

## ORIGINAL ARTICLE

# Depth-stratified community zonation patterns on Gulf of Alaska rocky shores

Brenda Konar<sup>1</sup>, Katrin Iken<sup>1</sup> & Matthew Edwards<sup>2</sup>

<sup>1</sup> School of Fisheries and Ocean Sciences, University of Alaska Fairbanks, Fairbanks, AK, USA

<sup>2</sup> Department of Biology, San Diego State University, San Diego, CA, USA

## Keywords

Census of Marine Life (NaGISA); Gulf of Alaska; intertidal and subtidal vertical zonation; invertebrate abundance; macroalgal biomass; regional variability.

## Correspondence

Brenda Konar, School of Fisheries and Ocean Sciences, University of Alaska Fairbanks, Fairbanks, AK 99775, USA.  
E-mail: bkonar@guru.uaf.edu

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## Abstract

Vertical zonation patterns have been considered ubiquitous in intertidal ecosystems but questions remain about their generality for individual taxonomic groups and over broad spatial scales, and whether they continue into adjacent shallow subtidal habitats. Taxon richness, invertebrate abundance, and macroalgal biomass were examined in the summer of 2003 along a vertical gradient in the rocky intertidal and shallow subtidal habitats around Kodiak Island, Kachemak Bay, and Prince William Sound, all within the Gulf of Alaska. Replicate samples of benthic organisms were taken in the high (~ 7 m), mid (~ 4 m) and low (~ 0 m) intertidal (relative to MLLW), and at 1, 5, 10 and 15 m water depths at three sites in each region, and identified to the lowest possible taxonomic level. Our primary goals were to assess (1) how estimates of taxon richness, invertebrate abundance, and macroalgal biomass vary among intertidal heights and subtidal depths and (2) how general these patterns are when considered across the Gulf of Alaska. Our results show that when all invertebrates were considered together, most of the variation in taxon richness was accounted for by differences among depths (*i.e.* intertidal heights and subtidal depths) (~ 51%), and among replicate samples within each depth (~ 26%). Little to none of the variation was accounted for by differences among sites within each region (~ 1%) or among regions themselves (~ 0%). When considered across the Gulf of Alaska, total taxon richness and organism abundance were greatest in the low intertidal/shallow subtidal and decreased with increasing height/depth. When separated by phylum and examined together with macroalgae, variation in abundance and/or biomass among depths was significant and accounted for most of the variability. Differences among regions and sites within each region were not significant and accounted for little to none of the variance. Because the pattern of zonation varied among sites within each region, it reduced the generality of a single zonation pattern for the Gulf of Alaska. Likewise, when community composition was compared among depths, geographic regions and sites within each region using multivariate analyses, vertical zonation patterns were evident at a regional scale, but high variability in these patterns among sites within each region reduced the generality of these patterns.

## Problem

Zonation patterns along elevation and depth gradients are common in rocky intertidal and subtidal ecosystems

(Underwood 1985; Foster & Schiel 1985; Hawkins *et al.* 1992; Bertness *et al.* 2006; and many others) and universal patterns in taxon composition, richness and abundance have been suggested (*e.g.* Stephenson & Stephenson

1949; Lewis 1964; Connell 1972). However, although numerous studies have described these zonation patterns in terms of organism biomass, abundance, morphology, and mobility at local scales (e.g. Mann 1972; Vermeij 1972; Gambi *et al.* 1994; Schiel *et al.* 1995; Davidson *et al.* 2004), recent work has suggested these patterns may not be generalizable across broad geographic regions (Ingólfsson 2005; Bertness *et al.* 2006) in the sense that there may not be a consistent peak in abundance and/or biomass at a particular depth stratum at all sites and regions for different taxonomic groups. This may be especially true for whole-community zonation patterns, which are influenced by numerous complex biological and physical processes acting on multiple species across local to regional spatial scales (Lubchenco & Menge 1978; Sousa 1979). As a result, many studies have used metrics such as taxon richness rather than individual species abundances to compare communities among geographic regions (e.g. Zacharias & Roff 2001; Witman *et al.* 2004) and intertidal heights within regions (e.g. Benedetti-Cecchi 2001). Consequently, discerning how taxon richness as well as organism abundance changes across elevation and depth gradients both within and among sites can be an important step in understanding whether general patterns in variation of depth-stratified community composition exist in coastal ecosystems across broad geographic regions.

Intertidal taxon richness generally increases from the high intertidal, seawards (Davidson *et al.* 2004; Ingólfsson 2005), reaching a maximum in the lower intertidal zones where physical conditions (*i.e.* temperature and immersion time) may be less stressful for many marine organisms but where biological interactions among organisms (*i.e.* predation and competition) may be stronger (Connell 1978). It is largely unknown, however, if this pattern continues into the subtidal where taxon richness can be higher due to increased macroalgal abundance (Foster & Schiel 1985). Marine macrophytes create a three-dimensional structure that provides food and shelter for a variety of invertebrate species, many of which show obligate associations with these algae and therefore can enhance species richness, survival, and reproduction (e.g. Ray 1996; Van Oppen *et al.* 1996; Duarte 2000; Bulleri *et al.* 2002). As a result, species richness in areas where macroalgae are abundant may be much greater than in areas where macroalgae are uncommon (McLean 1962; Mann 1972; Aleem 1973). Thus, assessing variation in macroalgal biomass along depth gradients from the high intertidal to the subtidal may provide a greater understanding of taxon richness patterns of associated fauna along the same depth gradients.

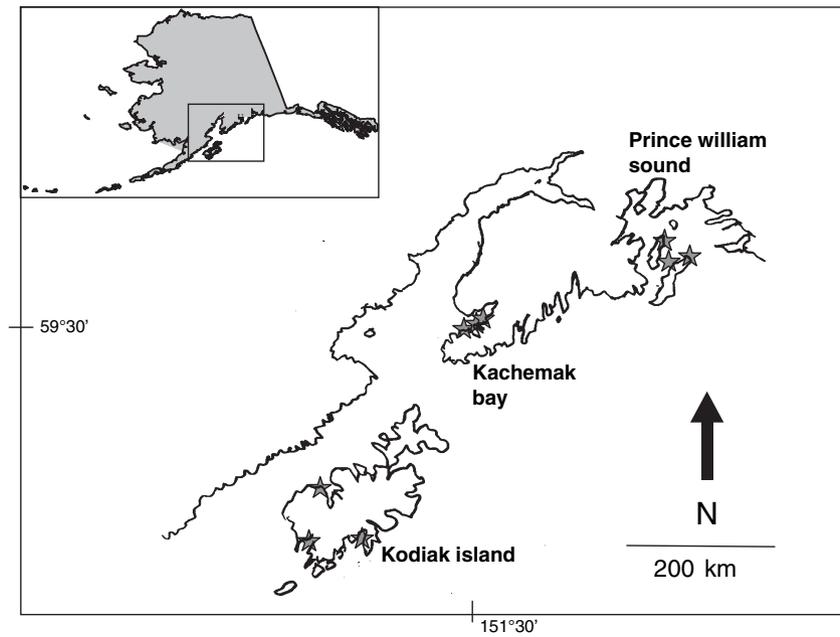
Over large geographic areas, taxon richness is influenced by processes acting at a broad range of spatial scales (Menge & Olson 1990; Chapman *et al.* 1995; Connell *et al.* 1997; Tilman & Kareiva 1997; Karlson &

Cornell 1998). However, making inferences to a single spatial scale may miss the important local factors structuring these communities (Dayton & Tegner 1984; Weins 1989; Levin 1992, 2000; Edwards 2004). Consequently, sampling designs that rely on hierarchical (fully-nested) protocols may be useful for studying both local and broad-level patterns of taxon richness (Carpenter 1998; Turner & Dale 1998). Such designs may also be amenable to analyses that partition variability (Graham & Edwards 2001), thus providing insights into the relative importance of processes acting at each scale (Hughes *et al.* 1999; Edwards 2004).

Whereas many studies have examined variation in zonation for specific taxa or groups of similar taxa (*i.e.* species grouped according to lower taxonomic affiliation or morphological similarity) within particular locations (e.g. Pearse & Hines 1979; Riedman *et al.* 1981; Witman 1987; Zuschin *et al.* 2001; Goldberg & Kendrick 2004), less is known about how consistent these patterns are, *i.e.* how zonation patterns for multiple taxa vary simultaneously across larger geographic regions. It is widely accepted, however, that local-scale patterns are strongly influenced by variation in topography, substrate profile, aspect angle, and biological interactions (Paine 1974; Konar 2000; Bertness *et al.* 2006; and many others), whereas regional-scale patterns are strongly influenced by oceanographic events, temperature, salinity, upwelling, and currents (Menge *et al.* 1997, 2003; and many others). Therefore, comprehensive assessments of how overall taxon richness, invertebrate abundance and macroalgal biomass compare between local and regional scales can provide considerable insight into the generality of zonation patterns over larger geographic areas. This study examined vertical zonation patterns in the distribution and abundance of intertidal and shallow subtidal rocky shore organisms with special attention to how these patterns vary from different taxonomic groups within and among geographic regions in the Gulf of Alaska. Special attention also was given to identifying the intertidal heights and subtidal depths where overall taxon richness, invertebrate abundance, and macroalgal biomass are greatest, and whether overall and larger taxonomic group invertebrate abundance is correlated with macroalgal biomass.

## Material and Methods

During summer 2003, three regions separated by 200–400 km and spanning a linear distance of approximately 600 km (longitudinally from 147°06' to 154°15' W and latitudinally from 56°45' to 60°39' N) were selected in the Gulf of Alaska (Fig. 1). Within each region (Kodiak Island, Kachemak Bay and Prince William



**Fig. 1.** Map of the Gulf of Alaska showing the three study sites (denoted by stars) at each of the three study regions (Kodiak Island, Kachemak Bay and Prince William Sound).

Sound), three sites were chosen based on the presence of rocky reef habitat and qualitative assessments of similar hydrodynamic forces and slope (personal observations by B.K. and K.I.). All sites (Kodiak Island – Old Harbor, Alitak, and Uyak Bay; Kachemak Bay – Elephant and Cohen Islands, and Outside Beach; Prince William Sound – Montague, Knight and Green Islands) were characterized by moderate slopes with approximately 15–20 m distance between high and low tide and tightly packed boulders of approximately 50–70 cm diameter (although the high-tide region at some sites had bedrock). Temperatures during summer 2003–2004 were monitored using HOBO Water Temp Pro data loggers (Onset Computers) and found to be similar, ranging over the annual cycle from approximately 3 to 15 °C in the subtidal and –15 to 35 °C in the intertidal. Intertidal winter freezing events can occur periodically in the Gulf of Alaska, especially during extreme (e.g. 9–10 m) tides (Carroll & Highsmith 1996; Patterson 2004), which may further influence species distribution and abundance patterns.

Macroalgal biomass and invertebrate abundance were estimated using standardized protocols developed for the Natural Geography In Shore Areas (NaGISA) program within the Census of Marine Life (Rigby *et al.* 2007). At each site, a stratified random sampling design was used in which five replicate samples were taken at randomly selected positions along a 30-m transect in each of the high (~ 7 m), mid (~ 4 m), and low (~ 0 m) intertidal strata, and the 1, 5, 10, and 15 m subtidal depth strata (relative to MLLW (Mean Low Level Water)). Intertidal heights were easily identifiable based on prevailing macroalgal biobands

(i.e. 'high' included the barnacle/*Fucus* bands, 'mid' included mussel and red algal bands, 'low' included red and brown algal bands), and subtidal depths were identified using a dive computer. At two sites [Outside Beach (Kachemak Bay) and Old Harbor (Kodiak Island)], the 15 m depth stratum was not sampled because there had been a transition of the substrate to 100% sand. Replicate samples along the transects consisted of two nested quadrats (a 25 × 25 cm quadrat nested within a 50 × 50 cm quadrat). Within each 25 × 25 cm quadrat, all macrofauna and macroalgae were removed and placed in a 63- $\mu$ m mesh bag. These were then sieved over a 0.5-mm screen immediately after collection and the invertebrates and macroalgae separated. Within the remaining portion of each 50 × 50 cm quadrat, only macroalgae were collected.

Macroalgae from both quadrats were combined, sorted to the lowest possible taxonomic level, and weighed to the nearest 1 g (wet weight). Encrusting coralline algae were recorded as being present for estimates of taxon richness analyses but were not included in the biomass analyses. Invertebrates collected in the 25 × 25 cm quadrats were preserved in 10% formalin and later transferred to 50% isopropyl alcohol. Individual organisms were sorted to the lowest possible taxonomic level and counted. Taxonomic resolution was equal for all macroalgal and invertebrate taxa at all sites and regions. Mollusks, echinoderms, and polychaetes were identified to species when possible, and other invertebrates were grouped by higher taxonomic affiliation. Arthropod groupings included: amphipods, isopods, harpacticoid copepods, tanaids, cumaceans, ostracods, cirripeds,

decapods (including brachyurans, lithodids, and pagurids), insects, pycnogonids, and euchelicerates (mites and pseudoscorpions). Other invertebrate groups were cnidarians (anemones, stauromedusae, and hydroids), oligochaetes, sipunculids, nemerteans, plathyhelminthes, bryozoans, brachiopods, and solitary ascidians. As these broader taxonomic groups were not identified to species, the reported taxonomic richness is likely an underestimate of true species richness. Further, some organism abundances (e.g. copepods) are likely an underestimate as they were often smaller than 0.5 mm and could pass through the mesh while sieving. Invertebrates that could not be distinguished as individuals upon removal from the substrate were recorded as present for the taxon richness analyses but were not included in the abundance analyses. Voucher specimens for all organisms are being held at the University of Alaska Fairbanks and are available for review.

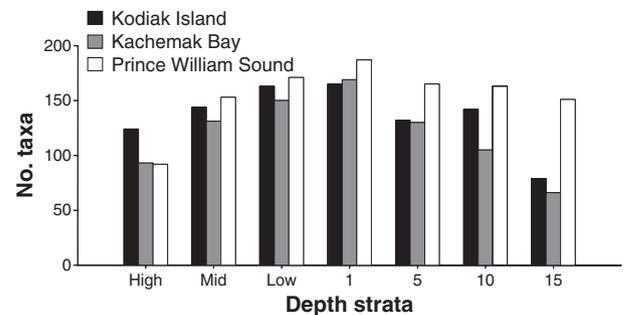
All statistical analyses were done using SYSTAT version 10 and PRIMER 6. Prior to testing, data were examined for normality by graphical examination of residuals (univariate analyses) and/or Draftsman plots (multivariate analyses), and for homogeneity of variances with Cochran's C test. Data for total invertebrate (all taxa combined) as well as mollusk, polychaete, and echinoderm abundances, and for algal biomass were each heteroscedastic and thus  $\log(x + 1)$  transformed to meet parametric requirements. Variation in abundances and/or biomass among study regions, sites within regions, and depth strata for each taxon group was examined with separate three-way Model III ANOVAs. Within these, Region was treated as a fixed factor, and Sites nested within Region, and Depth strata as random factors. Following this, the proportion of variation accounted for by each factor (*i.e.* the magnitude of effect) was determined using variance components analysis according to Graham & Edwards (2001). The relationship between average macroalgal biomass and invertebrate abundance for each depth was assessed within each region and across all regions using Pearson correlation analyses. Estimates of species richness are sensitive to low sample sizes. Inspection of species accumulation curves showed that the asymptote was not quite reached with five replicates per depth, although the rate of increase of the curves was clearly declining, indicating that the majority of species were recorded. Therefore, and because the level of taxonomic resolution varied among invertebrates, we did not statistically analyse richness data, but present them graphically. Community composition data based on abundance (invertebrates) and biomass (macroalgae) were analysed using Analysis of Similarity and non-metric multidimensional scaling after fourth-root transformation to normalize these data.

## Results

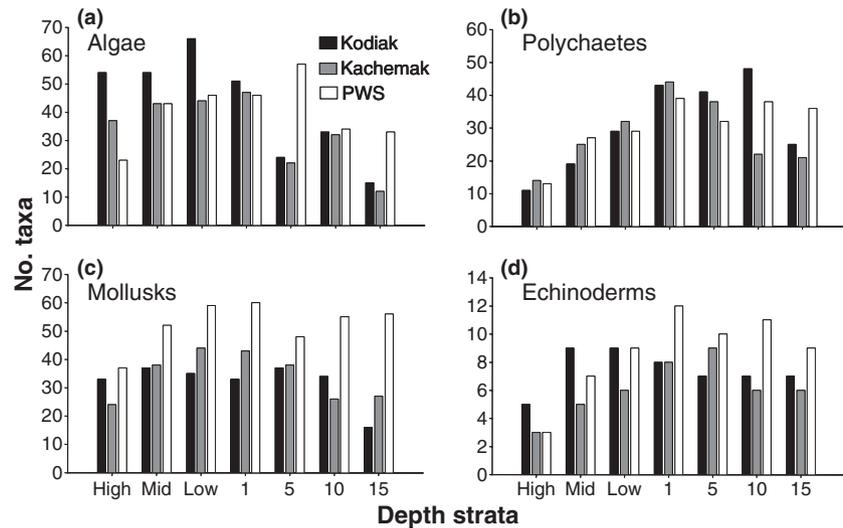
### Taxon and species richness

A total of 559 species and/or taxonomic groups were identified in this study. Of these, 220 species were macroalgae, 155 were mollusks, 107 were polychaetes, and 25 were echinoderms. The other 52 invertebrate taxa could not be identified to species and were grouped as 'miscellaneous invertebrates'. These included numerous groups of crustaceans, worms, sponges, bryozoans, ascidians, and unidentifiable 'others'. The 155 mollusk species included 101 gastropods, 27 bivalves, and 27 polyplacophorans. Of the 25 echinoderm species, 14 were asteroids, 6 holothuroids, 3 ophiuroids, and 2 echinoids. Of the 220 macroalgal species, there were 30 chlorophytes, 57 ochrophytes (phaeophytes) and 133 rhodophytes.

When data for all taxa were combined, similar trends among the three study regions showed that overall taxon richness was greatest at the 1-m depth and low intertidal strata and decreased with both increasing subtidal depth and intertidal height (Fig. 2). However, when species were separated into their respective taxonomic groups (*i.e.* macroalgae, polychaetes, echinoderms and mollusks), trends were less clear due to large taxon-dependent variation among the three regions (Fig. 3). For example, there were more algal species in the low to high intertidal at Kodiak Island than in the other two regions, but similar numbers or fewer species of macroalgae in the subtidal (Fig. 3a). Mollusk richness, in contrast, was greatest in the low intertidal and 1 m subtidal at Kachemak Bay and Prince William Sound, but equally rich at the other depths except the high intertidal, where richness was lowest (Fig. 3b). Polychaete richness was greatest in the shallow subtidal to 10 m depth and declined with increasing height in the intertidal, although the strength of this pattern varied among regions (Fig. 3c). Echinoderm richness was greatest in the mid



**Fig. 2.** Total number of taxa observed at each tidal height at each study region (Kodiak Island, Kachemak Bay and Prince William Sound). Data are based on presence/absence of taxa. Depth strata are defined as high, mid and low intertidal, and 1, 5, 10, and 15 m depth subtidal.



**Fig. 3.** Total number of taxa for (a) algae, (b) mollusks, (c) polychaetes, and (d) echinoderms at each study region. Data are based on presence/absence of each taxon. Depth strata are defined as high, mid and low intertidal, and 1, 5, 10, and 15 m depth subtidal.

and low intertidal at Kodiak Island, 5 m subtidal at Kachemak Bay, and 1 m subtidal at Prince William Sound (Fig. 3d), with no consistent pattern observed across the three regions. Together, this indicated that although general patterns in species richness across depths could be discerned when all taxa were grouped and examined together (Fig. 2), regional variation within and among the different taxa prevented such trends from being generalized to lower taxonomic groups across the Gulf of Alaska.

#### Abundance and biomass

A total of 197,184 invertebrates were enumerated in this study, of which there were 107,484 (55%) mollusks, 56,611 (29%) crustaceans, 18,174 (9%) polychaetes, 2873 (1%) echinoderms, and 12,042 (6%) miscellaneous invertebrates (Table 1). When all invertebrate taxa were combined, total invertebrate abundance did not vary significantly among the three regions (ANOVA:  $P \leq 0.405$ ) or the three sites within each region ( $P \leq 0.115$ ), but did vary among the seven depths ( $P \leq 0.001$ ; Table 2). Consequently, variability among the depths accounted for the largest amount ( $\sim 51\%$ ) of the variance in invertebrate abundance, whereas variability among sites within each region ( $\sim 1\%$ ) and among regions ( $\sim 0\%$ ) accounted for little to none of the variance in overall invertebrate abundance. Variability among replicate samples within each depth at each site accounted for approximately 26% of the total variability in invertebrate abundance, indicating that within-site variation greatly exceeded among-site and among-region variation. Further, differences among depths varied significantly among the three regions (region  $\times$  depth interaction:  $P \leq 0.001$ ), which accounted for approximately 19% of the

total variance in organism abundance (Table 2). This pattern, however, was largely driven by a few highly abundant invertebrate taxa in specific regions. For example, maximum invertebrate abundance at Prince William Sound occurred in the high intertidal zone due to high abundances of the mussel *Mytilus trossulus* and the gastropod *Littorina* spp., whereas the greatest invertebrate abundance at Kachemak Bay occurred in the low intertidal zone due to high gastropod (primarily *Lacuna vincta*) abundances. Differences among depths also varied significantly among the three sites within each region [site(region)  $\times$  depth interaction:  $P \leq 0.025$ ], which accounted for approximately 3% of the total variance in invertebrate abundance (Table 2; Fig. 4).

When the abundances of invertebrates were analysed by phylum, mollusks and polychaetes varied significantly by depth ( $P \leq 0.001$  and  $P \leq 0.005$ , explaining 47% and 28% of the total variance, respectively), but echinoderms did not ( $P \leq 0.175$ , explaining  $\sim 30\%$  of the variance; Table 2; Fig. 5). Although the abundance of mollusks varied significantly among regions ( $P \leq 0.015$ , 13% of the variance), significant variation was not detected for polychaetes or echinoderms ( $P \leq 0.205$  and  $P \leq 0.549$ , explaining  $\sim 2\%$  and 0% of the variance, respectively). Further, no significant variation in abundance was detected among sites within a region for any phylum or group ( $P \leq 0.366$ ,  $P \leq 0.679$  and  $P \leq 0.195$ , explaining  $< 1\%$ , 0% and  $\sim 30\%$  of the variance for mollusks, polychaetes, echinoderms, respectively). Similar to total invertebrate abundance, mollusk and polychaete variability among replicate quadrats within each depth at each site was much greater than variability among sites within a region or among regions. This was not observed for echinoderms. In all cases, however, the differences among

	echinoderms	mollusks	polychaetes	misc inverts	total inverts	total algae
Kodiak Island						
high	82	6615	235	2036	8968	2625
mid	78	3824	1609	1982	7493	7370
low	20	2437	685	3610	6752	11,613
1 m	20	1871	2868	11,129	15,888	32,316
5 m	16	933	1431	1273	3653	20,213
10 m	55	403	859	348	1665	8362
15 m	20	68	162	128	378	2118
total	291	16,151	7849	20,506	44,797	84,617
Kachemak Bay						
high	41	7904	330	4348	12,623	10,667
mid	472	3611	1350	9664	15,097	10,451
low	766	7949	1391	20,223	30,329	11,958
1 m	98	6475	2022	5493	14,088	13,022
5 m	51	470	938	526	1985	19,400
10 m	18	145	161	300	624	8901
15 m	17	99	136	112	364	690
total	1463	26653	6328	40,666	75,110	75,089
Prince William Sound						
high	183	37,000	388	1986	39,557	11,722
mid	55	9383	499	1422	11,359	11,708
low	255	7785	592	1267	9899	17,923
1 m	177	7867	1165	1658	10,867	19,669
5 m	43	1544	419	351	2357	11,819
10 m	71	410	312	382	1175	10,672
15 m	335	691	622	415	2063	2804
total	1119	64,680	3997	7481	77,277	86,317
grand total					197,184	246,023

**Table 1.** Total abundance of invertebrates and total biomass of macroalgae observed in the five replicate quadrats for each region and depth stratum.

depths depended on which site within a region was examined [*i.e.* the site(region)  $\times$  depth interactions were significant for all taxonomic groups]. These depth differences were often driven by only one or two species (see Table 2 for ANOVA results and variance components for individual taxonomic groups). Further, except for polychaetes, differences among depths for each taxonomic group also depended on which region was examined (*i.e.* the region  $\times$  depth interactions were significant). Many of these differences, however, were again driven primarily by only one or a few species in a specific region. For example, high mollusk abundance at Prince William Sound resulted primarily from large numbers of the mussel *M. trossulus* and the gastropod *Littorina* spp. in the high intertidal (Fig. 5b). Echinoderms were generally more abundant in the mid and low intertidal and at 15 m, primarily due to locally dense aggregations. Holothurians (*e.g.* *Cucumaria vegae*) and juvenile asteroids (*e.g.* *Leptasterias* spp.) were highly abundant in the mid and low intertidal at Kachemak Bay, and ophiuroids occurred in high densities at 15 m in Prince William Sound (Fig. 5d). Likewise, peaks in crustacean abundances were driven by high amphipod abundances at

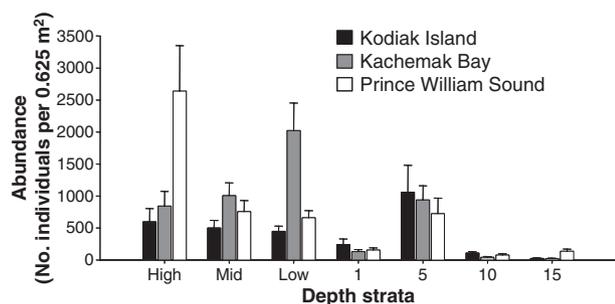
1 m at Kodiak Island, whereas high copepod abundances were observed in the low intertidal at Kachemak Bay (Fig. 5a).

Macroalgal biomass varied significantly among depths within each region ( $P \leq 0.016$ , explaining  $\sim 62\%$  of the variance) but not among sites within each region ( $P \leq 0.571$ ) or among regions ( $P \leq 0.866$ ), both of which explained approximately 0% of the variance (Table 2, Fig. 6). However, differences among depths varied significantly depending on which site within each region [site (region)  $\times$  depth interaction,  $P \leq 0.001$ , explaining  $\sim 9\%$  of the variance] or regions (region  $\times$  depth interaction,  $P \leq 0.036$ , explaining  $\sim 3.5\%$  of the variance) were examined (Table 2). In general, the greatest macroalgal biomass occurred at 1 m and decreased with both increasing depth and intertidal height (Fig. 6). This was primarily due to high abundances of large individual kelps, such as *Saccharina* spp., *Hedophyllum sessile*, and *Alaria* spp. in the shallow subtidal. Further, although macroalgal biomass exhibited similar trends to invertebrate abundance when considered across all regions, the two were not significantly correlated with one another (Pearson's  $r = 0.220$ ,  $n = 61$ ,  $P \leq 0.088$ ). However, when examined

**Table 2.** Results of separate three-way Model III ANOVAs testing variation in taxon abundance among study regions, sites within region, and depth strata for each taxonomic group (total invertebrates, mollusks, polychaetes, and echinoderms, and algae).

source	SOS	df	MS	F-statistic	P-value	$\omega^2$
total inverts						
region	16.551	2	8.276	0.981	0.405	0
site(region)	32.292	6	5.382	1.862	0.115	1.3
depth	340.328	6	56.721	19.627	<b>0.001</b>	51.0
region $\times$ depth	92.747	11	8.432	4.613	<b>0.001</b>	18.7
site(region) $\times$ depth	101.135	35	2.890	1.581	<b>0.025</b>	3.0
error	440.512	241	1.828			26.0
mollusks						
region	81.138	2	40.569	6.071	<b>0.015</b>	12.7
site(region)	30.132	6	5.022	1.130	0.366	0.1
depth	348.815	6	58.136	13.076	<b>0.001</b>	47.0
region $\times$ depth	80.187	12	6.682	4.841	<b>0.001</b>	13.9
site(region) $\times$ depth	151.153	34	4.446	3.221	<b>0.001</b>	8.1
error	334.009	242	1.380			18.2
polychaetes						
region	10.429	2	5.214	1.866	0.205	1.7
site(region)	21.731	6	3.622	0.664	0.679	0
depth	131.498	6	21.916	4.064	<b>0.005</b>	28.1
region $\times$ depth	27.955	10	2.795	1.421	0.173	4.2
site(region) $\times$ depth	163.722	30	5.457	2.774	<b>0.001</b>	16.3
error	419.076	213	1.967			49.7
echinoderms						
region	4.703	2	2.351	0.631	0.549	0
site(region)	30.772	6	5.129	1.537	0.195	27.9
depth	27.409	5	5.482	1.643	0.175	29.8
region $\times$ depth	44.738	12	3.728	4.157	<b>0.001</b>	19.2
site(region) $\times$ depth	116.782	35	3.337	3.721	<b>0.001</b>	18.2
error	218.822	244	0.897			4.9
algae						
region	0.824	2	0.412	0.146	0.866	0
site(region)	20.469	6	3.411	0.808	0.571	0
depth	77.854	6	12.976	3.073	<b>0.016</b>	61.6
region $\times$ depth	30.977	11	2.816	1.932	<b>0.036</b>	3.5
site(region) $\times$ depth	147.789	35	4.223	2.897	<b>0.001</b>	9.3
error	355.588	244	1.457			25.6

Bold types denote significant differences in the abundance and/or biomass among levels of that treatment.  $\omega^2$  denotes model fit expressed as the amount (%) of variability explained by each factor in the ANOVA model according to Graham & Edwards (2001).

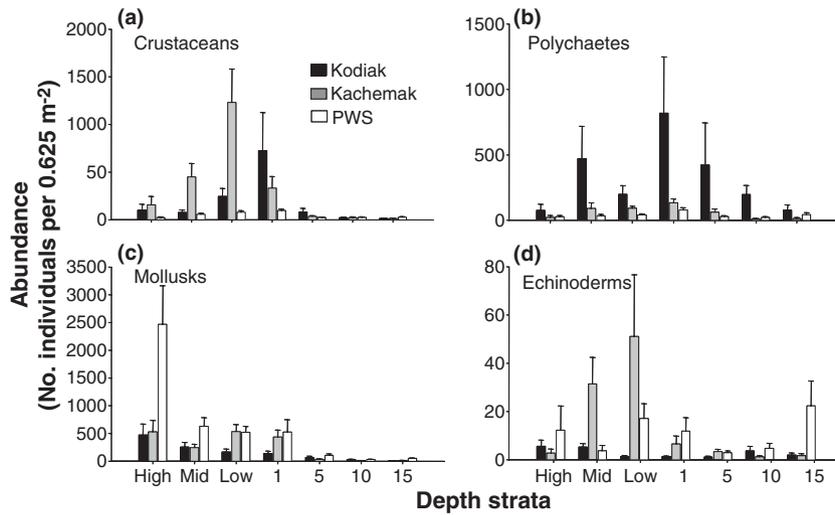


**Fig. 4.** Mean ( $\pm$  s.d.) invertebrate abundance (all individuals) for the seven depth strata at each study region.

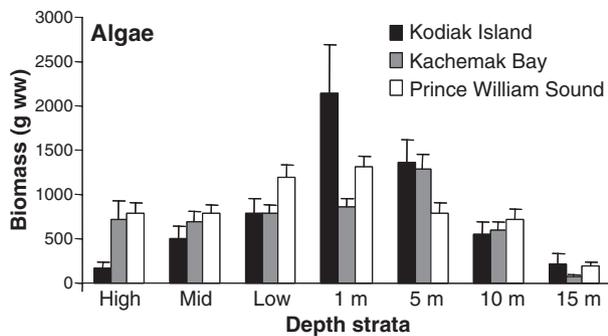
within each region separately, algal biomass was correlated with invertebrate abundance at Kodiak Island ( $r = 0.605$ ,  $n = 20$ ,  $P \leq 0.005$ ), but not at either

Kachemak Bay ( $r = -0.060$ ,  $n = 20$ ,  $P \leq 0.810$ ) or Prince William Sound ( $r = 0.156$ ,  $n = 21$ ,  $P \leq 0.480$ ).

When invertebrates and macroalgae were combined, and sites within each region pooled, benthic community composition varied significantly among the three geographic regions (ANOSIM:  $P \leq 0.008$ ) and among depths ( $P \leq 0.001$ ). Further, when depths within each site were pooled, community composition varied significantly among the three sites within each region ( $P \leq 0.021$ ) but not among regions ( $P \leq 0.154$ ). Community composition assessed using nMDS plots was similar within each depth when considered at the regional scale (Fig. 7a), but not at the smaller site scale (Fig. 7b). This suggests that overall zonation patterns in community composition are evident at the regional scale, but variation among sites obscures



**Fig. 5.** Mean abundance (+1 SE) for (a) crustaceans, (b) mollusks, (c) polychaetes, and (d) echinoderms for each of the seven depth strata at each study region.



**Fig. 6.** Mean algal biomass (mean + 1 SE) for the seven depth strata at each study region.

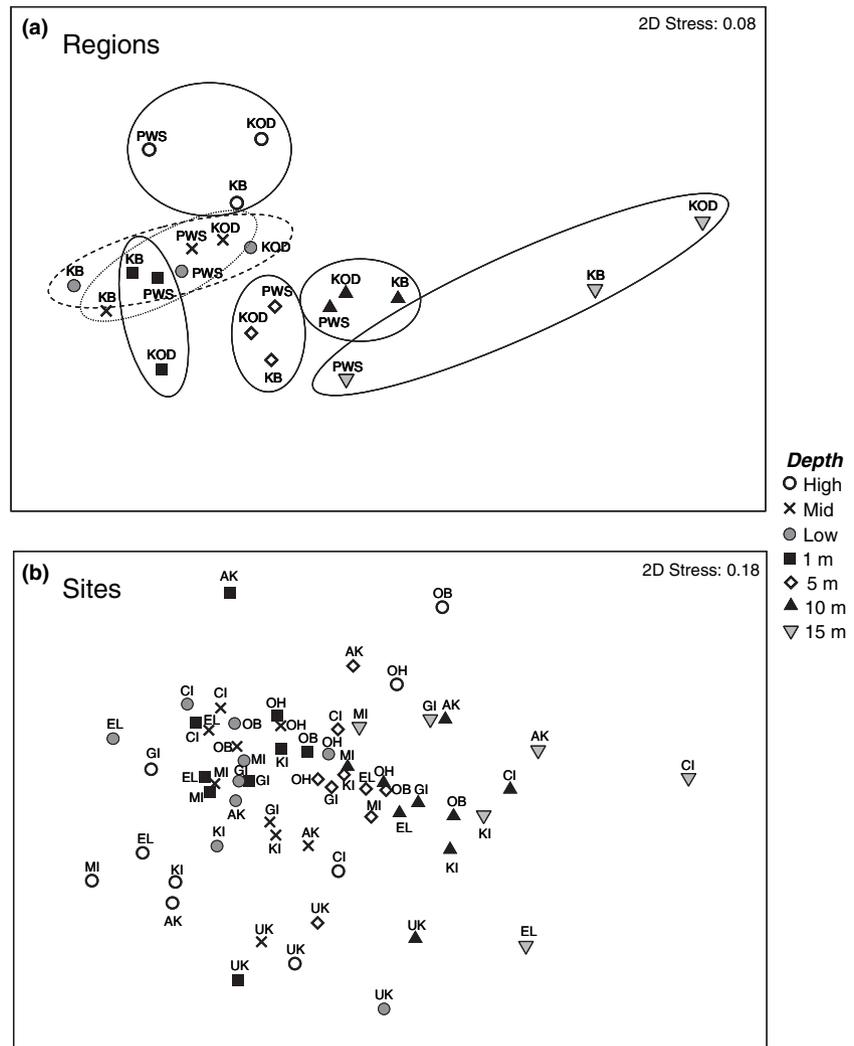
the regional uniformity of zonation patterns across the Gulf of Alaska.

**Discussion**

Vertical zonation patterns in species distribution are believed to be a global phenomenon that is particularly obvious in marine rocky shore communities (Stephenson & Stephensen 1949; Connell 1972). Components that describe these zonation patterns include mainly species richness (total number of species) and their abundance (density and biomass). Our results suggest that, across all taxa, a general zonation pattern was evident for all regions. Maximum organism abundance and richness occurred in the low intertidal/shallow subtidal and decreased with increasing tidal height and subtidal depth. Although this general zonation pattern (e.g. Stephenson & Stephensen 1949; Lewis 1964) was observed among various regions across the Gulf of Alaska, variability among taxa and among sites within regions obscured this overall zonation pattern when examined on smaller scales or for

specific taxa. Although our study regions were fairly close together (~ 300 km between adjacent regions) and belong to the same body of water (Gulf of Alaska), different taxonomic groups were responsible for establishing some of the invertebrate and algal zonation patterns in each region. For example, polychaetes were dominant at Kodiak Island, crustaceans and echinoderms dominated at Kachemak Bay, and mollusks were dominant at Prince William Sound. Within these groups, single species often dominated within a region to drive overall patterns of vertical trends within that region. Interestingly, similar results were found when comparing intertidal sites in Iceland, southern Alaska, and the Magellan region (Ingólfsson 2005, 2006). On that large spatial scale, taxonomic composition varied greatly across regions with no recurrent distinct zonation patterns.

Macroalgal biomass patterns have been reported to increase from the high intertidal, seawards (Ingólfsson 2005), and to decrease with increasing subtidal depth (Aleem 1973). Similarly, we found that macroalgal biomass was generally more abundant at 1 m subtidal depth and decreased with increasing intertidal height and subtidal depth, although these patterns varied significantly among our study sites. Despite this emerging pattern, generalizations need to be regarded with care because the large subtidal biomass at a few of these sites was due primarily to a few large kelps, namely *Agarum clathratum*, *Laminaria* spp, and *Saccharina* spp. While we emphasize that the large tidal range in the Gulf of Alaska renders the 1 m depth effectively and ecologically an intertidal environment, a large proportion (26%) of total algal biomass at this depth was contributed by kelps, such as *Alaria* spp., *Hedophyllum sessile* and *Saccharina* spp. Invertebrate abundance patterns indicated that mollusks were most abundant in the higher intertidal, and crustaceans and



**Fig. 7.** Results of nMDS examining relative differences in community composition (invertebrates and macroalgae combined) among depths at the scale of (a) region (all sites within each region pooled; regions are: KOD, Kodiak; KB, Kachemak Bay; PWS, Prince William Sound) and (b) sites within region (all quadrats within each site pooled; sites are: OH, Old Harbor; AK, Alitak Bay; UK, Uyak Bay; EL, Elephant Island; CI, Cohen Island; OB, Outside Beach; MI, Montague Island; KI, Knight Island; GI, Green Island). Circles in (a) indicate sites located at the same depths. Various dashed circles are used for clarity where overlap between depths occurred.

polychaetes at intermediate depths. Echinoderms, in contrast, had two abundance peaks, one in the low and mid intertidal and one at 15 m depth. Such taxon-specific distribution patterns may be associated with their ability to adjust to the interplay of physical and biotic interactions (Connell 1961), or because some echinoderm groups are intertidally abundant whereas others are subtidally abundant.

This study demonstrated that vertical zonation patterns in the rocky intertidal and the relative contributions of individual taxa to those patterns can be highly variable among geographic regions. Because intertidal depth strata were easily identified from dominant biobands, we were surprised by the absence of a consistent zonation pattern across the Gulf of Alaska. We believe that this is related to the high variation in the abundance of subordinate taxa among sites and depths, although the dominant taxa used to assign biobands were evident at all sites. Overall,

this study suggests that taxon-specific zonation patterns observed within a particular site may not be generalizable across larger geographic regions or to the taxa. This taxon-specific variation is likely to be driven in the main by abiotic and biotic factors. The environmental drivers are presumably numerous and may vary among different spatial scales (Levin 1992, 2000), and likely include physical factors such as regional and local circulation patterns, sedimentation, wave exposure, and light. Biological interactions usually include competition and predation. All these drivers have been shown to be important in establishing patterns of organism distribution and abundance (Benedetti-Cecchi 2001; Dayton & Tegner 1984; Edwards 2004; Karlson & Cornell 1998; Menge & Olson 1990).

In summary, our findings suggest that the observed variation in vertical zonation patterns and the inability to generalize across large geographic regions or for multiple taxa, should be considered when single locations and or

single taxa are used as regional representatives in comparisons of taxon richness among latitudes or other large geographical scales. The question of how many sites are needed to adequately describe a region will thus vary from region to region. These issues have to be important considerations when conservation and management plans are developed based on single-taxon or single-site information.

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