

**Who's on fish: comparing macro-scavenger communities on fish and kelp bait
across an intertidal-subtidal depth gradient.**

Collin P. Gross^{1,2}

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¹ Department of Biology, University of Washington, Seattle, WA 98195

² Friday Harbor Laboratories, University of Washington, Friday Harbor, WA 98250

Contact information:

Collin Gross

University of Washington

Department of Biology

Box 315800

Seattle, WA 98195-1800

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Abstract

The importance of scavenging communities, and the detritus and carrion on which they feed, has been well studied from the perspectives of spatial food subsidies (marine to terrestrial, terrestrial to marine, and marine to marine) and community structure (e.g. whale and wood falls in the deep sea). Most of these studies focus on comparing scavenging rates or scavenger diversity within a single habitat, usually deep-sea or intertidal, and seldom make comparisons between these regions. A baited trap experiment was conducted to quantify the macro-scavenger community and scavenging rates on aged fish and kelp at intertidal, shallow subtidal, and deep subtidal sites around San Juan Island, WA, USA. Bray Curtis cluster analysis showed a distinction between macrofaunal communities in the intertidal and both subtidal sites, with higher scavenging rates on fish than kelp at all sites. Differences in the Shannon-Weiner diversity index were found in trap macrofaunal communities between sites, although further study is needed to show if these differences are really the result of different communities of scavengers or merely the influx of ambient macrofauna into the traps at different sites.

Introduction

One of the most significant differences between marine and terrestrial communities is the relatively low importance of primary productivity in the ocean (Nybakken and Bertness 2005, Polis et al. 1997). Areas like eelgrass beds and kelp forests in which primary production occurs *in situ* are remarkably productive and diverse habitats (Mann 1973, Edgar 1990), both because of the structure they provide and the biomass of primary producers, but these only make up a small percentage of available

benthic habitat (Polis 1996). Much of the marine benthos is far removed from any source of photosynthetic production, and both shallow and deep-water benthic ecosystems are fed by the spatial subsidies of allochthonous primary and secondary productivity in the form of phytodetritus, macroalgae, carcasses, and other sources, which are often highly patchy and/or periodic (Smith and Demopoulos 2003, Britton-Simmons et al. 2009). Because of this scenario, when large strandings or food falls occur, especially highly labile carbon sources like fish and cetacean carcasses, large diverse aggregations of scavenging organisms form, many of which are found nowhere else in such high densities (Higgs et al. 2014, Goffredi et al. 2004).

Many studies have been undertaken on the influences of carrion and macroalgal detrital flux on intertidal (Polis and Hurd 1996, Colombini and Chelazzi 2003, Ince et al. 2007, Gonçalves and Marques 2011), subtidal (Duggins et al. 1989, Krumhansl and Scheibling 2012) and deep-sea (Dayton and Hessler 1972, Smith 1985, Fleury et al. 2013, Higgs et al. 2014) communities, but very relatively few studies have made direct comparisons between the community structures of the scavengers that feed on these allochthonous food sources across different habitats. Furthermore, most of these studies have looked at scavenger communities of different size classes; the accessibility of the intertidal means that studying macro- and meiofaunal scavengers can be done with much greater ease than in the deep sea. There, direct, targeted sampling is nearly impossible and photographic sampling techniques are more common, resulting in a bias towards megafaunal observation and sampling (Hecker 1990, Priede et al 1994, Yeh and Drazen 2009).

This study sought to make direct intertidal-subtidal comparisons in macrofaunal scavenging communities by quantifying the diversity of macros scavengers present in traps with two bait types, aged kelp and aged fish, across an intertidal-subtidal depth gradient. I hypothesized that given the higher C:N ratio present in aged kelp (~14-10 for aged *Nereocystis luetkeana*, Dethier et al. 2014) relative to aged fish (2.5-5.5, North Country Organics 2014), scavenging rates on this bait would be lower than those on aged fish, and that the community of scavengers present would contain mostly generalist species. In addition, as the distance from *in-situ* marine primary and secondary production increases, i.e. the intertidal and subtidal areas below kelp and eelgrass beds, scavenging species will be present in greater diversity and abundance.

Materials and Methods

Traps were constructed from half-liter plastic water bottles. The bottom was replaced with 500- μ m mesh and the top was inverted to form a funnel entrance. Bait was wrapped in a 1.5-mm mesh bag and suspended from the inner surface with microfilament line. Prior to deployment, bait bags were weighed, and bait was blotted and weighed wet. Two sets of traps were deployed in triplicate per site for a total of 18 traps across all sites: kelp-baited traps were supplied with blades of bull kelp (*Nereocystis luetkeana*) discovered after at least 2 days as beach wrack before aging in the dark for 4 days, and fish-baited traps were supplied with cod steaks purchased frozen, thawed two days and aged in the sun for one day prior to deployment.

Six traps each were deployed for 24 hours at 3 sites around San Juan Island (fig. 1), selected for their low flow regimes and substrate type (coarse sand to silt). False Bay, selected as an intertidal site, is a shallow embayment approximately 1 km wide, characterized by current speeds less than 0.5 m s^{-1} and semidiurnal tides ranging from -0.8 to +2.6 m (Stempien 2005). Traps were deployed here along a transect approximately



Figure 1. Map of San Juan Island, depicting intertidal (A), shallow subtidal (B) and deep subtidal (C) deployment sites.

230 m from the head of the bay, approximately 50 m from a rocky region further inland characterized by large swathes of the green alga *Ulva* sp. Shallow subtidal traps were secured off the Friday Harbor Labs breakwater at a depth of 14 m. Deep subtidal traps were deployed in a 30-m deep hole in the southeast edge of Friday Harbor. Ideally, a site below 100 m would have been selected, but due to the high current speeds present in local areas in this depth range, successful trap deployment was impossible.

After a 24-hour period, traps were recovered, their contents sieved through a 300- μm sieve, and fixed in 10% formalin. Macrofauna, excluding nematodes, were removed by hand. All except copepods and ostracods were keyed out as close to species level as possible by examination under compound and dissecting microscopes. Copepods were identified as calanoid, harpacticoid, or cyclopoid (*Oithona* sp.) and assigned a morphospecies number. Ostracods were assigned a morphospecies number as ostracods only. Bait bags and their contents were blotted and weighed wet together.

In Primer (Clarke and Gorley 2006), Shannon and Gini-Simpson diversity indices (H' and $1-\lambda'$), Margalef community diversity index, Pielou's evenness values were calculated for all traps, and total diversity was estimated using rarefaction analysis. Community resemblance across traps was quantified using non-metric multidimensional scaling (nMDS) and S17 Bray Curtis similarity analyses, with a fourth-root transformation. Due to the small sample sizes and high variances across and within treatments, direct comparisons of diversity and species richness and bait consumption/loss were conducted in R using Kruskal-Wallis tests.

Results

Bait was consumed or lost to a much greater degree in fish-baited traps than kelp-baited traps (fig. 2A, $p = 0.0003246$; Kruskal-Wallis test), with 14.5% of the original bait mass lost on average in kelp-baited traps and 58.8% lost in fish-baited traps. Although no significant difference in bait loss was found across depths in kelp-baited treatments, an apparent decreasing trend in fish mass lost was found with increasing depth; differences between depth treatments were nearly significant (fig. 2B, $p = 0.1258$; Kruskal-Wallis test). In the case of the intertidal fish-baited traps and one of the shallow subtidal fish-

baited traps, the mesh bottom of the trap was detached and the bait (including the bag) was removed.

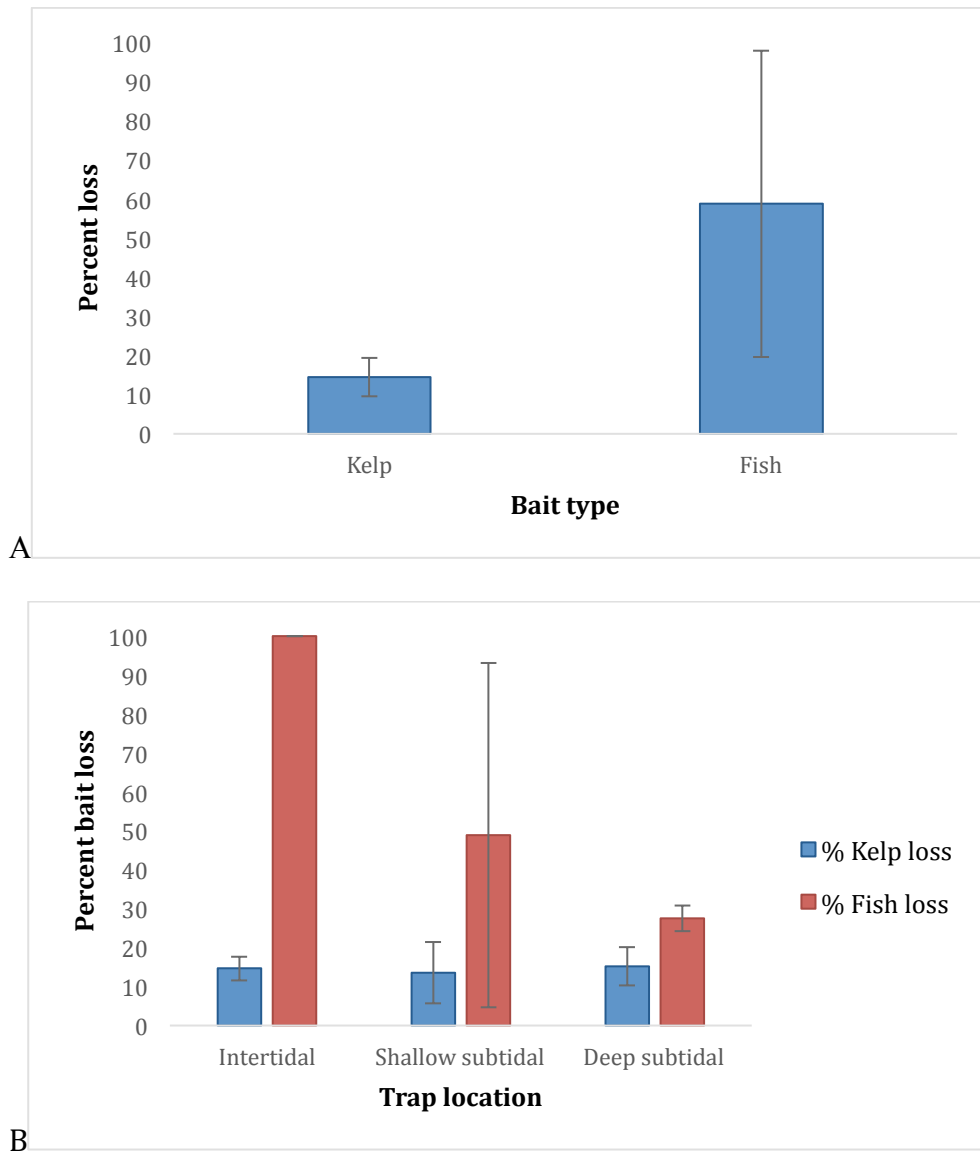


Figure 2. Comparison of bait consumption across traps with different baits (A, $p = 0.0003246$, Kruskal-Wallis test) and in different locations (B, $p = 0.1258$, Kruskal-Wallis test). Error bars are one standard deviation from the mean.

A total of 48 morphospecies were observed across all traps, falling into 16 higher taxa (fig. 3). Of these, 62.5% were found in only 1 trap. In general across all treatments, traps were dominated by one or two strongly or weakly dominant species, most of which

were crustaceans, and only one of which, harpacticoid 1 (fig. 4A), was dominant in more than one treatment.

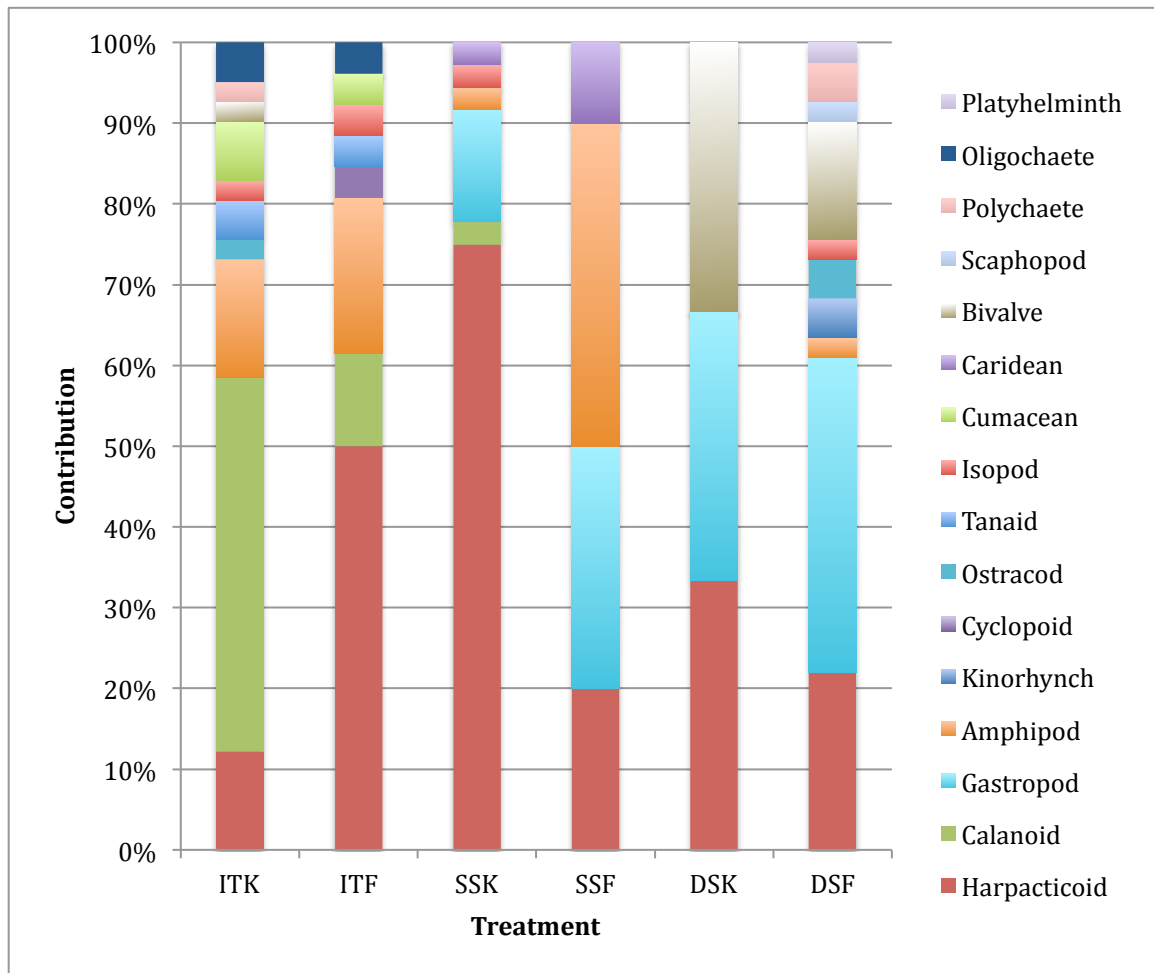


Figure 3. Macrofaunal community structure compared across the six different depth and bait treatments. IT = Intertidal, SS = Shallow Subtidal, DS = Deep Subtidal; K = Kelp-baited, F = Fish-baited.

The most diverse and commonly encountered animals in all traps were crustaceans, with a total of 32 species making up an average of 67.9% of all individual animals encountered. Copepods accounted for 68.0% of these, falling into 14 species. Mollusks were second in species richness and abundance, making up an average of 28.8% of all individual animals, distributed across 11 species. No apparent pattern was found in the relative contributions of mollusks vs. crustaceans to traps set at different depths or with different bait types.

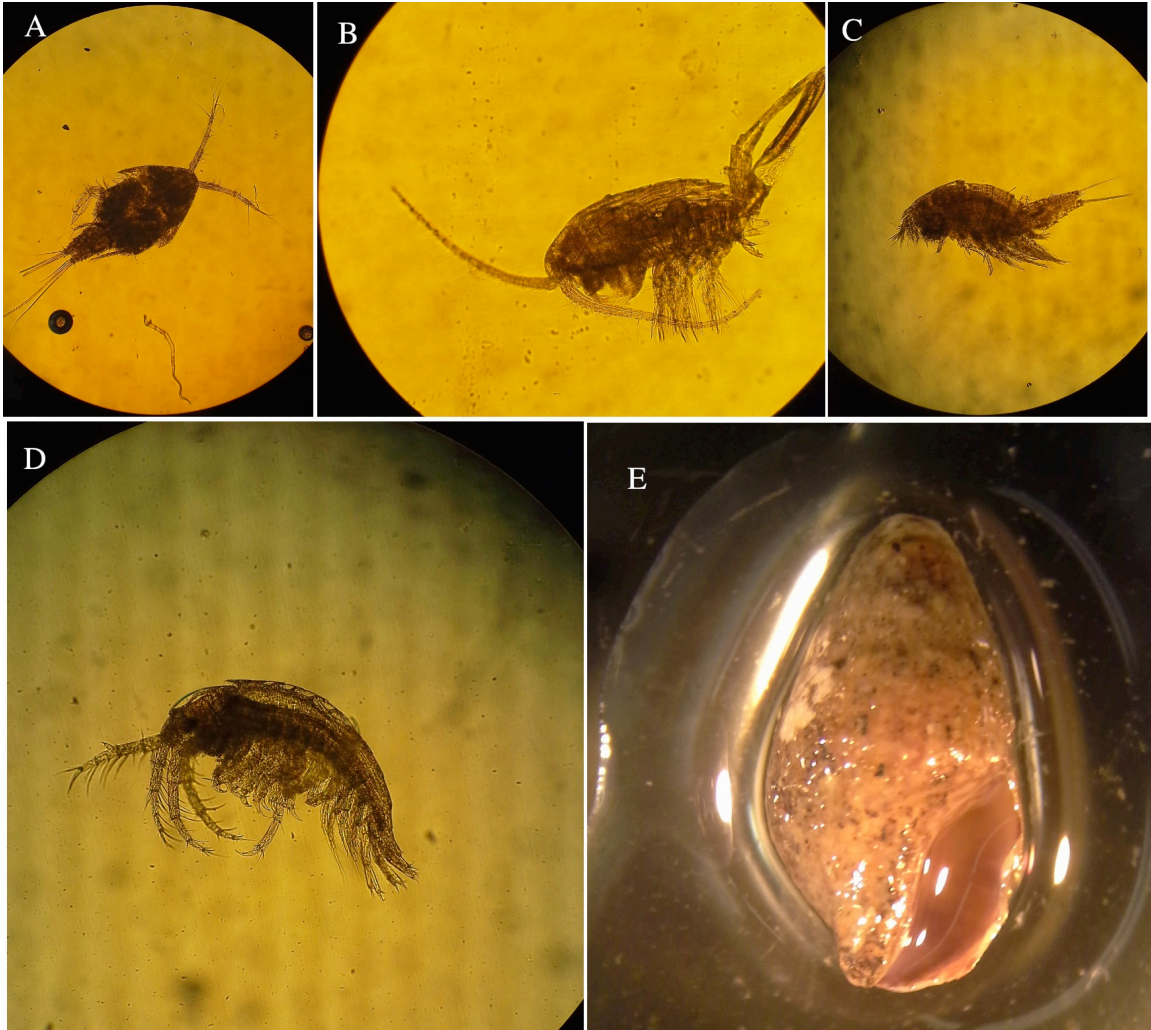


Figure 4. Dominant species present across the six different treatments including A) Harpacticoid sp. 1, SSK and DSK; B) Calanoid sp. 1, ITK; C) Harpacticoid sp. 5, ITK; D) *Ischyrocerus anguipes*, ITF; E) *Alia tuberosa*. Treatment names are as described in fig. 3.

No clear patterns in species richness appear across depths or bait types; shallow subtidal fish, shallow subtidal kelp, and deep subtidal kelp treatments appeared to plateau between 1 and 3 species while intertidal fish, intertidal kelp, and deep subtidal fish treatments had much greater richness. No significant difference in species richness was found between differently baited traps or between traps deployed at different depths (Kruskal-Wallis test). With the exception of H' across the three depth treatments ($p =$

0.038, Kruskal-Wallis test; fig. 5) all diversity and evenness indices did not differ significantly across different depth and bait treatments.

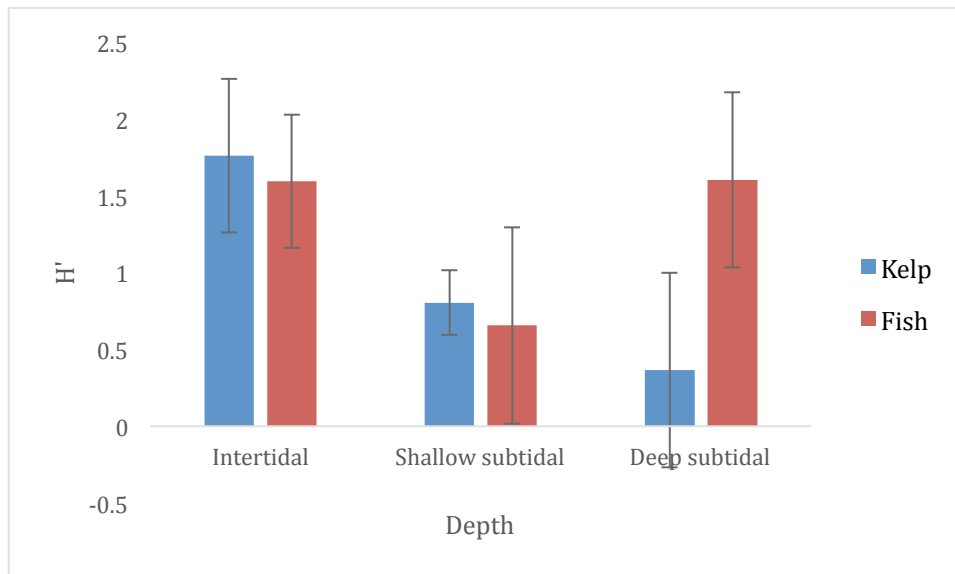


Figure 5. Shannon-Weiner diversity indices of macrofaunal communities present in the three depth treatments, $p = 0.038$, Kruskal-Wallis test.

Non-metric multidimensional scaling and cluster analyses based on a Bray Curtis distance matrix revealed a strong separation between intertidal macro-scavenger communities and both sets of subtidal communities, while subtidal treatment communities could not be separated from each other (fig. 6). Within the intertidal treatments, communities found in kelp-baited traps formed a distinct group. SIMPER analyses revealed an average similarity of 16.9% based on Bray Curtis similarity measure for shallow subtidal traps, 37.5% average similarity between intertidal traps, and 12.4% average similarity for deep subtidal traps. *Lacuna vincta*, harpacticoid sp. 5, and harpacticoid sp. 1 accounted for 37.0, 28.9, and 76.9% of the similarities across replicates in the shallow subtidal, intertidal, and deep subtidal, respectively. Across treatments, shallow subtidal and intertidal traps were 98.8% dissimilar, shallow subtidal and deep subtidal traps were 84.9% dissimilar, and intertidal and deep subtidal traps were 98.4%

dissimilar. .

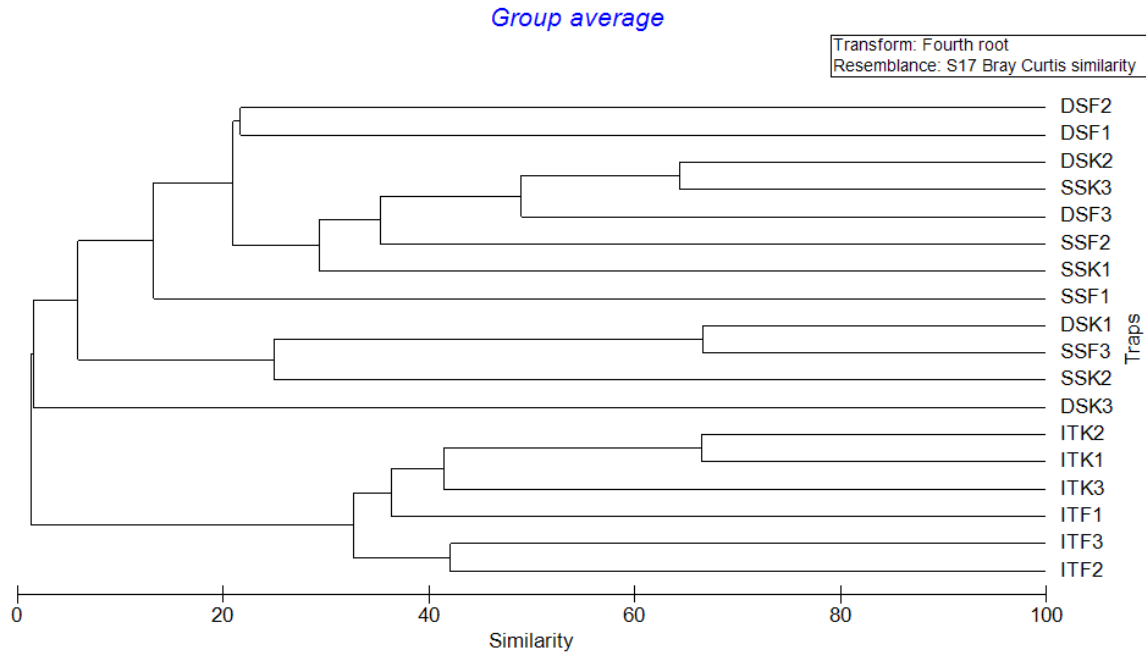


Figure 6. Dendrogram based on Bray Curtis distance representing the similarity between macrofaunal communities found in kelp- and fish-baited traps across intertidal, shallow subtidal, and deep subtidal depths. Treatment abbreviations are as in fig. 3.

Discussion

Clustering of intertidal and subtidal traps into two groups makes sense given the radically different abiotic factors that contribute to the overall structure of intertidal vs. subtidal communities (Connell 1961, Moran 1999, Perez et al. 2009), including scavengers. Within the intertidal group, the clustering together of kelp-baited traps is likely a result of the fish-baited traps being torn open, potentially exposing them to the ambient infaunal community or allowing scavengers that would otherwise accumulate to escape or pass through the trap. The intermixed clustering of deep and shallow subtidal traps may be due to either the close proximity of deep and shallow subtidal sites relative to the intertidal site (~2.5 km vs. ~6 km), or due to the lack of a strong change in background macrofaunal community structure with depth in the subtidal, two factors that

are probably interrelated. Given the large number of rare morphospecies across treatments overall and the high proportion of morphospecies found in only one replicate, it is almost impossible to make any generalizations about community structure across bait types or depths on the morphospecies level.

The apparent decreasing trend in bait consumption with depth can most obviously be explained by the complete loss of the bait and the bait bags after 24 hours deployment in the intertidal site, most likely the result of a crab or a large terrestrial predator rather than the macroscavengers that were the focus of this study. Despite this, given the relatively high proportion and higher taxonomic diversity of scavenging and detritivorous species present in intertidal traps (isopods, amphipods, tanaids, cumaceans, copepods, annelids, ostracods), it may be safe to say that scavenging rates would be higher in the intertidal outside of the influence of larger scavengers like crabs and foxes, although likely not on the scale observed in this experiment. In addition, given the relatively low productivity of sandy intertidal areas like False Bay, and the importance of marine carrion and algal detritus in these areas, scavenging rates could conceivably be higher in these areas (Polis and Hurd 1996, Polis et al. 1997, Gonçalves and Marques 2011). Subtidal areas, especially those in Friday Harbor, with their close proximity to macroalgal and eelgrass beds as well as fish, would likely have lower scavenging rates concentrated on small pieces of aged kelp or fish simply because of the greater abundance of similar food sources in these areas (Duggins et al. 1989, Britton-Simmons et al. 2009, Krumhansl and Scheibling 2012).

In addition to potentially skewing scavenging rate results, opening traps may have also compromised diversity results by allowing the escape of animals that would have

otherwise been retained. On the other hand, keeping the traps closed in many cases lead to the entrainment of sediment and associated infauna. In all intertidal kelp-baited traps, and many of the deep subtidal traps, a significant amount of sediment was found in the trap after deployment, which may explain the presence of non-scavenging infauna like bivalves and scaphopods in these traps. In the future, traps could be deployed with a wide base to minimize sinking into the substrate, suspended above the seafloor, or be more carefully placed so as to avoid tidal currents that might bring in sediment and ambient infauna.

One obvious flaw of this experiment is that it did not include control treatments at any of the depths tested, making it impossible to tell how the community structure of “scavengers” present in the trap differed, if at all, from the ambient macrofauna. The snail *Lacuna vincta*, for example, is well documented as an important herbivorous species (Duggins et al. 2001, Britton-Simmons et al. 2011), and was present in two of the shallow subtidal kelp-baited traps, but was also found in one deep subtidal and shallow subtidal fish-baited trap each. If the traps were doing their jobs and attracting only scavengers, I would expect to see a greater abundance of scavenging species present in the traps, and perhaps less diversity as only scavenging and detritivorous species would theoretically be present in the baited traps. Scavenging could also be inferred using stable isotope analyses to compare trap macrofauna to the bait, but external food sources and unknown assimilation times might confound this information.

Extensive and more carefully thought-out further study is needed to build a better picture of the different communities of scavengers present on these bait types at the depths tested. In the case of a future study, it would be interesting to see how the

relatively shallow subtidal sites sampled in this study compare to deeper ones (below 100 m) in terms of macro-scavenger abundance and community structure. Because both the sandy intertidal and deep sea are much further removed from large sources of marine primary and secondary production, I hypothesize that scavengers would occur with greater abundance in both areas.

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