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Pronounced effect of red seaweed (Gloiopeltis coliformis) diet on intake and growth of small sea urchin Mesocentrotus nudus

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Abstract

Body growth was measured for the small sea urchin *Mesocentrotus nudus* fed on the frozen or dried diets of three species of small red or brown seaweeds growing on intertidal reefs: *Gloiopeltis coliformis* (GF, frozen; or GD, dried), *Mazzaella japonica* (MF, frozen only) and *Scytosiphon lomentaria* (SlF, frozen only). The effects of these different seaweed preparations were investigated in comparison with sea urchins fed on frozen *Saccharina japonica* (SjF) kelp as a positive control. All diet experiments were conducted for two months during October–December. GF contained high levels of crude protein (16.2%) and carbohydrate (59.4%) which were not significantly different from MF. The sea urchins fed on GF or GD increased in weight significantly more than those fed other diets. Significantly higher diet conversion efficiencies led to the highest body increase rates. Test diameter increased by approximately 7 mm and body weight doubled. The cost effectiveness of feeding wild *M. nudus* juveniles can be greatly improved by using *G. coliformis* thalli, which remain after harvesting (when they are of no commercial value) and have a significantly high dry-weight to wet-weight ratio (facilitating air-drying for efficient diet storage).

Introduction

World sea urchin production has markedly decreased from a peak of 109,736 t in 1995 to 58,624 t in 2023 (FAO 2025). Research to boost production through aquaculture dramatically increased during the late 1990s and early 2000s (Pearce 2010). However, substantial increases in production have happened only in the Yellow Sea in northern China, where production peaked at 13,591 t in 2021 (FAO 2025). Sea urchin aquaculture production in Hamanaka Town, on the eastern Pacific coast of Hokkaido, Japan, steadily increased to 80.47 t in 2023 (Hamanaka Town Office Fisheries Division 2025). In both regions, fresh *Saccharina* kelp growing on the seafloor of the natural habitat or in cultivation are fed to the sea urchin *Strongylocentrotus intermedius* from hatchery-raised juveniles to adults of marketable size (Unuma and Kayaba 2015; Lawrence et al. 2019).

In contrast, unlike seaweed diets, the development of practical feeds composed of consistent ingredients was assumed to be able to support aquaculture production. Consequently, much research from the late 1990s to 2000s has been aimed at increasing sea urchin body growth up to marketable size and/or to enhance gonad production and improve gonad quality using prepared, formulated and extruded feeds (Lawrence et al. 1997, 2011; McBride et al. 1997, 1999; Robinson et al. 2002; Pearce et al. 2002; Chang et al. 2005; Daggett et al. 2005; Hammer et al. 2006). However, there is no evidence that sea urchin aquaculture using such practical feeds has led to a significant increase in commercial production to date.

To succeed in commercial sea urchin aquaculture production, survival rate, body growth, gonad production and gonad quality, as biological traits, and economic cost-effectiveness are the essential key factors. If the rate of body growth of sea urchin juveniles to a marketable size can be increased, the duration of aquaculture will be shortened, leading to improved cost-effectiveness. In sea urchin juveniles, digested food is primarily allocated to test growth (e.g. Fuji 1967), and this is mainly attributed to dietary

protein contents, as shown for *Pseudocentrotus depressus* (Akiyama et al. 2001), *Lytechinus variegatus* (Hammer et al. 2004, 2012; Heflin et al. 2016), and *Strongylocentrotus droebachiensis* (Dagget et al. 2005; Eddy et al. 2012; Kennedy et al. 2005), which were fed on formulated feeds. With natural diets, higher juvenile body growth rates have been demonstrated in *S. droebachiensis* and *S. franciscanus* fed on the large kelps *Saccharina latissima* and *Nereocystis luetkeana*, respectively (Larson et al. 1980; Morris and Campbell 1996). In contrast, some researchers have found high growth rates in sea urchin juveniles fed on small seaweeds. Inomata et al. (2013) compared the body growth of *S. intermedius* juveniles fed on either thawed *Pyropia yezoensis* (containing 36.7% crude protein) or thawed *Saccharina japonica* var. *ochotensis* (containing low crude protein of only 5.9%). The results showed that *P. yezoensis* diet promoted better growth than *S. japonica* var. *ochotensis*. Cárcamo (2015) compared the growth of *Loxechinus albus* juveniles fed one of four fresh small seaweed species (*Pyropia* sp., *Gracilaria chilensis*, *Sarcothalia crispata* or *Ulva* sp.) or fresh giant kelp *Macrocystis pyrifera*. *Pyropia* sp. and *G. chilensis* showed the highest growth rates.

The production volume of *Mesocentrotus nudus* is the largest of six commercial sea urchin species in Japan (Unuma 2015). The yearly mean price of sea urchin gonads at the Tokyo Metropolitan Central Wholesale Market, which is the largest dealing in sea urchins from around the world, increased from JP¥ 6,625 kg $^{-1}$ in 2011 (Sun and Chiang 2015) to JP¥ 26,157 kg $^{-1}$ in 2024 (Metropolitan Central Wholesale Market 2025). The price of these gonads has recently risen even further, and at the first auction held at the market on 5 January 2025, a 400 g fresh gonad of *M. nudus* from Hakodate in southern Hokkaido was sold for the surprisingly high price of JP¥ 7,000,000 (SUIKEI 2025), which is about US$ 44,253 at the exchange rate for that day.

The larvae of *M. nudus* settle mainly on crustose coralline algae (CCA; Sano et al. 1998), so this species is widely distributed in high-density populations on barren grounds devoid of macroalgae and dominated by CCA on subtidal reefs in northern Japan (Agatsuma et al. 2014, 2024; Horikoshi et al. 2025). However, its body growth rate and gonad production are markedly low (Agatsuma 2014). Recently, Takagi et al. (2020a,b,c,d,e,f) demonstrated that adult *M. nudus* collected from barren grounds and fed the basal frond portions of fresh *S. japonica* kelp or the sporophylls of fresh *Undaria pinnatifida* kelp (for a short period of around two months between May and July) could greatly improve in its gonad qualities, with respect to size, color, texture, flavor and taste. Based on these results, the standard for high-quality gonads of *M. nudus* has been established (Takagi et al. 2020f). If the body growth of small *M. nudus* from barren grounds can be rapidly increased, this species could be used for short-duration aquaculture.

Using fresh *U. pinnatifida*, Agatsuma et al. (2002) reported that the body growth rate of small *M. nudus* fed on the blades was faster than those fed on the sporophylls or stipes. However, little is known about the effects of small seaweed species on the body growth of small *M. nudus*. If seaweed is only available for feeding sea urchins during a limited period, it must be stored. Gonad growth in adult *Strongylocentrotus intermedius* fed dried *Saccharina longissima* or frozen green seaweed *Ulva australis* was lower than in those fed the same fresh plants (Machiguchi et al. 2012). However, the effect of different storage methods on sea urchin body growth remains unknown. In the present study, three small

seaweed species were chosen which grow seasonally in large quantities on upper-intertidal to upper-subtidal reefs, where collection is easy on the Pacific coast of northeastern Honshu, Japan. The study aims to describe (1) the diet intake, body increase rate, diet conversion efficiency and gonad production of *M. nudus* juveniles fed on the three small seaweed species, frozen or dried; and (2) the advantage of the small red seaweed *Gloiopeltis coliformis* from the viewpoints of cost-effectiveness and the expected protocol for use as diet in *M. nudus* aquaculture.

Materials and methods

Experimental design

Using SCUBA diving, 210 small *Mesocentrotus nudus* of test diameter ca. 17 mm were collected from a barren ground at depths of 6–7 m off Nojima Island, Shizugawa Bay, Miyagi Prefecture (38°40′N, 141°30′E) on 4 October 2017. Immediately after collection, the sea urchins were transported to the research facility (Yuriage Factory, Riken Food Co., Ltd., Natori City, Miyagi Prefecture; 38°17′N, 140°96′E). Ten sea urchins were deployed in each of 21 rectangular 10 L tanks (30 × 15 × 25 cm). The sea urchins were held in running and aerated seawater, which was pumped up from offshore waters, sand-filtered and UV-sterilized. The seawater in each tank was exchanged twice an hour during the experiment. A polyethylene net with a mesh size of 7.5 mm was placed at the bottom of each tank to prevent sea urchins from ingesting their feces. The sea urchins were first starved for eight days and then feeding experiments were conducted for two months from 12 October to 12 December 2017. Thirty sea urchins in three tanks randomly chosen were used for gonad examination on the first day of the experiment.

The collection sites, dates, and storage methods for each seaweed species fed to the sea urchins are shown in Table 1. The species used were the small red seaweeds *Gloiopeltis coliformis* and *Mazzaella japonica*, the small brown seaweed *Scytosiphon lomentaria*, and the large brown seaweed *Saccharina japonica*. *Gloiopeltis coliformis* collected on the coast at Oya, Kesennuma City, Miyagi Prefecture, was frozen at − 30°C (GF) or air-dried (GD). *Mazzaella japonica* (MF) and *S. lomentaria* (SlF) collected on the coast at Taneichi, Hirono Town, Iwate Prefecture and *S. japonica* (SjF) cultivated off Hashikami, Kesennuma City were frozen at − 30°C. Feeding the sea urchins with GF, GD, MF, or SlF are termed the ‘treatments’ GF, GD, MF, and SlF as experimental groups (n = 3 for each treatment). Those fed SjF (= treatment SjF) formed a positive control group (n = 3); those that were unfed formed a negative control group (n = 3).

A total of 18 tanks were arranged using a random table. Each seaweed diet was fed to sea urchins *ad libitum* 16 times (every 3–4 days during the experiment). To investigate the changes in wet weight of the five seaweed diets without sea urchins during the experiment, an amount of each diet almost equivalent to the amount fed to experimental and positive control sea urchins was deployed in another 15 rectangular 10 L tanks (n = 3), which were randomly arranged. The wet seaweed diets (administered 16 times) were weighed (0.01 g accuracy, using an electronic balance) at the start and end of each 3–4 day

feeding session. The weight of each seaweed fed to the sea urchins during the experiment was calculated according to the changes in each seaweed weight using the mean value (of n = 16).

The seawater temperature in the tanks was measured every 10 min using a wireless data logger (RTR-500C, T&D, Nagano, Japan). Daily water temperature was calculated as the mean of 144 data points over 24 h. One sea urchin fed SlF and four unfed sea urchins died during the experiment.

Diet intake

Before presenting diets GF, MF, SlF or SjF to the sea urchins, they were thawed, excess moisture was removed by blotting with paper towels, and they were weighed (0.1 g accuracy) using an electronic balance. To calculate diet intake as dry weight, the ratio of dry-weight to wet-weight for each diet was determined using frozen/thawed or dry (GD) samples that were dried for 4–5 days at 80ºC in a convection oven.

Uneaten pieces of each seaweed and feces were also weighed after they had been siphoned through a 200 µm mesh sieve and sorted from each other every 3–4 days before feeding. The wet diet intake (g. ind.$^{-1}$) was calculated as the difference between the weight of each diet administered and the weight of uneaten diet. The dry diet intake (g. ind.$^{-1}$) was calculated as wet diet intake multiplied by the ratio of dry weight to wet weight for each diet.

Body increase rate and diet conversion efficiency

For each treatment, the test diameter (TD, 0.1 mm accuracy, using a vernier caliper) and body weight (BW, 0.1 g accuracy, using an electronic balance) were measured for all individuals on the first day and 175 individuals (except the five dead animals) on the last day of the experiment. After measurement of TD and BW, 30 individuals not assigned to any treatment groups on the first day and all individuals on the last day were dissected, and the gonad wet weight (0.01 g accuracy) was measured. Calculations were performed to obtain increase rates for TD and BW (as percentage difference of the mean values on the last day and the first day); gonad indices (gonad wet weight as percent body weight); and diet conversion efficiency (difference in mean BW on the last day and the first day as a percentage of wet diet intake).

Proximate constituents in seaweed diets

The seaweeds used to prepare GF (11.8–21.2 g), MF (12.3–14.9 g) and SlF (29.2–30.4 g) were freshly collected, frozen at − 30°C, weighed, freeze-dried and pulverized. Three samples of each seaweed were analyzed. The ash content was determined by measuring the weight loss after ignition in a muffle furnace (GT-P2S, Shirota, Tokyo, Japan) at 600°C for 24 h. The nitrogen content was determined by the micro-Kjeldahl method (Kjeldahl 1883), and the percentage nitrogen was multiplied by 6.25 to give an estimate of crude protein content. Crude lipid was extracted with diethyl ether using a Soxhlet apparatus

(Soxhlet 1879). The carbohydrate content was calculated by subtracting the ash, crude protein, and crude lipid contents from the total dry matter. The proximate constituents in SjF (n = 5) were inferred from measurements of *S. japonica* var. *ochotensis* by Inomata et al. (2013). Each proximate constituent of GF samples was treated as equivalent to those of GD samples.

Statistical analysis

All data were log-transformed because no normality was detected by the Shapiro-Wilk test or the homogeneity of variance by Levene's test. Significant differences in TD and BW on the first day among tanks, TD and BW on the first and last day, total wet and dry diet intakes, dry-weight to wet-weight ratios, body increase rates, diet conversion efficiencies among treatments and gonad indices among treatments, including initial gonad index, and proximate constituents among seaweed diets were analyzed by One-way ANOVA. The significance of the data was then analyzed by Tukey's HSD as a *post hoc* test. All statistical analyses were performed using JMP (14.3.0; SAS Institute Inc., NC, USA).

Results

Proximate constituents in seaweed diets, and water temperature

Proximate constituents for each seaweed diet are shown in Table 2. Significant differences in each constituent were detected among seaweed diets (Table 3). GF, MF and SlF contained significantly more crude protein than SjF ($p < 0.01$). GF and MF contained significantly more carbohydrate than SlF ($p < 0.05$), significantly less crude lipid than SlF ($p < 0.05$), and less ash than SlF and SjF ($p < 0.05$).

The daily water temperature in each tank decreased from 20.1°C on 4 October to 9.3°C on the last day of the experiment.

Diet intake

Total wet and dry diet intakes for each treatment during the experiment and the dry-weight to wet-weight ratios are shown in Table 4. Significant differences in these values were detected among treatments (Table 3). The total wet intakes of treatments GF, GD and SjF were significantly more than for MF ($p < 0.05$). The total dry intake of GF was significantly more than with MF or SlF ($p < 0.05$). Intake of MF was significantly less than for GD or SjF ($p < 0.05$). The dry-weight to wet-weight ratio of GF was significantly more than with the other three diets ($p < 0.01$), and that of MF was significantly more than SlF or SjF ($p < 0.05$).

Body increase rates and diet conversion efficiencies

There were no significant differences in TD and BW among the 18 tanks on the first day of the experiment (Table 3). The initial and final values for TD and BW for each treatment measured on the first and last day of the experiment are shown in Table 5. Significant differences in the final values were detected among treatments (Table 3), with GF and GD exhibiting significantly greater TD and BW values than the other diets ($p < 0.01$). On the first day of the experiment, the mean TD and BW of both treatments were 17.5 mm and 3.3 g. Over the course of the experiment, TD increased by approximately 6 mm, and BW was 1.6 times. The BW of the unfed group was significantly less than with other treatments ($p < 0.01$), and for MF was significantly more than treatments SlF and SjF ($p < 0.01$).

Significant differences in the increase rates of TD and BW were detected among treatments (Table 3), with values for GF and GD significantly higher than for other treatments ($p < 0.05$; Fig. 1). The diet conversion efficiencies for each treatment are shown in Fig. 2, with significant differences among treatments (Table 3). The conversion efficiency with GF was significantly higher than for treatments MF, SlF and SjF ($p < 0.05$). No significant difference in conversion efficiency was detected between GF and GD. Diet conversion efficiency of MF was significantly higher than that of SlF and SjF ($p < 0.05$).

Gonad indices

The mean TD and BW of the sea urchins for which the gonad indices were examined were 17.1 mm and 2.5 g, respectively, on the first day of the experiment. The initial gonad index of the sea urchins, and that for each treatment on the last day of the experiment are shown in Fig. 3, revealing a significant difference for all groups (Table 3). The gonad index of treatment GD was significantly highest ($p < 0.01$), followed by treatments GF and MF, whose gonad indices were significantly higher than those of the other three treatments ($p < 0.05$).

Discussion

Effect of seaweed diets on body growth

A sharp decrease in water temperature, from 20.1ºC to 9.3ºC, between October and December during the experiment is generally observed along the Pacific coast of the Tohoku region (Japan Fisheries Research and Education Agency 2023). The diet intake values of small *M. nudus* (20–30 mm TD) do not differ significantly between water temperatures of 14 and 8ºC, but deceased significantly at 6ºC (Feng et al.2021). In addition, the intake of small *M. nudus* (15.6 mm TD) fed on fresh *Saccharina japonica* var. *religiosa* did not decrease between October and December, despite a decrease in water temperature from 19ºC to 10ºC (Agatsuma 2014). These studies reveal that diet intake was not affected by the decrease in water temperature.

Regardless of the lack of any significant difference in the proximate constituents of GF and MF, urchins fed with MF showed significantly lower body increase rate, diet conversion efficiency and gonad index. This is attributed to the significantly lower total diet intake than with treatments GF and GD. Substances that deter sea urchins from feeding on red seaweed, such as monoterpenes, diterpenes,

phenylpropanoids, bromodiphenyl ethers and pyrones, may be present in MF, resulting in decreased intake of diet based on MF (reviewed by Paul et al. 2001 and Lawrence et al. 2020).

Digestibility (absorption efficiency), which represents the difference between the amount of feed intake and amount of feces produced, is important in interpreting the quality of ingested nutrients (Watts et al. 2020). Hammer et al. (2004) reported that digestibility of dry protein matter in small *Lytechinus variegatus* fed prepared feed containing varying concentrations of protein (9, 15, 21 and 33% dry weight) was 77.7, 89.4, 92.2 and 94.7%, respectively. Consequently, growth was significantly slower in animals fed a 9% protein feed than in those fed higher rations. Thus, a high protein content (≥ 15%) in diets is known to contribute to the promotion of body growth of small sea urchins (Akiyama et al. 2001; Hammer et al. 2004, 2012; Dagget et al. 2005; Kennedy et al. 2005; Eddy et al. 2012; Inomata et al. 2013; Heflin et al. 2016). The highest growth rates and diet conversion efficiency in the treatments GF and GD were due to their high protein content of 16.2%.

The total diet intake values for treatments SlF and SjF were not significantly different from those for treatments GF and GD except for significantly lower dry intake values for SlF than for GF. The crude protein content in SlF and carbohydrate content in SjF were not significantly different from GF and MF. Carbohydrates include a large amount of carbon and serve as an important energy source for sea urchins (Powell et al. 2020). In *Lytechinus variegatus* fed on a formulated feed with high protein content, the body growth rates declined if the carbohydrate content was low (Schlosser et al. 2005; Hammer et al. 2006). In the present study, the body increase rate, diet conversion efficiency, and gonad index of urchins fed on SlF and SjF were lower than for those fed on GF or MF. These results are possibly due to significantly lower dry diet intake and carbohydrate content in SlF, and lower protein content in SjF, with a consequently higher proportion of ash content in both these diets. Takagi et al. (2020b,c) reported that the protein content of *S. japonica* blades cultivated in June was 3.2%, 3.2%, and 3.7% in the apical, middle and basal portions, respectively. The protein content of the basal portion increased significantly from 3.3% in late May to 5.6% in early July, which coincide with an increase in the carbon and nitrogen content for regrowth to form a second plant (Li et al. 2007; Takagi et al. 2020a). These findings suggest that the actual protein content would be less than the value of 5.9% reported by Inomata et al. (2013).

High levels of neutral lipids in feed negatively affect sea urchin growth (Kennedy et al. 2007; Hammer et al. 2010; Gibbs et al. 2015), although the dietary lipid requirement of sea urchins has yet to be determined (Watts et al. 2020). Hence, the effect of significantly higher crude lipid content in SlF (2.1%) than in GF (0.8%) on the growth of the sea urchin remains unknown. Regardless of significantly lower diet intake for MF than SlF or SjF, significantly higher diet conversion efficiency associated with higher crude protein or carbohydrate content in MF would contribute to the significantly higher BW and gonad index observed on the last day of the experiment.

In the present study, there were no significant differences in total diet intake, body increase rate or diet conversion efficiencies between the treatments GF and GD. The results suggest that the thallus tissue of the red alga can withstand drying and freezing during the low tide periods between winter and early

summer. To elucidate the mechanism underlying the significantly higher gonad index observed with treatment GD (1.76) in comparison with GF (0.95), the differences in nutrient availability, digestibility and/or allocation to the gonads of small *M. nudus* fed on GF and GD need to be examined.

Aquaculture using small seaweed diet

In the present study, TD and BW for sea urchins fed on GF and GD increased from 17.5 mm to 22.6–23.0 mm and from 3.3 g to 5.1–5.2 g, respectively, for the two-month experimental period during October–December. To promote the body growth of small sea urchins, when the sea urchin juveniles reach a visible size of > 10 mm TD (Horikoshi et al. 2025) and should continue for approximately eight months until early spring the following year when they grow to > 40 mm TD. After April, digested food is also allocated to increase gonad production toward the first maturation at two years of age in the September and October spawning season (reviewed by Agatsuma 2014, 2020). The modest protein content of a feed for gonad production in adult *M. nudus* is 12% (Takagi et al. 2022). The high concentrated protein diets GF or GD are predicted to cause an increase in the bitter-tasting free amino acids (lysine, valine, arginine, methionine and leucine) in the gonads (Liyana-Pathirana et al. 2002; Inomata et al. 2016). Therefore, it is necessary to switch the diet of GF or GD to fresh *Saccharina* kelp to improve gonad qualities (color, texture, flavor, taste) prior to harvesting (Takagi et al. 2020a,b,c,d,e,f).

Gloiopeltis coliformis (Fig. S1) is a small annual red seaweed widely distributed along the coast of Japan (Arasaki and Tokuda 2002; Tokuda et al. 1987; Yoshida 1998). It dominates the upper intertidal reefs and forms widespread beds and is harvested as an edible seaweed (for human consumption) in late winter and early spring in the Tohoku and Hokkaido regions of Japan. The thalli remaining after harvesting are as long as 15 cm in length (Yokohama 2013) and increase their biomass during May–June, decaying in summer. These remaining elongate, hard thalli contain sand and have no commercial value, yet they are adequate as diet for small sea urchins. In the present study, a significantly high dry-weight to wet-weight ratio of GF, compared with MF, SlF, or SjF, indicates a low moisture content and therefore suitability for air-drying. After air-drying, this seaweed should be sealed with oxygen absorbers during storage, which would reduce costs compared to freezing.

In conclusion, *G. coliformis* (GF and GD) is an excellent diet, containing high levels of crude protein and carbohydrate. This diet increases the intake and conversion efficiency of small *M. nudus*, accelerating growth. Using wild small *M. nudus* and air-dried *G. coliformis* has the potential to greatly improve the cost-effectiveness of sea urchin aquaculture. To succeed in sea urchin aquaculture using the red seaweed, an assessment of its stock size, the implementation of appropriate management practices and the evaluation of the cost effectiveness is needed. Using a large number of wild small sea urchins would contribute to restore diverse and productive kelp forests on barren grounds.

Declarations

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Tables

Tables are available in the Supplementary Files section.

Figures

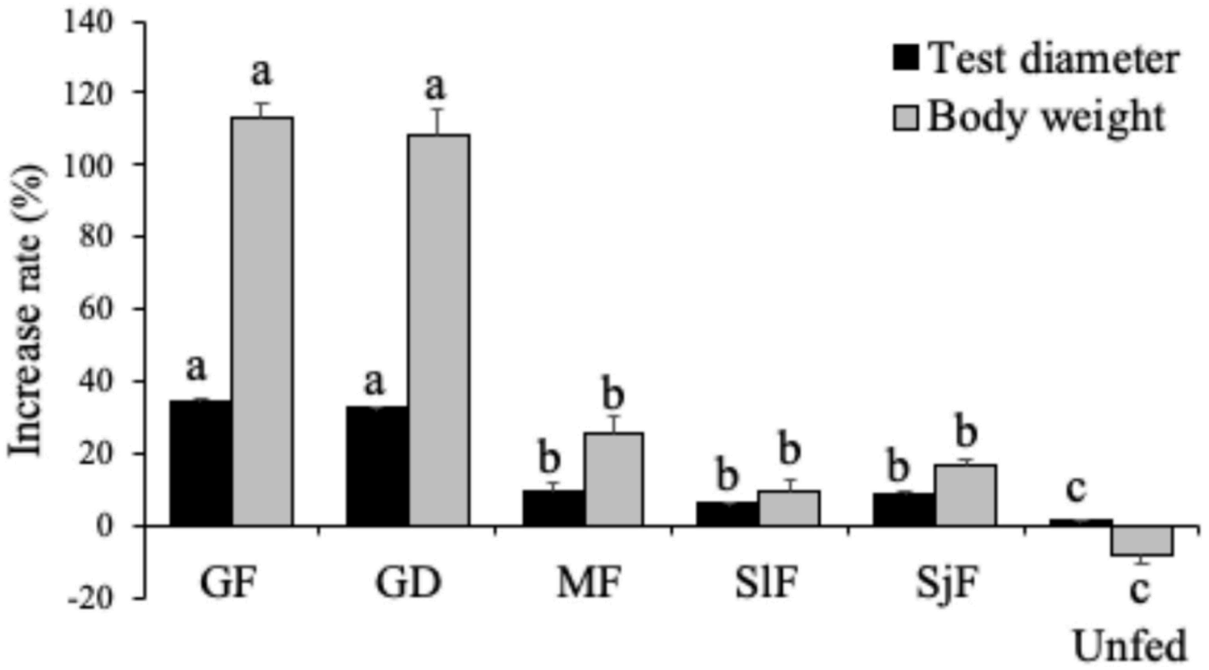


Figure 1

Increase rates of test diameter and body weight of small *Mesocentrotus nudus* in each treatment during the experiment. Lower-case letters denote significantly different values among treatments. Vertical bars indicate SE. An explanation of GF, GD, MF, SlF and SjF is provided in Table 1.

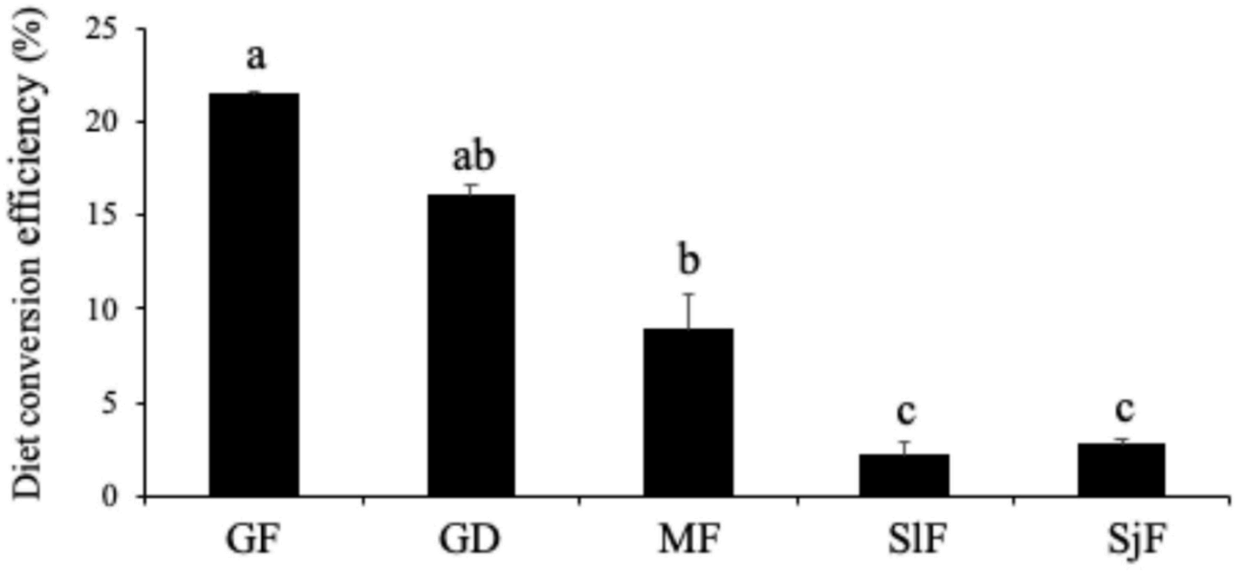


Figure 2

Diet conversion efficiencies of small *Mesocentrotus nudus*in each treatment during the experiment. Lower-case letters denote significantly different values among treatments. Vertical bars indicate SE. An explanation of GF, GD, MF, SlF and SjF is provided in Table 1.

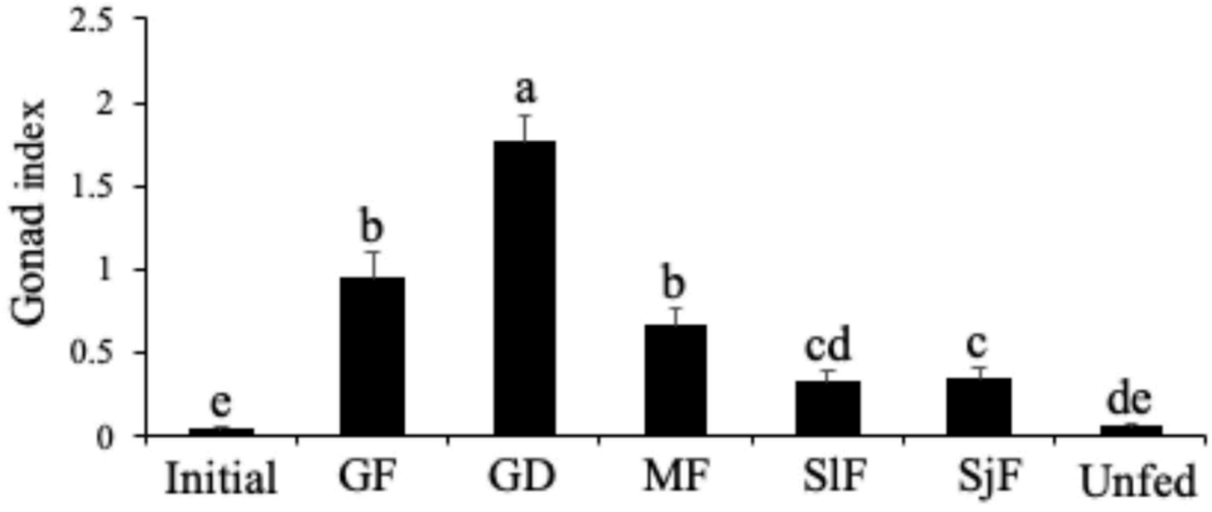


Figure 3

Gonad indices of small *Mesocentrotus nudus* on the first day ('Initial'), and for each treatment on the last day of the experiment. Lower-case letters denote significantly different values among treatments, including initial gonad index. Vertical bars indicate SE. An explanation of GF, GD, MF, SlF and SjF is provided in Table 1.

Supplementary Files

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