

Spatial synchrony of amphipods in giant kelp forests

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Abstract Amphipods are abundant in marine ecosystems worldwide and are important as prey and as consumers of macrophytes and detritus in food webs. Due to the spatially complex and dynamic nature of giant kelp (*Macrocystis pyrifera*) forests, assessment of the abundances of giant kelp and amphipods through time and space should provide insight into their potential interactions within the system. In an extensive field study within the surface canopy of giant kelp, the abundance of amphipods was quantified on artificial substrates at an array of 18 sites within kelp forests along Point Loma, California, USA, from July to October 2009 and 2010. Biomass of giant kelp canopy was estimated using remotely sensed imagery, and the spatial synchrony (autocorrelation through time) of kelp canopy was compared with synchrony of caprellid and non-caprellid amphipods. Caprellids exhibited high spatial synchrony that did not decrease with distance, while non-caprellids were synchronous on local scales, indicating high spatial heterogeneity in abundance through time. Gammarids showed a rapid exponential decrease in synchrony within the first 550 m that was consistent with synchrony of giant

kelp. This suggests a local-scale biotic link between non-caprellids and giant kelp canopy, whereas caprellid synchrony is more likely to be influenced by regional-scale environmental variables. Caprellids and other amphipods are important prey resources for common kelp forest fishes, so these differences may in turn affect the spatial distributions of these predators. Moreover, excretion by amphipods may be an important source of nitrogen to giant kelp during periods of nitrogen limitation.

Introduction

Amphipod crustaceans are fundamental players in marine ecosystems (Chapman 2007a) and are often a primary component of the invertebrate assemblage in macrophyte-based systems around the world (Taylor and Cole 1994; Christie et al. 2009; Guerra-García et al. 2010; Ronowicz et al. 2013). Amphipods are important grazers (Poore 1994; Duffy and Hay 2000; Pérez-Matus and Shima 2010), nutrient cyclers (Taylor and Rees 1998; Hepburn et al. 2012), and prey (Bray and Ebeling 1975; Schneider and Harrington 1981; Moore et al. 2003; McCurdy and Forbes 2005; Feary et al. 2009; Okamoto et al. 2012). From work in multiple systems, it is clear that amphipods can be highly variable in space and time (Guerra-García et al. 2000; Nakaoka et al. 2001; Thiel et al. 2003). Recognition of spatial heterogeneity in the abundance of organisms within a landscape may be key to understanding ecosystem complexity (Wiens 1989; Wagner and Fortin 2005). Despite this acknowledged importance, we know little about their spatial and temporal fluctuations within well-studied ecosystems such as giant kelp (*Macrocystis pyrifera*) forests, especially at landscape scales.

Amphipods consume significant amounts of organic material. Most species of caprellid amphipods are

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detritivorous (Guerra-García and Tierno de Figueroa 2009) and with a few obligate carnivores (Guerra-García and Tierno de Figueroa 2009). Many species have shown high dietary plasticity (Saunders 1966; Caine 1977, 1980), and detritivorous species can opportunistically prey on small crustaceans (Guerra-García and Tierno de Figueroa 2009). Many other amphipod taxa (e.g., many gammarideans) are also primarily detritivores, but feeding strategies vary by species (Cruz-Rivera and Hay 2000; Farlin et al. 2010). Herbivorous taxa (e.g., Ampithoidae) are important grazers in seagrass and macroalgae-based systems (Duffy and Hay 2000; Pérez-Matus and Shima 2010). In Southern California kelp forests, herbivorous amphipods and other mesograzers cause reduced performance of giant kelp (Davenport and Anderson 2007). During unfavorable growing conditions, reproductive collapse (Graham 2002) and sometimes complete mortality (Dayton et al. 1992) have been attributed to amphipod outbreaks.

As a consequence of their prevalence and feeding strategy, amphipods may play an important role in nutrient retention and cycling within macroalgae-based systems, especially during periods of nutrient limitation (Taylor and Rees 1998; Hepburn et al. 2012). Amphipods and other epifauna excrete ammonia (Regnault 1987), which can be readily utilized by brown algae (Hanisak 1983). In one temperate system, it was estimated that epifauna excrete 1.5–2.1 times as much nitrogen as fucal algal hosts uptake (Taylor and Rees 1998). Giant kelp requires high levels of nitrogen to undergo rapid growth and is thus nitrogen limited at times (Zimmerman and Kremer 1984; North and Zimmerman 1984), but it has the ability to transport nitrogen from older blades to areas of active growth (Hepburn et al. 2012). Transport of nitrogen from locations with of dense epifauna (e.g., holdfasts) could be a mechanism for individuals to tolerate nitrogen limitation (Hepburn et al. 2012), and would be an indirect positive interaction between epifauna and macroalgae. Spatial and temporal heterogeneity in amphipod abundance could then result in a patchy and more complex nutrient environment than is typically assumed in kelp forests.

All amphipods lack a planktonic larval stage (Chapman 2007a). It is hypothesized that they disperse on more local scales than many other marine invertebrates (Caine 1979), but rafting on floating substrates is common and contributes to the cosmopolitan distribution of many caprellid species (e.g., Thiel et al. 2003). Caprellid reproduction may occur year-round (Jessen 1969), and abundances vary seasonally, often by at least an order of magnitude (Takeuchi et al. 1990). Field colonization experiments have shown caprellids and other amphipods to readily colonize habitats on local scales (Edgar 1992; Poore 2005; Rule and Smith 2005), but across multiple systems, amphipod abundances are spatially and temporally patchy (Poore 2004; Rule and

Smith 2005). Colonization studies in macroalgae and seagrass systems have found that habitat structural complexity (Edgar and Robertson 1992; Hauser et al. 2006), proximity to food resources (Poore 2004), patch size (Eggleston et al. 1999; Roberts and Poore 2006), and habitat type (Edgar 1992; Smith and Rule 2002; Page et al. 2007) can all influence the abundance and species composition of amphipods. Physical parameters such as temperature and conductivity have also been correlated with caprellid abundance and diversity (Guerra-García et al. 2010).

Due to the high spatial and temporal variation exhibited by amphipods, traditional statistical methods may fail to detect clear patterns. It is common for sampling sites to be averaged together in a region, and the specific position of the site in the landscape is not considered. However, the combination of conditions operating across multiple spatial and temporal scales suggests the importance of position and neighborhood context within a landscape (Wagner and Fortin 2005), and the variation experienced at each site may be an important descriptor of ecosystem forces. Sampling of epifaunal colonization to artificial substrates at multiple spatial scales has revealed differences in large-scale and small-scale colonization of substrates (Rule and Smith 2005), and some amphipods prefer habitat adjacent to food sources (Poore 2004). One method for characterizing variation across a landscape is to measure spatial autocorrelation through time, a phenomenon known as synchrony (Moran 1953; Buonaccorsi et al. 2001). Spatial autocorrelation is inversely related to spatial heterogeneity; low spatial autocorrelation indicates that abundance in one position is not correlated with abundance in adjacent positions. When synchrony is low, organism abundance at one location does not fluctuate similarly with organisms at nearby locations, so spatial heterogeneity through time is high.

Mechanisms of synchrony include recruitment, top-down control, and bottom-up processes, all of which can occur over different spatial scales. Giant kelp may be synchronous on local scales through time (Cavanaugh et al. 2013), and synchrony of giant kelp canopy decreases rapidly between 50 m and 1.3 km, closely resembling the synchrony of urchin populations over the same area (Cavanaugh et al. 2013). Because amphipods lack a planktonic larval phase and presumably have relatively short dispersal, we might predict that recruitment would result in local-scale synchrony (relatively low autocorrelation at large scales). In addition, strong effects of spatially heterogeneous predators or high heterogeneity in preferred substrata could result in local-scale synchrony (Moran 1953; Bjørnstad et al. 1999). Alternatively, regional-scale variation in environmental variables (e.g., temperature, nutrients) could serve as a large-scale synchronizing mechanism (Moran 1953; Bjørnstad et al. 1999). Moreover, if dispersal distances are farther than assumed, abundances may be

spatially autocorrelated at large scales due to recruitment pulses. Although spatial and temporal heterogeneity of amphipods may translate to variation in community level processes within kelp forests (e.g., nutrient cycling, availability as food for fishes), we do not know the degree to which amphipods fluctuate synchronously, nor the scale at which this might occur.

Our objective was to assess the spatial synchrony of abundant amphipod groups and giant kelp canopy within kelp forests. To address this objective, we used spatial statistics to analyze data collected by remote sensing and field sampling of invertebrates via artificial substrates.

Methods

Study system and design

This study was conducted in the expansive giant kelp forests off Point Loma, San Diego, California, USA (Fig. 1). The spatial extent of the Pt. Loma kelp forests is large enough that patches of giant kelp at either end of the reef function relatively independently of one another (Cavanaugh et al. 2014), and there are sand channels, rubble piles, and several limestone reefs interspersed throughout the area. The methods that follow were originally designed to detect variation in settlement of invertebrates through kelp forests (Morton and Anderson 2013). In the process of completing that study, we observed high abundances of amphipods on our settlement collectors. This provided us with an unexpected opportunity to examine their abundances across space and their relationship to kelp forest habitat. We recorded the abundance of all invertebrates found on our collectors, including both settling organisms and “brooders,” allowing us to examine fluctuations in amphipod abundance through space and time.

A complete randomized block array was established, with two alongshore blocks (north and south) separated by approximately 1.5 km (Fig. 1). Within each block, we randomly established three cross-forest transects spaced 100–500 m apart. We haphazardly placed three sites along each transect, with one in each of the following alongshore strata: (1) the “outer edge,” 10 m west of the offshore edge of the kelp forest, (2) the “middle,” approximately in the middle of the kelp forest and at least 100 m east of the outer edge (this minimum distance accounted for narrower regions of kelp stands), and (3) the “inner edge,” 10 m east of the inshore edge of the kelp forest. Thus, this sampling design consisted of two regions, three cross-forest transects within each region, and three sampling sites positioned along each transect for a total of 18 sites (see Morton and Anderson 2013 for additional details).

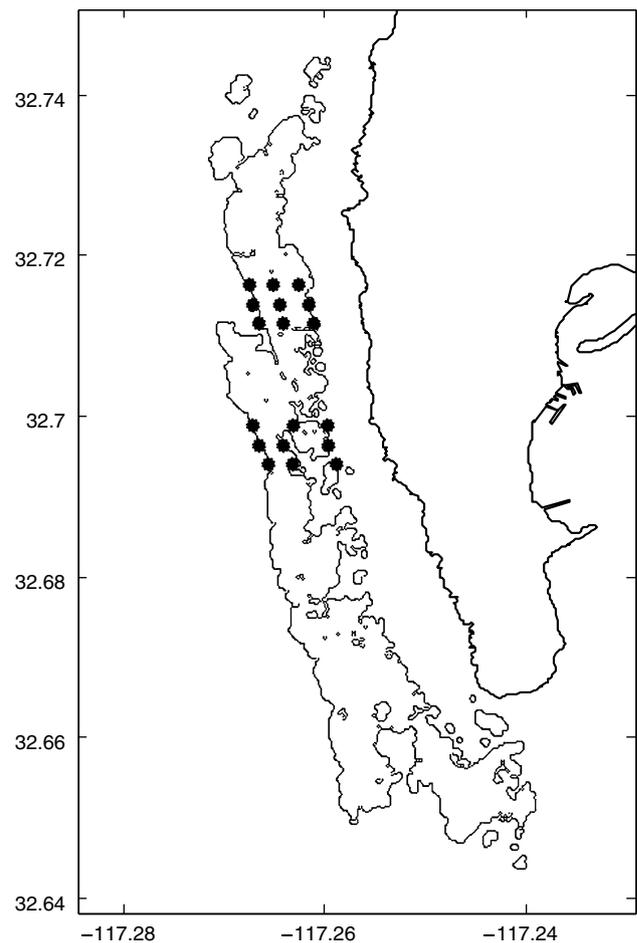


Fig. 1 Block array of invertebrate sampling sites, indicated by black circles. The thick outlined region is Point Loma, California; the thin outline indicates the edge of the region where giant kelp canopy was observed at any point in 2009 and 2010 Landsat image time series

At each site, we deployed two moorings to account for potentially high variability in invertebrate abundance. We placed the first mooring haphazardly and the second mooring 10 m south of the first. As part of our original study, we cleared all giant kelp within a 10-m radius of each mooring to prevent entanglement with moorings and standardize the amount of structure immediately surrounding invertebrate collectors; colonization of artificial substrates by amphipods may not decrease at 10 m distance from natural habitat (Roberts and Poore 2006). We maintained clearings throughout sampling periods in 2009 and 2010.

Estimating biomass of giant kelp canopy

We estimated biomass of giant kelp canopy throughout the entire Point Loma reef system during summer and fall (May–November) 2009 and 2010 using 30-m-resolution

multispectral imagery from Landsat 5 TM and Landsat 7 ETM+ sensors. We identified 11 usable images of the Point Loma kelp forest for 2009 and 10 usable images for 2010. The methods used to process and calibrate the reflectance measurements from the Landsat satellites into giant kelp canopy biomass (kg m^{-2}) are described in detail in Cavanaugh et al. (2011). Briefly, radiometric signals from all images were standardized to a single atmospherically corrected image using fixed ground control points. Fractional cover of giant kelp was then modeled using multiple endmember spectral mixing analysis, and kelp canopy biomass was estimated using the observed relationship between diver-estimated biomass and Landsat kelp pixel fraction. Canopy biomass at each pixel was matched to each sampling period using a cubic interpolation (MATLAB function *interp1* “cubic”; Bell et al. 2015).

Estimating amphipod abundance

We used dish-scrubbing pads (S.O.S. Tuffys, Clorox, Oakland, California, USA; hereafter Tuffys) as passive invertebrate collectors. As stated earlier, we were originally interested in quantifying the abundance of settling invertebrates, and Tuffys are well established as artificial substrata for collection of various invertebrate phyla (Mace and Morgan 2006; Lagos et al. 2007; Menge et al. 2009). Complex artificial substrata are readily colonized by amphipods (Kendall et al. 1996; Smith and Rule 2002; Rule and Smith 2005; Hauser et al. 2006). Comparisons of artificial substrata to natural complex habitats have shown variable results (Smith and Rule 2002; Edgar and Klumpp 2003), but artificial substrata can be used to quantify relative abundances in space and time, even if community composition on the substratum does not exactly match natural habitat (Edgar and Klumpp 2003). In kelp forests, caprellids are most dense in finely branching benthic algae and sessile invertebrates (Page et al. 2007), and are more common at shallow depths (Holbrook and Schmitt 1986). Gammarideans are most abundant on kelp fronds in the mid-water column portion (from about 1 m below the water surface to 2 m from the seafloor) (Coyer 1984). The complex structure of the pot scrubber is similar to the fine-scale complexity that many amphipods inhabit, and we observed high abundances of amphipods on Tuffys throughout sampling.

One Tuffy was deployed at 7 m depth on each of the two moorings per site and sampled every 2 weeks during two consecutive summers, July–October 2009 and 2010. We selected this depth to maximize the species of invertebrates sampled, capture dispersing individuals (rather than crawling migrants), and limit confounding structural effects of kelp canopy at the water surface. Every 2 weeks, divers on SCUBA collected Tuffys using a plastic bag and deployed clean, seawater-conditioned Tuffys. Samples were stored at

$-20\text{ }^{\circ}\text{C}$ until processing. We removed our collectors more frequently than in many studies, so abundances should reflect production of amphipods from surrounding habitat, rather than establishment and production on the substrate. In the laboratory, we passed all samples through a 500- μm sieve, and organisms were fixed in 10 % formalin and then preserved in 75 % ethanol. After preservation, we sorted amphipods as either Caprellidea or Gammaridea, which were separate suborders at the time of sorting. However, in between data collection and analyses, the suborder Senticaudata was established, which incorporated 95 families from Gammaridea, including Caprellidae (Lowry and Myers 2013). Thus, our amphipod groups will be hereafter referred to as either “caprellid” (referring to the family Caprellidae) or “non-caprellid” (all other amphipods collected, including members of the still existing suborder Gammaridea, as well as some members of Senticaudata).

Synchrony analyses

For kelp canopy synchrony analysis, we used log-transformed canopy biomass (kg m^{-2}) through time in each kelp pixel and the nonparametric correlation function R package NCF (Sncf function; Bjørnstad et al. 1999) to calculate the autocorrelation between kelp pixels through time as a function of distance. The strength of these correlations provided a measure of synchrony in kelp canopy biomass.

Caprellid and non-caprellid amphipods were analyzed separately. To assess spatial autocorrelation of amphipod abundance through time, amphipod abundance for each sample was standardized to a 14-day sampling period, and the average of the two Tuffys per site was calculated. We used the NCF package (Sncf function; Bjørnstad et al. 1999) to calculate spatial synchrony of each amphipod group and used the default number of degrees of freedom for each nonparametric correlation function ($\sqrt{\text{sampling locations}}$). Although the greatest distance between any two sampling sites was 2.75 km, there were twice as many samples for distances <2.25 km; therefore, we set 2.25 km as a maximum distance for all spatial analyses. Confidence intervals were generated by bootstrap resampling with 1000 iterations.

Results

Kelp canopy biomass was variable throughout our study area, and total canopy biomass was greater in 2009 than in 2010 (Fig. 2). In 2010, there was a reduction in canopy biomass along the inner edge of kelp (with some sites losing their kelp canopy entirely) coupled with an increase in canopy biomass along the outer edge. Kelp canopy biomass behaved synchronously at scales less than 660 m (spatial

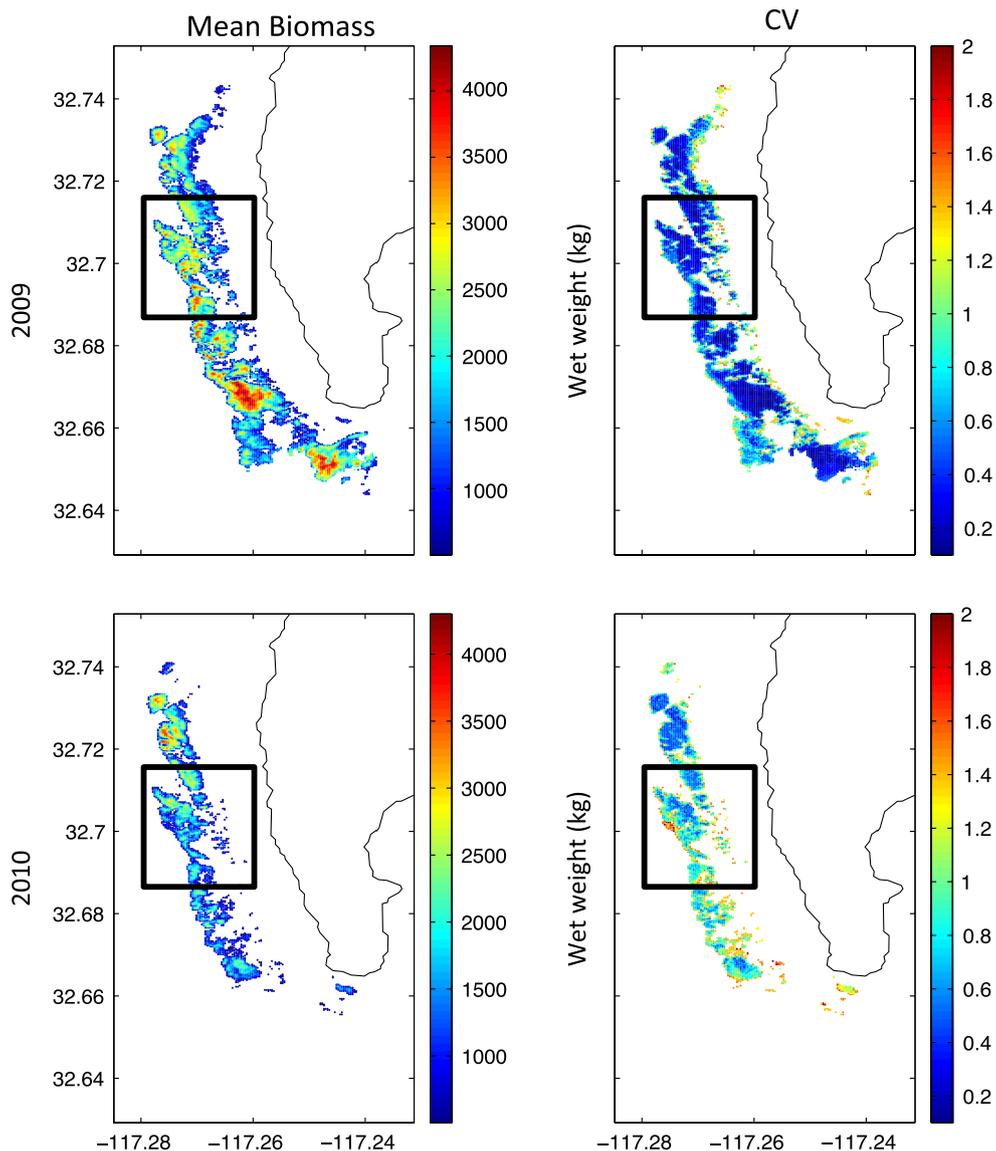


Fig. 2 Mean kelp canopy biomass and coefficient of variation (CV) within the Point Loma region from May to November 2009 and 2010. The *black rectangle* indicates the invertebrate sampling area. The

coefficient of variation is a standardized measure of dispersion, calculated by dividing the standard deviation of canopy biomass by the mean canopy biomass at each point

correlation was greater than the mean) within our study area (Fig. 3a). Spatial correlation ranged between 0.26 and 0.72, and the decline in synchrony with distance was best described by a double exponential decay function.

Over 350,000 invertebrate specimens were collected from Tuffys, 325,412 of which were amphipods. Caprellid amphipods were most abundant, comprising 83.5 % of the total number of amphipods collected. Caprellid abundances were variable in time, with peak abundance during August of 2009 and September of 2010. These pulses in abundance were observed at multiple sites simultaneously, indicating low spatial heterogeneity (Fig. 4). This pattern was captured by our synchrony analysis. Spatial correlation

through time was high (0.69–0.73) and did not decrease with increasing distance within the study area (Fig. 3b).

Non-caprellid amphipods were an order of magnitude less abundant than caprellids, constituting 16.5 % of amphipods collected (52,065 individuals). Pulses in abundance were observed in clusters of sites (Fig. 5). A very strong pulse was observed at a single site on August 19, 2009, but at most sites abundances were highest in October of 2010 (Fig. 5). Non-caprellid spatial correlation through time ranged from 0.38 to 0.70 and was greater than its mean at scales of less than 530 m (Fig. 3c), indicating that non-caprellids were as synchronous as caprellids at smaller scales within our system, but synchrony declined quickly

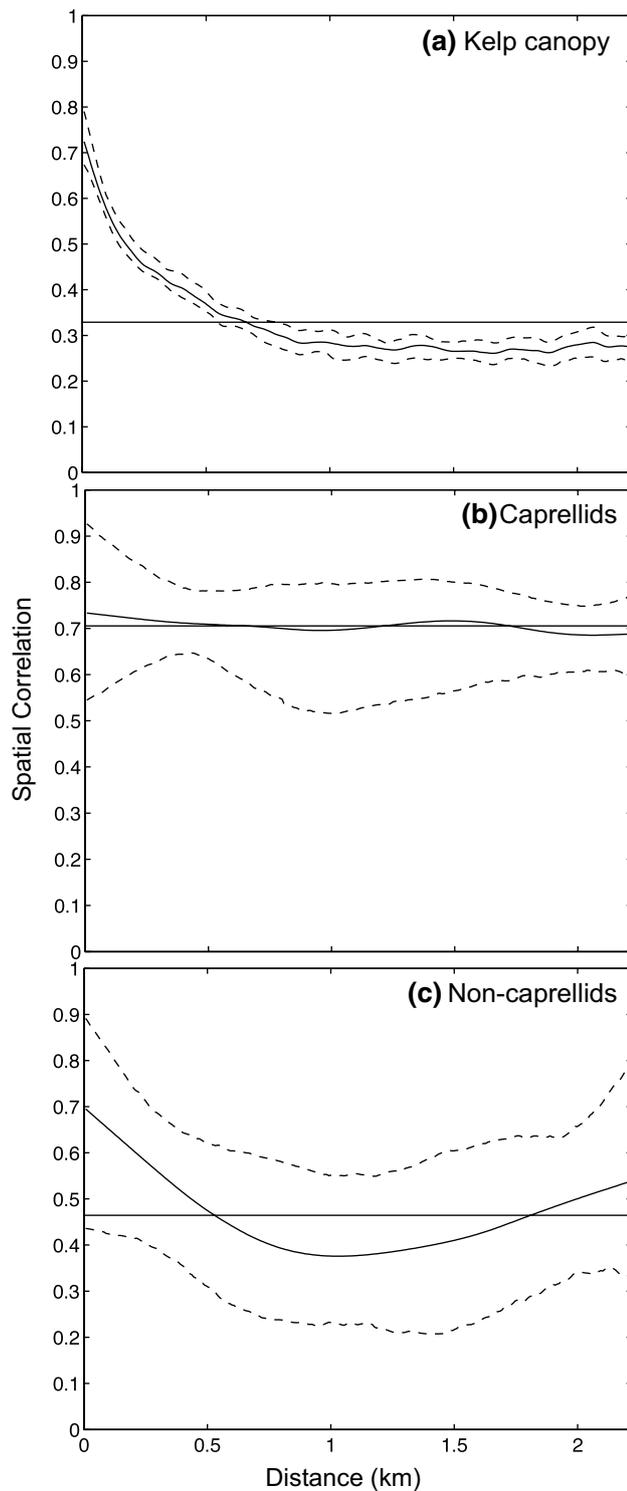


Fig. 3 Nonparametric spatial correlation functions (NCFs) as the solid black line for **a** giant kelp, **b** caprellids, and **c** non-caprellids. The NCFs show how correlation between points through time varies with distance. The *dashed lines* show 95 % bootstrap confidence intervals, and the *horizontal lines* shows the regional mean spatial correlation. The kelp NCF was constructed from 1142 Landsat pixel time series from the Point Loma kelp forest, while the crustacean NCFs were constructed from time series from the 18 sampling sites

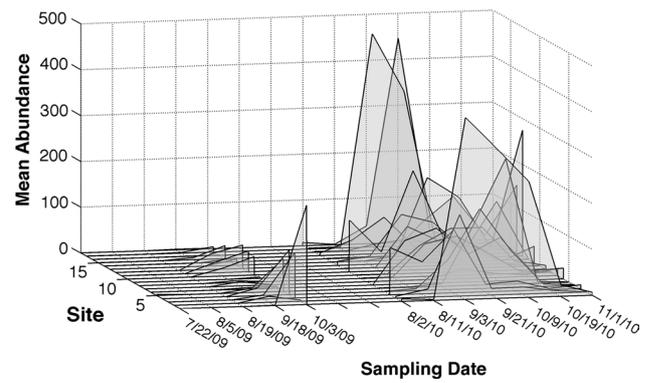


Fig. 4 Mean daily abundance of caprellid amphipods at all sites for all sampling dates

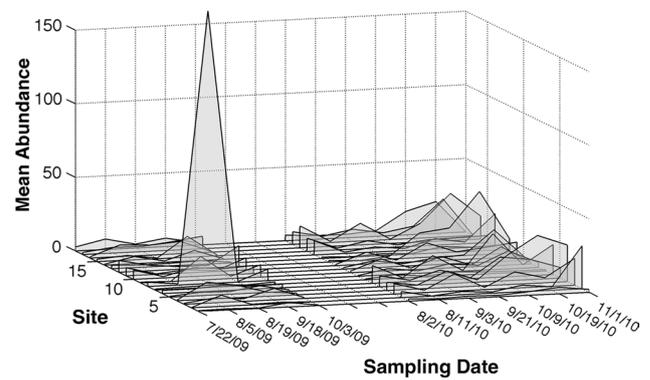


Fig. 5 Mean daily abundance of non-caprellid amphipods at all sites for all sampling dates

with increasing distance, in contrast to caprellids. The decline with distance was best described by a double exponential function, similar to that of kelp canopy biomass.

Discussion

Spatial heterogeneity of organisms at multiple scales affects both local and regional ecological processes (review by Tilman and Kareiva 1997). The recognition of heterogeneity as important in ecological complexity (Wiens 1989) has led to the development of landscape ecology, which assumes that ecological processes within a plot are not necessarily independent of neighboring plots (Wagner and Fortin 2005). The ecological effects of heterogeneity may be particularly strong for foundation species (e.g., giant kelp) and those that are central within food webs (e.g., amphipods).

Previous work has shown that over large scales, giant kelp synchrony experiences two exponential decreases with distance. A first rapid decrease occurs between 50 m and 1.3 km and a second, large-scale decrease occurs at

distances between 1.3 and 172 km (Cavanaugh et al. 2013). Scales of synchrony of sea urchins and young kelp recruits corresponded to the 50 m and 1.3 km spatial scale, suggesting that small-scale synchrony of kelp populations may be influenced by local drivers of predation and recruitment (Cavanaugh et al. 2013). The larger scale between 1.3 and 172 km was similar to spatial correlation patterns of environmental variables, indicating regional environmental variability was affecting synchrony at larger scales (Cavanaugh et al. 2013). Here, we examined synchrony at a higher resolution within a smaller area (one-dimensional 50-m coastline segment in Cavanaugh et al. 2013 vs. two-dimensional 30-m pixels in our study) and established that the same local-scale pattern held true within the kelp forests of Pt Loma.

Non-caprellid amphipod abundances were synchronous across a similar scale as giant kelp canopy (scales < 550 m). Both follow a double exponential decay function, and the synchrony function for giant kelp falls entirely within the confidence interval of the non-caprellid synchrony function. This suggests that forces influencing non-caprellid abundance operate over similar spatial scales as forces structuring giant kelp canopy biomass, suggesting a link between them. We are unable to tease-apart factors affecting synchrony, but kelp canopy biomass and non-caprellid amphipods appear to be influenced by local-scale drivers.

The synchrony function does not indicate whether this link is positive or negative, or indirect or direct. There are multiple scenarios of varying likelihood where giant kelp could influence amphipods via a combination of bottom-up and top-down forces. Some amphipod species graze giant kelp (amphipods), but these were probably not well sampled by our substrates (Edgar and Klumpp 2003). Furthermore, many more species are detritivores (Chapman 2007a) so a direct trophic link between herbivorous amphipods and giant kelp is not the most plausible mechanism for the observed patterns. Alternatively, dense kelp canopy alters the flow regime over a reef, which could retain food particles in the system and induce a positive association between giant kelp and non-caprellids, or dense kelp could slow delivery of material from outside the kelp forest (Eckman 1983; Gaylord et al. 2007) and induce a negative association. Dense kelp may also create a positive, non-trophic link if reduced flow enhances retention of kelp spores and dispersing amphipods. A subsequent increase in recruitment of both giant kelp and amphipods could induce local-scale synchrony.

In addition, predation by kelp-associated fishes may produce a positive or negative indirect link between giant kelp and non-caprellids. Particular fishes are positively correlated with kelp density (e.g., Anderson 1994), and several common juvenile and adult kelp forest-associated fishes feed extensively on non-caprellid amphipods (formerly

known as gammarideans) (Bray and Ebeling 1975). Non-caprellid amphipods make up a significant percentage of the diet of kelp perch (*Brachyistius frenatus*), kelp bass (*Paralabrax clathratus*), and kelp rockfish (*Sebastes atrovirens*) (Coyer 1979), and for black surfperch (*Embiotoca jacksoni*) and striped seaperch (*Embiotoca lateralis*) (Holbrook and Schmitt 1986). Dense kelp canopy may reduce amphipod mortality due to predation by providing refuge (inducing a positive association), or dense kelp canopy may attract enough predators to overwhelm any benefit of additional refuge, with a net negative effect on non-caprellid amphipods. The nature of the effect of kelp density on amphipod mortality due to predation may not be linear and may depend on the species of predators present at a given time. Non-caprellid amphipods may represent a more patchy food resource for multiple predator species, and interactions with linked members of the kelp forest community may be influenced by the spatial heterogeneity observed in these taxa.

In contrast, caprellids were synchronous over the entire spatial scale of our study. This suggests the importance of forces operating over scales at least as large as our sampling array. In seagrass beds, estuarine zones, and *Sargassum* beds, caprellids have exhibited strong seasonal patterns in reproduction, with high population densities during peak times (Woods 2009), consistent with our observations. Population cycles of several caprellid species have been linked to biomass of their host substratum (Guerra-García et al. 2000; Nakaoka et al. 2001). Caprellids readily colonize many substrata, but within kelp forests, the highest densities are found on hydroids and bryozoans (Page et al. 2007), with relatively few found on fronds of giant kelp (Coyer 1984). It is possible that the high densities observed on Tuffys indicate regionally high biomass on natural benthic substrata, supporting large caprellid populations. However, synchrony at this spatial scale is more suggestive of regional fluctuations in temperature and/or productivity as opposed to small-scale biotic interactions (the Moran effect; Moran 1953; Bjørnstad et al. 1999). As detritivores and opportunistic feeders with rapid reproduction and dispersal, caprellids have the ability to respond quickly to influxes of productivity and rapidly colonize new habitats (Jessen 1969; Woods 2009; Guerra-García and Tierno de Figueroa 2009).

Predation on caprellids was probably not responsible for regional synchrony, but may have had an important influence on caprellid temporal variability, specifically the crashes observed following spikes. Some common fish species prey on caprellids preferentially, including the painted greenling (Page et al. 2007) and shiner surfperch (Caine 1991). Shiner surfperch moving into a seagrass bed are capable of reducing caprellid densities by nearly two orders of magnitude within a month (Caine 1991). The extreme

temporal variability observed coupled with large-scale spatial synchrony could be explained by the combination of large-scale bottom-up forces leading to increased production, followed by rapid utilization of caprellids as a food resource by fishes.

Artificial substrata provide standardized structure that can be used to determine relative differences among sites, but we are unable to make inferences concerning the absolute abundances of amphipods on natural substrates in the system. Multiple studies have compared the communities colonizing artificial substrates with natural communities, with varying results (Smith and Rule 2002; Edgar and Klumpp 2003; Rule and Smith 2005; Hauser et al. 2006; Cole et al. 2007). A few relevant points emerge from previous work using similar substrata. First, the timing of deployment of substrata matters (possibly more than length of deployment) (Underwood and Chapman 2006) and colonization of substrata may be linked to stochastic supply and ability of colonists to disperse to the novel habitat (Chapman 2007b). By sampling frequently and over a long timescale (relative to the reproductive cycle of amphipods), much of this variation was captured in our samples. Second, host-specific species are not typically well sampled by artificial substrata (Edgar and Klumpp 2003), and colonization on them is influenced by direct contact with natural substrata (Smith and Rule 2002; Cole et al. 2007). By positioning Tuffys in the mid-water column and clearing a 10-m radius, we reduced this effect, while also increasing our sampling bias toward good dispersers with lower substratum specificity. Although the communities collected by artificial substrata are not necessarily representative of the natural community (Smith and Rule 2002; Chapman 2007b), they are valid tools for examining relative differences among locations (Edgar and Klumpp 2003; Rule and Smith 2005) and allowed us to characterize synchrony over multiple spatial scales without confounding effects of biogenic habitat structure.

It was not logistically feasible for us to identify our samples to species or to collect data on the size distributions of individuals because these data were collected as part of another study with different objectives. This limitation prevents us from making conclusions concerning recruitment as well as statements concerning the interactions between individual species and macroalgae. Consequently, we have restricted our conclusions to those that are valid for multiple feeding guilds and age classes of amphipods. Even with these limitations, we have been able to characterize relative differences in abundance of a foundation species (giant kelp) and abundant, trophically important invertebrates (amphipods), which allows us to make inferences concerning the spatial heterogeneity and the scales of structuring forces in this ecosystem.

Nutrient supply by large animals has been recognized recently as an important component of nutrient cycling in aquatic ecosystems (Burkepile et al. 2013; McCauley et al. 2015), and crustacean epifauna have the potential to be an important source of nitrogen for macroalgae (Taylor and Rees 1998). This type of positive interaction has not been thoroughly investigated. Interactions between amphipods and macrophytes are usually considered with respect to grazing (Thom et al. 1995; Duffy and Hay 2000; Davenport and Anderson 2007; Lewis and Anderson 2012), with positive effects of amphipods on seagrass growth attributed to “cleaning” of epiphytes (van Montfrans et al. 1984; Hughes et al. 2004). Availability of nutrients to giant kelp has historically been considered on regional scales (North and Zimmerman 1984; Reed et al. 2011), and during periods of upwelling, regional nutrient delivery likely overwhelms any local-scale variation in nutrient supply. The local-scale synchrony of both giant kelp and non-caprellids suggests interaction between these organisms, so it is possible that during periods of regional nutrient limitation, excretion by non-caprellids could contribute to giant kelp growth or maintenance. Caprellids were two orders of magnitude more abundant than non-caprellids at peak abundances, and they responded to regional-scale processes. Excretion by caprellids would provide a pulse of nutrients to the system over a larger spatial scale. If caprellid synchrony is an effect of nutrient delivery, consumption of detritus and excretion could extend the residence of nutrients in the system beyond what would occur based on water residence times alone. The canopy of giant kelp is synchronous over small and large scales and is linked to regional productivity (Cavanaugh et al. 2013), so any nutrient subsidy by caprellids may be masked by this effect. Further research should assess spatial correlations of environmental variables with amphipod abundances and possible feedbacks between amphipods and giant kelp.

Our study provides a higher resolution image of kelp canopy synchrony within kelp stands over large areas of rocky reef and indicates that the double exponential decay of kelp canopy synchrony is consistent across small and large spatial scales. The small-scale synchrony observed in giant kelp canopy and non-caprellid amphipod abundance suggests biotic interaction between these organisms, while regional synchrony of caprellids suggests environmental drivers are important. Due to the central food web position of both groups of amphipods and structural importance of giant kelp, these differences may affect the spatial distributions of upper trophic levels that use these food resources, and the consumptive effects of amphipods may have a strong influence on cycling of detritus in this system. Studies of amphipods in other systems should consider the spatial scale of potential synchronizing mechanisms as well as the ecological implications of amphipod synchrony. Our

study demonstrates the utility of sampling across multiple spatial scales and the application of spatial statistics to improve our understanding of kelp forest communities at landscape scales.

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