

Secondary production of *Jassa slatteryi* (Amphipoda, Ischyroceridae) on a *Zostera marina* seagrass bed in southern Korea

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ABSTRACT: On the basis of monthly samples, we measured the secondary production of the amphipod *Jassa slatteryi* Conlan 1990, on a *Zostera marina* L. seagrass bed in Gwangyang Bay, southern Korea. The standing crop of seagrass showed 2 peaks in spring and fall, with maximum biomass in May. Biomass distribution of *J. slatteryi* was positively correlated with the standing crop of seagrass ($p < 0.05$), suggesting that there is a biological interaction between these 2 species. *J. slatteryi* displays 2 main breeding periods during the year; in spring (March to May) and in fall (October to December). The biomass of *J. slatteryi* and the standing crop of seagrass in the spring was much higher than in the fall. The annual secondary production of *J. slatteryi* in the Gwangyang Bay seagrass bed ($20.07 \text{ g dry weight m}^{-2} \text{ yr}^{-1}$) is the highest reported in amphipods inhabiting seagrass beds. However, the annual production:biomass (*P:B*) ratio, at 5.21, was lower than recorded previously in both temperate and tropical seagrass beds because the number of generations decreases the *P:B* ratio. The combination of high abundance and secondary production suggests an important role for *J. slatteryi* in the seagrass-bed ecosystem as a trophic link from primary producers to higher consumers.

KEY WORDS: Secondary production · Seagrass bed · *Jassa slatteryi*

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INTRODUCTION

Seagrass beds are among the highest producing habitats of marine ecosystems and, from a trophic structure point of view, occupy an important position in coastal ecosystems (Thayer et al. 1984). Seagrass meadows support a high abundance and diversity of associated fauna, microphytobenthos and microorganisms (Stoner 1980, Cariou-Le Gall & Blanchard 1995), which are consumed by higher predators (e.g. crabs, fish, and waterfowl) utilizing the seagrass beds as feeding areas (Thayer et al. 1975). A notable feature of seagrass beds is the high density of invertebrate fauna (resident infauna and epifaunal invertebrates) relative to that in adjacent, unvegetated habitats (Orth et al. 1984). The abundance and density of invertebrate fauna in seagrass beds is an important factor determining production in coastal ecosystems.

Small and migratory isopods, amphipods and mysids are characterized by rapid turnover rates (Drake & Arias 1995), and may predominate in seagrass beds (Jeong et al. 2004). In particular, amphipods are considered to be one of the most important secondary producers in seagrass beds (Fredette & Diaz 1990). Amphipods utilize primary food sources such as detritus and phytoplankton, and are in turn prey for higher-level consumers such as fishes and large crustaceans (Nelson 1979, Vetter 1995, Derrick & Kennedy 1997).

The amphipod crustacean *Jassa slatteryi* Conlan, 1990 is an epibenthic, abundant species of intertidal vegetated habitats, living at a depth of about 1 to 30 m below spring tide low water (Barnard 1958, Hong 1983). On the basis of a year-round survey, Jeong et al. (2004) reported that *J. slatteryi* was a dominant species on the *Zostera marina* L. seagrass bed of southern Korea. A few studies have briefly addressed the distri-

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bution and systematics of *J. slatteryi* (Hong 1983, Jeong et al. 2004). Many studies have been carried out on the secondary production of amphipods (see Yu & Suh 2002). However, most of these studies were concentrated on amphipod species inhabiting unvegetated habitats. The secondary production of amphipods in seagrass beds remains largely unknown. Moreover, no attempts to measure secondary production of *J. slatteryi* have been made. The objectives of this study are 2-fold: (1) to measure the annual variation of biomass and (2) to estimate the secondary production of *J. slatteryi* on seagrass beds in southern Korea.

MATERIALS AND METHODS

Sampling. The sampling station was a sublittoral seagrass bed surrounded by rock in the northwestern part of Namhae-do, Gwangyang Bay (Fig. 1). Tidal levels were measured as the distance (m) above and below mean sea level (MSL) at Gwangyang (NORI 2002). The annual tidal range varied from 415 cm above to 22 cm below MSL. The seagrass beds along the shoreline and are 10 to 30 m wide and 90 to 100 m long. Water temperature and salinity ranged from 9.2 to 26.4°C and from 10.9 to 31.6 psu, respectively (Fig. 2). During the rainy season, the lowest salinity in August was clearly linked to the runoff of Seomjin River near the sampling station.

Epibenthic amphipods on *Zostera marina* seagrass leaves were sampled monthly from January to Decem-

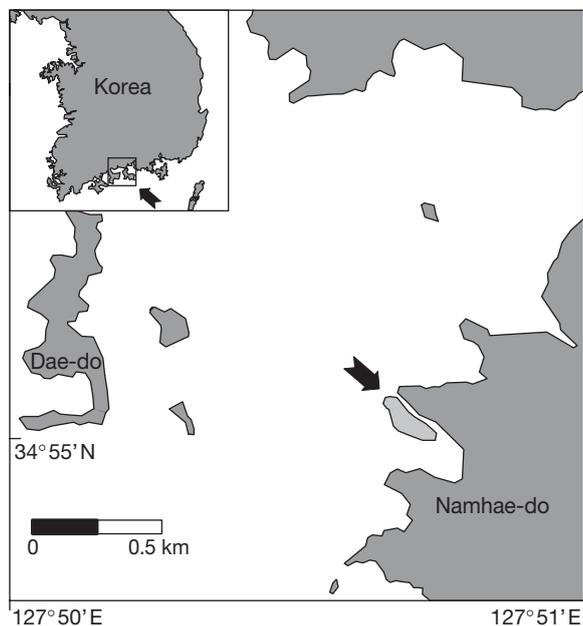


Fig. 1. Location of the sampling site in Gwangyang Bay, southern Korea. The arrows indicate the seagrass bed investigated

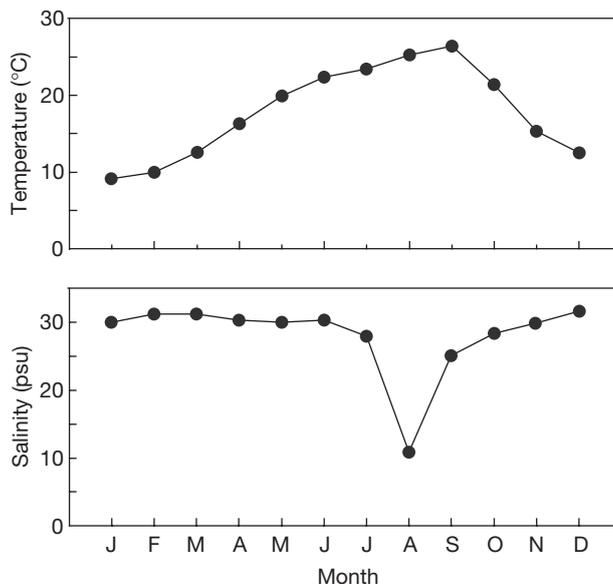


Fig. 2. Monthly variation of temperature and salinity

ber 2002 at the spring tide low water mark. Three replicate samples were collected using a diver-operated hand-held net (15 × 15 cm mouth, 0.15 mm mesh size). The hand-held net was carefully placed over seagrass and covered from the tip of leaves to the shoot rhizome. Next, the mouth of the net was closed before cutting the rhizomes. To avoid disturbance of sediment, sampling was carried out in the upper ~15 cm of the water. The seagrass samples were transported to the laboratory, where the animals were separated from seagrass by rinsing with filtered sea water.

The dry weight (DW) of seagrass was measured after drying for 24 h at 60°C and weighed to the nearest 0.01 g using an electronic microbalance (Mettler Instrument, UMT2). The animals separated were immediately preserved in 5% borate-buffered formaldehyde with filtered sea water. Individuals of *Jassa slatteryi* were sorted and counted under a dissecting microscope. The size of individuals was determined by measuring the length of the animal from the tip of the rostrum to the end of the telson under a stereomicroscope fitted with an image analysis system (Image Pro Plus 2.0).

Biomass. Additional samples to measure biomass were collected from March to May 2004. After collection, live individuals of *Jassa slatteryi* were sorted under a dissecting microscope and placed separately in a vial filled with filtered sea water. They were transported to the laboratory to clear the gut. Next, all live *J. slatteryi* were incubated for 48 h without food. After incubation, live animals were rinsed with distilled water and their body length (BL) measured in cm. For DW measurement, specimens were dried for 24 h at 65°C and individually weighted to the nearest 0.1 µg

using an electronic microbalance (Mettler Instrument, UMT2). The regression of DW (in mg) was obtained in an equation of the form: $DW = aBL^b$, where a and b are constants.

Secondary production. Because the cohorts of amphipods inhabiting seagrass beds were difficult to separate, secondary production of *Jassa slatteryi* was estimated using the size-frequency method. The conceptual basis of this method is the use of the average size-frequency distribution to sum the total losses between size groups based on samples taken monthly throughout the year. Benke's (1979) modification of the basic production equation of Hynes methods (Hynes 1961, Hamilton 1969) is used here:

$$P = \left[I \sum_{j=1}^i (\bar{N}_j - \bar{N}_{j+1}) \times \sqrt{\bar{W}_j \bar{W}_{j+1}} \right] \times (365 / CPI)$$

where P is the annual production, I is the number of times loss factor, i is the number of size classes, N_j is the mean number of individuals in size class j (averaged over the entire year), W_j is the mean DW of individuals in size class j , and CPI the cohort production interval (in days) from hatching to reaching the largest size class. When a difference in maximum length between females and males occurred, we selected the lower times loss factor to avoid overestimation of production (Waters & Hokenstrom 1980). The annual production was the summation of the production of each size class multiplied by $365/CPI$ to account for multiple broods (Benke 1979). The life cycle of *J. slatteryi* is nearly 1 yr (S. J. Jeong unpubl. data), therefore the value of $365/CPI$ was not modified. The accuracy of the size-frequency method increases with the use of smaller size intervals (Cushman et al. 1978). Because the mean size of newly hatched juveniles of *J. slatteryi* was 0.75 mm (see Fig. 4), we used 1 mm size classes to estimate secondary production.

RESULTS

Biomass

The relationship between the standing crop of seagrass and biomass of *Jassa slatteryi* was highly significant (Pearson's correlation test, $n = 185$, $r^2 = 0.88$, $p < 0.05$). The standing crop of seagrass showed 2 peaks throughout the year (Fig. 3). The standing crop increased from 60 g DW m⁻² in February to 838.51 g DW m⁻² in May and then decreased to 240.43 g DW m⁻² in August. After September, the standing crop increased again and reached a value of 338.60 g DW m⁻² in November.

The significant relationship between BL and DW of *Jassa slatteryi* is presented by the regression equation:

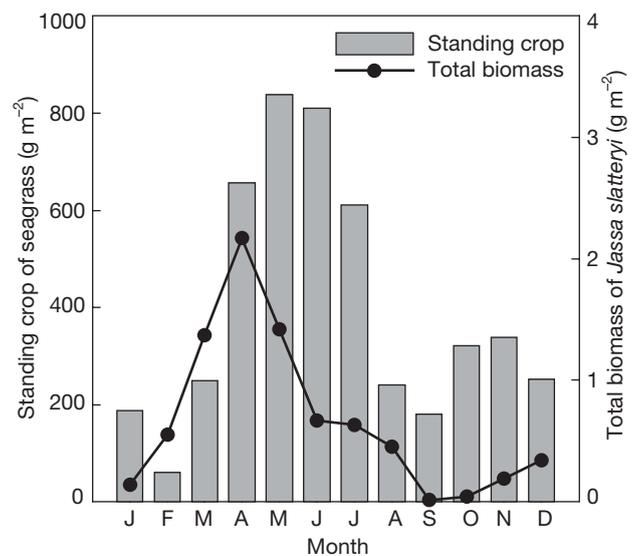


Fig. 3. *Jassa slatteryi*. Seasonal variation in total biomass (DW) of *J. slatteryi* and the standing crop (DW) of seagrass

$DW = 0.0048BL^{2.44}$ ($n = 131$, $r^2 = 0.87$, $p < 0.05$). Biomass distribution of *J. slatteryi* was similar to the variation pattern of the standing crop of seagrass, and showed 2 peaks in April and December (Fig. 3). It rapidly increased from 0.14 g DW m⁻² in January to 2.27 g DW m⁻² in April and then decreased to 0.01 g DW m⁻² in September. The biomass increased again and showed a value of 0.34 g DW m⁻² in December.

Biomass of *Jassa slatteryi* is also closely related to the growth periods of seagrass (Fig. 3). The biomass of each size class was lower in the early fall than in the other seasons, but the proportion of small individuals was higher in fall (Fig. 4). The total biomass was very low in late summer and winter (Fig. 3). Biomass of small individuals (<3 mm) was greater than that of large individuals (>3 mm) in spring and fall, whilst the biomass of large individuals increased during spring and early winter before the breeding period (Fig. 4). In the spring and fall breeding periods, the BL of *J. slatteryi* ranged from 3.0 to 8.0 mm. Mean DW of *J. slatteryi* was very high during fall and then rapidly decreased in the early winter (Fig. 5). Maximum mean DW was 17.12 mg m⁻² in November. Density was negatively related to mean DW (Fig. 5).

Production

Before the estimation of secondary production, the number of times loss factor was reduced from 10 to 9 because the maximum lengths of males and females were 8.25 and 9.75 mm, respectively. The total produc-

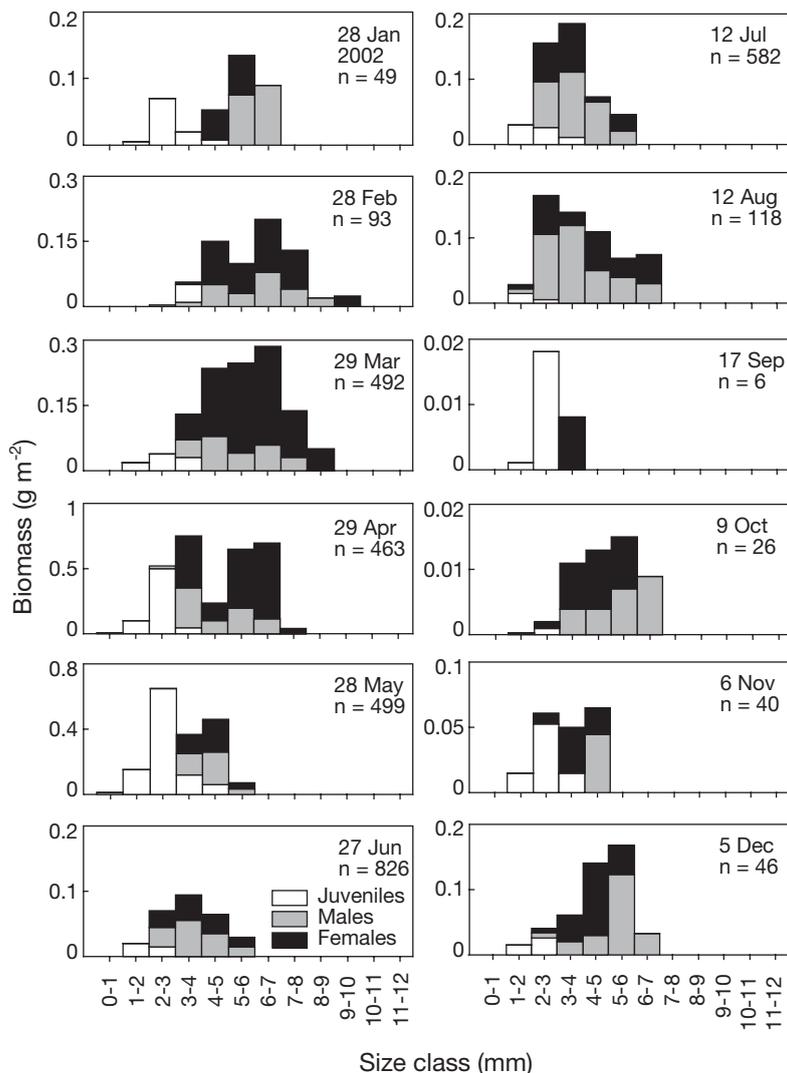


Fig. 4. *Jassa slatteryi*. Seasonal variation in biomass (DW) structure

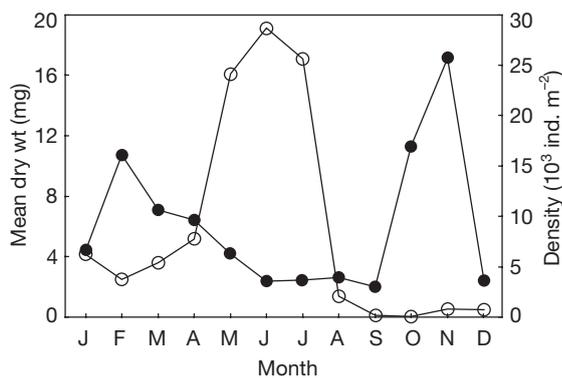


Fig. 5. *Jassa slatteryi*. Seasonal variation in mean DW (●) and density (○)

tion of *Jassa slatteryi* was estimated as 20.07 g DW m⁻² yr⁻¹, and annual biomass as 3.85 g DW m⁻² yr⁻¹. The annual P:B ratio was estimated as 5.21 (Table 1).

DISCUSSION

Based on foregut content analysis, Jeong et al. (2004) reported that the main food items of *Jassa slatteryi* consist of seagrass tissues and benthic diatoms. Thus, *J. slatteryi* is a herbivorous feeder. The growth pattern of seagrass was closely correlated with the biomass structure of *J. slatteryi*, as was previously observed by Fredette & Diaz (1986) for *Gammarus mucronatus*. The growth of seagrass is clearly linked to the secondary production of *J. slatteryi*.

Marine amphipods exhibit a wide range of secondary production according to species and

Table 1. *Jassa slatteryi*. Estimation of secondary production of *J. slatteryi* on the seagrass beds of Gwangyang Bay by the size-frequency method. Biomass expressed as DWs. No. lost: lost individual number between 2 successive size groups; Wt. at lost: geometric mean of individual weights between 2 successive size groups; wt. lost: lost production in each size group; No. times lost: number of size groups through which *J. slatteryi* grows

Size group (mm)	Density (No. m ⁻²)	Mean wt (mg)	Standing stock (g m ⁻²)	No. lost (m ⁻²)	Wt. at lost (mg)	Wt. lost (g m ⁻²)	No. times lost	Production (g m ⁻²)
0–1	44.45	0.00	0.00	-1009.52	0.01	-0.01	9	-0.06
1–2	1053.97	0.01	0.01	-11292.25	0.03	-0.28	9	-2.55
2–3	12346.22	0.05	0.58	4065.04	0.07	0.29	9	2.60
3–4	8281.18	0.11	0.88	4065.31	0.15	0.60	9	5.37
4–5	4215.87	0.20	0.85	1053.97	0.25	0.26	9	2.37
5–6	3161.90	0.31	0.98	2159.20	0.38	0.82	9	7.37
6–7	1002.70	0.47	0.47	949.37	0.55	0.52	9	4.70
7–8	53.33	0.65	0.03	26.66	0.77	0.02	9	0.18
8–9	26.67	0.91	0.02	8.89	1.02	0.01	9	0.08
9–10	17.78	1.15	0.02	17.78	0.00	0.00	9	0.00
Total biomass		3.85			P:B ratio	5.21	Total production	20.07

Table 2. Secondary production, P (g DW m⁻² yr⁻¹) and annual $P:B$ ratio for amphipods

Species	Location and depth (m)	Habitat	P	$P:B$ ratio	Source
<i>Ampelisca agassizi</i> (Judd, 1896)	Georges Bank, USA (84)	Marine sublittoral zone	2.2	1.5	Collie (1985)
<i>Uinctola inermis</i> Shoemaker, 1945	Georges Bank, USA (84)	Marine sublittoral zone	2.8	2.5	Collie (1985)
<i>Erichthonius fasciatus</i> (Stimpson, 1853)	Georges Bank, USA (84)	Marine sublittoral zone	2.3	4.4	Collie (1985)
<i>Haploops fundiensis</i> Wildish and Dickinson, 1982	Bay of Fundy, NW Atlantic (80)	Marine sublittoral zone	0.1 ^a	1.3	Wildish (1984)
<i>Photis reinhardi</i> Krøyer, 1842	Bay of Fundy, NW Atlantic (80)	Marine sublittoral zone	0.1 ^a	2.8	Wildish (1984)
<i>Casco bigelowi</i> (Blake, 1929)	Bay of Fundy, NW Atlantic (80)	Marine sublittoral zone	0.2 ^a	2.5	Wildish (1984)
<i>Harpinia propinqua</i> Sars, 1895	Bay of Fundy, NW Atlantic (80)	Marine sublittoral zone	0.01 ^a	3.1	Wildish (1984)
<i>Ampelisca araucana</i> Gallardo, 1963	Coast, Chile (65)	Marine coast	9.8	3.7–4.5	Carrasco & Arcos (1984)
<i>Ampelisca macrocephala</i> Liljeborg, 1852	Chirikov Basin, N Bering Sea (35–50)	Marine coast	39.8	0.9	Highsmith & Coyle (1990)
<i>Ampelisca tenuicornis</i> Liljeborg, 1856	Bay of Morlaix, English Channel (17)	Marine coast	0.7	3.12	Dauvin (1988a)
<i>Ampelisca brevicornis</i> (Costa, 1853)	Bay of Morlaix, English Channel (17)	Marine coast	0.04–0.3	0.4–3.5	Dauvin (1988b)
<i>Ampelisca typica</i> (Bate, 1857)	Bay of Morlaix, English Channel (17)	Marine coast	0.07–0.16	4.1–4.4	Dauvin (1988c)
<i>Ampelisca armoricana</i> Bellan-Santini and Dauvin, 1981	Bay of Morlaix, English Channel (17)	Marine coast	0.1–10.4	1.8–2.7	Dauvin (1988d)
<i>Ampelisca sarsi</i> Chevreux, 1887	Bay of Morlaix, English Channel (17)	Marine coast	0.02–1.0	1.9–3.0	Dauvin (1989)
<i>Byblis japonicus</i> Dahl, 1944	Shijiki Bay, Japan (10)	Marine estuary	7.35	10.83	Sudo & Azeta (1996)
<i>Ampelisca abdita</i> Mills, 1964	Joco marsh, Jamaica Bay, USA (10)	Marine estuary	25.3	3.7	Franz & Tancredi (1992)
<i>Ampelisca abdita</i> Mills, 1964	Ruffle Bar, Jamaica Bay, USA (1)	Marine estuary	47	3.5	Franz & Tancredi (1992)
<i>Pontoporeia femorata</i> Krøyer, 1842	St. Margaret's Bay, Canada (4–10)	Marine estuary	2.3–2.8 ^a	3.6–4.8	Wildish & Peer (1981)
<i>Ampelisca abdita</i> Mills, 1964	Fountain Avenue, Jamaica Bay, USA (8)	Marine estuary	32.4	4.2	Franz & Tancredi (1992)
<i>Rhepoxynius abronius</i> Barnard, 1960	Yaquina Bay, USA (5)	Marine estuary	0.7–1.1	1.29–2.09	Kemp et al. (1985)
<i>Ampelisca tenuicornis</i> Liljeborg, 1856	Maritime Rance, English Channel (4)	Marine estuary	0.7–1.7	4.2–3.7	Dauvin (1988a)
<i>Corophium volutator</i> (Pallas, 1766)	Maritime Rance, English Channel (4)	Marine estuary	0.3–0.5	2.1–4.0	Dauvin (1988b)
<i>Ampelisca brevicornis</i> (Costa, 1853)	Western Sweden (0.5)	Marine tidal zone	1.6	5.1	Moller & Rosenburg (1982)
<i>Hausitorius Canadensis</i> Bousfield, 1962	Derbyhaven, Isle of Man	Marine tidal zone	1.3–1.7	2.5–3.2	Hastings (1981)
<i>Synchelidium lenorostratum</i> Hirayama, 1986	Maine, USA	Marine tidal zone	1.02	1.5	Donn & Croker (1986)
<i>Parhyale basrensis</i> Salman, 1986	Dolsando, Korea (1)	Marine tidal zone	1.09	5.68	Yu & Suh (2002)
<i>Microdeutopus gryllotalpa</i> Costa, 1853	Shatt al-Arab River, Iraq	Marine tidal zone	5.58	3.06	Ali & Salman (1987)
<i>Gammarus mucronatus</i> Say, 1818	Cadiz Bay, Spain (<0.1)	Marine lagoon	4.6 ^a	12.8	Drake & Arias (1995)
<i>Gammarus mucronatus</i> Say, 1818	Massachusetts, USA (<2)	Salt marsh	12.5–15.8	12.5–15.8	LaFrance & Ruber (1985)
<i>Gammarus mucronatus</i> Say, 1818	Chesapeake Bay, USA (0.3–1.0)	Seagrass beds	14.3	23.6–76.8	Fredette & Diaz (1990)
<i>Gammarus mucronatus</i> Say, 1818	York River, USA	Seagrass beds	5–10	15.8–36.8	Fredette & Diaz (1986)
<i>Jassa slatteryi</i> Conlan, 1990	Gwangyang Bay, Korea (1–1.5)	Seagrass beds	20.07	5.21	This study

^aValues converted to g DW using the weight-to-weight conversion factors of Ricciardi & Bourget (1998)

habitat (Table 2). In unvegetated habitats, the highest production value reported was 47 g DW m⁻² yr⁻¹ for *Ampelisca abdita* in Jamaica Bay, New York (Franz & Tanacredi 1992). However, the production of most amphipods inhabiting unvegetated habitats ranges from 0.1 to 15.8 g DW m⁻² yr⁻¹; *Ampelisca macrocephala* is an exception with a production of 39.8 g DW m⁻² yr⁻¹ in the Bering Sea (Highsmith & Coyle 1990). In seagrass beds, on the other hand, the highest production value reported was 14.30 g DW m⁻² yr⁻¹ for *Gammarus mucronatus* from the lower Chesapeake Bay (Fredette & Diaz 1990). In this study, the secondary production of *Jassa slatteryi* was 20.07 g DW m⁻² yr⁻¹, the highest value for amphipods inhabiting seagrass beds.

The high production measured in this study can be explained in 2 possible ways. One reason could be the difference in mesh size of the sampling nets. To investigate the life cycle of *Gammarus mucronatus*, Fredette & Diaz (1986) collected samples using net with a mesh size of 0.25 mm. However, for measuring secondary production, Fredette & Diaz (1990) used a net with a mesh size of 0.5 mm, without commenting on the change of mesh size. Considering the size of newly hatched juveniles of *G. mucronatus*, it is possible that juveniles of *G. mucronatus* were not quantitatively sampled. The size class containing the newly hatched amphipods was the largest of all the size classes of *G. mucronatus* tested (see Fredette & Diaz 1986, Figs. 8 to 10). We suggest, therefore, that the secondary production of *G. mucronatus* could have been underestimated. In our study, a hand-held net with a mesh size of 0.15 mm allowed us to collect all newly hatched juveniles quantitatively, since the smallest newly hatched juveniles of *Jassa slatteryi* are 0.5 mm.

The second reason for the high production measured in this study could be the large brood size (number of embryos per brood) of *Jassa slatteryi*. Yu & Suh (2002) suggested that amphipods with large brood size have a greater chance of survival than those with small brood size. The high survival rate may contribute to success in rebuilding the population of the next generation (Yu et al. 2002) and is directly related to the increase of biomass of amphipods. The mean brood size of *Gammarus mucronatus* ranges from 15 to 39 eggs (Steele & Steele 1975, Borowsky 1980), and that of *Jassa slatteryi* ranged from 31 to 49 eggs per brood. Thus, it is possible that the large brood size of *J. slatteryi* affects the high secondary production.

It has been empirically demonstrated that the *P:B* ratios of benthic amphipods are higher in vegetated than unvegetated habitats (Orth et al. 1984). For example, the *P:B* ratios of *Gammarus mucronatus* inhabiting seagrass beds ranged from 15.8 to 76.8, whilst amphipods living in unvegetated habitats were low,

ranging from 0.4 to 15.8 (Table 2). The annual *P:B* ratio of *Jassa slatteryi* was 5.21 (Table 1). Compared with *P:B* ratios of amphipods inhabiting other seagrass beds, this value is relatively low even if generally higher than in unvegetated habitats (Table 2). Dauvin (1989) reported that the *P:B* ratio appeared to be closely related to the number of generations. For many generations, a high *P:B* ratio was evident and was a characteristic of short-lived, multivoltine species (Kemp et al. 1985, Donn & Croker 1986). The number of generations of *J. slatteryi* was lower than that of other amphipods and we suggest that this causes a decrease of the *P:B* ratio in *J. slatteryi*.

Seagrass beds provide better habitats for diverse and abundant invertebrate communities than many other habitats (Orth et al. 1984). In seagrass beds, benthic amphipods are an important food for fishes and crustaceans. The high abundance and secondary production of *Jassa slatteryi* in the seagrass beds depends not only on the high egg production of *J. slatteryi* but also on the growth of seagrass. It is clear that the dominant herbivorous feeder *J. slatteryi* may play an important role in the energy flow between primary production and higher consumers in the seagrass beds of southern Korea.

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