

Role of forest-origin coarse particulate organic matter for the brackish water amphipod *Anisogammarus pugettensis*

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We assessed how litter piles (i.e., terrestrial leaves and twigs) in the river mouth act as a refuge for the marine amphipod (*Anisogammarus pugettensis*) from predation. We compared the survival rates of *A. pugettensis* under predation pressure from flounder (*Pleuronectes schrenki*) using different organic debris particle size classes and different amounts of debris (batch sizes). Particle size classes were <10, 10–50, and 50< mm, which were supplied in 0-, 5-, or 50-g batches. After 24 h, *A. pugettensis* survival was higher in larger batches of debris regardless of particle size. In addition, we conducted feeding experiments using kelp and terrestrial leaves as food resources for *A. pugettensis* in June and October 2005 to estimate the usage of these food resources. Although *A. pugettensis* that were fed only terrestrial leaves exhibited negative growth rates, carbon stable isotope analysis in both experimental seasons indicated that terrestrial leaves were part of the *A. pugettensis* diet. From these experiments, we concluded that terrestrial leaves are occasionally used as a food resource by *A. pugettensis*, although their principal role is as a refuge.

Key words: carbon stable isotope, CN ratio, flounder, food resource, growth rate, lignin, macroinvertebrate, refuge, total phenol

Introduction

Organic debris produced in upstream forests is used by a variety of stream- and river-dwelling species (e.g., Peterson and Cummins, 1974; Richardson, 1992; Wallace *et al.*, 1995) during transportation to the sea with the current flow. Mangrove systems (Skov and Hartnoll, 2002) and rivers with relatively short channel lengths and steep slopes do not conform to the river continuum concept (Vannote *et al.*, 1980). The river continuum concept applies to large rivers with long channel lengths, overhanging tree canopy which becomes more open downstream, and as the influence of the forest decreases, primary production by the alga-based food web becomes dominant. In short rivers, not all coarse particulate organic matter (>1 mm; Cummins, 1974) that enters the stream from riparian forest (Kochi *et al.* 2004) is decomposed in freshwater section of the river, and is carried into the neritic regions beyond the river mouth (Sakurai and Yanai, 2006). Sakurai and Yanai (2006) indicated that riparian forest-origin leaf litter piles in river mouth areas play an important role as feeding site for young cresthead flounder (*Pleuronectes schrenki*), an important fishery resource in Japan (Murakami, 2003) because the litter piles

form a habitat for their food resource, the amphipod (*Anisogammarus pugettensis*). Near Atsuta in Hokkaido, Japan, *A. pugettensis* has been found to comprise approximately 80% of the total annual gut contents of the flounder (Sakurai and Yanai, 2006).

A. pugettensis is widely distributed from the west coast of North America to coastal areas of the Kamchatka Peninsula and Sakhalin Island (Bousfield, 1957; Waldichuk and Bousfield, 1962; Kussakin *et al.*, 2001) as well as Hokkaido (Sakurai and Yanai, 2006). This species is an important food resource of salmon in coastal North America (Chang and Parsons, 1975) and flounder (*P. schrenki*) in Hokkaido, Japan (Sakurai and Yanai, 2006). In coastal areas of the Sea of Japan, *A. pugettensis* is the dominant species in leaf piles and clumps of kelp (Sakurai and Yanai, 2006).

Amphipods have been shown to use organic detritus as a habitat and as a food resource in freshwater and marine environments (Marchant and Hynes, 1981; Mancinelli and Rossi, 2002). As *A. pugettensis* does not occur in sandy bottom areas around the litter piles (Sakurai and Yanai, 2006) *A. pugettensis* are also considered to utilize litter piles as a habitat and for their food resource. Consequently, as the litter piles function as feeding sites for young cresthead flounder, the piles may also function as a refuge for *A. pugettensis*.

In the litter piles, we can observe twigs, leaves and pine cones of terrestrial-origin as well as seaweed fragments. Because the shape, size and composition of litter

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piles vary, their function as a habitat and food resource are considered to differ. In our previous study, although we showed that *A. pugettensis* consumed terrestrial leaves (Kochi and Yanai, 2006), it was uncertain if these leaves were assimilated or if they only passed through their digestive system. The function of litter piles for lower consumers in coastal areas is important to understand whole coastal food web and mechanism of fish propagation.

In this study, our purpose is first to clarify the importance of litter piles as refuges of *A. pugettensis*. We examined differences in the survivorship of *A. pugettensis* in the presence of a predator (the flounder *P. schrenki*) among different sizes and amounts of litter piles. Second, our purpose is to estimate importance of terrestrial leaves for *A. pugettensis* as a food resource.

Materials and Methods

Experiment 1

The experiment was conducted from June 23 to July 30 in 2004. Flounders (BL; 70–100 mm, one-year age; Murakami, 2003) were collected by diving near the mouths of the Atsuta and Gokibiru rivers. A total of 24 fish were immediately transported to the Hokkaido Central Fisheries Experimental Station, where they were acclimated at 14–15°C (ambient seawater temperature at the time of the experiments) in a large aerated aquarium (58 cm in diameter and 45 cm in height) for 2 weeks. During the rearing period, filtered seawater was supplied. The rearing water in the container was renewed every 48 h. Before the experiment, *A. pugettensis* was provided *ad libitum* as food for the flounders.

Litter piles that consisted of leaf fragments, twigs of terrestrial-origin and seaweed fragments were collected from the mouth of the Atsuta River. The litter piles were brought back to the laboratory and dried at 50°C for 48 h. The material was then sieved into the three particle sizes: <10 mm, 10–50 mm, and >50 mm in diameter. Macroinvertebrates were removed from the dried organic matter by hand sorting. After sieving, the particles were weighed to the nearest 0.1 g into 5-g and 50-g batches. Debris <10 mm in diameter was composed of fragmented wood (96%) and fragmented leaves (4%). Debris 10–50 mm in diameter was composed of fragmented wood and leaves, and occasionally cones of Japanese larch. Debris >50 mm in diameter was made up entirely of twigs. All particles were soaked in seawater for 24 h to rewet before the experiments.

A. pugettensis were collected from the Atsuta River 1 day before starting the experiment and transported to the laboratory in a cooler. They were kept in an aquarium until needed. The length range of *A. pugettensis* used in the experiment was 8–10 mm based on our earlier observations (Sakurai, unpublished data) that the gut contents in floun-

ders 70–100 mm long comprised mostly *A. pugettensis* in the length range of 1.5–10.0 mm.

Smaller cubic aquaria (with a thin black plastic frame, acrylic transparent case and no cover) containing 50 L of aerated and filtered seawater were placed apart from each other in a large tank. This tank was large enough to contain all smaller aquaria and can be used to change water level and temperature depending on an experimental design. This tank consisted of steel, which surface was coated by dark green color. Water temperature in the large tank was set at 14–15°C, and photoperiod corresponded to natural conditions.

We conducted three experiments with nine treatments to estimate the effect of particle size (<10 mm, 10–5 mm, >50 mm) and batch size (0 g as control, 5 g, 50 g) of the litter pile on *A. pugettensis* as a refuge. One fish was released into each small aquarium, followed by 20 *A. pugettensis*. In this study, we did not consider any behavioral difference of *A. pugettensis* possibly caused by sexual difference, and we used 20 randomly selected individuals. The 20 *A. pugettensis* that were released into the aquaria immediately hid among the litter piles. In the control aquaria, because there were no hiding spaces for *A. pugettensis* they tended to stay in the corners of the aquaria where they tried to conceal themselves by pressing flat against the side of the aquaria. In our pilot study, flounder of 70–100 mm body length were found to be able to consume more than 20 *A. pugettensis* within 24 h. Therefore we judged that the *A. pugettensis* that survived after 24 h did not arise from the flounder being satiated.

The *A. pugettensis* used for the experiments were renewed every time. However, we used the same fish up to three times for the experiments. To diminish any possible problems regarding learning by using the same flounder specimens for the experiments, we took 10 day intervals between each set of experiments (one litter size group × three litter amount). During the interval, they were kept in a large aquarium together as described above for the initial 2 week rearing. Therefore, the experimental procedure assumed no violation of the assumption of independence, i.e., using the same fish repeatedly had any effect on their consumption rate of *A. pugettensis*. We established six to eight replicates per treatment.

Experiment 2

Feeding experiments were conducted in June and October 2005, for 30 and 25 days, respectively. In June, *A. pugettensis* were collected from coastal brackish water in Atsuta, on the first day of the experiment (20 June). They were collected from woody debris using nets, kept in cooler box, and then transported to the laboratory. Random individuals were weighed (to the nearest 0.01 mg of wet weight) and then placed in a polyethylene chamber C-AP cup (Chuo

Kagaku Inc., Kounosu, Japan) containing 90 ml of seawater. Water in the chambers was renewed once every 2 days, with pre-filtered seawater from Atsuta that had been kept in an incubator at 15.5°C. We changed the chamber for larger polyethylene C-AP cups (diameter=12 cm, height=8.6 cm) filled with 400 ml of seawater after day 14 of the experiment. In this case seawater was renewed once every 3 days. Senescent kelp (*Laminaria religiosa*) and terrestrial leaves were also collected from Atsuta. *L. religiosa* is typically an annual plant that is widely distributed along the coast of the Sea of Japan (Nabata and Akino, 2003). We used only terrestrial leaves and pieces of kelp that had sufficient leaf area to cut the disks (see below) and discarded samples with holes. For most terrestrial leaves, we were unable to identify the species.

The experiment included three treatments each with ten replicates: “kelp”, “terrestrial”, and “mixed” (kelp and terrestrial leaves together). In the litter piles in the river mouth, kelp was predominant in addition to terrestrial woody debris. To simulate natural conditions, leaves were not dried. Disks (1 cm diameter) of kelp or terrestrial leaves for the experiment were obtained using a cork borer. For the kelp and terrestrial treatments two disks were added, while one disk of each was provided in the mixed treatment. Disks were added when necessary to compensate for losses due to feeding by *A. pugettensis*. The average (\pm SE) initial wet weight of *A. pugettensis* was 11.5 ± 1.8 mg ($N=30$) and initial values were not different among treatments ($\chi^2=0.44$, $P=0.80$, $N=30$). During the experiment, both the day length and the water temperature (15.5°C) simulated natural conditions. On day 30, we removed leaves from the chambers in every treatment. Seawater was renewed, and *A. pugettensis* were returned to each chamber to defecate. After 24-h incubation, we dried all *A. pugettensis* for 48 h at 50°C and measured the individual dry weights.

We estimated the water content of *A. pugettensis* using 25 additional individuals. We dried them for 48 h at 50°C, and then measured the dry weight of each individual to the nearest 0.01 mg. *A. pugettensis* water content was calculated as the difference between the wet and dry weights. The average water content (\pm SE) of 25 individuals was 67.1(\pm 1.3)%. The dry weight of *A. pugettensis* at the start of the experiment was calculated using this value. The daily growth rate (G) of *A. pugettensis* was calculated from the following equation.

$$G = (W_t - W_0) / (W_0 \cdot t) \times 100$$

W_0 is the initial dry weight and W_t is the dry weight at time t (in days).

After measuring the dry weight, individuals were ground into a fine powder and 1N-HCl solution added to remove the inorganic carbon. We then determined the stable

carbon isotope ratio ($\delta^{13}\text{C}$) of *A. pugettensis* in each treatment using an element analyzer (EA 1112, ThermoElectron, Waltham, Massachusetts, USA) and a mass analyzer (DELTA plus; Finnegan MAT, San Francisco, California, USA). Details concerning the isotope analysis are described in Yanai and Kochi (2005). At the beginning of the experiment, some *A. pugettensis* individuals were kept in filtered seawater for 24 h to allow them to excrete feces and were also used for isotope analysis. Kelp and terrestrial leaves were dried and ground to pass through a 0.4-mm mesh for isotope analysis. Because the $\delta^{13}\text{C}$ of an animal is influenced by its food and increases by +1‰ compared to its food (Fly, 1988), we discuss the relationship between *A. pugettensis* and its food resources (i.e., kelp and terrestrial leaves) using the results of the isotope analysis. In this study, because we could obtain only $\delta^{13}\text{C}$ of kelp and terrestrial leaves, we referred to Sakurai *et al.* (in press) for values for diatoms.

Powders of kelp and terrestrial leaves were also used to determine C:N ratios, total phenol, and lignin content. Kelp and terrestrial leaf carbon and nitrogen were analyzed using an element analyzer (EA 1110; CE Instruments, Milan, Italy). Total phenol (% dry weight) was determined using the Folin-Ciocalteu method, following Julkunen-Titto (1985). Klason lignin content (% dry weight) of terrestrial leaves was determined following the method of Effland (1977).

For the experiment in October, we collected *A. pugettensis* on the first day of the experiment (October 13), as described above for the June experiment. The average (\pm SE) initial wet weight of *A. pugettensis* was 2.19 ± 0.17 mg ($N=30$), and initial values were not different among treatments ($\chi^2=0.53$, $P=0.77$, $N=30$). We used the same chambers as in June (diameter=12 cm, height=8.6 cm) for incubations. Water temperature was maintained at 17.0°C, and the day length simulated natural conditions. After the 25-d experiment, we used identical methods to those described above for all analyses. We also used the same value to calculate the water content of *A. pugettensis*.

Statistical analysis

For experiment 1, survival rate values were square root transformed and analyzed using two-way analysis of variance (ANOVA) to estimate the effects of particle size (three levels: <10 mm, 10–50 mm, >50 mm), batch size (three levels: 0, 5, or 50 g), and their interaction. For experiment 2, we conducted χ^2 tests to compare survival rates between experimental seasons (June and October) and leaf type (kelp, terrestrial, and mixed). In addition, we used two-way ANOVA to compare differences in growth rates and carbon stable isotope values, C:N ratios and total phenol content. The two main factors were experimental season and leaf type. All data were log ($x+1$)-, radial-, or square root-trans-

formed for standardization and to improve normality. When differences were significant in a two-way ANOVA, Tukey's HSD test was performed to differentiate statistically mean values. We also used a non-parametric Kruskal-Wallis test to explore the difference in lignin content of terrestrial leaves between seasons. All statistical analyses were performed using SYSTAT ver. 8.0 (1988, SPSS Inc., Chicago, Illinois, USA).

Results

Experiment 1

In the control treatment, after the release of *A. pugettensis* in each aquarium, young flounder immediately found *A. pugettensis* and preyed on them. However, in the 5-g, and the 50-g batch treatments, because *A. pugettensis* hid among the litter, the young flounder searched for them by swimming among the litter. In these litter treatments, concomitantly to the flounder's swimming, litter was disturbed. Based on our observation, it seemed difficult for young flounder to find *A. pugettensis* in larger amounts of the litter.

After 24 h, in all litter size classes of the experiment, the remaining number of *A. pugettensis* was smallest in control, ranged from 0.2 to 1.1 individuals. Litter batch size significantly affected the *A. pugettensis* survival (two-way ANOVA $F_{2,53}=24.01$ $P<0.001$). Survival of *A. pugettensis* increased with the increase of the batch size. However, a significant difference was not found either among the particle size classes ($F_{2,53}=2.58$ $P=0.085$) or for the interaction of litter batch and particle size ($F_{4,53}=0.70$ $P=0.59$) (Fig. 1). By this experiment, we concluded that although the amount of litter affected *A. pugettensis* survival, litter particle size did not affect *A. pugettensis* survival.

Experiment 2

A. pugettensis survival rates differed among treatments in June. Individuals that were fed only terrestrial leaves exhibited a 60% survivor rate although individuals in the other treatments all survived during the experiment ($F=2$, $\chi^2=9.23$, $P<0.01$). In October, survivorship of *A. pugettensis* was not different among the treatments; 90% in kelp treatment and 80% in both terrestrial and mix treatments ($F=2$, $\chi^2=0.48$, $P=0.78$). *A. pugettensis* growth rates differed significantly among seasons ($F_{1,45}=26.09$, $P<0.001$) and leaf types ($F_{2,45}=25.15$, $P<0.001$), but there was no interaction between factors ($F_{2,45}=1.99$, $P=0.14$; Fig. 2). Interestingly, *A. pugettensis* exhibited positive growth rates when fed kelp or a mixture of kelp and terrestrial leaves, but growth rates were negative when they were fed only terrestrial leaves. In all treatments, *A. pugettensis* growth rates were higher in October than in June. A two-way ANOVA revealed that the $\delta^{13}\text{C}$ of *A. pugettensis* was significantly affected by season ($F_{1,30}=5.98$, $P<0.05$) and leaf type

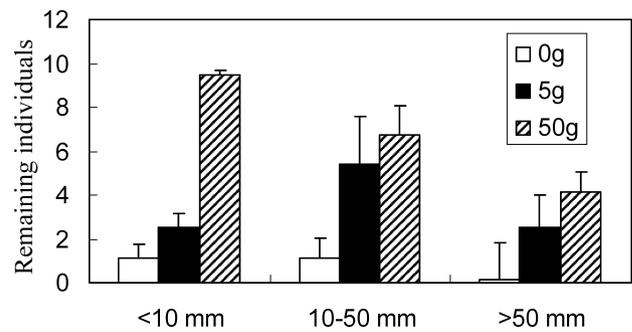


Figure 1. Survivorship (mean±SE) of *A. pugettensis* (20 individuals) under flounder predation as a function of organic detritus particle size (<10 mm vs. 10–50 mm vs. 50< mm) and batch size (0 g vs. 5 g vs. 50 g). N=8 at each batch size for <10 mm, 7 for 10–50 mm, 6 for 50< mm. Litter batch size significantly affected the *A. pugettensis* survival (ANOVA $P<0.001$).

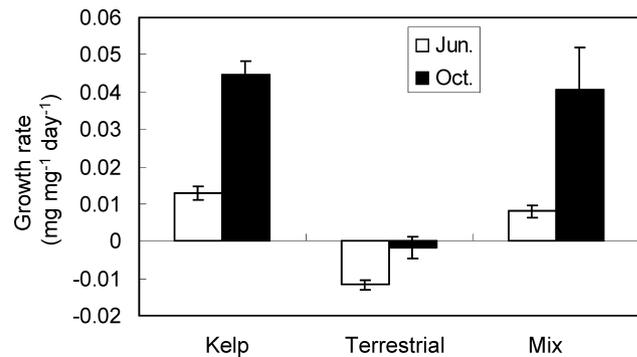


Figure 2. Daily growth rates (mean±SE) of *A. pugettensis* during the two feeding experimental seasons. Growth rates differed significantly among seasons (ANOVA, $P<0.001$) and leaf types (ANOVA, $P<0.001$). Growth rates of kelp and mix treatments were significantly higher than that of terrestrial treatment (Tukey's HSD test, $P<0.05$). N=10 at each treatment.

($F_{3,30}=50.35$ $P<0.001$), although their interaction was also significant ($F_{3,30}=3.50$, $P<0.05$) (Fig. 3). The $\delta^{13}\text{C}$ values of *A. pugettensis* after *A. pugettensis* were fed terrestrial leaves did not differ from the initial values in June and shifted to terrestrial leaf values in October. On the other hand, *A. pugettensis* $\delta^{13}\text{C}$ values in the kelp and mixed treatments clearly shifted towards those of the kelp $\delta^{13}\text{C}$.

The C:N ratio differed between the kelp and terrestrial leaf (ANOVA: $F_{1,16}=6.07$, $P<0.05$), but not between seasons ($F_{1,16}=0.19$, $P=0.67$) (Fig. 4). Terrestrial leaves had a higher C:N ratio than kelp. Total phenol content differed between seasons (ANOVA: $F_{1,8}=76.67$, $P<0.001$) and leaf types ($F_{1,8}=89.04$, $P<0.001$), with no interaction ($F_{1,8}=1.56$, $P=0.26$). Terrestrial leaves had a higher total phenol content than kelp. In addition, both kelp and terres-

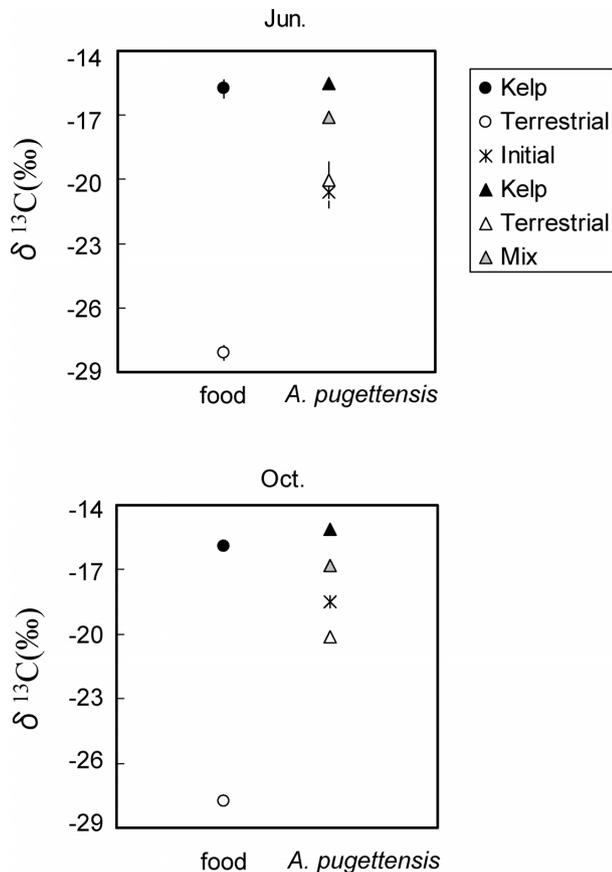


Figure 3. $\delta^{13}\text{C}$ (mean \pm 2SE) of the *A. pugettensis* and their food resources (kelp and terrestrial leaves). N=5 at each treatment.

terrestrial leaves had higher total phenol contents in October than in June. In contrast, the lignin content of terrestrial leaves was higher in June than in October (Kruskal-Wallis test: $P<0.05$) (Fig. 5).

Discussion

Everett and Ruiz (1993) reported that the survival of glass shrimp (*Palaemonetes pugio*) under fish (*Fundulus heteroclitus*) predation pressure in the laboratory was approximately 2–2.5 times higher in the presence of coarse woody debris (30 cm long and 10 cm in diameter) than in tanks without refuges. Although the woody fragments used in our study were of a smaller particle size than those used by Everett and Ruiz (1993), we observed a similar refuge effect. It is reasonable to assume that larger amounts of organic matter yield more refuges and resulted in higher *A. pugettensis* survival. Although we found no statistical differences among organic matter size classes, we observed variation in *A. pugettensis* hiding behavior, perhaps owing to differences in the physical structure of the organic matter. For <10-mm organic matter that was composed of frag-

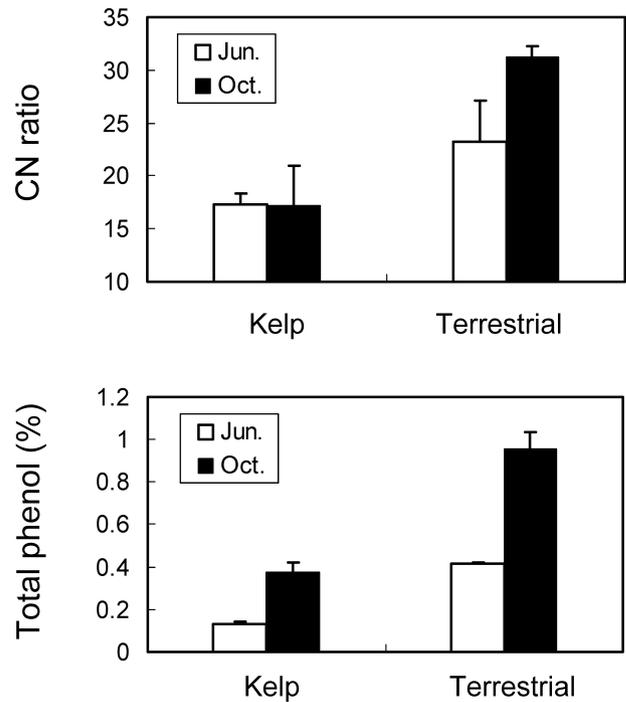


Figure 4. C:N ratio and phenol content (mean+SE) of kelp and terrestrial leaves. N=5 for C:N ratio and N=3 for phenol content at each group. C:N ratio differed between the kelp and terrestrial leaves (ANOVA, $P<0.05$). Total phenol content differed between seasons (ANOVA, $P<0.001$) and leaf types (ANOVA, $P<0.001$).

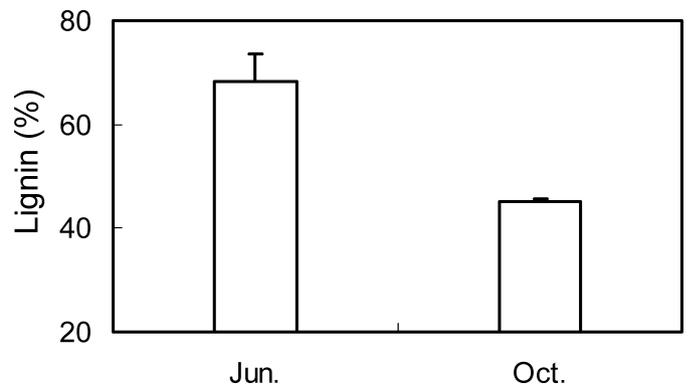


Figure 5. Lignin content (mean+SE) of the terrestrial leaves. N=3 at each season. The lignin content of terrestrial leaves was significantly higher in June than in October (Kruskal-Wallis test: $P<0.05$).

mented twigs and leaves, there were no interparticle voids in fragments. Thus, *A. pugettensis* could only hide within cracks between twigs and leaves. Because these cracks served as refuges, increases in the amount of organic matter should be directly correlated with increases in the availability of refuges, allowing individuals to survive. In contrast,

>10 mm organic matter often contained pore spaces, such as empty spaces within Japanese larch cones or hollows within twigs. In general, greater habitat complexity reduces predation pressure (Russo, 1987; Tatrai and Herzig, 1995). Therefore, increases in the structural complexity of organic matter could augment *A. pugettensis* survivorship.

Although we observed differences in *A. pugettensis* growth rates between the experimental seasons, patterns of growth rates corresponding to the three leaf-type treatments were similar between the seasons. Terrestrial leaves alone appeared to be a poor-quality food resource, as *A. pugettensis* exhibited negative growth rates when fed this leaf type alone. In our experiment, the relative nitrogen content was lower and phenol content was higher in terrestrial versus kelp leaves in both seasons. Moreover, terrestrial leaves contained much more lignin, although algae in general (including kelp) do not contain true lignin (Swain, 1979; Ragan and Glombitza, 1986). In freshwater environments, oak leaves kept in stream water for 24 h contained about 2% phenol and about 25% lignin (Kochi and Kagaya, 2005). In this study, terrestrial leaves collected from seawater contained much lower levels of phenol and higher levels of lignin than leaves from the above experiment in freshwater, indicating that leaves from seawater had already been well decomposed and fragmented during the river transport and/or drifting in seawater. However Sakurai *et al.* (in press) showed in their experiment that *A. pugettensis* in November did not preferentially consume kelp to terrestrial leaves when kelp and terrestrial leaves were supplied together. Seasonal differences of chemistry in leaves and kelp may affect their availability for *A. pugettensis*.

Stable isotope analysis revealed that the $\delta^{13}\text{C}$ of *A. pugettensis* differed between the kelp, terrestrial and mixed treatments. $\delta^{13}\text{C}$ of *A. pugettensis* reflected $\delta^{13}\text{C}$ of kelp and mixture of kelp and terrestrial leaves during both experimental seasons. It is interesting that although terrestrial leaves had little potential as a food resource for *A. pugettensis*, $\delta^{13}\text{C}$ of *A. pugettensis* moved toward the value of terrestrial leaves after they fed on terrestrial leaves in October. However, they could not depend on all of the nutrient derived from terrestrial leaves. As Sakurai *et al.* (in press) indicated, they would use epiphytic diatoms, which have 16.85 of $\delta^{13}\text{C}$, on the leaves and/or kelp in addition to the terrestrial leaves and kelp. The initial $\delta^{13}\text{C}$ value of *A. pugettensis* was intermediate of terrestrial leaves and kelp leaves in June and shifted a little to kelp in October. Therefore, in both seasons, especially in June, it was possible that senescent kelp leaves were scarce, thus, *A. pugettensis* had to use terrestrial leaves as a supplementary food resource in addition to kelp leaves.

In October, *A. pugettensis* growth rates were approximately four times higher in the same treatments than in

June. In addition to the leaf quality, the difference may be related to the initial body weights of *A. pugettensis*. *A. pugettensis* used in October were smaller in size than those used in June. In a freshwater growth experiment, Sutcliffe *et al.* (1981) demonstrated that growth rates of *Gammarus* amphipods decrease with age. In addition, water temperature may have affected the differences in growth rates between seasons. Sutcliffe *et al.* (1981) showed that the growth rates of younger *Gammarus* increased with increases in water temperature. Rearing water temperature was higher in October than in June in our experiments. We also obtained higher growth rates of *A. pugettensis* than the present rates in June when they were bred in higher water temperatures in the previous study (Kochi and Yanai, 2006).

Leaves and twigs in seawater that serve as a refuge for *A. pugettensis* are potentially a hindrance to flounder, which may feed less effectively in the presence of this prey refuge. However, young flounder could also take advantage of litter piles for use as habitat and refuge from predators. Similarly, juveniles of many flatfishes occur in nursery areas where they experience abundant food resources, favorable temperatures, and shelter from predation (Reichert, 2003).

Future research should focus on the amount, distribution of mixture of kelp and forest-origin leaf litter pile in seawater, and seasonal changes of their composition and availability.

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河口域に流下した落葉が海産ヨコエビ *Anisogammarus pugettensis* に果たす役割

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森林域から河口域に流下した粗大有機物が、沿岸に生息するトンガリキタヨコエビ(*Anisogammarus pugettensis*)の隠れ場所や食物資源としてはたす役割を明らかにするために飼育実験を行った。1, 粒径と量の異なる落ち葉だまり内において、クロガシラガレイ若齢魚を捕食者として24時間後のトンガリキタヨコエビの生残率を測定した。ヨコエビの生残率はどの粒径においても量が多い場合に最大であった。2, 落葉と海藻(ホソメコンブ)を食物資源としてト

ンガリキタヨコエビの飼育実験を行い、成長速度と炭素安定同位体比を調べた。ヨコエビの安定同位体比からは、海藻に加え、体内に落葉も取り込んでいる事が示された。トンガリキタヨコエビは、落葉を主に隠れ場所として利用するが、予備的に食物資源としても利用していると推察され、河口域の落葉だまりは、低次消費者の涵養の場として重要な役割を果たしていると考えられた。

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