FAS http://e-fas.org
Fisheries and Aquatic Sciences

Original Article
Fish Aquat Sci 18(1), 57-63, 2015

Effects of Rearing Density on Growth of the Polychaete Rockworm *Marphysa sanguinea*

Hossein Parandavar[1,a], Kyeong-Hun Kim[2] and Chang-Hoon Kim[1,2]*

[1]Department of Marine Bio-materials and Aquaculture, Pukyong National University, Busan 608-737, Korea
[2]Department of Interdisciplinary Program of Biomedical, Mechanical and Electrical Engineering, Pukyong National University, Busan 608-737, Korea
[a]Present address: International Sturgeon Research Institute, Rasht, Iran

Abstract

Effects of rearing density on growth and survival of the polychaete rockworm *Marphysa sanguinea* have been investigated in order to develop rearing techniques for this species. This study was examined over a nine-month period in the Fisheries Science and Technology Center of Pukyong National University. Three rockworm densities, 500, 1,000 and 2,000 worms·m^{-2} with weight ranges of < 0.5 g, 0.6-1.5 g, and 1.6-2.5 g, and the no feed control treatment, were stocked in triplicate 0.10 m^2 boxes with sand bottoms. Growth rates were checked with 15 randomly sampled rockworms from each box at months 3, 6 and 9. Results showed that SGRs in all treatments were higher during the first period (0-3 months) than the second (3-6 months) and third periods (6-9 months) for all treatment densities, while SGRs decreased with increasing density. However, survival and growth of worms at high density was not better than low density, but daily biomass production in medium and high density groups was 6.28 g m^{-2}day^{-1} for the rockworms of 0.6-1.5 g with 2,000 inds·m^{-2}, and 12.6 g m^{-2}day^{-1} for group between 1.6-2.5 g with 2,000 inds·m^{-2}, and 14.7 g m^{-2}day^{-1} for the group of individuals <0.5 g with 1,000 inds·m^{-2}. Results showed that *M. sanguinea* can be one of the most suitable species to commercially exploit in a farming system. In particular, specified densities permit elevated pure production.

Key words: Polychaete, *Marphysa sanguinea*, Density, Growth

Introduction

The ecological role of polychaetes in marine benthic communities is very important (Giangrande et al., 2005). They are known to be good indicators of species richness (Olsgart and Somerfield, 2000) and as bio-indicators of the marine environment (Pocklington and Wells, 1992; Giangrande et al., 2005).

The rockworm *Marphysa sanguinea* (Montagu) that belongs to the Eunicidae family has been important bait for fisheries and sport fishing in Korea. There are several other families such as Arenicolidae, Nereidae, Glyceridae and Nephtyidae also exploited worldwide for sport and commercial fishing. Moreover, the demand for these species has increased rapidly in recent years because these worms are also very important nutrient sources for stimulating gonad maturation and spawning of fish and crustaceans in hatcheries for aquaculture purposes (Olive, 1999). The other main point of the culture and commercial use of this bait is to reduce the substrate harvesting disturbance, and the great biogeochemical and benthic community impact (Gambi et al., 1994).

The production costs of polychaete worms in an intensive worm aquaculture system should be efficient enough to make profits (Nesto et al., 2012). Therefore, one of the most important factors for culturing these species is production density

Received 23 February 2015; **Revised** 19 March 2015
Accepted 23 March 2015

***Corresponding Author**
E-mail: chkpknu@hanmail.net

(Olive, 1999; Prevedelli, 1994; Safarik et al., 2006). The role of density dependent processes in the regulation of animal populations has also been a subject of interest for many ecologists, and density-dependent factors, including competition for space and food, are also important structuring agents for populations of a number of sediment dwelling polychaete species (Scaps et al., 1998; Buekema et al., 2000; Omena and Zacagnini, 2000; Reise et al., 2001).

Preliminary information on the life cycle of these populations and the influence of several environmental variables was acquired from Prevedelli's laboratory study (1994). It showed a positive correlation between the growth and developmental rate of juveniles and water temperature was observed. The present study examined the effects of density on growth and mortality of the rockworm *Marphysa sanguinea*.

Materials and Methods

A nine month long on-site controlled experiment was conducted with 3 density groups and 1 no feed group for 3 different body size groups (< 0.5 g, 0.6 to 1.5 g and 1.6 to 2.5 g) of the rockworm *M. sanguinea* in the Fisheries Science and Technology Center, Pukyong National University, Goseong, South Korea. The three different rearing density groups were: 500 inds·m^{-2} (low, T1), 1,000 inds·m^{-2} (medium, T2) and 2,000 inds·m^{-2} (high, T3). The number of animals per boxes was set at 50, 100 and 200, in order to obtain densities of 500 inds·m^{-2} (T1), 1,000 inds·m^{-2} (T2) and 2,000 inds·m^{-2} (T3), respectively. Along with the 3 density treatments, a no feed treatment (TC) was set with the density of 1,000 inds·m^{-2}. Therefore each body size group was subject to 4 different treatments: 3 density groups (T1, T2, and T3) and 1 no feed control (TC).

The worms were reared in PVC boxes (0.1 m^2), measuring 40 cm (L) × 25 cm (W) × 20 cm (D). The boxes were half-filled with sand (150-500 μm), which was sun dried and then rinsed several times with freshwater. For each different body size group (< 0.5 g, 0.6 to 1.5 g and 1.6 to 2.5 g), three boxes were allocated per density group (T1, T2, and T3) and the no feed control (TC). This totaled twelve boxes per weight group, and 36 boxes total for the experiment. All boxes were connected to a seawater flow through system and the water was pumped from Jaran Bay in front of the Center. In order to examine the growth rates, 15 worms were randomly sampled from each box for every 3 month period. Water temperature was maintained at 20 ± 2℃ using a Thermo Control Unit. Water quality (temperature, salinity, dissolved oxygen and pH) was measured three times per week by the Hydrolab Surveyor 4a device.

M. sanguinea in each treatment box were fed with commercial high protein fish food pellets (Aquanet Co. Ltd. Korea; 54% protein), with the amount of 3.5% of body weight three times a week, except the TC group. Mortality of the worms was assessed at the completion of the nine months study.

Growth was evaluated as follows;

Specific growth rate (SGR) (%) = 100 [ln(Wf−Wi)] t^{-1},
Weight gain (WG) (%) = [100 × (Wf−Wi)/Wi],

where Wf is the final weight, Wi is the initial weight and t is the time interval in days. The survival rate was calculated with the number of surviving organisms at each time with respect to their initial number. The number of surviving organisms at the end of the experiment was used to calculate the final density (inds·m^{-2}), final biomass production, i.e. product of final density and individual mean wet weight (g m^{-2}) and daily biomass production (g m^{-2} day^{-1}).

Statistical Analysis

Confirming normality and homogeneity of variance of data were tested using the Kolmogorov-Smirnov test. Statistically significant differences among measured parameters were computed using a one-way ANOVA by SPSS 15 software for Windows (SPSS Inc., Chicago, IL, USA). Significant differences between treatments ($P < 0.05$) were evaluated using the Duncan's Multiple Range Test.

Results

During the nine-month study, there was little variation in salinity (34-35.5 psu) and pH (7.5-8.2) in the treatment boxes. Dissolved oxygen concentrations within the treatment boxes ranged from 5.8-6.9. As shown in Table 1, significant differences ($P < 0.05$) were detected among the three density groups of rockworms with different treatments in final weight (FW), specific growth rate (SGR), weight gain (WG) and survival rate (SR).

In group 1 (less than 0.5 g body size), significant differences in total weight ($P < 0.05$) were observed among the treatments, where 4.4 g in T1 was significantly higher than in other treatments (T2, 3.5 g; T3, 2.7 g and TC, 0.12 g) (Table 1). For T1, the growth rate in the first 3 month period (1.43 g) was higher than the second (1.3 g) and the third 3 month period (1.23 g). The T2 growth rate in the first 3 months was 1.1 g, the same in the second 3 months (1.11 g), but declined in the third 3 months (0.84 g). The growth rate of T3 in the first 3 months was 0.67 g, and for the second and third 3 month periods reached to 0.73 g and 0.85 g, respectively. The growth rate in TC group decreased during the first, second and third experimental period (Fig. 1).

In this group, the highest SGR was found in T1 and the lowest one to TC. The SGRs of T1, T2, T3 and TC groups were 0.84%, 0.75%, 0.64% and -0.43%, respectively. The SGRs of T1 and T2 were significantly higher than those of T3 and TC. The SGR of TC was the lowest among the treatments (Table 1).

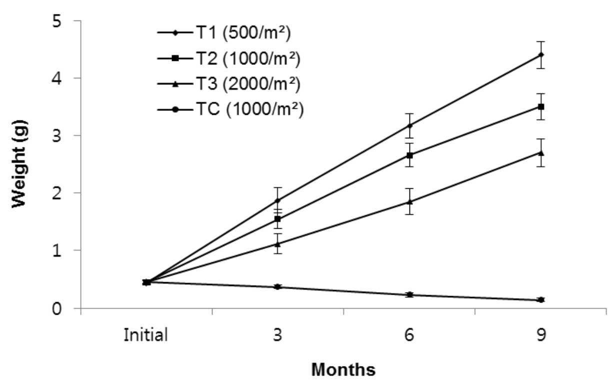

Fig. 1. Growth in total weight of small size (< 0.5 g) group of rockworm, *Marphysa sanguinea* reared under 3 different densities and a non-feeding condition. Error bars represent the standard deviation of the means.

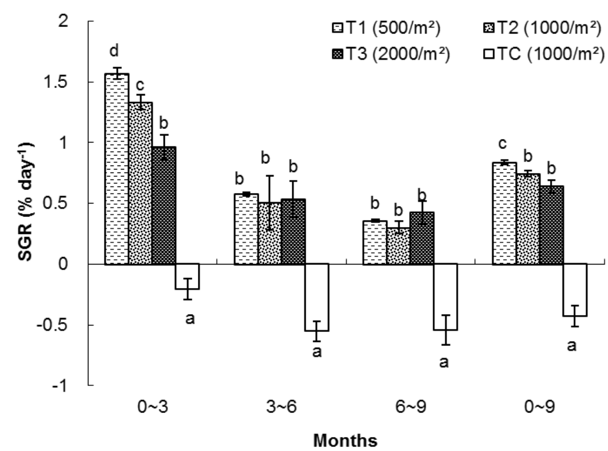

Fig. 2. Specific growth rate (SGR) of small body size (< 0.5 g) group of rockworm *Marphysa sanguinea* reared under 3 different densities (T1, T2, T3) and non-feeding (TC) for 9 months.

As shown in Fig. 2, in the first 3 months there were significant differences in SGR between treatments but in the second and third 3 month periods of the experiment there were no significant differences between treatments (without considering the control). The highest specific growth rates were evident for all samples in the first 3 months, followed by a general decrease. At the end of the experiment, survival rates of the T1, T2, T3 and TC groups were 78%, 62%, 45% and 15%, respectively.

The growth measured in weight in group 2, indicated significant differences in weight among the density treatments (Fig. 3). In T1, the growth rate in the first 3 months (1.94 g) was higher than the second (1.58 g) and third 3 months (1.05 g). In T2, growth rate in the first, second and third 3 months were 1.51 g, 1.35 g and 1.39 g, respectively, while those in T3 were 1.24 g, 1.36 g and 0.85 g, respectively. The growth rate of TC in the first, second and third 3 months were - 0.17 g, - 0.22g and - 0.33 g, respectively.

In particular, the growth rate was significantly lower in the highest density group. After nine months, average total weights of rockworms in T1, T2, T3 and TC treatments reached to 5.94 ± 0.31 g, 5.52 ± 0.24 g, 4.66 ± 0.24 g and 0.52 ± 0.12 g, respectively.

Table 1. Growth performance of the different body size (Group 1, 2, 3) of rockworm *Marphysa sanguinea* reared under 3 different densities (T1, T2, and T3) and a no feed treatment (TC) for 9 months[1]

	Treatments ($inds \cdot m^{-2}$)	IW [2] (g)	FW [3] (g)	SGR [4] (% day^{-1})	WG [5] (%)	SR [6] (%)
Group 1 (< 0.5 g)	T1 (500)	0.44 ± 0.04	4.4 ± 0.24^{d}	0.84 ± 0.02^{c}	897.2 ± 62^{d}	78 ± 4^{d}
	T2 (1000)	0.45 ± 0.03	3.5 ± 0.23^{c}	0.75 ± 0.03^{c}	672.2 ± 59^{c}	62 ± 5^{c}
	T3 (2000)	0.45 ± 0.02	2.7 ± 0.24^{b}	0.64 ± 0.05^{b}	488.0 ± 84^{b}	45 ± 4^{b}
	TC (1000)	0.45 ± 0.03	0.12 ± 0.03^{a}	-0.43 ± 0.09^{a}	-68.9 ± 8^{a}	15 ± 2^{a}
Group 2 (0.6–1.5 g)	T1 (500)	1.37 ± 0.08	5.94 ± 0.31^{d}	0.53 ± 0.02^{b}	332.6 ± 18^{c}	76 ± 4^{c}
	T2 (1000)	1.27 ± 0.10	5.52 ± 0.24^{c}	0.54 ± 0.02^{b}	334.9 ± 28^{c}	71 ± 5^{c}
	T3 (2000)	1.21 ± 0.12	4.66 ± 0.24^{b}	0.49 ± 0.03^{b}	284.4 ± 31^{b}	63 ± 7^{b}
	TC (1000)	1.24 ± 0.06	0.52 ± 0.12^{a}	$- 0.33 \pm 0.1^{a}$	-58 ± 12^{a}	52 ± 4^{a}
Group 3 (1.6–2.5 g)	T1 (500)	2.33 ± 0.10	7.2 ± 0.22^{d}	0.41 ± 0.02^{c}	209 ± 13^{c}	74 ± 7^{b}
	T2 (1000)	2.32 ± 0.09	6.71 ± 0.27^{c}	0.39 ± 0.02^{bc}	189.1 ± 14^{c}	76 ± 5^{b}
	T3 (2000)	2.34 ± 0.09	6.05 ± 0.25^{b}	0.35 ± 0.02^{b}	158.4 ± 11^{b}	72 ± 6^{b}
	TC (1000)	2.35 ± 0.08	1.44 ± 0.13^{a}	$- 0.18 \pm 0.03^{a}$	-38.5 ± 5^{a}	65 ± 6^{a}

[1]Values are mean ± SD. Within a column, means with different superscript letters differ significantly ($P < 0.05$). Absence of superscript indicates no significant difference between treatments.
[2]IW, Initial weight.
[3]FW, Final weight.
[4]SGR (Specific growth rate) (% day^{-1}): [(log final weight - log initial weight) / day] ×100.
[5]WG (Weight gain) (%): [(final weight - initial weight) / initial weight] ×100.
[6]SR (Survival rate) (%): (final individuals / initial individuals) ×100.

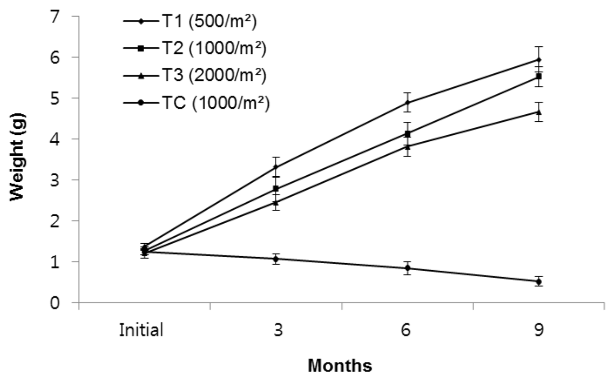

Fig. 3. Growth in total weight of medium body size (0.6~1.5 g) group of rockworm *Marphysa sanguinea* reared under 3 different densities (T1, T2, T3) and a non-feeding (TC) condition for 9 months. Error bars represent the standard deviation of the means.

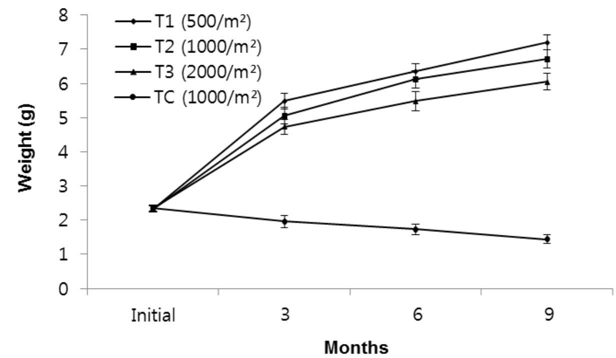

Fig. 5. Growth in total weight of high body size (1.6~2.5 g) group of rockworm *Marphysa sanguinea* reared under 3 different densities (T1, T2, T3) and a non-feeding (TC) condition for 9 months. Error bars represent the standard deviation of the means.

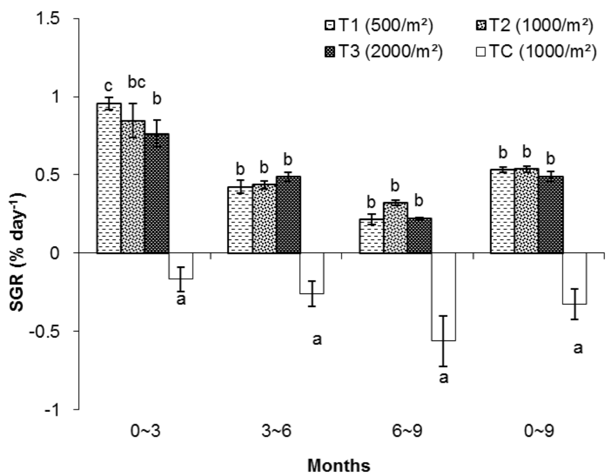

Fig. 4. Specific growth rate (SGR) of medium body size (0.6~1.5 g) group of rockworm *Marphysa sanguinea* reared under 3 different densities (T1, T2, T3) and non-feeding (TC) for 9 months.

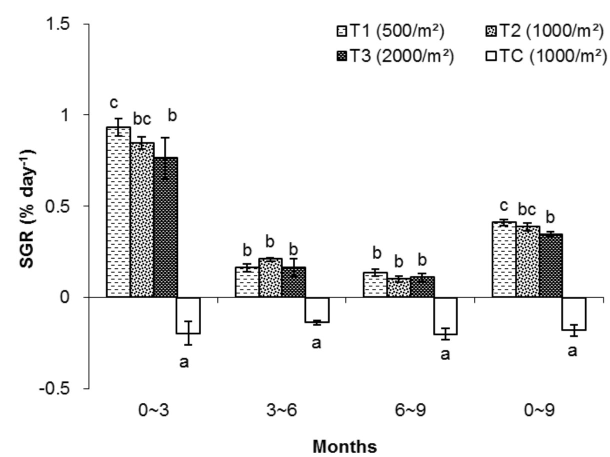

Fig. 6. Specific growth rate (SGR) of high body size (1.6~2.5 g) group of rockworm *Marphysa sanguinea* reared under 3 different densities (T1, T2, T3) and non-feeding (TC) for 9 months.

In the T1 (500 inds·m^{-2}) treatment, the specific growth rate was higher than in other treatments but there was no significant differences in SGR between T1 and T2 as for T1, T2, T3 and TC: 0.53%, 0.54%, 0.49% and -0.33% day^{-1}, respectively (Table 1). As shown in Fig. 4, in the first 3 months there were significant differences in SGR between T1 and T3 and control but there was no significant difference between T1 and T2, also no significant difference observed between T2 and T3. In the second and third 3 month period of the experiment there were no significant differences in SGR between treatments (except the TC). Similar to group 1, high specific growth rates, were evidenced for all samples in the first 3 months, followed by a general decrease. In group 1, at the end of the experiment, the survival rate of the treatment with low density (T1) was higher (76%) than the other treatments as those were 71%, 63% and 52% for T2, T3 and TC, respectively.

In group 3 (1.6-2.5 g), the average weights of worms at the densities of 500 inds·m^{-2}, 1,000 inds·m^{-2}, 2,000 inds·m^{-2} and TC (1,000 inds·m^{-2}) were 7.2 g, 6.71 g, 6.05 g and 1.44 g, respectively (Fig. 5, Table 1). These results showed that there were significantly large differences in mean weight among all treatments as the highest weight belonged to T1 and the lowest belonged to the control group (P < 0.05). In T1, the growth rate in the first 3 months (3.16 g) was higher than in the second 3 months (0.86 g) and third 3 months (0.85 g). In T2, the growth rate in the first 3 months was 2.73 g and decreased in the second 3 months (1.07 g), and in the third 3 months decreased to 0.59 g. The growth rate for T3 in the first 3 months was 2.39 g, and for the second 3 months was 0.75 g, and for the third 3 months decreased to 0.57 g. Also in this group, the results showed that there was not a positive growth rate in the control group as it decreased in weight throughout the experimental period showing a -0.39 g, -0.23 g and -0.29 g decrease in weight at first, second and third 3 month periods, respectively.

The specific growth rate in T1 (500 inds·m^{-2}) was higher than in other treatments, but there was no significant difference in SGR between T1 and T2. Also, no significant difference was observed in SGR between T2 and T3 as those were 0.41, 0.39, 0.35 and -0.18% for T1, T2, T3 and TC, respectively ($P > 0.05$) (Table 1). As shown in Fig. 6, in the first 3 months there were significant differences in SGR between T1-3 and TC, but there was no significant difference between T1 and T2, and no significant difference observed between T2 and T3. In the second and third 3 month periods there were no significant differences in SGR among treatments (not considering TC). The highest specific growth rates for all groups were evidenced for all samples in the first 3 months, followed by a general decrease. In this group, at the end of the experiment, survival rates of treatments was not related to density, unlike in other groups, as those were for T1, T2, T3 and TC: 74%, 76%, 72% and 65%, respectively.

Discussion

Rearing density effects on growth of rockworms were apparent in the long term. As expected, means of weight and survival were highest at low density and the lowest growth was at high density, following 3, 6 and 9 months (Figs. 1, 3 and 5) of incubation. In the whole experiment, the organisms kept at the highest density (2,000 inds·m^{-2}) showed the lowest value of specific growth rates suggesting the negative influence of increasing intra-specific competition, as observed in some nereidid polychaetes (Miller and Jumars, 1986; Zajac, 1986; Nesto et al., 2012). At all density levels, estimated specific growth rate during the first 3 months was higher than during the second and third trimester. Our results are in agreement with the results of Nesto et al. (2012) on *Hediste diversicolor*.

The final density and biomass per unit area and the daily biomass production are shown in Table 2. The maximum values of biomass were reached by the highest density sample, but organism mean weight was lower than in other densities. In group 1, after 9 months the best pure production observed was in T2 at 1,720 g·m^{-2}. T2's final biomass was approximately 5 times greater than polychaete weight following the start of incubation with daily biomass production of 6.28 g m^{-2} day^{-1}. These results are in line with the results of Nesto et al. (2012) about *Hediste diversicolor* and in contrast to groups 2 and 3, the highest value was revealed by organisms maintained at high density. In group 2, after 9 months the best pure production was observed in T3 (2,000 inds·m^{-2}) with 3452 g m^{-2} and daily biomass production of 12.6 g m^{-2} day^{-1}. This treatment's final biomass was 3.5 times greater than polychaete weight following the start of incubation. In group 3, after 9 months the best pure production observed was in T2 with 4032 g·m^{-2} (daily biomass production 14.72 g m^{-2} day^{-1}). It's final biomass was approximately 2 times greater than polychaete weight following the start of incubation, consistent with the results of Bridges (1996) and Pesch et al. (1987) about *Neanthes arenaceodentata*.

In all groups, maximum growth rate was noticed in the first 3 months. Thereafter, declines in growth rate were observed in all treatments but were most marked for polychaetes at high

Table 2. Production parameters calculated in *Marphysa sanguinea* maintained at different densities

	Treatments (inds·m^{-2})[c]	Final density[a] (inds·m^{-2})	Final biomass[a] (g m^{-2})	Pure production (g)	Daily biomass production[b] (g m^{-2} day^{-1})
Group 1 (< 0.5 g)	T1 (500)	390	1,716	1,496	5.46
	T2 (1,000)	620	2,170	1,720	6.28
	T3 (2,000)	900	2,430	1,530	5.58
	TC (1,000)	150	18	- 432	-1.58
Group 2 (0.6–1.5 g)	T1 (500)	380	2,257	1,572	5.74
	T2 (1,000)	710	3,919	2,649	9.67
	T3 (2,000)	1,260	5,872	3,452	12.60
	TC (1,000)	520	270	- 970	- 3.54
Group 3 (1.6–2.5 g)	T1 (500)	370	2,664	1,499	5.47
	T2 (1,000)	760	5,100	2,780	10.15
	T3 (2,000)	1,440	8,712	4,032	14.72
	TC (1,000)	650	936	-1,414	-5.16

[a]Data calculated at the end of experiment trials (9 months).
[b]Data calculated on the basis of pure production/culture days (274 days).
[c]Each treatment was done in triplicate.

density, which showed little further increase in weight. Individual worm growth in high density was not better than in low density. Negative effects on individual growth in high densities probably were due to stress associated with finding of feed and suitable space.

The observed negative density-dependent effects on growth of juvenile and late juvenile *M. sanguinea* are similar to those reported for a number of other polychaete species (Miron et al., 1991; Scaps et al., 1998; Safarik et al., 2006). Adverse effects on growth related to high rearing density have already been described for other species of polychaetes such as *Neanthes arenaceodentata* (Dillon et al., 1993; Pesch et al., 1987), *Scoloplos* spp. (Rice et al., 1986), *Capitella* sp. (Tenore and Chesney, 1985) and *Polydora ligni* (Zajac, 1986). In contrast, there has been one report to have mentioned positive growth effects with increasing polychaete (*Neanthes arenaceodentata*) density (Bridges et al., 1996).

It is evident that polychaete *M. sanguinea* possesses the ability to grow better in low density but biomass production is not related as it was with the survival factor because survival rate can be one of the main factors in this case. Survival was negatively influenced by high rearing density, as also already reported for *N. arenaceodentata* (Pesch et al., 1987; Dillon et al., 1993), *D. aciculata* (Safarik et al., 2006) and *Hediste diversicolor* (Nesto et al., 2012). The decreasing survival percentages are likely to be related to the increasing intra-specific competition. Rearing density related patterns in growth and mortality provide evidence for negative density dependent interactions with neighboring worms.

Considering 3.5–4 g as the best market weight for the polychaete *M. sanguinea*, this study showed that after 3, 6 and 9 months fed with commercial feeds and maintained at declared stocking densities, this species is suitable for commercial exploitation within indoor farming systems. For this species, if an initial weight of less than 0.5 g is used for rearing, according to the results of survival and growth in this study, the best density and time period to achieve approximately market weight and obtain more profit, is 1,000 inds·m^{-2} after 9 months. For the group 0.6-1.5 g, this is ,2000 inds·m^{-2} after 6 months, and for the group with 1.6-2.5 g, 2,000 inds·m^{-2} after 3 months.

Acknowledgments

This work was supported by a Research Grant of Pukyong National University (2013 year) and was conducted by using all experimental worms produced from the project (CD20120651) of Technology Development Program for Fisheries (on iPET), Ministry of Oceans and Fisheries, Republic of Korea. The authors also extend their appreciation to Mr. Ji-Il Kim and Ji-Hong Lee of the Fisheries Science and Technology Center of Pukyong National University for their valuable help for this experiment.

References

Bridges TS, Farrar JD, Gamble EV and Dillon TM. 1996. Intraspecific density effects in *Nereis* (*Neanthes*) *arenaceodentata* Moore (Polychaeta: Nereididae). J Exp Mar Biol Ecol 195, 221–235.

Buekema JJ, Essink K and Dekker R. 2000. Long term observations on the dynamics of three species of polychaetes living on tidal flats of the Wadden Sea: the role of weather and predator-prey interactions. J Anim Ecol 69, 31-44.

Dillon TM, Moore DW and Gibson AB. 1993. Development of a chronic sublethal bioassay for evaluating contaminated sediment with the marine polychaete worm *Nereis* (*Neanthes*) *arenaceodentata.* Environ Toxicol Chem 12, 589-605.

Gambi MC, Castelli A, Giangrande A, Lanera P, Prevedelli D and Vandini RZ. 1994. Polychaetes of commercial and applied interest in Italy: an overview. In: Actes de la 4ème Conférence Internationale des Polychètes.Memoires du Muséum National d'Histoire Naturelle. Dauvin JC, Laubier L and Reish DJ, eds. Muséum National d'Histoire Naturele, Paris. 162: 593-603.

Giangrande A, Licciano M and Musco L. 2005. Polychaetes as environmental indicators revisited. Review. Mar Pollut Bull 50, 1153–1162.

Miller DC and Jumars PA. 1986. Pellet accumulation, sediment supply, and crowding as determinants of surface deposit-feeding rate in *Pseudopolydora kempi japonica* Imajima & Hartman (Polychaeta:Spionidae). J Exp Mar Biol Ecol 99*,* 1-17.

Miron G, Desrosiers G, Retière C and Lambert R. 1991. Dispersion and prospecting behaviour of the polychaete *Nereis virens* (Sars) as a function of density. J Exp Mar Biol Ecol 145, 65–77.

Nesto N, Simonini R, Prevedelli D and DaRos L. 2012. Effects of diet and density on growth, survival and gametogenesis of *Hediste diversicolor* (O.F. Müller, 1776) (Nereididae, Polychaeta). J Aquaculture 363, 1–9.

Olive PJW. 1999. Polychaete aquaculture and polychaete science: a mutual synergism. Hydrobiologia 402, 175–183.

Olsgart F and Somerfield PJ. 2000. Surrogates in benthic investigations. Which taxonomic units? J Aquatic Ecosys Str Recov 7, 25–42.

Omena EP and Zacagnini ACC. 2000. Population dynamics and secondary production of *Laeonereis acuta* (Treadwell, 1923) (Nereididae: Polychaeta). Bull Mar Sci 67, 421-431.

Pesch CE, Zajac RN, Whitlatch RB and Balboni MA. 1987. Effect of intraspecific density on the history traits and population growth rate of *Neanthes arenaceodentata* (Polychaeta: Nereidae) in the laboratory. Mar Biol 96, 545-554.

Prevedelli D. 1994. Influence of temperature and diet on the larval development and growth of juveniles *Marphysa sanguinea* (Montagu) (Polychaeta, Eunicidae). Actesde la 4ème Conférence Internationale des polychètes: Memories du Museum d'Histoire Naturelle (Fr) 162, 521–526.

Reise K, Simon M and Herre E. 2001. Density-dependent recruitment after winter disturbance on tidal flats by the lugworm *Arenicola marina*. Helgol Mar Res 55, 161-165.

Rice DL, Bianchi TS and Roper EH. 1986. Experimental studies of sediment reworking and growth of *Scokoplos* spp. (Orbiniidae: Polychaeta). Mar Ecol Prog Ser 30, 9-19.

Safarik M, Redden AM and Schreider MJ. 2006. Density-dependent growth of the polychaete *Diopatra aciculata*. Scientia Marina 70S3, 337–341.

Scaps P, Brenot S, Retière C and Desrosiers G. 1998. Space occupation by the polychaetous annelid *Perinereis cultrifera*: Influence of substratum heterogeneity and intraspecific interactions on burrow structure. J Mar Biol Ass UK 78, 435-449.

Smith HS. 1935. The role of biotic factors in the determination of population densities. J Econ Ent 28, 873-898.

Tenore KR and Chesney Jr EJ. 1985. The effects of interaction of rate of food supply and population density on the bioenergetics of the opportunistic polychaete, *Capitella capitata.* Univ. South Carolina Press, SC, p.429.

Zajac RN. 1986. The effects of intra-specific density and food supply on growth and reproduction in an infaunal polychaete, *Polydora ligni* Webster. J Mar Res 44, 339–359.