed were not identified to the species level. We used comparisons of taxon richness to assess distributional patterns of relative biodiversity (i.e., percent of

Table 1 Level 2 classification summary for Southeast Alaska estuaries

Estuary class summary		Attribute categories				Estuaries by domain			
Class	Description	Glaciers[a]	Snow[b]	Discharge[c]	Exposure[d]	1	2	3	Total number
1	Very exposed large glacier	L	H	H	VH	1	–	–	1
2	Very exposed medium glacier	M	H	H	VH	9	–	–	9
3	Very exposed small glacier	S	H	H	VH	4	–	–	4
4	Very exposed snow	–	S	M	VH	18	–	–	18
5	Very exposed rain	–	R	L	VH	26	–	–	26
6	High exposed snow	–	S	M	H	21	15	–	36
7	High exposed rain	–	R	L	H	27	–	8	35
8	Moderate exposed large glacier	L	H	H	M	–	1	–	1
9	Moderate exposed medium glacier	M	H	H	M	–	3	–	3
10	Moderate exposed small glacier	S	H	H	M	2	16	–	18
11	Moderate exposed snow	–	S	M	M	24	110	17	151
12	Moderate exposed rain	–	R	L	M	29	8	52	89
13	Low exposed large glacier	L	H	H	L	–	1	–	1
14	Low exposed medium glacier	M	H	H	L	1	19	2	22
15	Low exposed small glacier	S	H	H	L	–	12	9	21
16	Low exposed snow	–	S	M	L	24	78	83	185
17	Low exposed rain	–	R	L	L	49	8	42	99
						235	271	213	719

There are 719 estuaries distributed among 17 estuarine classes and 3 marine domains. Not all classes are represented in each domain. Column 1 lists the estuary class, and column 2 provides a summary description of each class. Columns 3–6 show the estuary attribute categories defined below. Columns 7–9 show the distribution of estuaries by class within each marine domain, and column 10 lists the total number of estuaries in each class

Fig. 7 *Box and whisker plots* of environmental attributes for each estuary class within each marine domain. Plots **a**, **d**, **g**, and **j** are for domain 1, the outer coast; plots **b**, **e**, **h**, and **k** are for domain 2, the north inside coast; and plots **c**, **f**, **i**, and **l** are for domain 3, the south inside coast. Class categories 1–17 and descriptions are listed in Table 1. All attribute values are log transformed
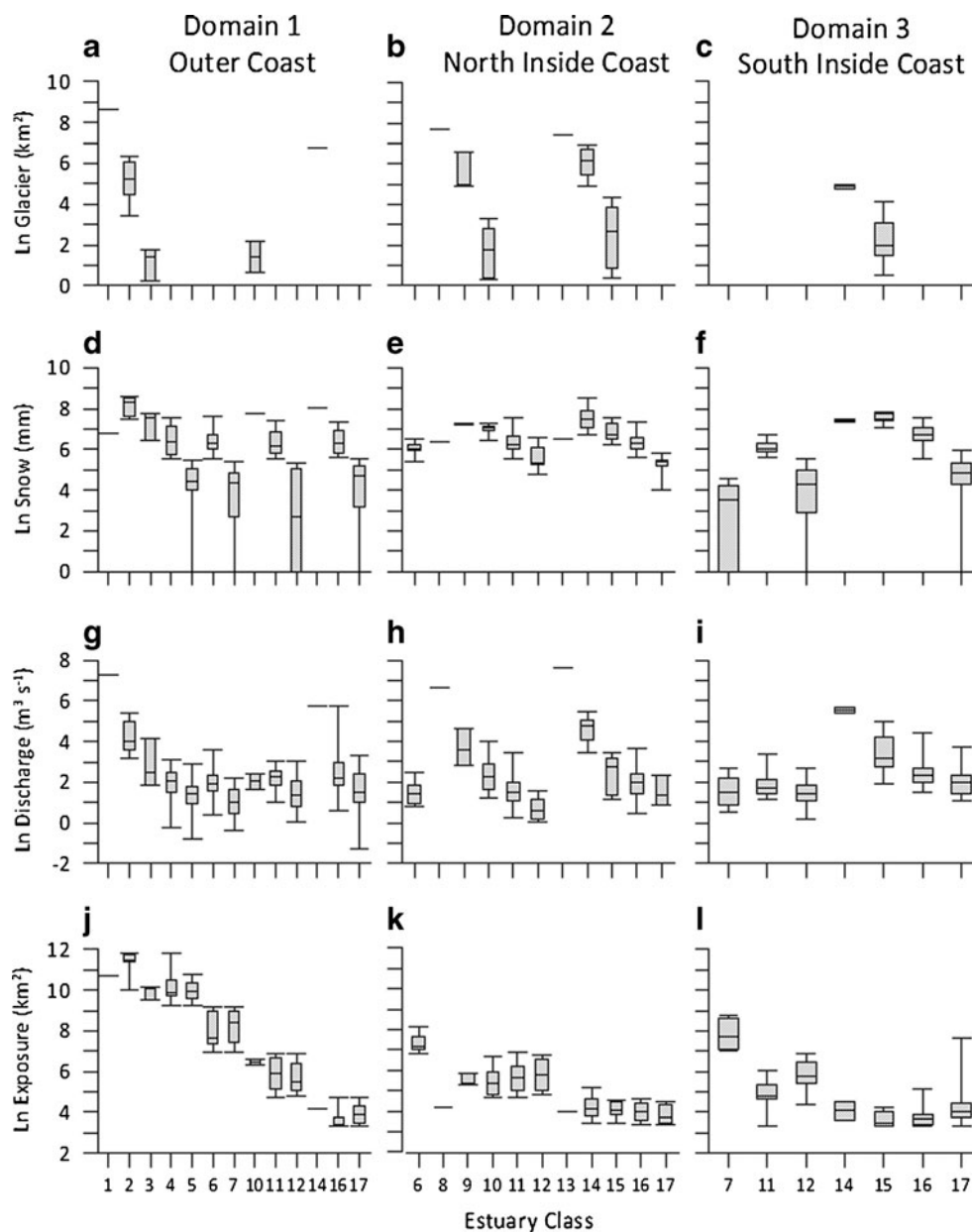
total number of taxa observed). Linear regressions were used to test for a relationship between relative biodiversity and marine exposure, and watershed hydrography using S-Plus (Mathsoft Inc., Seattle, WA, USA). We evaluated the relationship among level 2 estuary classes in each level 1 domain and across all domains and the results were plotted.

Results

Level 1: Marine Domains

Figure 3 shows a plot for the unique temperature and salinity combinations characterizing three distinct marine domains. Domain 1 represents the relatively cold euhaline

outer coast, domain 2 represents the colder glacier dominated polyhaline northern inside waters, and domain 3 represents the warmer river dominated polyhaline waters of the southern inside coast. One-way ANOVA tests showed significant differences among the domains in both temperature ($F_{2, 3,133} = 2,791$, $p < 0.001$) and salinity ($F_{2, 3,133} = 5,353$, $p = 0.001$). The spatial extents of the three marine domains for the Alexander Archipelago are shown in Fig. 4.

Level 2: Estuarine Mixing Zones

Figure 5 shows the relative magnitudes of the attributes used to define the hydrodynamic environment of the 719 estuaries of the Alexander Archipelago. Typical annual discharge profiles for Southeast Alaska streams are shown in Fig. 6. Note

that large, medium, and small glaciated streams differ only in magnitude (i.e., the hydrographic profiles are similar). The snow-dominated streams have an early summer freshet when the snow begins to melt at high elevation and a fall flood with the autumnal rains. The rain-dominated systems generally show a more uniform flow regime throughout the year, typically with a lower discharge during the drier summer months. The estuaries were grouped into 17 unique classes (see Table 1) and spatially nested into the marine domains. There are 235 estuaries in domain 1, 271 in domain 2, and 213 in domain 3. Note that combinations of small, medium, and large glaciated watersheds of highly exposed estuaries do not occur in this region. Box and whisker plots for the environmental attributes for each estuary class are shown in Fig. 7. Figure 8 shows the spatial distribution of the 17 estuary classes.

The two-dimensional solution of the MDS ordination for each domain is plotted in Fig. 9. The final stress values are shown for each analysism and all are within the good to excellent range (Clarke 1993). There are varying degrees of heterogeneity within each estuary class, but in general, smaller clusters represent estuaries that are more similar. Furthermore, classes farther apart are interpreted to be less similar than those closer together. In domain 1 (Fig. 9a), the pattern of among estuary class separation was best explained by marine exposure ($r^2=0.71$) and snow ($r^2=0.57$). The ANOSIM tests for among estuary class similarity (or dissimilarity) indicate that estuary classes within domain 1 along the outer coast were clearly distinguished from each other (global $R=0.678$ with maximal separation when $R=1$, $p=0.001$). In domain 2 (Fig. 9b), the pattern of class separation was best explained

Fig. 8 The spatial distribution of estuary classes in Southeast Alaska. *Symbols* representing estuaries are listed by class number in the legend and defined in Table 1. Note that not all estuary classes are represented in each domain
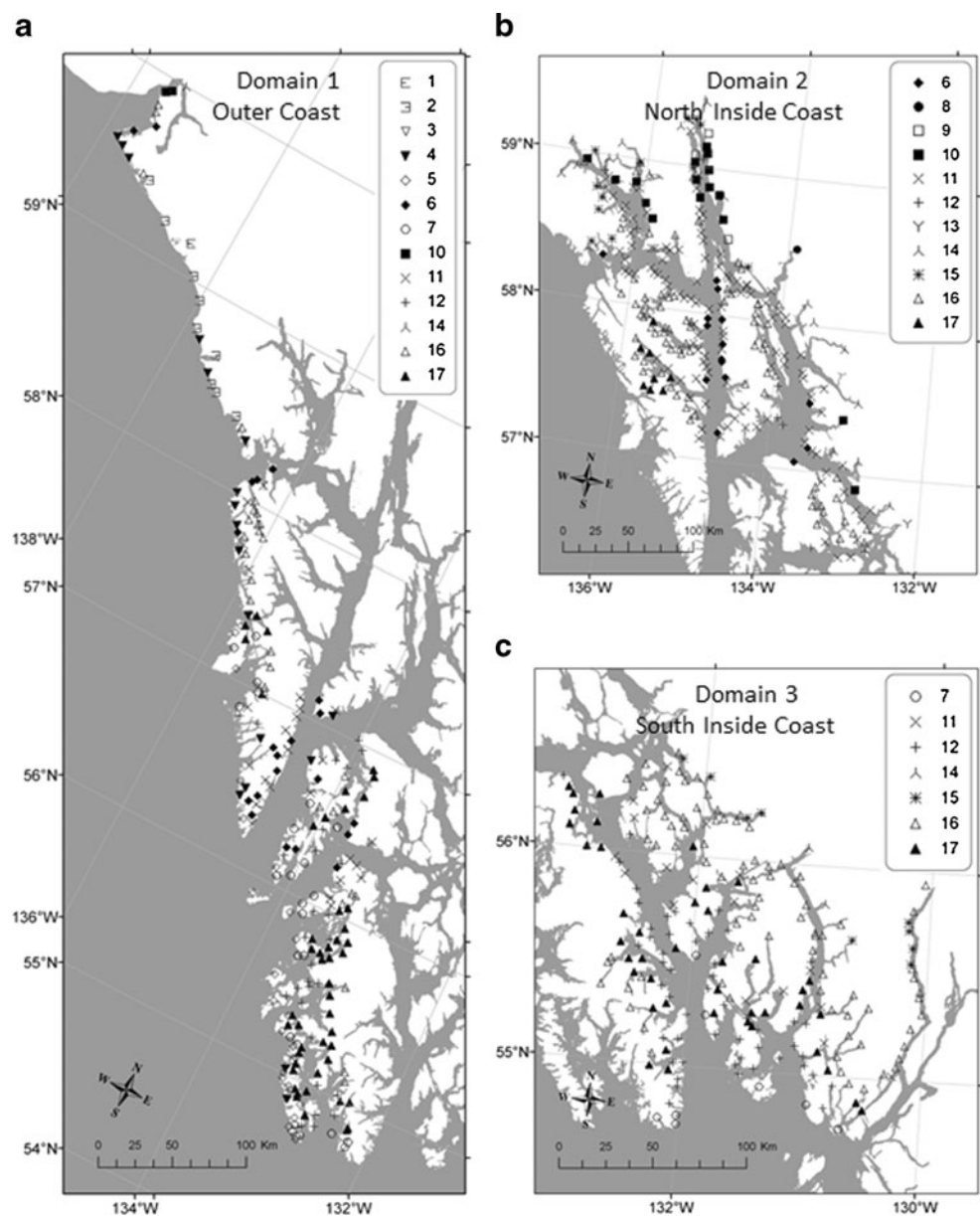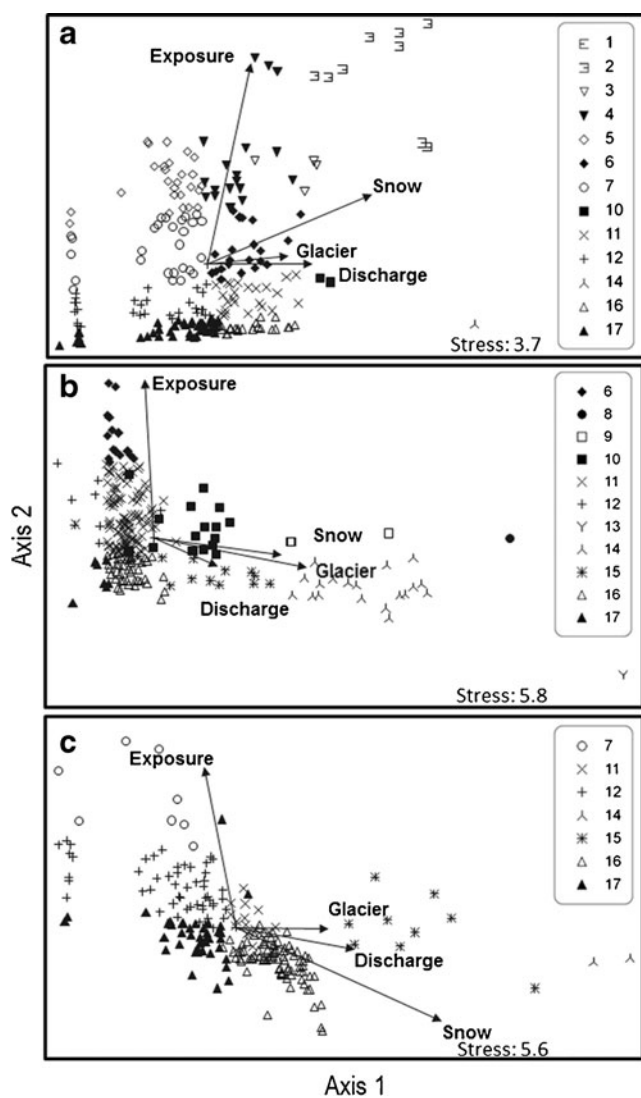
Fig. 9 MDS plots for the ordination analysis of estuary attributes. Plots show the two-dimensional view of a multidimensional cloud of points. *Plotted points* are shown with symbols corresponding to the estuary classes shown in the legend, listed in Table 1, and mapped in Fig. 8. The plot for estuaries in domain 1 are shown in **a**, for domain 2 in **b**, and for domain 3 in **c**. Results of attribute correlations with the principal axes are listed in Table 2

by exposure (r^2=0.71), glacier size (r^2=0.68), and snow (r^2= 0.57), and the ANOSIM tests indicate that estuary classes were clearly distinguished (global R=0.673, p=0.001). In domain 3 (Fig. 9c), the pattern of class separation was best explained by snow (r^2=0.72) and discharge (r^2=0.56), and the ANOSIM tests indicate significant estuary class separation (global R=0.610, p=0.001).

Table 2 lists the analysis results of within-class multivariate dispersion and similarity percentages. In domain 1, the estuaries in class 2 showed the greatest relative separation (1.406), and class 10 showed the least (0.518). Within-class similarity was forced mostly by snow and marine exposure. In domain 2, the estuaries of class 14 showed the greatest

relative separation (1.505), and class 17 showed the least (0.699). Within-class estuary similarity in domain 2 was forced mostly by snow and discharge. In domain 3, the estuaries of class 15 were the most dispersed (1.615), and those of class 14 the least (0.831) and within-class similarity was forced mostly by river discharge.

Level 3: Nearshore Habitats

Figure 10 summarizes the estuarine nearshore habitats classified with the ShoreZone mapping system. Additional data are tabulated in Online Resource 1. The 719 estuaries include 88,575 nearshore segments. There are 45,720 segments in 233 estuaries in domain 1 representing 13,527 km of shoreline. Rock is the dominant habitat type (23 %), followed by gravel and sand (21 %), then rock and gravel habitats (20 %), and river channels (1 %). There are 19,657 segments in 236 estuaries in domain 2 representing 7,379 km of shoreline. Gravel and sand habitats are dominant (18 %), followed by rock and gravel (11 %), all rock (2 %), and glaciers (1 %). In domain 3, there are 23,204 segments in 213 estuaries representing 7,910 km of shoreline. Rock and gravel is the main habitat type (38 %), followed by gravel and sand (19 %), and all rock (12 %).

Analysis of Ecological Patterns

The distribution of the taxa and taxonomic groups among the 17 estuary classes is plotted in Fig. 11. Anadromous fishes are represented in all classes except for estuary class 10 in domain 1. Terrestrial grasses and salt marshes are present in all estuary classes. Marine invertebrates are found in all estuaries except those in class 1 in domain 1. Marine vascular plants were not observed in classes 1, 2, 10, and 14 in domain 1, or in classes 8 and 14 in domain 2. Marine algae were observed in all classes except for class 1 in domain 1. Canopy kelps were not found in classes 1, 10, and 14 in domain 1, and classes 9 and 13 in domain 2, and classes 14 and 15 in domain 3.

The frequency of observation by estuary class for the selected fishes, plants, and invertebrates included in this study are tabulated in Online Resource 2. Frequencies are expressed as a percent of the total number of estuaries in a class. The highest relative biodiversities (> 90 %) were found in estuary classes 4, 5, 6, 7, and 17 in domain 1, 11 in domain 2, and 6 and 12 in domain 3. The lowest relative biodiversity (< 50 %) was found in estuary classes 1 and 10 in domain 1, and 12 in domain 2; however, these classes are represented by only one or two estuary members.

Figure 12 illustrates the results of multivariate ordination analyses to explore taxa associations with the different estuary classes. In this analysis, the vectors represent taxa, the angle and length of the radiating lines in each plot relate to the direction and relative magnitude of the Pearson's

Table 2 Results of estuary group similarity analysis

| Estuary class | Group dispersion domain | | | Attribute percent contribution to group similarity | | | | | | | | | | | |
| | 1 | 2 | 3 | Domain 1: outer coast | | | | Domain 2: north inside coast | | | | Domain 3: south inside coast | | | |
				Glacier	Snow	Discharge	Exposure	Glacier	Snow	Discharge	Exposure	Glacier	Snow	Discharge	Exposure
1	—			—	—	—	—								
2	1.406			20.24	22.20	16.27	41.29								
3	1.343			6.86	50.17	34.25	8.72								
4	1.170			0.00	30.30	10.10	59.60								
5	0.979			0.00	62.49	9.63	27.88								
6	0.915	0.818		0.00	48.04	15.84	36.11	0.00	27.71	19.96	52.34				
7	1.158		1.574	0.00	73.82	4.25	21.93					0.00	24.45	26.19	46.37
8		1.376		—	—	—	—	40.05	0.38	54.28	5.28				
9	0.518	1.114		68.96	0.10	27.20	3.74	11.90	18.81	36.04	33.25				
10	0.753	1.091		0.00	71.93	11.34	16.73	0.00	44.07	17.19	38.74				
11	1.153	1.207	0.833	0.00	90.67	4.95	4.38	0.00	45.90	17.30	36.80	0.00	8.14	55.18	36.67
12			1.233									0.00	46.97	24.19	28.84
13		—		0.831	—	—	—	—	—	—	—				
14		—	1.505	1.615	—	—	—	—	13.90	53.27	27.20	5.63	23.90	2.94	40.75
32.41															
15			1.256					25.58	43.17	27.41	3.85	48.40	1.61	48.90	1.09
16	0.734	0.786	0.885	0.00	72.61	25.66	1.73	0.00	54.96	35.53	9.51	0.00	21.21	70.10	8.69
17	1.008	0.699	1.079	0.00	88.37	10.91	0.71	0.00	60.52	25.34	14.15	0.00	25.03	44.00	30.97

Column 1 lists the estuary classes, and columns 2–4 list the relative dispersion index by marine domain. Larger numbers indicate relatively greater dispersion or attribute variability within estuarine classes. Columns 5–8 for domain 1, columns 9–12 for domain 2, and columns 13–16 for domain 3 list the percent contribution of each attribute to within group similarity
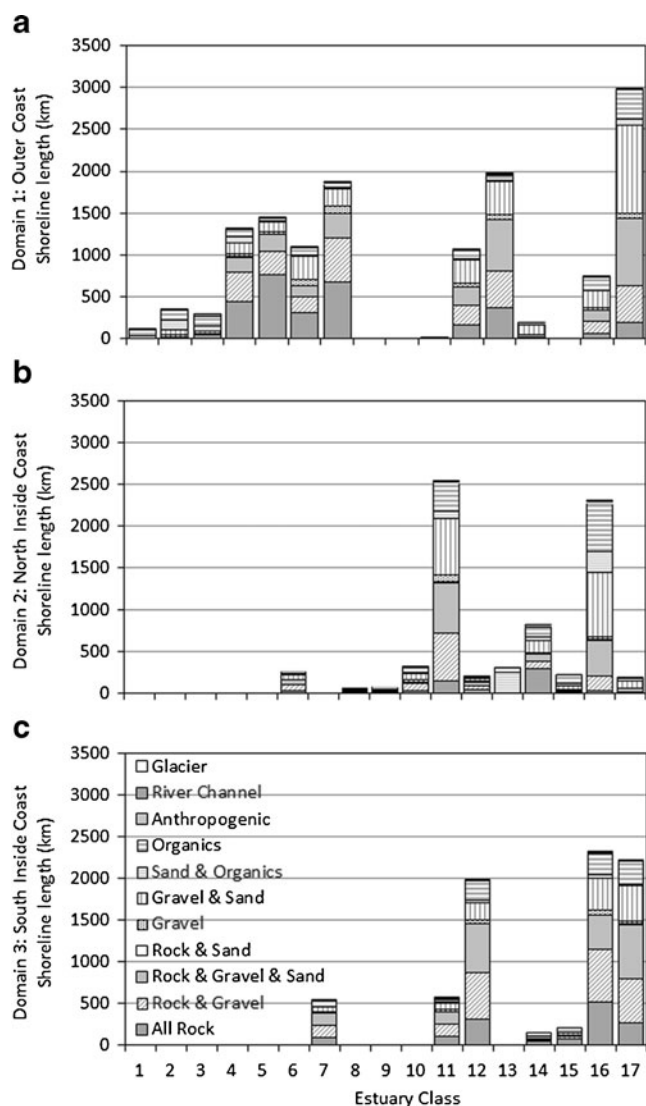
Fig. 10 Distribution of shoreline habitat types by estuary class for domain 1, the outer coast in **a**; domain 2, the north inside coast in **b**; and domain 3, the south inside coast in **c**. Data were compiled from ShoreZone mapping surveys. See text for details and Online Resource 1 for additional data
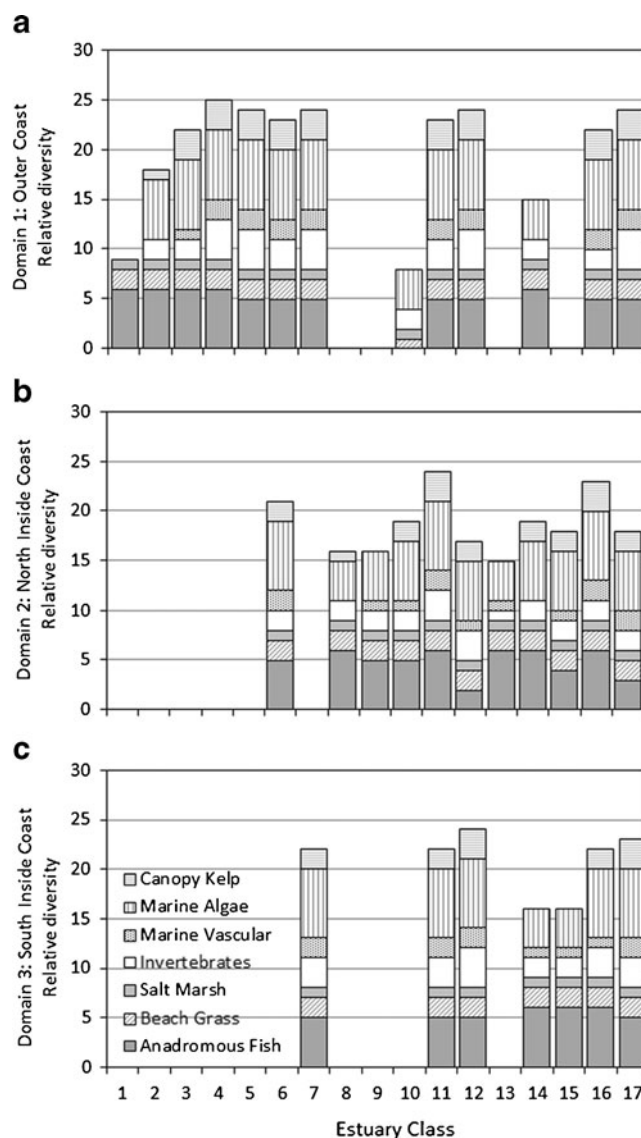

Fig. 11 Distribution of estuarine biota by estuary class for domain 1, the outer coast in **a**; domain 2, the north inside coast in **b**; and domain 3, the south inside coast in **c**. Data were compiled from Alaska Department of Fish and Game anadromous stream surveys and observations from ShoreZone surveys. Possible totals are six anadromous fishes, two grasses, one salt marsh, four invertebrates, two vascular plants, seven marine algae (understory), and three canopy kelps. See text for details and Online Resource 2 for additional data

correlation (in two-dimensional ordination space). In domain 1 (Fig. 12a), the taxa most highly associated with the pattern of estuary classes include Chinook salmon (*Oncorhynchus tshawytscha*) in exposed glaciated estuaries (classes 2 and 4), surf grass (*Phyllospadix* sp.), and giant kelp (*Macrocystis integrifolia*) in exposed rain dominated estuaries (classes 5 and 7), and eel grass (*Zostera marina*) and Chum salmon (*Oncorhynchus keta*) in low exposed rain dominated estuaries (class 17). In domain 2 (Fig. 12b), the strongest associations include Chinook salmon in low exposed glaciated estuaries (classes 14 and 15), ribbon kelp (*Alaria* sp.) in exposed snow-dominated estuaries (class 6), and eel grass in low exposed rain-dominated estuaries (class 17). In domain 3 (Fig. 12c), the strongest associations are

among Chinook salmon in low exposed glaciated estuaries (class 15), surf grass, giant kelp, bull kelp (*Nereocystis luetkeana*), and urchins (*Strongylocentrotus* sp.) in exposed rain-dominated estuaries (class 7), and ribbon kelp in moderate exposed rain-dominated estuaries (class 12). Table 3 lists the Pearson's *r* and the coefficients of determination for each taxon or taxa group most highly correlated with the estuary classes ($r > 0.25$), as well as the estuary class best characterized by each taxon or taxa group. In domain 1, there are 16 taxa or taxa groups with a statistically significant ($\alpha = 0.05$) indicator value
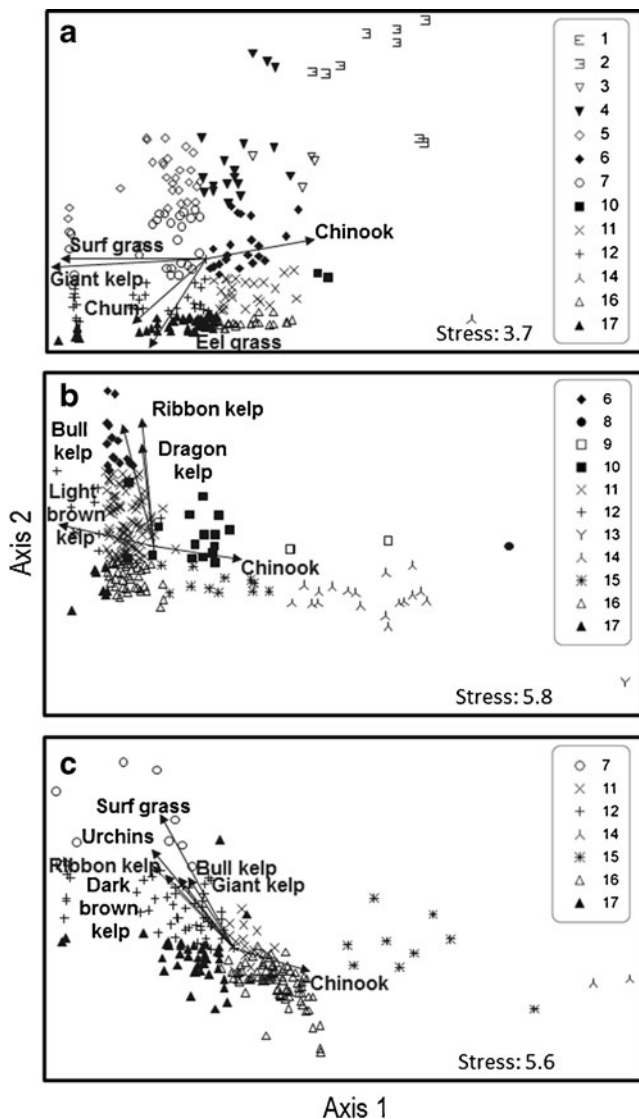
Fig. 12 Vectors representing the association between taxa and the estuary classes (for Pearson's $r > 0.25$) are shown on the ordination plots of estuarine environmental attributes. See Table 3 for statistical results

for at least one estuary class; in domain 2, there are 10, and in domain 3, there are 8.

We examined the effects of marine exposure and watershed hydrography on relative biodiversity using linear regressions (Fig. 13a–h) and found that, in most cases, marine exposure was positively correlated (i.e., higher exposure=higher relative biodiversity) and watershed hydrography was negatively correlated with relative biodiversity (i.e., more fresh water= lower relative biodiversity). Across all domains, exposure explained 91 % of the variation in relative biodiversity ($F_{3, 678} = 28.53$, $p < 0.05$) and watershed hydrography explained 93 % ($F_{4, 677} = 47.87$, $p < 0.05$). Exposure explained 89 % of the variation in domain 1 ($F_{3, 299} = 7.96$, $p < 0.05$), 64 % of the variation in domain 2 ($F_{3, 233} = 9.93$, $p < 0.05$), and 98 % of the variation in domain 3 ($F_{3, 210} = 14.30$, $p < 0.05$).

Hydrography explained 80 % of the variation in domain 1 ($F_{4, 228} = 31.79$, $p < 0.05$), 88 % of the variation in domain 2 ($F_{4, 231} = 9.43$, $p < 0.05$), and 83 % of the variation in domain 3 ($F_{4, 209} = 24.08$, $p < 0.05$).

Discussion

Our habitat classification is able to resolve environmental differences among estuaries that significantly alter biological structure in the Alexander Archipelago. We found that many taxa or taxa groups show strong fidelity to one or a few estuary classes while others were relatively ubiquitous. These results are similar to other nearshore studies in the Northeast Pacific that suggest benthic habitats with similar environmental attributes have similar biological communities (Schoch et al. 2006), and relative biodiversity increases predictably with increasing habitat complexity, marine exposure, and decreasing freshwater (Dethier and Schoch 2005). The ShoreZone aerial synoptic surveys were adequate for identifying common macro epifauna and flora, but finer scale ground surveys are needed to further refine the relationship between estuary class, nearshore habitat, and biodiversity in this system. Nevertheless, the biota identified by the ShoreZone surveys, while limited in numbers of categories, are almost all habitat forming organisms, and thus proxies for larger and more diverse communities. A limitation of the aerial surveys is not identifying benthic infauna or taxa that do not form large surface aggregations. However, more detailed ground surveys by Dethier and Schoch (2005) found that biodiversity generally decreases in estuaries even though total biomass may increase, and this lends a reasonable rationale against the relevance of benthic macro infauna to observed patterns of relative biodiversity in this particular system.

The marine exposure index is a proxy for wave climate that, as a mechanism of disturbance, has been shown by Denny (1995) and others to significantly alter biotic composition of the nearshore. Most of the shoreline habitat in Southeast Alaska is rock on wave-exposed coasts, rock and gravel on more sheltered shorelines where there may only be locally generated wind waves, and mixed gravel and sand where wave energy is mostly attenuated. Silty sediments with organics are confined to heads of protected bays and inlets. On the outer coast where wave energy creates very dynamic gravel beaches, the substrate is devoid of interstitial fine-grained particles and likely biologically depauperate. In sheltered estuaries, interstitial spaces in gravel beaches are often filled with sand and silt. Here, slight increases in wave energy, as could be expected during winter storms, will likely resuspend fine sediments and remove these grains from the substrate, causing significant seasonal disturbance to infaunal populations.

Table 3 Pearson's correlation coefficients and coefficients of determination are listed for the environmental attributes that best explain the distinction among estuary classes and for the taxon or taxa group that is best correlated with the estuary classes (Pearson's r>0.25)

Taxon or taxa group	Example taxa / group	Domain 1: outer coast				Domain 2: north inside coast				Domain 3: south inside coast				Estuary class by domain		
		Axis 1		Axis 2		Axis 1		Axis 2		Axis 1		Axis 2		1	2	3
		r	r²	r	r²	r	r²	r	r²	r	r²	r	r²			
Snow	Physical	0.756	0.572	0.491	0.241	0.752	0.566	−0.269	0.072	0.851	0.416	−0.282	0.080			
Exposure		0.387	0.150	0.840	0.706	−0.203	0.041	0.842	0.709	−0.333	0.111	0.750	0.563			
Discharge		0.497	0.247	0.122	0.015	0.531	0.282	−0.353	0.124	0.645	0.416	−0.282	0.080			
Glacier		0.455	0.207	0.115	0.013	0.824	0.679	−0.308	0.095	0.570	0.325	−0.084	0.007			
Coho	*Oncorhynchus kisutch* (Anadromous fishes)	−0.173	0.030	−0.299	0.089									12	9	14
Chinook	*Oncorhynchus tshawytscha*	0.438	0.192	0.186	0.034	0.327	0.107	−0.117	0.014	0.517	0.268	−0.289	0.084	3	14	14
Sockeye	*Oncorhynchus nerka*	0.268	0.072	0.065	0.004	0.264	0.069	−0.169	0.029					3	9	14
Chum	*Oncorhynchus keta*	−0.028	0.001	−0.377	0.142									11	17	14
Pink	*Oncorhynchus gorbuscha*	−0.239	0.057	−0.308	0.095									12	17	14
Steelhead	*Oncorhynchus mykiss*									0.252	0.064	−0.307	0.094	16	9	14
Salt marsh	e.g., *Puccinellia* sp.	−0.050	0.003	−0.251	0.041	−0.253	0.055	0.125	0.016					10	9	14
Dune grass	e.g., *Leymus mollis* (Grasses)					−0.252	0.064	0.155	0.024					10	9	14
Sedges	e.g., *Carex* sp.					0.061	0.004	−0.250	0.062					2	17	14
Barnacles	e.g., *Balanus* sp., *Semibalanus* sp. (Invertebrates)	−0.361	0.130	−0.362	0.131									10	9	14
Urchins	*Strongylocentrotus* sp.									−0.542	0.293	0.588	0.346	5	12	7
Blue mussel	*Mytilus trossulus*									0.279	0.078	−0.227	0.051	10	9	14
California mussel	*Mytilus californianus*													5	–	12
Surf grass	*Phyllospadix* sp. (Vascular)	−0.313	0.098	0.295	0.087					−0.511	0.261	0.684	0.468	5	17	7
Eel grass	*Zostera marina*	−0.505	0.255	0.027	0.001	−0.292	0.085	−0.161	0.026	−0.427	0.182	0.195	0.038	17	17	17
Rockweed	e.g., *Fucus* sp. (Algae)	−0.428	0.183	−0.516	0.266									17	9	14
Green algae	e.g., *Ulva* sp.	−0.439	0.193	−0.487	0.237									10	9	14
Bleached algae	Unid. red algae	−0.290	0.084	−0.332	0.110					−0.327	0.107	0.146	0.021	12	17	17
Red algae	Unid. red algae	−0.382	0.145	−0.290	0.084	−0.273	0.074	0.225	0.050					10	6	14
Ribbon kelp	*Alaria* sp.	−0.310	0.096	−0.172	0.029	−0.142	0.020	0.434	0.189	−0.534	0.285	0.536	0.287	5	6	7
Light brown kelp	e.g., *Saccharina* spp.	−0.251	0.063	0.179	0.032	−0.379	0.144	0.161	0.026					10	6	14
Dark brown kelp	e.g., *Laminaria* spp.	−0.323	0.105	−0.503	0.253	−0.162	0.026	0.250	0.063	−0.444	0.197	0.499	0.249	5	6	7
Dragon kelp	*Alaria fistulosa* (Canopy)	−0.255	0.065	0.299	0.089	−0.129	0.017	0.388	0.151					6	6	17
Giant kelp	*Macrocystis integrifolia*	−0.543	0.295	−0.089	0.008	−0.171	0.029	0.422	0.178	−0.403	0.162	0.498	0.248	7	16	7
Bull kelp	*Nereocystis luetkeana*	−0.397	0.158	−0.069	0.005					−0.495	0.244	0.505	0.255	5	6	7

The last three columns list the estuary class statistically preferred or best characterized by each taxon or taxa group in each marine domain. Values in italics are statistically significant (α=0.05)
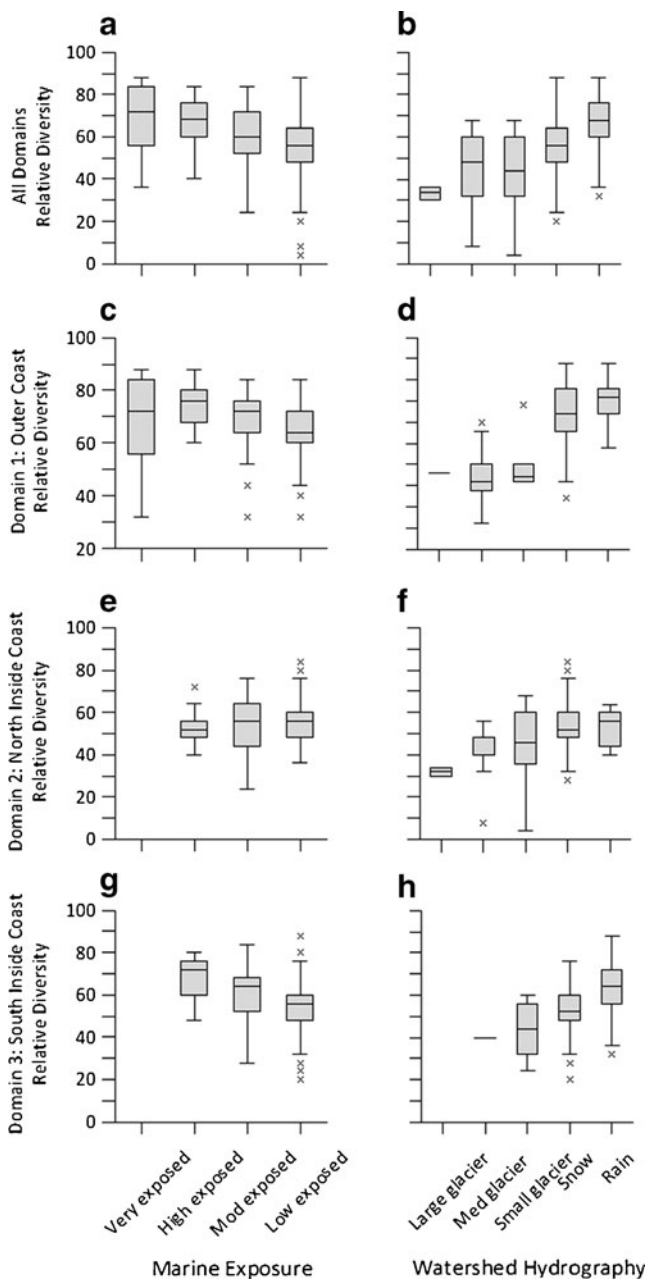
Fig. 13 *Box and whisker plots* of relative biodiversity from all marine exposure classes (**a**, **c**, **e**, and **g**) and from all hydrographic classes (**b**, **d**, **f**, and **h**) for each domain and for all domains combined. Outliers are represented by *X*'s

estuary may differ from that of another having similar morphology but different hydrographic characteristics.

Our analyses suggest that estuarine biodiversity is also a function of the amount and diversity of nearshore benthic habitat. Biodiversity generally increases within an estuary when a broad range of nearshore benthic habitats are available, thus more species niches. It follows that estuary classes with more shoreline length are also more geomorphologically diverse and, therefore, more biodiverse, particularly when marine exposure is high and freshwater input is low.

The estuarine environment of Southeast Alaska is a region of high biological productivity and diversity, but can be heavily influenced by anthropogenic perturbations such as oil spills, chronic pollution, development, and industrial and recreational resource extraction. Understanding the relationships between physical features of shorelines and nearshore populations allows us to assess the vulnerability and sensitivity of estuarine ecosystems to both natural and anthropogenic perturbations. The classification system described here provides an objective approach for organizing and grouping complex estuarine ecosystems based on oceanic, watershed, and benthic environmental drivers. We evaluated the statistical associations between various groups of biota and estuary classes, and because these associations are correlative and not causative, we are careful to not over interpret the results, but they certainly point to new hypotheses about the mechanisms of association for the different estuaries in this study. While environmental classifications are important tools to aid our understanding of complex systems, management applications should be tempered by the limitation that all classifications force natural gradients into discrete categories and in the process may encounter problems, especially near edges or boundaries, since ecosystems, and estuaries in particular, are multidimensional continua. In that regard, information needed to further refine our understanding of these systems includes higher resolution mapping of the shoreline, better estimates of key environmental variables (e.g., salinity, stream discharge, precipitation, etc.), finer scale biodiversity surveys, and process oriented studies that account for variability at time scales ranging from tidal to climatological. Advancing our ecological understanding of this remote ecosystem will be a laborious and time-consuming process, and in the interim, this classification is a useful management tool for identifying ecologically sensitive shorelines for strategic conservation planning.

In Puget Sound, Washington, USA, Dethier et al. (2010) found a strong response in benthic biota to subtle differences in water temperature and salinity. Many nearshore organisms, especially algae, are extremely sensitive to the salinity range of the water (Costanza et al. 1993). Therefore, the seasonal variability and magnitude of freshwater runoff can significantly influence the structure and distribution of marine organisms and are often the primary drivers of estuarine functions (Hume et al. 2007). Since some organisms are better adapted to lower salinity than others, the entire community structure of one

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