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Macroalgal substitution effect in diet on growth, body composition, and stress resistance of juvenile sea cucumber (*Apostichopus japonicus*) subjected to air and low salinity exposures

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Abstract
Effect of various macroalgae substitution for *Sargassum thunbergii* in diet on growth, body composition, and survival of sea cucumber (*Apostichopus japonicus*) subjected to air and low salinity exposures was determined. Nine hundred juvenile sea cucumber were distributed into 18 tanks (50 sea cucumber per tank). Six experimental diets were prepared. *Sargassum thunbergii* was included in the control (Con) diet. The macroalgae *Sargassum horneri*, *Undaria pinnatifida*, *Saccharina japonica*, *Ulva australis*, and combined *U. pinnatifida* and *S. japonica* were included to replace *S. thunbergii* in the Con diet, referred to as the SH, UA, UP, SJ, and combined diets, respectively. All diets were assigned to triplicate groups of sea cucumber. Sea cucumbers were fed daily for 8 weeks. After the 8-week feeding trial, sea cucumbers were subjected to 30-h air and 12-h low salinity at 10 psu exposures. Weight gain and specific growth rate of sea cucumber fed the Con, SH, and UA diets were significantly greater than those of sea cucumber fed the UP, SJ, and combined diets. The chemical composition of the whole sea cucumber, except for moisture content, was not affected by the experimental diets. No difference in survival of sea cucumber fed all experimental diets was observed at the end of 4-day post observation period after the 30-h air and 12-h low salinity exposures. In conclusion, *S. thunbergii* can be substituted with either *S. horneri* or *U. australis* in sea cucumber feed without retarding growth and stress resistance against air and low salinity exposures.

Keywords Sea cucumber (*Apostichopus japonicus*) · Macroalgal substitution effect · Air exposure · Low salinity exposure

Introduction

Sea cucumber (*Apostichopus japonicus*) exhibiting cryptic nocturnal behavior (Chang et al. 2004; Guancang et al. 2011) is a commercially important aquaculture species in China, Republic of Korea, Japan, and the Russian Federation (Yuan et al. 2006; Gu et al. 2010; Seo and Lee 2011; Oh et al. 2014; Shahabuddin and Yoshimatsu 2015; Ru et al. 2019). In the Republic of Korea, the annual aquaculture production of sea cucumber reached 93 tonnes in 2019 (KOSIS 2020). Dried sea cucumber has been used as an ideal tonic food with high protein and low fat (Chen 2003). Production of sea cucumber has become a commercially lucrative area and needs to be extended to satisfy the high demand for the increasing human population (Ru et al. 2019), which can be largely supplied by aquaculture (Shahabuddin et al. 2017).

Sea cucumbers are known to feed on sedimentary organic litter like other holothurians in the wild (Yuan et al. 2006). In the aquaculture industry, formulated diets mainly composed of macroalgae powder and sea mud are commonly applied to improve the production of sea cucumber (Chang et al. 2003). The brown macroalga, *Sargassum thunbergii*, is one of the most common feeds for sea cucumber farming in the Republic of Korea, China, and Japan (Sui 1989; Battaglene et al. 1999). However, the wild resource of *S. thunbergii* has dramatically decreased due to its high demand resulting from the expanded sea cucumber farming, and it has eventually resulted in an increased price of this macroalga (Yuan 2005).

As *S. thunbergii* is not being produced commercially, it is difficult for local suppliers or collectors to satisfy an increasingly high demand for this macroalga for the

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expanded sea cucumber farming in Asia. Therefore, development of formulated feed is highly needed to achieve stable production of sea cucumber. Sea cucumber fed diets substituting 50% of *S. thunbergii* with different macroalgae (*Undaria pinnatifida* and *Saccharina japonica*) and plant ingredients (*Brassica oleracea var. capitata* and rice straw powder) or diets substituting 25% of *S. thunbergii* with other plant ingredients (fermented soybean meal and distiller dried grain powder) achieved superior SGR to the control diet containing *S. thunbergii* at 40% (Seo et al. 2011). Wu et al. (2015) evaluated dietary substitution effect of corn (*Zea mays*) leaf for *S. thunbergii* on growth of sea cucumber when 25, 50, 75, and 100% of *S. thunbergii* were substituted with corn leaf in sea cucumber feed composed of 30% *S. thunbergii* and 70% sea mud and recommended the combined use of 18.8% *S. thunbergii* and 11.2% corn leaf in sea cucumber feed for the best growth performance. Searching for an alternative source for *S. thunbergii* is highly needed to reduce the overharvesting pressure of *S. thunbergii* in the wild and achieve stable and effective production of sea cucumber.

Macroalgae, such as *U. pinnatifida*, *S. japonica*, *U. australis*, and *S. horneri*, are commonly found in the shallow coastal areas of Republic of Korea. As these macroalgae are rich in proteins, soluble dietary fibers, minerals, vitamins, phytochemicals, antioxidants, and polyunsaturated fatty acids containing low caloric value, and defensive and storage compounds (Fleurence 1999; Colombo et al. 2006; Mohamed et al. 2012; Wan et al. 2019; Gao et al. 2020), they can be considered as feed ingredients in aquafeeds, especially *U. pinnatifida* and *S. japonica*, some of the most common feeds adopted by the farmers to raise abalone and sea urchins (Yone et al. 1986; Agatsuma et al. 2002; Qi et al. 2010; Cho et al. 2011). Anisuzzaman et al. (2017) described that dietary inclusion of macroalgae (*Ulva lactuca* or *S. japonica*) and microalgae (*Nannochloropsis oculata*) at 15% improved growth of sea cucumber compared to the control diet containing the same amount of wheat flour. Xia et al. (2012a) also reported that sea cucumber fed diets containing different seaweed (*S. thunbergii*, *S. polycystum*, *Zostera marina*, *U. lactuca*, *S. japonica*, and boiled *S. japonica*) powders and sea mud powders at the ratio of 3:7, respectively greatly affected growth, ingestion rate, digestibility, and ammonia–nitrogen production of sea cucumber, and suggested that *U. lactuca*, *Z. marina*, and fresh *S. japonica* would be the optimum seaweeds for the commercial culture of sea cucumber. However, knowledge on a suitable and sustainable substitute for *S. thunbergii* is still insufficient to expand the commercial culture of sea cucumber.

Abiotic factors, such as air exposure and salinity change, are the most important ecological factors affecting growth and metabolism of aquatic animals (Vidolin et al. 2002; Hou et al. 2019). Therefore, these abiotic stressors resulted in severe economic and resource losses, and strongly limit the expansion of sea cucumber industry (Huo et al. 2018). Salinity change mainly caused by water exchange, evaporation, and precipitation (Wang et al. 2014) can lead to osmotic stress and severe mortality of sea cucumber (Meng et al. 2011). Sea cucumber is also frequently subjected to air exposure (desiccation) stressor during various farm activities and transportation without water (Hou et al. 2019). Minimizing the undesirable effect of air exposure during transportation of mollusk is critical for successful aquaculture since it affects survival and growth (Malham et al. 2003; Morash and Alter 2016). Balanced nutrition in formulated feed can help to improve the metabolic and physiological status of aquatic animals and strengthen their resistant capacity against various abiotic stressors, such as air exposure and salinity change stressors (Liu et al. 2015; Lee et al. 2016; Ansary et al. 2019a, b).

In this study, therefore, dietary substitution effect of various macroalgae (*S. horneri*, *U. australis*, *U. pinnatifida*, *S. japonica*, and the combined *U. pinnatifida* and *S. japonica*) for *S. thunbergii* on growth, body composition, and stress resistance of sea cucumber subjected to air and low salinity exposures was evaluated.

Materials and methods

Rearing condition of the experimental animals

Juvenile sea cucumbers purchased from a private hatchery (Namhae-gun, Gyeongsangnam-do, Korea) were moved and acclimated to the experimental conditions for a couple of weeks before starting the feeding trial. During the acclimation period, sea cucumbers were daily fed with a commercial diet (the mixture of *Sargassum* spp. and sea mud) at 3–5% biomass.

A total of 900 juvenile (initial weight of 1.46 g) sea cucumbers were randomly disseminated into indoor 18 300-L round-shaped tanks (50 juveniles per tank) with flow-through system. Sand-filtered seawater temperature fluctuated from 8.7 to 15.5 °C (mean ± SD; 12.0 ± 0.16 °C) and flow rate of tank was 3 L min^{-1}. Continuous aeration was provided into each tank and a photoperiod of 10 h: 14 h (light: dark) cycle was adapted based on Guancang et al. (2011)'s study, in which the optimal photoperiod for rearing sea cucumber was 6–15 h light per day. The diets were mixed well with seawater in a 50-mL tube and fed to sea cucumber once a day (14:00) to satiation (ca. 2–5% of total biomass) with a little leftover for 8 weeks. Aeration and water supply stopped for 3 h after the designated daily feed supply. Aeration was supplied at 17:00 again, but sand-filtered seawater was again supplied at the morning (09:00) in the following day until the next designated feed supply. To maintain the water quality, the bottom of the tank was cleaned and dead sea cucumbers were removed daily.

Preparation of the experimental diets

Six experimental diets were prepared (Table 1). The control (Con) diet contained 40% defatted soybean meal and 10% brown fish meal as the protein source. Thirty five percent *Sargassum thunbergii* was included in the Con diet. *Sargassum thunbergii* in the Con diet was replaced with an equal amount of *S. horneri*, *U. australis*, *U. pinnatifida*, *S. japonica*, and the combined *U. pinnatifida* and *S. japonica* (= 1:1, dry weight basis) powder, referred to as the SH, UA, UP, SJ, and combined diets, respectively. Fresh clean seaweeds were collected in the wild, air-dried at 40 °C for 48 h, and then ground to powders. All diets were assigned to triplicate groups of sea cucumber. All feed materials were sieved with 250 µm mesh sieve (Samwoo Industry Co., Korea) and mixed well. All experimental diets satisfied the protein and lipid requirements of sea cucumber (Seo and Lee 2011). All diets were stored in a freezer (− 15 °C) and used in small amounts whenever necessary.

Sample collection and measurements

All surviving sea cucumbers from each tank were counted and collectively weighted to measure weight gain at the end of the 8-week feeding trial. Specific growth rate (SGR) (% day^{-1}) was calculated as follows: SGR = (*ln* final weight − *ln* initial weight) × 100 / day of feeding.

Analyses of the chemical composition of the experimental diets and animals

Ten sea cucumbers from each tank were randomly selected and sacrificed for the chemical analysis. The chemical composition of the experimental diets and sea cucumber was determined according to the standard AOAC (1990) methods. Crude protein (N × 6.25) was measured by the Kjeldahl method (Buchi B-324/435/412, Auto Kjeldahl System, Switzerland), crude lipid content was analyzed using an ether-extraction method, moisture content was calculated by oven drying at 105 °C for 24 h, and ash content was estimated by a muffle furnace at 550 °C for 4 h.

Table 1 Ingredient and chemical composition of the experimental diets (dry matter basis, %)

	Experimental diets					
	Con	SH	UA	UP	SJ	Combined
Ingredient (%)						
Defatted soybean meal	40	40	40	40	40	40
Brown fish meal	10	10	10	10	10	10
Sargassum thunbergii	35					
Sargassum horneri		35				
Ulva australis			35			
Undaria pinnatifida				35		17.5
Saccharina japonica					35	17.5
Combined *U. pinnatifida*:*S. japonica* (1:1)						
Wheat flour	10	10	10	10	10	10
Cellulose	1	1	1	1	1	1
Vitamin premix[a]	2	2	2	2	2	2
Mineral premix[b]	2	2	2	2	2	2
Nutrients (%, DM)						
Dry matter	91.1	91.3	91.7	91.4	91.5	91.8
Crude protein	28.9	29.0	29.1	29.2	28.8	28.5
Crude lipid	2.8	2.8	2.7	3.0	2.9	2.9
Ash	19.1	19.2	19.1	19.1	19.0	19.2

[a]Vitamin premix contained the following amounts which were diluted in cellulose (g kg^{-1} mix): L-ascorbic acid, 200; α-tocopheryl acetate, 20; thiamin hydrochloride, 5; riboflavin, 8; pyridoxine, 2; niacin, 40; Ca-D-pantothenate, 12; myo-inositol, 200; D-biotin, 0.4; folic acid, 1.5; p-amino benzoic acid, 20; K3, 4; A, 1.5; D3, 0.003; cyanocobalamin, 0.003. [b]Mineral premix contained the following ingredients (g kg^{-1} mix): NaCl, 7; $MgSO_4.7H_2O$, 105; $NaH_2PO_4.2H_2O$, 175; KH_2PO_4, 224; $CaH_4(PO_4)_2.H_2O$, 140; Ferric citrate, 17.5; $ZnSO_4.7H_2O$, 2.8; Ca-lactate, 21.8; CuCl, 0.2; $AlCl_3.6H_2O$, 0.11; KIO_3, 0.05; $Na_2Se_2O_3$, 0.007; $MnSO_4.H_2O$, 1.4; $CoCl_2.6H_2O$, 0.07

Monitoring survival of sea cucumber subjected to air exposure stressor

After the 8-week feeding trial, 15 sea cucumbers were randomly chosen from each tank and the rest of the sea cucumbers were removed. Seawater was completely drained out from all experimental tanks and exposed to air for 30 h. Then all tanks were refilled with sand-filtered seawater and other rearing conditions were maintained as same as the 8-week feeding trial conditions except for feeding. Sea cucumber was starved and survival was monitored for the next 4 days after the 30-h air exposure. Dead sea cucumbers were removed every 3 h for the first 2 days and every 6 h for the remaining 2 days. Sufficient oxygen was supplied to seawater in tanks during the 4-day post observation period.

Monitoring survival of sea cucumber subjected to low salinity stressor

Fifteen sea cucumbers were randomly selected from each tank at the end of the 8-week feeding trial to evaluate resistance against low salinity change stressor. Eighteen round-shaped plastic bottom–screened containers (30 cm in diameter and 8.5 cm in height) were placed in one 3-t rectangular water tank adjusted at 10 psu salinity by mixing tap water with sand-filtered seawater (32 psu). Salinity was measured by using YSI 6-Series Multi Parameter (YSI, USA). Sea cucumbers were exposed to 10 psu saline water for 12 h, which was then drained out and then refilled with sand-filtered seawater to monitor survival of sea cucumber for the next 4-day post observation period. Other rearing conditions were maintained as same as the experimental conditions except for feeding. Sea cucumber was starved and survival was monitored for the next 4 days after the 12-h low salinity exposure. Dead sea cucumbers were removed every 3 h for the first 2 days and every 6 h for the remaining 2 days. Sufficient oxygen was supplied to water in a tank during the 4-day post observation period.

Statistical analysis

Statistical analysis was accomplished by the software SAS version 9.3 (SAS Institute, USA). Percentage data were subjected to arcsine-transformation prior to analysis. One-way ANOVA and Duncan's multiple range test (Duncan 1955) were used to compare the means of treatment. Survival of sea cucumber during the 4-day post observation period after the 30-h air and 12-h low salinity exposure stressors was analyzed by using Kaplan–Meier survival curve, log-rank, and Wilcoxon tests.

Results

Survival and growth of sea cucumber at the end of the 8-week feeding trial

Survival of sea cucumber (≥ 98%) was not significantly ($p < 0.3$) affected by the experimental diets (Table 2). Significantly greater weight gain and SGR ($p < 0.004$ and $p < 0.003$, respectively) were obtained in sea cucumber fed the Con, SH, and UA diets than those of sea cucumber fed the UP, SJ, and combined diets. However, there was no significant ($p > 0.05$) difference in weight gain and SGR of sea cucumber fed the Con, SH, and UA diets.

Whole body proximate composition of sea cucumber

Moisture content of sea cucumber fed the UP diet was significantly ($p < 0.0001$) higher than that of sea cucumber fed the Con, SH, UA, and SJ diets, but not significantly ($p > 0.05$) different from that of sea cucumber fed the combined diet (Table 3). Crude protein content of sea cucumber ranged from 3.4 to 3.5%, crude lipid ranged from 0.3 to 0.4%, and ash ranged from 3.4 to 3.5%. These parameters were not significantly ($p > 0.05$) affected by the experimental diets.

Table 2 Survival (%), weight gain (g sea cucumber^{-1}), and specific growth rate (SGR) of juvenile sea cucumber fed the experimental diets for 8 weeks

Experimental diets	Initial weight (g sea cucumber^{-1})	Final weight (g sea cucumber^{-1})	Survival (%)	Weight gain (g sea cucumber^{-1})	SGR[a] (% day^{-1})
Con	1.46 ± 0.002	3.78 ± 0.020	100.0 ± 0.00	2.32 ± 0.020^a	1.70 ± 0.009^a
SH	1.46 ± 0.003	3.75 ± 0.020	100.0 ± 0.00	2.29 ± 0.017^a	1.68 ± 0.005^a
UA	1.46 ± 0.001	3.77 ± 0.029	98.0 ± 2.00	2.31 ± 0.030^a	1.69 ± 0.015^a
UP	1.46 ± 0.003	3.66 ± 0.013	100.0 ± 0.00	2.20 ± 0.011^b	1.64 ± 0.004^b
SJ	1.46 ± 0.002	3.65 ± 0.020	100.0 ± 0.00	2.19 ± 0.021^b	1.63 ± 0.011^b
Combined	1.46 ± 0.001	3.68 ± 0.029	99.3 ± 0.67	2.21 ± 0.030^b	1.64 ± 0.015^b
p-value			$p < 0.3$	$p < 0.004$	$p < 0.003$

Values (means of triplicate ± SE) in the same column sharing a common superscript are not significantly different ($p > 0.05$). [a]Specific growth rate (SGR) = [(ln (final weight) – ln (initial weight)) × 100 / days of feeding]

Table 3 Chemical composition (wet weight basis, %) of the whole body of juvenile sea cucumber fed the experimental diets for 8 weeks

Experimental diets	Moisture	Crude protein	Crude lipid	Ash
Con	91.2 ± 0.06^{b}	3.5 ± 0.03	0.3 ± 0.03	3.5 ± 0.03
SH	91.3 ± 0.15^{b}	3.4 ± 0.03	0.3 ± 0.03	3.4 ± 0.03
UA	91.3 ± 0.05^{b}	3.5 ± 0.00	0.4 ± 0.05	3.5 ± 0.00
UP	91.7 ± 0.03^{a}	3.5 ± 0.07	0.3 ± 0.00	3.5 ± 0.07
SJ	90.4 ± 0.12^{c}	3.4 ± 0.07	0.4 ± 0.00	3.4 ± 0.07
Combined	91.5 ± 0.12^{ab}	3.4 ± 0.07	0.3 ± 0.03	3.5 ± 0.07
p-value	$p < 0.0001$	$p > 0.4$	$p > 0.08$	$p > 0.4$

Values (means of triplicate ± SE) in the same column sharing a common superscript are not significantly different ($p > 0.05$)

Survival of sea cucumber exposed to the 30-h air exposure stressor

Sea cucumbers fed all experimental diets were all alive during the 30-h air exposure after the 8-week feeding trial (Fig. 1). Mortality was first observed in sea cucumbers fed the Con, SH, SJ, and combined diets at 9 h after the 30-h air exposure. However, survival of sea cucumber was not significantly ($p > 0.8$ for log-rank test) affected by the experimental diets at the end of the 4-day post observation period.

Survival of sea cucumber subjected to the 12-h low salinity stressor

Mortality of sea cucumbers fed the combined diet started at 6 h after the 12-h low salinity stressor. However, survival of sea cucumber was not significantly ($p > 0.4$ for log-rank test) affected by the experimental diets at the end of the 4-day post observation period (Fig. 2).

Discussion

Relatively high SGR values (1.63–1.70%/day) of sea cucumbers obtained in this study compared to −0.04–0.54 (Seo and Lee 2011), 0.15–1.0 (Seo et al. 2011), 0.29–1.47 (Song et al. 2017), 0.39–0.59 (Wu et al. 2015), 0.48–0.80 (Xia et al. 2012a), 0.83–1.16 (Li et al. 2021), and 0.96–1.42 % day^{-1} (Wen et al. 2016) reported in the same species of sea cucumber in other studies indicated that growth of sea cucumber was well achieved in this study. No difference in weight gain and SGR of sea cucumber fed the Con, SH, and UA diets indicated that *S. thunbergii* could be replaced with either *S. horneri* or *U. australis* in formulated feed without lowering the growth performance of sea cucumber.

Since *S. horneri* and *U. australis* are the main macroalgae causing golden and green tides, respectively, in Republic of Korea (Hawang et al., 2016; Kim et al. 2017), their availability as feed ingredients in aquafeed seems to be high over *S. thunbergii*. In addition, substitutability of those fouling macroalgae (*S. horneri* and *U. australis*) and their combination for *U. pinnatifida* in abalone (*H. discus*) feed was also well proved (Ansary et al. 2019a, b, c). This is another study to suggest substitutability of those fouling macroalgae for *S. thunbergii* in formulated sea cucumber feed. Similarly, Song et al. (2017) showed that green tide–causing macroalgae (*Chaetomorpha linum*) could be used as a replacer for *S. thunbergii* in sea cucumber feed because of its high protein and low cellulose content. Gao et al. (2011a) also suggested that red algae (*Gracilaria lemaneiformis*) would be more preferable feed for sea cucumber rather than *S. thunbergii* because the administration of *G. lemaneiformis* achieved superior SGR to *S. thunbergii* with or without a mixture of benthic matter.

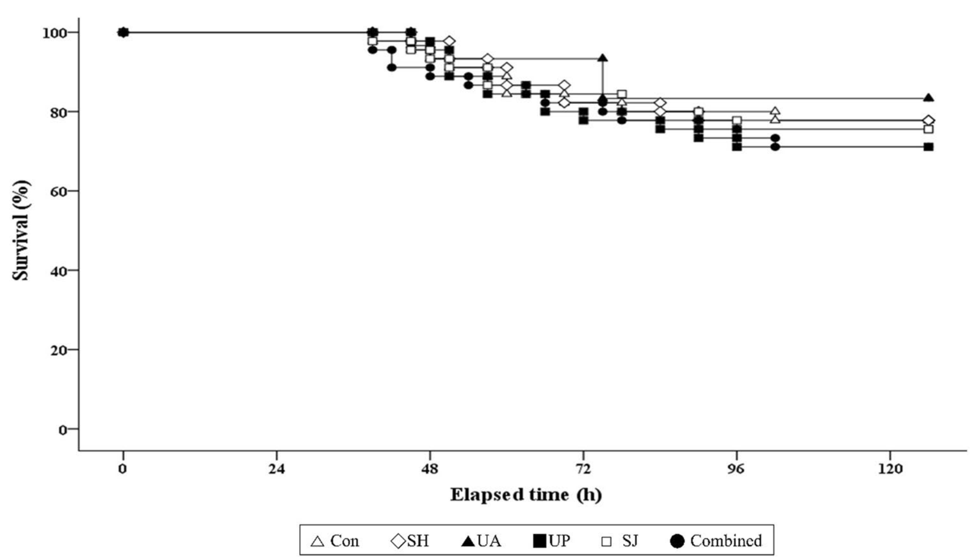

Fig. 1 Survival (%) of sea cucumber during the 4-day post observation period after the 30-h air exposure (means of triplicate ± SE) ($p > 0.8$ for log-rank test)

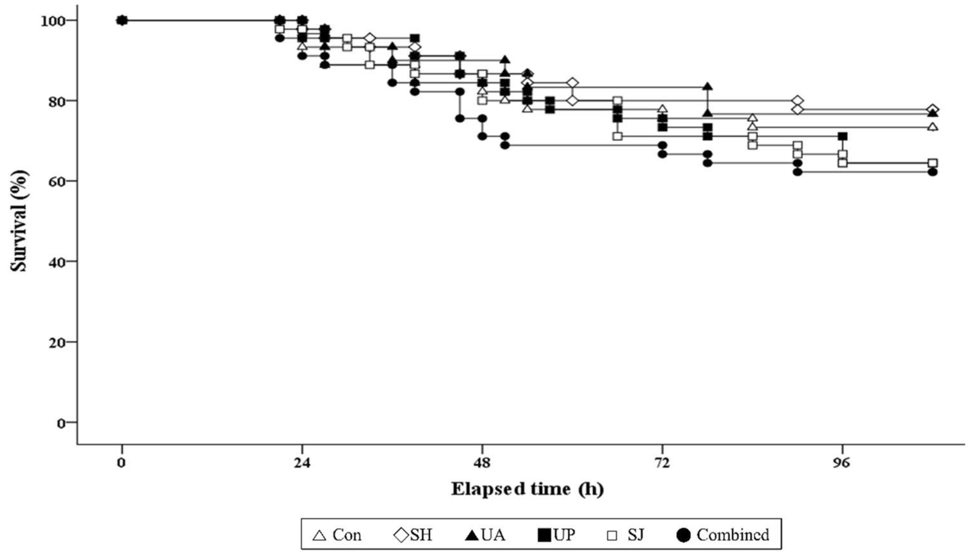

Fig. 2 Survival (%) of sea cucumber during the 4-day post observation period after the 12-h low salinity (at 10 psu) exposure (means of triplicate ± SE) ($p > 0.4$ for log-rank test)

Inferior weight gain and SGR of sea cucumber fed the UP, SJ, and combined diets to the Con diet in this study indicated that *U. pinnatifida* and *S. japonica* seemed to be less suitable than *S. thunbergii* in formulated sea cucumber feed. Unlike this study, however, Seo et al. (2011) reported that sea cucumber fed formulated diets substituting 50% of *S. thunbergii* with *U. pinnatifida*, *S. japonica*, and plant source (*Brassica oleracea* var. *capitata* and rice straw) achieved greater SGR compared to the control diet containing *S. thunbergii* at 40% without any substitution in the 10-week feeding trial. This difference could have resulted from differences in substitution ratio of *S. thunbergii* with macroalgae in diets (complete (100%) substitution of *S. thunbergii* with macroalgae (*U. pinnatifida* and *S. japonica*) in this study vs. 50% of substitution of *S. thunbergii* with macroalgae (*U. pinnatifida* or *S. japonica*) (Seo et al. 2011)). Similarly, combined macroalgae produced superior growth performance of abalone to a single macroalga (Naidoo et al. 2006; Robertson-Andersson et al. 2011; Viera et al. 2011). Nevertheless, the combined diet did not improve the growth of sea cucumber in this study because both UP and SJ diets produced inferior growth to the Con diet, and their combined effect had no desirable effect on growth.

Administration of a nutrition-balanced feed is one of the critical factors affecting the growth and development of all living animals. Generally speaking, sea mud is the main part of the diet for sea cucumber, which contains low nutrients (Zhao et al. 2012). This could be another reason for superior SGR of sea cucumber fed with nutrition-balanced diets to a diet containing sea mud powder (Xia et al. 2012a, b; Wu et al. 2015; Anisuzzaman et al. 2017; Song et al. 2017; Li et al. 2021). Substitutability of *S. thunbergii* with other macroalgae (either common feed for abalone (*U. pinnatifida* and *S. japonica*) or fouling macroalgae (*S. horneri* and *U. australis*)) seemed to be also closely related to with or without supplementation of sea mud powder in sea cucumber feed.

The chemical composition of the whole body sea cucumber, except for the moisture content, was not affected by the experimental diets in this study. Similarly, the whole body composition of the same species of sea cucumber was unaffected by diets substituting *S. thunbergii* with corn leaf (Wu et al. 2015) or substituting fish meal with red alga (*Pyropia*) spheroplasts (Shahabuddin et al. 2015). Unlike this study, however, the chemical composition of whole body of the same species of sea cucumber was affected by diets containing different feed ingredients (*Sargassum muticum*, *G. lemaneiformis*, *U. lactuca*, and benthic matter collected from an outdoor pond) (Wen et al. 2016) or substituting *S. thunbergii* with various plant ingredients (Seo et al. 2011). The chemical composition of sea cucumber was similar to that in this study, but varied seasonally (Gao et al. 2011b).

A nutrition-balanced feed may act as an immune regulator to lower the impact of various abiotic stressors in aquatic animals (Liu et al. 2015; Lee et al. 2016; Ansary et al. 2019a, b). No difference in survival of sea cucumber fed all experimental diets in the 4-day post observation periods after the 30-h air and 12-h low salinity exposures in this study indicated that dietary substitution of *S. thunbergii* with other macroalgae (*S. horneri*, *U. australis*, *U. pinnatifida*, *S. japonica*, and combined *U. pinnatifida* and *S. japonica*) did not deteriorate survival of sea cucumber. Similarly, Hou et al. (2019) reported that less than 6 h of air exposure did not cause irreparable damage to sea cucumber in handling and shipping when four groups of sea cucumber were resubmerged in aerated seawater for 24 h after 0 (control group), 1, 3, and 6 h of air exposure. Meng et al. (2011) showed that no mortality was observed during salinity decrease, but

40–50% mortality occurred when salinity was maintained at low levels when sea cucumbers were reared at 30 psu, acclimated at either 20 psu or 25 psu at a rate of 2.5 psu every 6 h, maintained at designated salinity for 4 days, and then returned at 30 psu for 4 days, and suggested that low salinity can cause mortality of sea cucumber partially due to the rapid drop of osmotic pressure in the coelomic fluid during hypo-osmotic stress after heavy rainfall in summer. Unlike this study, however, commercial diet supplemented with *U. lactuca* and grape seed extract improved productivity and lowered mortality of greenlip abalone (*H. laevigata*) during high summer water temperatures in Southern Australia (Lange et al. 2014).

Therefore, we can suggest that macroalgae (*S. horneri* and *U. australis*) can be effectively used as a substitute for *S. thunbergii* in sea cucumber feed without impairing growth performance and survival of sea cucumber against the 30-h air and 12-h low salinity exposures.

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Data availability The datasets generated during and/or analyzed during the current study are available from the corresponding author on reasonable request.

Declarations

Conflict of interest The authors declare no competing interests.

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