

# Macrobenthos of the nearshore Aleutian Archipelago, with emphasis on invertebrates associated with *Clathromorphum nereostratum* (Rhodophyta, Corallinaceae)

Heloise Chenelot · Stephen C. Jewett · Max K. Hoberg

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**Abstract** In the Aleutian Islands, Alaska, crustose coralline algae can be widespread in the low intertidal and shallow subtidal regions, and cover most available hard substrates. The longevity and slow growth-rate of coralline algae make them vulnerable to major disturbances, including anthropogenic disturbances and ocean acidification. Subtidal habitats dominated by crustose coralline algae are often associated with sea urchin-barren grounds and regarded as supporting limited invertebrate communities, especially compared with the adjacent kelp forests. *Clathromorphum nereostratum* is one of the most abundant crustose coralline algae found in the Aleutian Islands. Although the surface of this crustose alga exhibits little structural complexity, it can develop into crusts half-a-meter thick (2–10 cm in this study) that provide microhabitats for a variety of cryptic invertebrates. Despite the omnipresence of this alga throughout the nearshore Aleutians, very little is known about its associated faunal community. In the summers of 2006 and 2007, a benthic survey was conducted at 50 sites throughout the shallow (<20 m), nearshore Aleutian Islands as part of the Alaska Monitoring and Assessment Program.

The habitat encountered at each site was categorized as soft sediment, macroalgae-dominated, or crustose coralline-dominated. At each site, scuba divers sampled three 0.06-m<sup>2</sup> quadrats. Invertebrate communities associated with thick crustose coralline algae were compared with soft-sediment and macroalgae-dominated communities based on faunal abundance and diversity. Despite the depauperate appearance of crustose habitats, this study revealed that crustose environments support faunal communities as diverse and abundant as those found in rich macroalgal habitats.

**Keywords** Crustose coralline algae · Kelp holdfast · Soft sediment · Urchin barren · Ocean acidification · Biodiversity

## Introduction

The nearshore environment of the Aleutian Islands, Alaska, provides very diverse habitats ranging from soft sediments to bedrock and from sea urchin barrens to dense kelp forests. In many marine systems, highly heterogeneous habitats have been shown to support highly diverse floral and faunal communities (McCoy and Bell 1991; Coleman and Williams 2002; Steller et al. 2003). Tropical coral reefs are recognized as the most productive and diverse marine ecosystem and support the highest number of species per unit area (Knowlton 2001; Groombridge and Jenkins 2002; Roberts et al. 2002). In temperate and sub-boreal regions, kelp forests (North 1971; Foster and Shiel 1985; Graham 2004), and rhodolith beds (Foster 2001; Steller et al. 2003; Kamenos et al. 2004a, b; Nelson 2009) also sustain high invertebrate biodiversity. Those rich and diverse ecosystems all provide highly complex and heterogeneous physical environments. Kelp forests provide three-dimensional (3D) complexity by extending the benthic

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H. Chenelot (✉) · S. C. Jewett · M. K. Hoberg  
Institute of Marine Science, University of Alaska Fairbanks,  
Fairbanks, AK 99775-7220, USA  
e-mail: heloise@ims.uaf.edu

S. C. Jewett  
e-mail: jewett@ims.uaf.edu

M. K. Hoberg  
e-mail: mkhoberg@alaska.edu

habitat upward in the water column and offer high substrate heterogeneity to very diverse fish and invertebrate communities (Feder et al. 1974; Hicks 1980; Ebeling and Laur 1985; Bodkin 1988). The holdfasts of brown algae, in particular, harbor a great variety of organisms (Ghelardi 1971; Smith et al. 1996; Anderson et al. 2005).

Urchins are often found inhabiting kelp forests, but when urchin densities grow unchecked, urchin grazing pressure can remove most sessile organisms, including the prominent kelp, and transform lush kelp forests into urchin barrens. Urchin barrens are often considered the alternate state of kelp forests and, by removing the structural complexity offered by macrophytes, are believed to generate low biodiversity (Paine and Vadas 1969; Lawrence 1975; Steneck 1986; Estes et al. 2010). Urchin barrens are also frequently associated with red crustose coralline communities, and urchin grazing may in fact help maintain the presence and dominance of crustose communities (Paine and Vadas 1969; Steneck 1986). In contrast to macrophytes and rhodoliths, crustose algae are very low-relief features that provide very little structural complexity and heterogeneity (Smith 1944; Lebednik 1976; Steneck and Dethier 1994). At first glance, crustose coralline habitats resemble barren grounds and encrusting coralline algae are often referred to as primary substrate because of their bare-rock appearance (Menge 1976; Rowley 1989).

During the summers of 2006 and 2007, the Alaska Monitoring Assessment Program (AKMAP) conducted coastal surveys of the Eastern and Western Aleutians Islands, respectively (Jewett et al. 2008). Preliminary results for data collected in 2006 were presented in Chenelot et al. (2008). Several types of habitats were encountered during the assessment, but kelp forests were a prominent sight along the Aleutian Archipelago. Soft sediments, urchin barrens and crustose coralline habitats were also commonly present. In the Aleutians, the two most common red crustose coralline species are *Lithothamnion* spp. and *Clathromorphum nereostratum*. *Lithothamnion* spp. form a thin layer of crust that conforms to the substrate (Smith 1944; O'Clair and Lindstrom 2000). In contrast, *C. nereostratum* forms extensive pavement-like deposits that can be greater than 0.5 m in thickness and over 1 m in diameter (Lebednik 1976). Upon further observations during the sampling efforts, we recognized that the thick crustose coralline, despite its bare and barren appearance, harbored a great number of invertebrates. Despite the ubiquitous presence of *C. nereostratum* throughout the Aleutian Archipelago, very little is known about the faunal communities associated with this thick crustose coralline.

The objective of this investigation was to assess and compare the invertebrate communities (in terms of community assemblages, invertebrate abundance and species

diversity) associated with the thick crustose coralline *Clathromorphum nereostratum*, with communities commonly found in other coastal Aleutian habitats (soft sediments and kelp holdfasts).

## Methods

### Study area

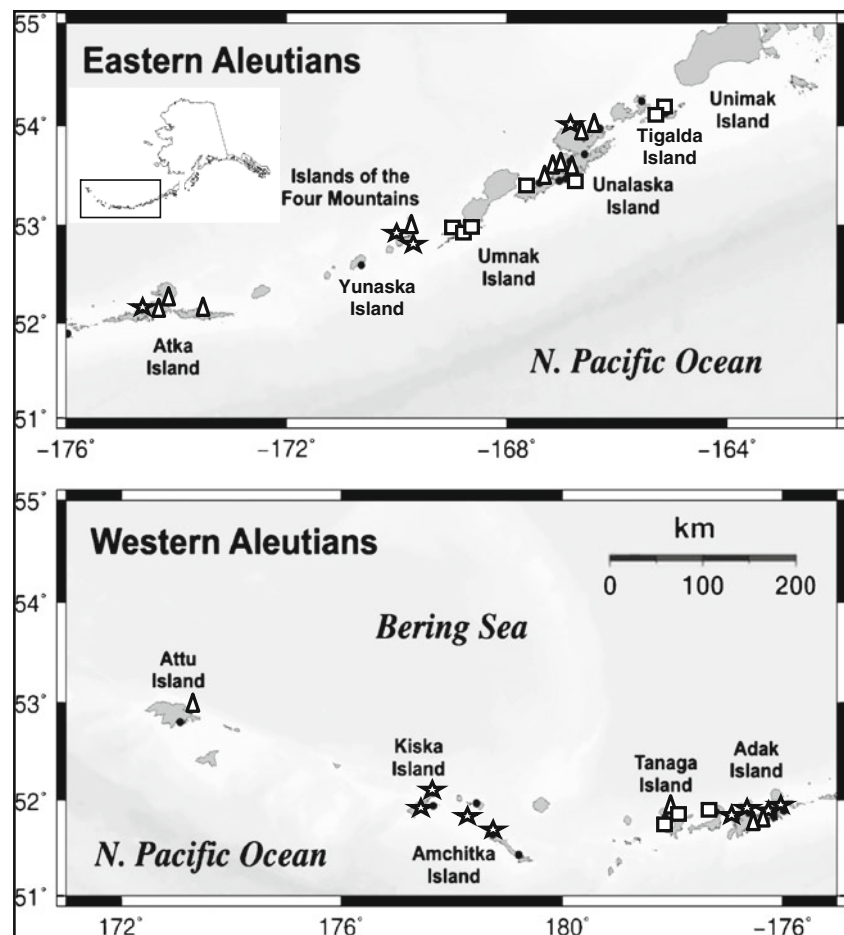
AKMAP conducted coastal surveys of the Eastern and Western Aleutians Islands, spanning a distance of approximately 1,900 km, during the summers of 2006 and 2007, respectively. In 2006, 23 sites were randomly selected between Tigalda Island, near the Alaska Peninsula, and Yunaska Island, west of the Islands of Four Mountains (Fig. 1). In 2007, 27 sites were sampled between Attu and Umnak Islands. Sites were located both on the Pacific Ocean and Bering Sea sides of the islands and were positioned on soft substrates (mud and sand) and hard substrates, including kelp forests, urchin barrens, and crustose coralline habitats.

Kelp forests in the study area were dominated by two canopy-forming species *Nereocystis luetkeana* and *Eualaria fistulosa*. Understory kelp often formed very dense mats and the dominant species included *Saccharina* spp., *Agarum* spp. and *Thalassiphyllum clathrum*. Urchin barrens were also frequent in the study area. Crustose coralline habitats were commonly found concurrent with urchin barrens. In the shallow subtidal region of the Aleutians, extensive coralline crusts were often ubiquitous and covered nearly all available substrate (bedrock, large boulders, and small rocks). Two types of red crustose coralline were encountered, the thin crustose coralline, mostly *Lithothamnion* spp., and the thick crustose coralline, *Clathromorphum nereostratum*. Sandy areas were also frequently found throughout the survey area.

### Community sampling

The randomly preselected sites were located by GPS and nautical charts, and surveyed for safety and acceptable depth range (<20 m). At each site, divers deployed a 30-m transect tape along a depth contour and placed three replicate 25×25-cm (0.06 m<sup>2</sup>) quadrats at random distances along the transect. If the quadrats were on soft substrates, the sediments were dredged to a depth of 10 cm. On rocky substrates, all invertebrates and all algae (foliose and crustose) were scrapped clear within the 25×25-cm frames. When thick crustose coralline was present, the entire thallus had to be pried off the substrate in order to access the invertebrates that were hiding underneath as well as within the crust (Fig. 2a–c). The destructive samples were collected in fine-mesh (500 μm) bags. Once on board the

**Fig. 1** Map of the 50 study sites in the Eastern (*top*) and Western (*bottom*) Aleutian Islands, Alaska. The sites that contained 0.06-m<sup>2</sup> quadrats categorized as soft sediment (*Soft*), kelp holdfast (*Holdfast*), or thick crustose coralline (*TCC*) habitat are marked with *white triangles*, *squares*, or *stars*, respectively. The *black dots* represent surveyed sites that were categorized as Mixed habitat and were not included in the analysis



ship, the samples were sieved through a 1-mm mesh screen, and preserved in 10% buffered formalin. In the laboratory, the samples were rinsed and transferred to 50% isopropanol for later processing.

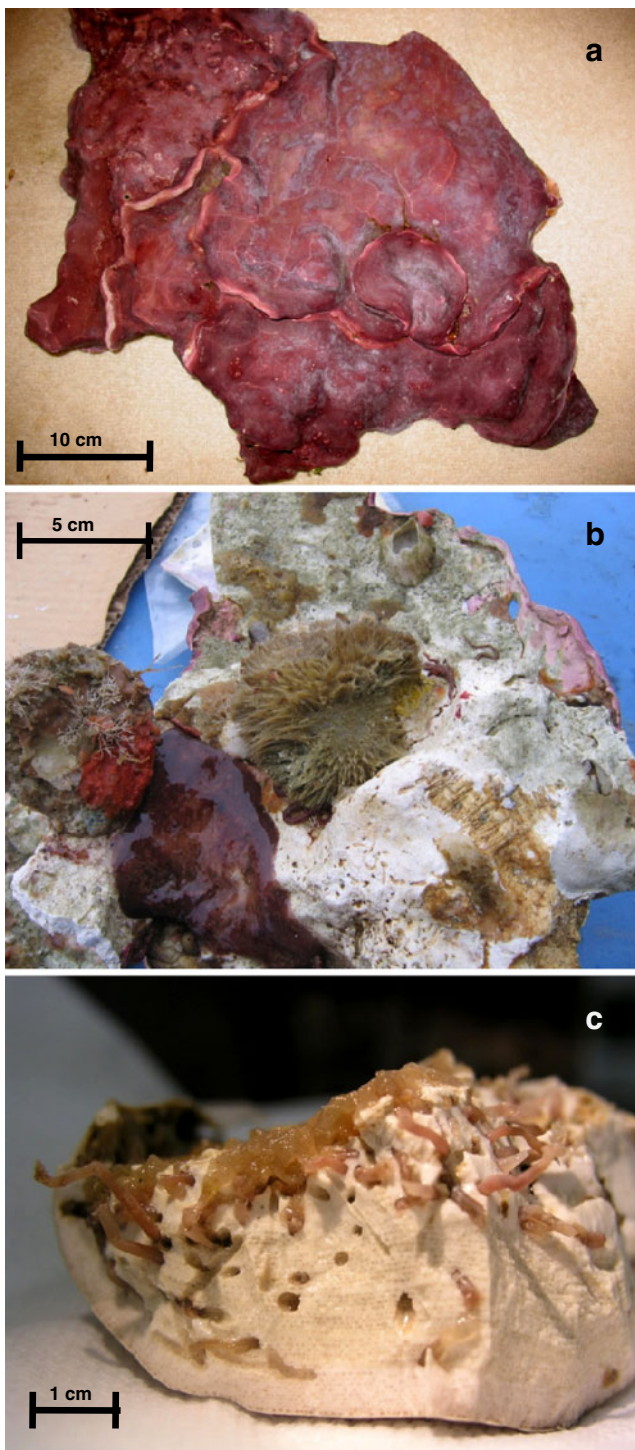
Invertebrates associated with the thick crustose coralline *Clathromorphum nereostratum* represented a challenge as most were nested deep inside the matrix of the thick crust. Under a dissecting microscope, the conspicuous invertebrates were removed first from the crust surface. The remaining invertebrates were extracted by fracturing the large calcareous chunks with a hammer. Smaller coralline pieces were then broken into small gravel-size pieces using wire cutters. Counts were recorded for solitary invertebrates. Colonial organisms were given a count of one so they could be included in the diversity and community analyses. All sorted invertebrates were identified to the lowest practical taxonomic level. For the present analysis, challenging groups (mostly Porifera, Hydrozoa, Bryozoa, and Ascidiacea) were only identified at the phylum or class level. Also, *Strongylocentrotus droebachiensis* and *S. polyacanthus* were the two dominant sea urchin species. Because of the difficulty in identifying individuals to the species level, and until

further taxonomic and genetic information become available, sea urchins were conservatively identified to the generic level.

#### Data analysis and quadrat selection

A total of 50 sites and 148 25×25-cm quadrats were sampled throughout the study area (two samples were accidentally lost). Because several types of substrate were encountered within a single site, individual quadrats along a single transect were categorized into one of four habitat types: Soft (soft sediment), Holdfast (kelp holdfast), TCC (thick crustose coralline), or Mixed. In order to standardize as much as possible our quadrat categories, any quadrats that did not match specific characteristics chosen for Soft, Holdfast, and TCC habitats were labeled as Mixed. The Mixed category encompassed very diverse and inconsistent types of substrate (coarse sediments, encrusting sponges, *Lithothamnion* sp., bedrock covered with debris, etc.); therefore Mixed quadrats were not included in our community analyses.

Quadrats categorized as Soft were mostly sand, but the grain size ranged from fine to coarse. Quadrats that contained small gravel and pebbles were not included in



**Fig. 2a–c** *Clathromorphum nereostratum* thalli and their associated fauna. The top surface of *C. nereostratum* shows low structural complexity, except for the low-relief sutures created by the growth of adjacent individual thalli (a). The underside surface reveals a greater relief and harbors relatively large organisms such as sponges (e.g., *Craniella villosa*), barnacles, hydroids, bryozoans, and ascidians (b). A closer look at the crustose matrix (upside-down in the photo) reveals a dense colony of burrowing invertebrates (mostly *Dipolydora* spp. polychaetes) (c)

our Soft category and were labeled as Mixed. Accordingly, quadrats that were located within kelp beds, but did not include holdfasts, were not included as Holdfast quadrats. To be categorized as TCC, *Clathromorphum nereostratum* had to cover the majority (>50%) of the quadrat surface area.

#### Statistical analysis

The biodiversity indices taxon richness ( $S$ ), abundance of individual organisms ( $N$ ), and the Shannon-Wiener Diversity Index (Shannon Index) ( $H'$ , log base  $e$ ) were calculated using Primer statistical software (PRIMER 6.0, Primer-E, Ivybridge, UK, 2001). All diversity and abundance values were  $\log(x+1)$  transformed prior to testing to satisfy assumptions of normality and equal variances. The statistical differences in those factors between habitat types were evaluated with one-way ANOVAs followed by Tukey's pairwise comparisons (PAST version 1.96 2009).

Non-metric multidimensional scaling (MDS) analyses were used to plot community similarity patterns based on abundance of invertebrate taxa from  $25 \times 25$ -cm quadrats within Soft, TCC, and Holdfast habitats (PRIMER 6.0, Primer-E, 2001). The data were  $\log(x+1)$  transformed and the Bray-Curtis coefficient was used as a resemblance parameter. The multivariate patterns, in terms of habitat type resemblances, were depicted in ordination plots. Because samples from hard-substrate habitats (Holdfast and TCC) clumped more closely together than with Soft samples, a subset MDS plot was produced to more clearly visualize how taxa composition of benthic fauna differed between Holdfast and TCC habitats.

The patterns depicted on MDS plots were derived from combined abundance data from individual taxa within each sample. The presence or absence, as well as the relative abundance, of certain influential species are responsible for the gradients observed (i.e., how closely or spread out samples are plotted). The Similarity Percentage routine (SIMPER; PRIMER 6.0, Primer-E, 2001) was performed in order to detect and list which taxa were most significantly contributing to the separation between the different habitat types.

One-way analysis of similarity (ANOSIM, randomization/permutation procedure; PRIMER 6.0, Primer-E, 2001) was carried out to assess the degree of difference in benthic invertebrate assemblages between habitats. The Null hypothesis that there were no significant differences amongst groups was rejected if the significance level ( $p$ ) was  $<0.05$ . The  $R$ -statistic value was used to evaluate the extent of any significant difference.  $R$  values close to 1.0 suggested that invertebrate communities of samples within a specific habitat were more similar to each other than to samples from another habitat.

## Results

### General

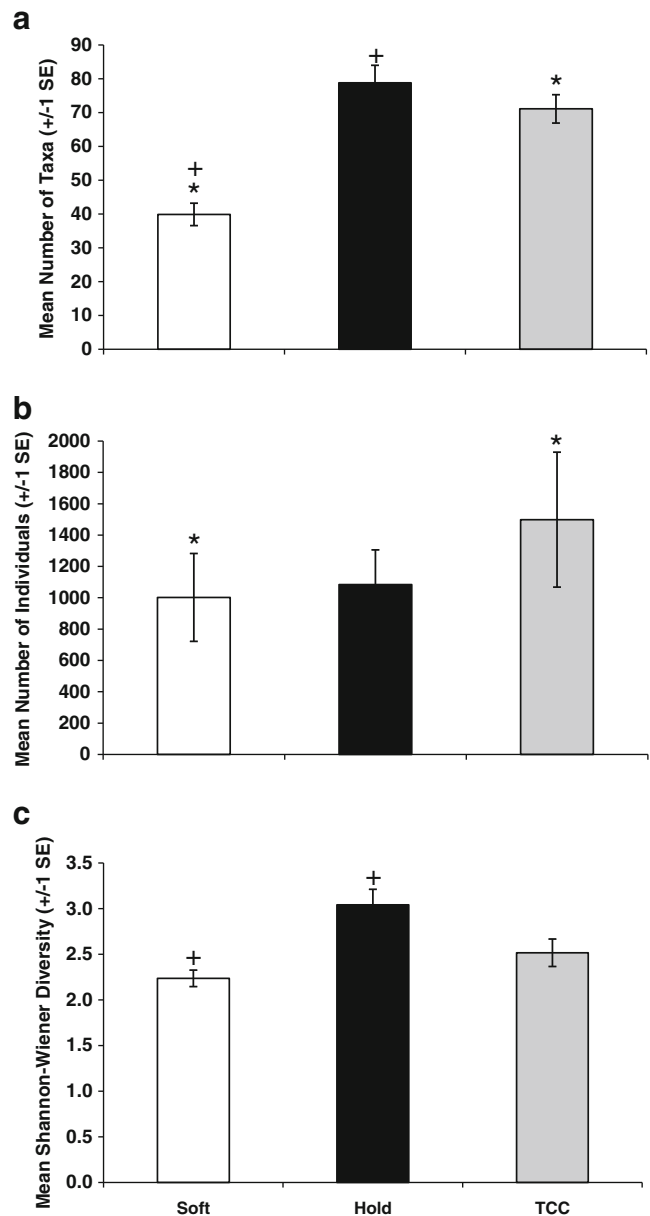
The survey of 50 sites, for a total of 148 0.06-m<sup>2</sup> quadrats, along the Aleutian Islands led to the collection of a total of 119,795 individual invertebrates belonging to a total of 707 different taxa. Not all organisms were identified to the species levels, but the taxonomic level of identification remained consistent throughout the samples. A total of 489 genera, 266 families, 92 orders, 38 classes, and 16 phyla were recorded. The most abundant phyla were Annelida (72,865 individuals), Arthropoda (31,673 individuals), and Mollusca (7,141 individuals). Approximately 4,620 h were required to process all invertebrate samples.

Of the 148 samples collected, 75 were classified as Mixed, 38 as Soft, 16 as Holdfast, and 19 as TCC samples. The following results pertain only to the 73 samples categorized as Soft, Holdfast, or TCC habitats. Depths at each of our habitat types varied from 8 to 19 m for Soft habitat, 6–15 m for Holdfast habitat, and 7–17 m for TCC habitat. There was no significant difference in mean depth between habitat types ( $p=0.499$ ). All habitat types were distributed throughout the entire study area (Fig. 1).

The number of taxa ( $S$ ) collected varied greatly between samples, ranging from 14 to 113 for Soft, 48–111 for Holdfast, and 54–133 for TCC quadrats (Fig. 3a). The mean taxa richness was significantly lower in the Soft habitat ( $40\pm 3.3$  taxa per quadrat; mean  $\pm$  SE) versus Holdfast ( $79\pm 5.2$ ) and TCC habitats ( $71\pm 4.2$ ) ( $p<0.001$ ). A total of 348 taxa were encountered within the 38 Soft quadrats. Three hundred and thirty-six taxa were collected from 16 Holdfast samples, whereas 362 taxa were accumulated from 19 TCC quadrats. When the cumulative number of individual taxa was divided by the number of quadrats per habitat, and when simplifying the relation between taxa accumulation and sample size to a linear relationship, TCC habitat averaged 19 new taxa, whereas Soft samples produced only nine new taxa per additional quadrat. Holdfast samples provided 21 taxa per additional quadrat.

The number of individuals ( $N$ ) counted within each sample varied greatly, ranging from 45 to 7,680 for Soft, 176–3,396 for Holdfast, and 244–8,346 for TCC quadrats (Fig. 3b). The mean number of individuals was significantly different between Soft and TCC habitats ( $p=0.012$ ). TCC habitat averaged the highest number of invertebrates per quadrat ( $1,499\pm 430.6$ ) compared with Soft ( $1,002\pm 280.4$ ) and Holdfast ( $1,085\pm 220.7$ ) habitats.

The Shannon Diversity Index ( $H'$ ) takes into account both the number of taxa as well as the number of individuals within each taxon. Invertebrate diversity varied between 1.16 to 3.10 for Soft, 1.10 to 3.74 for Holdfast,



**Fig. 3** Biodiversity indices for invertebrate taxa richness,  $S$  (a), abundance,  $N$  (b), and Shannon diversity,  $H'$  (c) based on all invertebrates collected within individual 0.06-m<sup>2</sup> quadrats in *Soft*, *Holdfast*, and *TCC* habitats. The number of quadrats sampled was 38, 16, and 19 from *Soft*, *Holdfast*, and *TCC* habitats, respectively. Mean taxa richness ( $S$ ) was significantly lower in *Soft* than in *Holdfast* and *TCC* habitats ( $p<0.001$ ). There was a significant difference in the mean number of individuals ( $N$ ) collected between *Soft* and *TCC* habitats ( $p=0.012$ ). There was a significant difference in the mean invertebrate diversity ( $H'$ ) between *Soft* and *Holdfast* habitats ( $p=0.001$ )

and 1.15 to 3.35 for TCC quadrats (Fig. 3c). Biodiversity was significantly lower within Soft habitat ( $2.24\pm 0.09$ ) than Holdfast habitat ( $3.04\pm 0.17$ ) ( $p=0.001$ ). TCC samples had an  $H'$  value of 2.52 ( $\pm 0.15$ ) that was not significantly different from Soft and Holdfast values.

A list of the ten most abundant families within each substrate type shows that polychaetes and amphipods were abundant in all habitat types, but certain families were often specific to each habitat (Table 1). Spionid polychaetes were the most dominant families in all three habitats, but the species *Dipolydora* spp. was characteristic of hard substrate (Holdfast and TCC) habitats, whereas *Pygospio elegans* was the most abundant spionid in Soft substrate. Syllid polychaetes were also abundant in all three habitats, with *Exogone* spp. being the dominant syllid on Soft as well as hard substrates. *Typosyllis* spp., however, were predominantly found associated with hard substrate. In contrast, other polychaete families (Oweniidae, Cirratulidae, Orbiniidae) were only abundant in Soft sediments, while terebellid polychaetes were abundant in both hard substrate habitats. Amphipods were an important group in all habitat types, but gammarids were characteristic of Soft sediments, as caprellids and ischyrocerids were abundant in Holdfast and TCC habitats. Bivalves were abundant in both Soft sediments and Holdfasts, with thyasirids being found only in Soft sediments, and mytilids being abundant mostly in Holdfasts. Similarly, ostracods (Philomedidae) were exclusively found in Soft sediments, whereas stronglylocentrodid urchins were only abundant in TCC habitat. Acrocirrid polychaetes were almost exclusively associated with TCC; few were collected from Holdfasts and none were found in Soft sediments. A complete list of species and their abundance within each habitat type is tabulated in Supplementary Table 1 and is available in electronic format only.

### Community analysis

Overall invertebrate community structure, as displayed with MDS plots, suggested discernible differences between soft-sediment and hard-substrate communities (Fig. 4a). Samples collected from soft-sediment quadrats were quite spread out on the plots, suggesting great variability in invertebrate community composition within that habitat, especially compared with the samples collected from Holdfast and

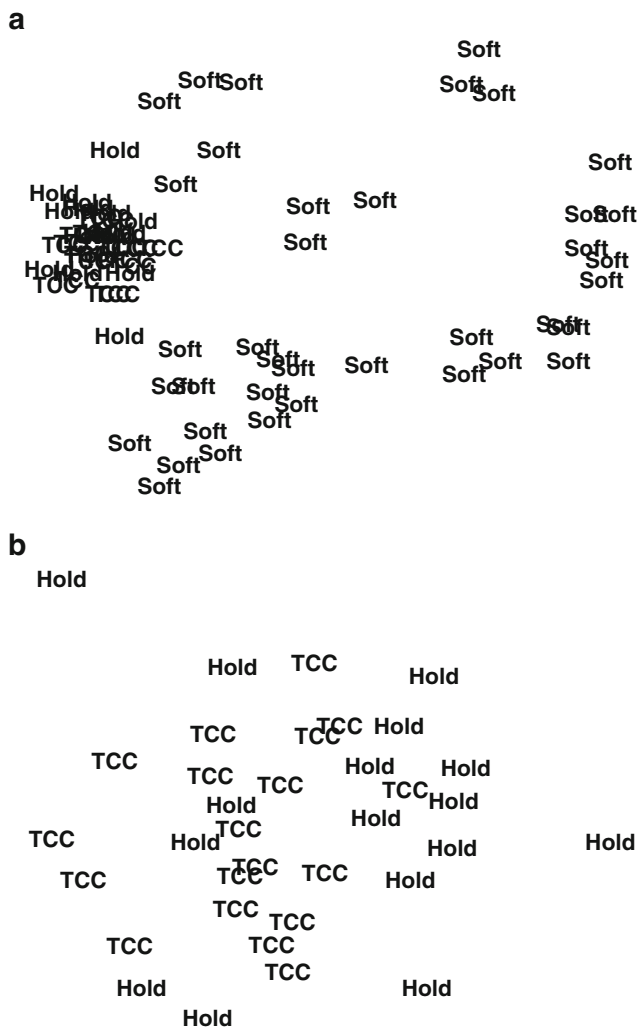
TCC quadrats. ANOSIM results validated the graphical observations that community compositions were significantly different between habitat types and that samples collected from similar habitats were more similar to each other than to samples from other habitat types ( $p=0.001$ ; global  $R$  value=0.204). Although hard-substrate samples (Holdfast and TCC) tended to clump together and segregate from soft-sediment samples, when the MDS plot focused on hard-substrate samples only, invertebrate communities also suggested some moderate partitioning between Holdfast and TCC quadrats (Fig. 4b;  $p=0.001$ , global  $R$  value=0.235).

Of the many taxa collected during the survey, some contributed most to the divergence observed in community composition among the different habitats. Examples of influential species that are highly typical of a particular substrate type or habitat are presented below. Good discriminating taxa are not necessarily abundant, but they tend to be consistently present (or in higher numbers) within samples characteristic of one habitat and absent (or in lower numbers) from samples from other habitats. Cumaceans (predominantly *Diastylis* spp. and *Lamprops* spp.), bivalves from the order Veneroidea (mostly *Axinopsida serricata*, *Cyclocardia* spp., *Macoma* spp.), and the amphipod *Grandifoxus vulpinus* were found in most soft-sediment samples but were typically absent from the hard-substrate samples (Holdfast and TCC). In contrast, chitons (mostly *Boreochiton beringensis*, *Juvenichiton saccharinus*, and *Micichiton* spp.), caprellid amphipods, and sabellid polychaetes were predominantly found within hard substrates. Although many taxa were jointly found in both Holdfast and TCC samples, some species were highly typical of either TCC or Holdfast habitats. Examples of taxa that are characteristic of Holdfast habitats were sea cucumbers of the order Dendrochirotida (primarily *Cucumaria* spp. and *Pentamera* spp.). Similarly, mytilid bivalves (chiefly *Vilasinia vernicosus*, which was never found in association with TCC) and the bryozoan *Microporina borealis* were principally collected from Holdfast quadrats.

The acrocirrid polychaetes *Acrocirrus* spp. were present in all but two TCC samples, but only in one-third of the Holdfast

**Table 1** List of the ten most abundant invertebrates (at the family or higher level) within each habitat type (Soft, Holdfast, and TCC). The taxa are listed in decreasing order of abundance

Soft	Holdfast	TCC
Spionidae (Polychaeta)	Spionidae (Polychaeta)	Spionidae (Polychaeta)
Oweniidae (Polychaeta)	Syllidae (Polychaeta)	Phoronida
Cirratulidae (Polychaeta)	Spirorbidae (Polychaeta)	Syllidae (Polychaeta)
Syllidae (Polychaeta)	Ischyroceridae (Amphipoda)	Caprellidae (Amphipoda)
Spirorbidae (Polychaeta)	Sabellidae (Polychaeta)	Sabellidae (Polychaeta)
Rissoiidae (Gastropoda)	Amphipoda, Juveniles	Amphipoda, Juveniles
Philomedidae (Ostracoda)	Caprellidae (Amphipoda)	Munnidae (Isopoda)
Gammaridae (Amphipoda)	Munnidae (Isopoda)	Acrocirridae (Polychaeta)
Thyasiridae (Bivalvia)	Mytilidae (Bivalvia)	Strongylocentrotidae (Echinoidea)
Orbiniidae (Polychaeta)	Terebellidae (Polychaeta)	Terebellidae (Polychaeta)



**Fig. 4a, b** MDS plots of benthic fauna composition based on abundance data of invertebrates within 0.06-m<sup>2</sup> quadrats. The community similarity patterns are plotted by habitat types, *Soft*, *Hold* (Holdfast), and (*TCC*). All three habitat types (**a**). Hard-substrate habitats (*Hold* and *TCC*) (**b**). The data were log(x+1) transformed and resemblance was based on Bray-Curtis similarities (2D stress=0.16 in **a** and 0.22 in **b**)

quadrats; they always were found in much greater numbers in TCC samples. Both *Dipolydora* spp. (spionid polychaetes) and *Strongylocentrotus* spp. (echinoids) were present in most Holdfast and TCC samples, but were consistently found in much greater abundance within TCC quadrats.

## Discussion

The Aleutian nearshore region supports a very diverse benthic community. A total of 35 animal phyla have been recorded from the entire world's ocean, all habitats, depths, latitudes, and longitudes combined (Groombridge and Jenkins 2002). During the investigation of the nearshore region of the Aleutian Islands, AKMAP encountered a total

of 16 benthic marine phyla or 707 taxa of invertebrates. Considering the relatively narrow bathymetry (6–20 m) explored, short coastal distance travelled (1,900 km), and relatively modest number of sites surveyed (50), the species richness of this Aleutian region is high. Those numbers are in fact comparable, if not richer, to previous AKMAP investigations. A total of 14 phyla and 441 taxa were collected in Southcentral Alaska in 2002 and 14 phyla and 531 taxa were collected by AKMAP in Southeast Alaska in 2004 (unpublished). However, those samples ( $n=50$  from each region) were only collected from soft sediments, ranging in depth from 3.5 to 503 m, using a 0.1 m<sup>2</sup> van Veen grab and most organisms were identified to the species level. We expect that if the taxonomic resolution for the Aleutian samples had been achieved to the species level for the challenging groups (e.g., sponges, ascidians, bryozoans), the number of taxa recorded from the Aleutian Islands would be even greater.

Some of the most common types of habitats encountered during the AKMAP of the Aleutian Islands were soft sediments, kelp beds, and urchin barrens and their associated crustose coralline communities. The present study revealed that the thick crustose coralline *Clathromorphum nereostratum* provides habitat to a much more diverse and abundant community of invertebrates than expected from its low-relief feature. Structural complexity is a key factor in explaining the association of high invertebrate biomass and biodiversity with certain habitats. High habitat heterogeneity provides increased microhabitats, resource partitioning and niche availability to a wide variety of organisms (McCoy and Bell 1991; Coleman and Williams 2002; Steller et al. 2003). Heterogeneous habitats provide refuge from predators (Taylor 1984; Lewis and Eby 2002) and are often nursery grounds for a wide variety of fishes and invertebrates (Ebeling and Laur 1985; Bodkin 1988; Kamenos et al. 2004a, b).

Kelp forests are often considered the temperate-boreal equivalent to tropical coral reefs. They are dominant nearshore habitats that are important to the entire ecosystem because they sustain high primary and secondary productivity and are very dynamic systems (Foster and Shiel 1985; Duggins et al. 1989; Graham 2004). Kelp forests support an extremely diverse fauna, including seabirds, marine mammals, fishes, and invertebrates (for review see North 1971; Foster and Shiel 1985). An extensive list of over 800 species of animals (ranging from protozoans to mammals) was recorded in association with the kelp beds of southern California (North 1971). Holdfasts are a structurally complex feature of kelp thalli; these networks of intertwined haptera (root-like projections) form an intricate lattice and produce numerous refuge spaces for various invertebrates. Holdfasts of many different kelp species have been documented to harbor a great variety of organisms

(Ghelardi 1971; Smith et al. 1996; Anderson et al. 2005). In their study of the fauna associated with the holdfast of *Ecklonia radiata*, Smith et al. (1996) reported 385 species belonging to 152 families and ten phyla. Those results are comparable to what Anderson et al. (2005) recorded (351 taxa, from 296 genera, 213 families, 72 orders, 26 classes, 15 phyla). The sampling protocol used by AKMAP was not specifically designed to address the biodiversity of particular habitats; however, the results from our study are comparable to others, regarding the diversity of kelp holdfast fauna. In addition, our study suggests that thick crustose coralline algae equally sustain a rich and diverse invertebrate community, i.e., 362 different taxa, from 177 families, 72 orders, 32 classes, and 14 phyla. Holdfast samples generated similar values. A more pronounced trend is observed in comparison with soft-bottom diversity, when TCC and Holdfast numbers are normalized by the number of samples for each habitat type (with 19 and 21 taxa per quadrat for TCC and Holdfast habitats, respectively, versus only nine for soft-bottom samples). In addition, TCC samples supported the highest abundance of invertebrates. Those results suggest that TCC habitats can support an unexpectedly high diverse invertebrate community. We believe that the actual biodiversity associated with TCC may have been underestimated because the AKMAP survey was not specifically designed to assess TCC diversity. For example, the TCC quadrats were not always 100% covered by *Clathromorphum nereostratum*; therefore, lessening the actual density of individuals and taxa measured per quadrat. In addition, colonial organisms such as sponges, hydroids, bryozoans, and ascidians seemed quite diverse and were predominantly observed on hard substrate, but because of their challenging taxonomy, they were not identified to lower taxonomic levels. This fact implies that the biodiversity of *C. nereostratum* may rise further as the taxonomic resolution of those groups improves.

The compositions of invertebrate communities found within each of the three habitats were significantly different and were dominated by different groups of organisms. The communities observed within Holdfast and TCC habitats were more similar to each other than to soft-sediment communities. Both crustose coralline algae and kelp require hard substrate to develop and grow and both types of habitat are often found adjacent to one another. In our study, grazers such as chitons, limpets and urchins were obviously more abundant in hard-substrate than in soft-sediment samples. Most herbivores are physically deterred by the resistance presented by the calcified coralline tissues (Steneck and Walting 1982; Steneck 1986; Steneck and Dethier 1994), and because of their low caloric values coralline algae are not very nutritious (Littler and Littler 1980). Calcified coralline algae are relatively resistant to grazing pressures, especially compared with the faster-

growing fleshy algae (Steneck and Dethier 1994). Urchins (*Strongylocentrotus* spp.) were the most conspicuous herbivores observed in the shallow hard-substrate habitats throughout the Aleutian Islands. Urchin barrens are often seen as an alternate state of lush kelp forests (Lawrence 1975; Steneck 1986; Estes et al. 2010). Many studies have demonstrated that in productive environments with intense herbivory, algal crusts dominate, but when herbivores are removed, larger canopy-forming macroalgae overgrow coralline crusts and diversity increases again (Paine and Vadas 1969; Lawrence 1975; Steneck 1982, 1986). Urchin grazing may actually help perpetuate the presence of crustose communities by removing fast-growing micro- and macroalgae that have the potential to overgrow and outcompete the slow-growing red crusts (Paine and Vadas 1969; Steneck 1982). But by grazing off most sessile organisms (in particular kelp), urchins also remove most of the structural complexity that macroalgae provide. In early studies, encrusting coralline algae were often designated as primary substrate because of their bare rock appearance (Paine and Vadas 1969; Menge 1976; Rowley 1989). Although crustose coralline communities are frequently overlooked because of their relatively low productivity, Ojeda and Dearborn (1989) observed that in the rocky subtidal zone of the Gulf of Maine, coralline communities support a high diversity of organisms and sustain relatively high secondary productivity. In their study, the authors recorded that crustose coralline covered most of the available primary substrate and that the sea urchin *Strongylocentrotus droebachiensis* was the most prominent organism. In addition, a total of 60 species of macroinvertebrates, representing nine phyla, were collected from 133 0.25-m<sup>2</sup> benthic samples. Although our sampling efforts of TCC were comparatively limited (only 19 0.06-m<sup>2</sup> samples), we enumerated 362 taxa, representing 14 phyla. The greater diversity observed in our Aleutian study, compared with Ojeda and Dearborn's, can be explained by the fact that the crustose coralline algae (*Lithothamnion glaciale*, *Lithothamnion lemoineae*, *Clathromorphum circumscriptum*, and *Phymatolithon rugulosum*) encountered in their study form only a thin crustose layer, whereas *Clathromorphum nereostratum* produces a thick crust.

Although the smooth crustose surface was often entirely dominated by sea urchins or seemed relatively denuded of conspicuous fauna, we found a surprisingly rich cryptic fauna hiding underneath the crust or within the calcareous matrix. Individual *Clathromorphum nereostratum* thalli can be wider than 50 cm in diameter, and adjacent plants can form extensive pavements that cover most of the available substrate and dominate the benthic floral community (Lebednik 1976; personal observations). In contrast to the thin crustose corallines, the thick crust of *C. nereostratum* does not conform to the substrate and forms a plethora of



crevices, cavities, and interstices, providing valuable hiding places for a vast variety of cryptic invertebrates. In addition, the calcite nature of the skeleton of *C. nereostratum* allows boring invertebrates to drill tunnels and burrows through the calcified matrix itself. The deep burrows inside the thick calcareous matrix of the TCC offer boring organisms shelter from predation and extreme environmental conditions (Sato-Okoshi 1999).

The assortment of invertebrates we found in association with *Clathromorphum nereostratum* ranges from sponges, hydrozoans, bryozoans, polychaetes, echinurans, sipunculids, mollusks, ophiuroids to ascidians. Some of the invertebrates found hidden between the primary substrate and the crust were of relatively large size, e.g., 10-cm diameter sponge *Craniella villosa*. Sabellids, nereids, sipunculids, echinurans, bivalves (*Hiatella arctica*), and ophiuroids (*Ophiopholis aculeata*) were often found underneath the thick crust. The most abundant groups of organisms found within the calcareous matrix itself were the spionid polychaetes (mostly *Dipolydora* spp.). Boring polychaetes belong to the families Eunicidae, Lumbrineridae, Dorvilleidae, Cirratulidae, Sabellidae, and Spionidae (Blake 1969; Hutchings 1986), and are predominantly suspension feeders and surface deposit feeders (Jumars and Fauchald 1977; Blake 1996; Sato-Okoshi 1999). Blake and Evans (1973) mentioned that at least five species of *Polydora* and three of *Boccardia* (both spionids) bore or nest into coralline algae (*Lithothamnion* sp., *Lithophyllum* sp., *Prolithion* sp.) and a total of 26 spionid species have been reported to only occur in calcium carbonate substrates. Sato-Okoshi (1999) examined 28 different types of calcareous substrate (i.e., coralline algae, barnacle tests, mollusk shells) and found a total of 13 boring species of spionids. Although some species of spionids are found in calcareous as well as non-calcareous substrates, most are always found within their self-excavated burrows and were only encountered in calcareous substrate (Blake and Evans 1973; Sato-Okoshi 1999). Most boring spionid species are unable to move, relocate, or form a new burrow if dislodged; therefore, the stability of the thick crustose coralline is essential to the survival of individual spionids (Sato-Okoshi 1999). The boring mechanisms are still not well understood, but Blake and Evans (1973) proposed that the spionid *Polydora* sp. uses a chemical process by secreting acid to dissolve the calcareous substrate, uses its modified setae on the 5th setiger to mechanically erode the substrate, or uses a combination of chemical and mechanical processes. Liu and Hsieh (2000) suggested that the burrow of *Polydora villosa* consists of two parts that are formed at different stages. *Polydora villosa* begins by actively boring into the coral and forming a U-shaped burrow, but as the coral grows, the spionid passively keeps elongated the tunnel. However, boring behaviors appear to be specific to each spionid species (Sato-Okoshi 1999).

Crustose coralline seems to be a key factor in supporting a rich community in the shallow subtidal of the Aleutians Islands by providing substrate, refuge, and food to a wide variety of infaunal (e.g., spionids) as well as epifaunal invertebrates (e.g., sea urchins). In return, infaunal borers may play a crucial role in maintaining the rich diversity of the entire community. Bioerosion has been reported to be extremely important in the dynamics of coral reefs. Polychaetes are some of the initial coral colonizers and are thought to make the substrate more attractive to other boring organisms. By creating burrows and tunnels, boring organisms also increase the habitat available to non-boring fauna (for review see Hutchings 1986). Bioerosion of the crustose coralline by spionids and other boring organisms tends to make the calcareous matrix more fragile (personal observations) and susceptible to physical disturbances (e.g., storms). When large pieces of coralline crust break off and detach, more of the primary substrate becomes available for recolonization. This erosion process is essential for the entire community, as many of the cryptic organisms that were hiding within or underneath the crust are now exposed and provide food to many predators. Most fauna associated with *Clathromorphum nereostratum* seem out of reach of predators. However, when large chunks of the thick crust were broken off during sampling, a plethora of food became available and attracted invertebrate predators such as urchins, sea stars and fishes (personal observations). In addition, several studies suggest that some invertebrate species are found almost exclusively in association with crustose coralline. The limpet *Tectura testudinalis* shares a symbiotic relationship with the crustose coralline *Clathromorphum circumscriptum* (Steneck 1982). Similarly, the lined chiton, *Tonicella lineata*, is found almost exclusively on crustose coralline (Barnes and Gonor 1973). Many invertebrates seem to preferentially settle and metamorphose on crustose coralline algae (chitons, Barnes and Gonor 1973; abalone, Morse et al. 1979; limpets, Steneck 1982; and urchins, Pearce and Schiebling 1988; Rowley 1989; Lambert and Harris 2000). Nelson (2009) offered a detailed review of the several important contributions non-geniculate calcified macroalgae can make as key components in their ecosystem, significant structural engineers, and important players in the global carbon cycles.

Besides playing a crucial role as a community former, *Clathromorphum nereostratum* has the potential to be used as a paleothermometer. Because red crustose coralline algae are long-lived and slow-growing, they can act as climate recorders, recording past temperatures and environmental variations in their skeleton (Foster 2001; Frantz et al. 2005; Halfar et al. 2007; Kamenos et al. 2008). Frantz et al. (2005) estimated the growth rate of a *C. nereostratum* specimen collected from Adak Island in the Aleutians to be  $0.30 \pm 0.03$  mm·year<sup>-1</sup>. Based on U/Th procedures, a live specimen of *C.*

*nerostratum* collected at Attu Island in the Aleutians was dated at  $850 \pm 28$  years cal BP (before present), making it the longest-lived marine organism known (Halfar et al. 2007). *Clathromorphum nereostratum*, in particular, can be an extremely valuable ‘climate archive’ because of its boreal distribution (Halfar et al. 2007). A recent study of the high-resolution Mg/Ca ratios in *C. nereostratum* from Amchitka Island, Western Aleutians, supports the great potential for the use of this alga, and possibly other coralline species, as a reliable paleotemperature proxy (Hetzinger et al. 2009).

The longevity and slow growth-rate of coralline algae also make them vulnerable to major disturbances, including anthropogenic disturbances (Steller et al. 2003; Nelson 2009). In addition, crustose corallines form by depositing magnesian calcite, a type of calcium carbonate ( $\text{CaCO}_3$ ) that is very sensitive to acidification. These algae are believed to be at increased risk from global ocean acidification. A study specifically investigating the effects of ocean acidification on crustose coralline algae reported a significant decrease in growth and recruitment rate under elevated  $\text{CO}_2$  conditions (Kuffner et al. 2007). A related study investigating the effects of acidified seawater on seagrass calcareous epibionts suggests that coralline algae are very sensitive to slight decrease in water pH (Martin et al. 2008). Additionally, organisms living in northern oceans may potentially be facing an even greater challenge as cold waters can hold more gas (i.e.,  $\text{CO}_2$ ) than warmer waters, making them more susceptible to increase acidification. Signs of ocean acidification have already been reported in Alaska’s coastal waters (University of Alaska Fairbanks 2009) and in the Western Arctic (Bates et al. 2009).

In conclusion, the smooth surface of crustose corallines exhibit very little structural relief and gives a deceptive notion that little life is associated with these algae. However, the majority of the invertebrates associated with the thick crustose coralline hides underneath or within the crust. Because of the important role crustose coralline plays in the nearshore ecosystem of the Aleutian Islands, should this habitat be adversely impacted, the repercussions could be dramatic for the associated invertebrate communities. Much more research is needed to better understand the role of the thick crustose coralline algae and their associated invertebrate communities in the food web of the nearshore region of the Aleutian Islands. Considering the major function *Clathromorphum nereostratum* may play in supporting a rich and diverse fauna and the dramatic implications global warming and ocean acidification could have on its health, we believe that this habitat deserves greater scientific scrutiny.

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