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Survival and growth of the Caribbean scallops, *Argopecten nucleus* and *Nodipecten nodosus*, in suspended systems at different culture depths and net replacement frequencies

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ABSTRACT: Survival of the Caribbean scallops *Argopecten nucleus* and *Nodipecten nodosus* in suspended culture is relatively low. The effects of culture depth and frequency of net replacement on survival and growth of both scallops were assessed, in addition to the effects on the amount of biofouling and presence of predators in the culture systems. Hatchery-produced juveniles were kept in pearl nets suspended at 3 different culture depths (6, 9 and 12 m) with 2 frequencies for net replacement (i.e. monthly and every second month, hereafter 'bimonthly'). Survival of both scallop species was higher at 12 m depth. *A. nucleus* also showed higher growth rates at 12 m depth, while *N. nodosus* exhibited higher growth rates at 6 m depth. *A. nucleus* and *N. nodosus* performed best under monthly and bimonthly net replacement schemes, respectively. Frequency of presence and size of cymatid predators did not differ between treatments, but greater frequency and size of portunids occurred at bimonthly net replacement in *A. nucleus* culture nets. In most months, the biofouling dry biomass in the pearl nets was higher in those maintained at a depth of 6 m with bimonthly net replacement. The results indicate that the survival of both scallops could be improved by maintaining the culture systems suspended at a depth of 12 m, under lower temperature conditions, and applying a monthly net replacement scheme in *A. nucleus* in order to minimize the biofouling on the nets and a bimonthly scheme in *N. nodosus* in order to minimize scallop perturbation associated with net replacement.

KEY WORDS: Biofouling · Predators · Bivalves · Epibionts · Temperature · Portunids · Cymatids

1. INTRODUCTION

Argopecten nucleus (Born, 1780) and *Nodipecten nodosus* (Linnaeus, 1758) are pectinid species from the Caribbean, which are cultured at experimental and pilot scale (Velasco & Barros 2008, Velasco et al. 2011, Valderrama et al. 2016). Both species are epibenthic and live on sandy or calcareous bottom habitats. *A. nucleus* is a species of moderate size (~50 mm) occurring over the sea bottom until 50 m depth, while *N. nodosus* reaches larger sizes (~150 mm) and lives attached to hard substrates at depths between 10 and 120 m (Díaz & Puyana 1994, Lodeiros et al. 1999). Both exhibit strong growth in suspended culture systems at low densities (25 to 40% of bottom net coverage) at depths between 6 and 32 m, reaching the commercial size (40 mm in *A. nucleus* and 70 mm in *N. nodosus*) at 9 to 12 mo old (Lodeiros et al. 1998, 2001, Velasco et al. 2009, 2011, 2013, Barros et al. 2018). Their survival, however, is variable and can be rather low: between 7 and 68% for *A. nucleus* (Lodeiros et al. 1993, Velasco et al. 2009, Barros et al. 2018) and between 14 and 80% for *N. nodosus* (Lodeiros et al. 1998, Acosta et al. 2000, Mendoza et al. 2003, Rupp 2007, Velasco et al. 2009, Gómez-León et al. 2010). The main factors related to the low survival of these species are predation, the presence of large amounts of biofouling and high temperatures (>28°C) (Freites & Núñez 2001, Rupp 2007, Velasco et al. 2009).

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Some of the main predator species for these scallops in suspended culture systems are portunid crabs (*Charybdis hellerii* and *Cronius ruber*) and cymatid snails (*Cymatium pileare* and *C. cingulatum*) (Freites et al. 2000, Ciocco & Orensanz 2001, Velasco et al. 2009). Larval states of such organisms enter through the net into the culture systems and rapidly grow at the expense of predating the cultured scallops (Ventilla 1982, Freedman & Bell 1996). In the case of the biofouling, most of the species found are macroalgae and filtering invertebrates (especially *Balanus* sp.), which cover the culture systems and, to a lesser degree, the scallop shells (Uribe et al. 2001, Velasco 2008, Cortés-Useche et al. 2011, Carraro et al. 2012). These biofouling species usually compete for resources and restrict the water inflow into the culture systems, and they are also able to parasitize and deteriorate the scallop shells (Lesser et al. 1992, LeBlanc et al. 2002, Pacheco & Garate 2005, Fitridge et al. 2012). In addition, the presence of biofouling reduces the useful life of the culture systems, and the disposal of used systems in water or on land could impair the environmental quality of marine and terrestrial ecosystems (Uribe et al. 2001, Dürr and Watson 2010, Adams et al. 2011).

Among the mitigation measures used to control biofouling and the presence of predators in the culture systems, some of the most common are physical removal, coating shells and nets with antifouling products, biocontrol and avoidance of natural recruitment (Fitridge et al. 2012). Removal monthly, or every 2 wk, of predators and biofouling, as well as the use of sea urchins inside the systems are practices that have been reported as helpful to control the settling of harmful organisms in culture systems of *A. nucleus* and *N. nodosus* at small scales (Velasco et al. 2009, Cortés-Useche et al. 2011). Nevertheless, the use of such practices at a larger scale is considered wasteful, expensive and inconsistent (Roma et al. 2009, Fitridge et al. 2012). Considering that the settling of predator larvae and biofouling is directly influenced by food availability (Pérez et al. 2016), the increase of culture depth could be a useful, cheaper and easier measure to limit the larval recruitment of harmful species, and possibly with less frequent net replacement.

With the goal of identifying operational practices that could improve the productivity of *A. nucleus* and *N. nodosus* cultured in suspended systems, the present study assessed the effects of culture depth and frequency of net replacement on the survival and growth of both species as well as on the degree of biofouling and presence of predators.

2. MATERIALS AND METHODS

A total of 7000 juveniles of *Argopecten nucleus* (mean ± SE shell length: 11.3 ± 0.14 mm) and 13 200 juveniles of *Nodipecten nodosus* (8.5 ± 0.08 mm shell length) were produced in the Laboratorio de Moluscos y Microalgas of the Universidad del Magdalena in Taganga, Santa Marta, Colombia (11° 16′ 03″ N, 74° 11′ 24″ W), following the protocols described by Velasco & Barros (2007, 2008, 2009) and Velasco et al. (2007).

In this study, a factorial experimental design was applied for both species using 3 different culture depths (6, 9 and 12 m) and 2 frequencies for net replacement (monthly and every 2 mo, hereafter 'bimonthly'), which resulted in 6 treatments with 3 replicates each. Juveniles of each species were randomly distributed in Netlon® pyramidal pearl nets (35 × 35 × 20 cm and 6 mm mesh size) at a stocking density of 30% of net bottom coverage. The number of scallops placed in each net was calculated on the basis of the area occupied in the bottom of each net (1225 cm^2) and the surface area of each specimen assuming a circular shape (387 and 731 ind. net^{-1} for *A. nucleus* and *N. nodosus*, respectively). The pearl nets were then individually suspended in a 100 m subsurface long-line at a depth of 5 m, leaving ~50 cm of separation between pearl nets. The long-line system was located in the aquaculture lease of the Universidad del Magdalena in Bahía Taganga (11° 16′ 04″ N, 74° 11′ 36″ W), where depths varied from 15 to 20 m.

Monthly or bimonthly, depending on the treatment, the pearl nets were taken out of the water and transported ashore for ~4 to 6 h in order to replace the nets as well as to estimate scallop growth and survival, the amount of biofouling and the abundance of predators in the nets. For this, the population of each net was transferred to containers (20 to 50 l) with seawater, and the living specimens were counted. Monthly survival for each replica was estimated as the proportion between the number of living bivalves at the end of the month or every second month and the initial number of animals placed in each net. The shell length of 30 randomly selected individuals was measured with calipers (0.01 mm). Potential predators (crabs and snails) that were present in culture nets were placed in plastic bags containing 4% seawater formalin for subsequent identification, enumeration and measurement of individual body size (shell length for cymatid snails and carapace width for portunid crabs). The biofouling dry biomass on the nets was also estimated based on the difference between the weight of the pearl net sun-dried for 7 d and the ini-

tial weight of the clean net. Finally, the scallops were placed in new pearl nets at their original densities with the number of animals readjusted in each net according to the method described above, and the culture systems were returned to the original depth. Every month, surplus animals extracted from each pearl net were distributed in extra replicates under the same conditions as those of the experimental juveniles in order to subsequently adjust the density in the case of high mortalities. The experiments lasted 6 mo for both species, between March and September 2011 for *A. nucleus* and between June and December of 2012 for *N. nodosus*.

Every 2 wk, 3 seawater samples (4 l) were collected using a Niskin bottle at the 3 culture depths. Seston concentration and organic content of each sample were determined following the methods of Strickland & Parsons (1972). Salinity was measured using a refractometer (Brixco, precision 1 ppt), and temperature was registered from glass maximum–minimum thermometers (Sper Scientific, precision 1°C) maintained at each depth. Due to administrative problems in the project, it was not possible to take water samples between June and July of 2012.

The existence of statistical differences in the growth and survival of scallops between culture depth and frequency of net replacement was analyzed using a 2-way ANCOVA, with time as the covariate variable. The frequency of presence and size of predators, as well as the biofouling dry biomass, were compared between treatments and different periods of time using a factorial ANOVA. Physical-chemical parameters (i.e. temperature, salinity, seston concentration and organic content) were compared between different culture depths and periods of time using a 2-way ANOVA. When differences among treatments and/or periods of time were detected, Bonferroni or Tukey multiple tests were performed to detect the specific intra-level differences. Before the analysis, data normality and homoscedasticity were confirmed in almost all cases, and transformations were applied when required. Thus, predator size data were log transformed, data for shell length in *N. nodosus* and biofouling dry biomass were ranked, and data for frequency of presence of predators were square-root transformed. Temperature data for *A. nucleus* culture did not comply with the normality and homoscedasticity requirements, so these data were analyzed using the Kruskal-Wallis test. Correlation analysis of the data (i.e. physical-chemical variables, monthly growth and survival rates of scallops, frequency of presence and size of predators, and biofouling dry biomass) was performed using Spearman's correlation. The Statgraphics Centurion XVII X64 software was used for all statistical analysis, with significance level of $\alpha = 0.05$.

3. RESULTS

3.1. *Argopecten nucleus*

Survival of *A. nucleus* after 6 mo in suspended culture varied between 29 and 48% (Fig. 1A), with the highest decrease (41–68%) registered in the first sampling, at 30 or 65 d culture time. Juveniles with

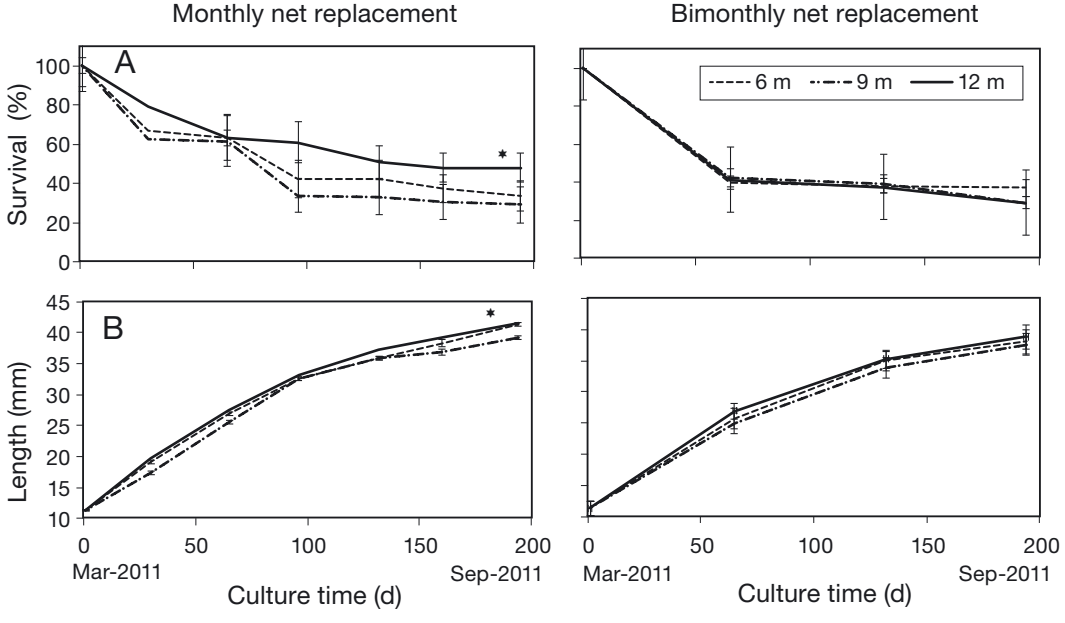

Fig. 1. Mean ± SE (A) survival and (B) growth in shell length of *Argopecten nucleus* maintained at different conditions (i.e. culture depths and net replacement frequencies. *$p < 0.05$

an initial shell length of 11.3 mm reached between 37.5 and 41.6 mm (Fig. 1B) at the end of the experiment, with growth rates between 0.14 and 0.16 mm d^{-1}. Highest survival and growth rates were found in animals cultured at a depth of 12 m and where net replacement was monthly (Table 1). The water temperature between March and September of 2011 varied between 23 and 29°C (Fig. 2A), with the lowest values at a depth of 12 m in March and the highest values at 6 and 9 m in July and August (K-W= 6.0, $p < 0.0098$). Salinity fluctuated between 34 and 37 ppt (Fig. 2B), with the highest values at depths of 9 and 12 m in March and the lowest values at 6 m in May (Table 2). Seston concentration fluctuated between 1.8 and 7.7 mg l^{-1} (Fig. 2C), being highest at depths of 9 and 12 m in April and June and lowest at 6 m from April to June (Table 2). Seston organic content oscillated between 17 and 82% (Fig. 2D), registering highest values at a depth of 12 m in May with lowest at 9 m from June to August (Table 2). Significant neg-

Table 1. ANCOVAs and ANOVAs of the survival and shell length of *Argopecten nucleus* and *Nodipecten nodosus* maintained at different suspended culture conditions (i.e. culture depths and net replacement frequencies)

Variable	Source of variation	SS	df	Square means	*F*	p
Survival	Covariable: Culture time	42762.10	1	42762.10	169.71	0.0000
	A: Depth	705.85	2	352.92	1.4	0.0216
	B: Net replacement	243.38	1	243.38	0.97	0.0283
	A × B Interaction	928.72	2	464.36	1.84	0.1642
Shell length	Covariable: Culture time	306162.00	1	306162.00	20117.48	0.0000
	A: Depth	605.75	2	302.87	19.9	0.0000
	B: Net replacement	1703.96	1	1703.96	111.97	0.0000
	A × B Interaction	57.03	2	28.51	1.87	0.1537
Cymatid frequency	A: Culture time	0.81	2	0.40	1.86	0.1698
	B: Depth	0.40	2	0.20	0.93	0.4041
	C: Net replacement	0.80	1	0.80	3.7	0.0624
	A × B Interaction	0.96	4	0.24	1.11	0.3685
	A × C Interaction	0.16	2	0.08	0.37	0.6967
	B × C Interaction	0.17	2	0.09	0.39	0.6774
	A × B × C Interaction	0.81	4	0.20	0.94	0.4535
Cymatid size	A: Culture time	4.37	2	2.19	1.67	0.2024
	B: Depth	2.77	2	1.38	1.06	0.358
	C: Net replacement	2.94	1	2.94	2.24	0.1428
	A × B Interaction	9.92	4	2.48	1.9	0.1325
	A × C Interaction	1.18	2	0.59	0.45	0.641
	B × C Interaction	3.24	2	1.62	1.24	0.3024
	A × B × C Interaction	4.21	4	1.05	0.8	0.5304
Portunid frequency	A: Culture time	2.90	2	1.45	3.31	0.0478
	B: Depth	1.85	2	0.92	2.11	0.1365
	C: Net replacement	1.56	1	1.56	3.56	0.0673
	A × B Interaction	3.16	4	0.79	1.8	0.1503
	A × C Interaction	0.83	2	0.41	0.94	0.399
	B × C Interaction	0.24	2	0.12	0.27	0.7637
	A × B × C Interaction	0.75	4	0.19	0.43	0.7894
Portunid size	A: Culture time	597.28	2	298.64	3.62	0.0368
	B: Depth	240.25	2	120.13	1.46	0.2462
	C: Net replacement	570.51	1	570.51	6.92	0.0125
	A × B Interaction	332.37	4	83.09	1.01	0.4161
	A × C Interaction	164.88	2	82.44	1	0.3777
	B × C Interaction	171.23	2	85.61	1.04	0.3642
	A × B × C Interaction	161.87	4	40.47	0.49	0.7423
Fouling	A: Culture time	3198.04	2	1599.02	17.43	0.0000
	B: Depth	6486.26	2	3243.13	35.34	0.0000
	C: Net replacement	9680.17	1	9680.17	105.5	0.0000
	A × B Interaction	21776.00	4	5443.99	59.33	0.0000
	A × C Interaction	80.11	2	40.06	0.44	0.6497
	B × C Interaction	1440.78	2	720.39	7.85	0.0015
	A × B × C Interaction	458.11	4	114.53	1.25	0.3082

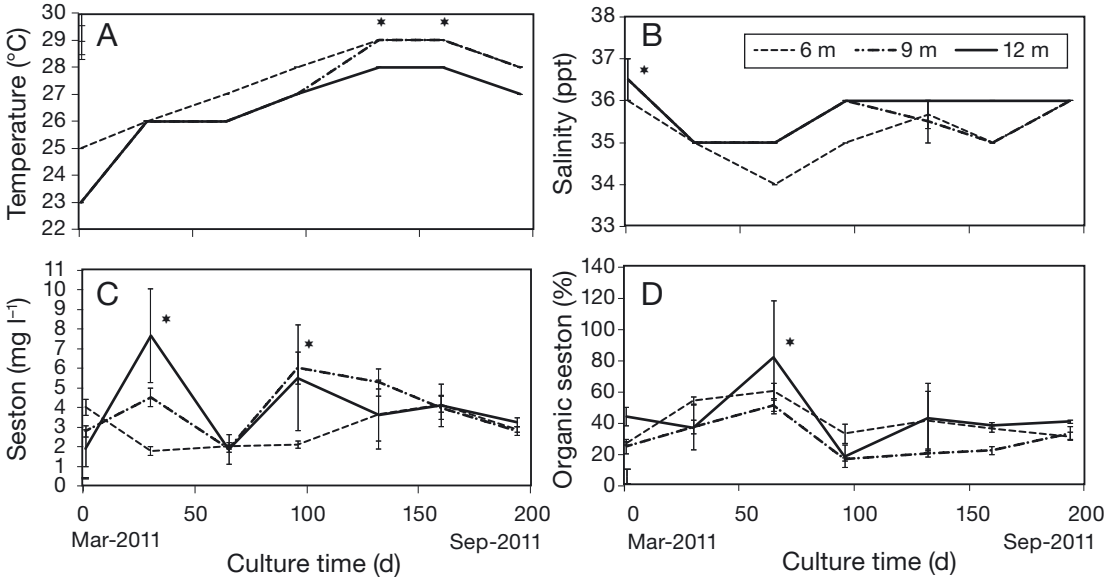

Fig. 2. Mean ± SE (A) temperature, (B) salinity, (C) seston concentration and (D) seston organic content in Taganga Bay during the experimental culture of *A. nucleus*. *$p < 0.05$

Table 2. ANOVAs of the physicochemical parameters of Taganga Bay (Santa Marta, Colombia) at different depths and months at which *Argopecten nucleus* and *Nodipecten nodosus* were cultured

Species	Variable	Source of variation	SS	df	Square means	*F*	p
A. nucleus	Salinity	A: Depth	2.78	2	1.39	20.55	0.0000
		B: Culture time	13.99	6	2.33	34.43	0.0000
		A × B Interaction	3.27	12	0.27	4.03	0.0008
	Seston	A: Depth	12.50	2	6.25	3.02	0.0631
		B: Culture time	43.57	6	7.26	3.50	0.0089
		A × B Interaction	63.03	12	5.25	2.53	0.0178
	Seston organic	A: Depth	1720.30	2	860.15	3.95	0.0293
		B: Culture time	7105.03	6	1184.17	5.44	0.0006
		A × B Interaction	1985.86	12	165.49	0.76	0.6844
N. nodosus	Temperature	A: Depth	3.60	2	1.80	2.50	0.0000
		B: Net replacement	52.80	4	13.20	10.11	0.0000
		A × B Interaction	2.40	8	0.30	0.33	0.0000
	Salinity	A: Depth	0.96	2	0.48	2.48	0.0000
		B: Culture time	13.00	4	3.25	16.71	0.0000
		A × B Interaction	1.06	8	0.13	0.68	0.0000
	Seston	A: Depth	0.02	2	0.01	0.08	0.9206
		B: Culture time	0.13	4	0.03	0.34	0.8481
		A × B Interaction	0.95	8	0.12	1.28	0.2912
	Seston organic	A: Depth	2026.17	2	1013.08	4.38	0.5215
		B: Culture time	495.90	4	123.98	0.54	0.7107
		A × B Interaction	1568.18	8	196.02	0.85	0.5701

ative correlations were found between the monthly growth rates of *A. nucleus* and water temperature (Table 3).

The frequency of presence of cymatid snails in the pearl nets oscillated between 0 and 16 ind. m^{-2}, their shell lengths fluctuated between 3 and 28 mm (Fig. 3A), and their growth rates ranged between 0 and 16 mm mo^{-1}. The frequency of presence of portunid crabs varied between 0 and 46 ind. m^{-2}, while their carapace widths were between 4 and 42 mm (Fig. 3B), and their growth rates were between 0 and 24 mm mo^{-1}. Significantly higher frequency and size of portunids were registered in April and/or June than in August (Table 1). No statistical differences

Table 3. Spearman correlation analysis between environmental parameters, the monthly growth rates and survival values of *Argopecten nucleus* and *Nodipecten nodosus* under different suspended culture conditions

Parameter	*A. nucleus*						*N. nodosus*					
	Growth rate			Survival			Growth rate			Survival		
	r	n	p	r	n	p	r	n	p	r	n	p
Temp	−0.9281	27	0.0000	0.5547	27	0.0514	0.4956	23	0.0201	−0.3013	24	0.1484
Salinity	0.1031	27	0.5990	−0.2234	27	0.2546	−0.1933	23	0.3647	0.0196	24	0.9252
Seston	−0.2326	27	0.2356	−0.0037	27	0.9851	−0.3323	23	0.1191	−0.0431	24	0.8363
Organic seston	0.1856	27	0.3440	0.0418	27	0.8311	−0.1286	23	0.5465	0.0274	24	0.8954
Cymatid frequency	−0.1244	27	0.5258	−0.2710	27	0.1670	0.1901	23	0.3726	−0.1251	24	0.5486
Portunid frequency	0.2670	27	0.1734	−0.2121	27	0.2794	0.0015	23	0.9943	−0.1698	24	0.4154
Cymatid size	0.1909	18	0.4312	−0.3849	18	0.1125	0.6571	6	0.1417	−0.3714	6	0.4062
Portunid size	0.4898	20	0.0327	−0.2521	20	0.2719	0.0214	15	0.9361	0.0321	15	0.9043
Cymatid growth rate	0.2819	17	0.2596	−0.4779	17	0.0559	0.3241	17	0.1949	−0.2028	18	0.4030
Portunid growth rate	0.7606	18	0.0017	−0.3127	18	0.1973	0.2022	17	0.4186	−0.2909	18	0.2303
Fouling	0.1043	18	0.6670	−0.3514	18	0.1474	0.2598	17	0.2987	−0.0320	18	0.8951

were found for the frequency of presence and size of cymatid predators found in the pearl nets at different culture depths or net replacement frequencies (Table 1). The biofouling dry biomass fluctuated between 215 and 1143 g m^{-2} (Fig. 3C), with the higher values found under a bimonthly net replacement scheme, in the month of August, and in pearl nets kept at a depth of 6 m, except in April when higher biofouling values were verified at 12 m (Table 1). Significant positive correlations were found between the size of portunid crabs, the crab growth rate and the monthly growth of *A. nucleus* (Table 3).

3.2. *Nodipecten nodosus*

Survival of *N. nodosus* juveniles after 6 mo in suspended culture fluctuated between 0 and 44% (Fig. 4A), with marked declines (35–54%) registered in the first sampling at 30 or 65 d culture time. Survival values were significantly higher in animals maintained at a depth of 12 m and under a bimonthly net replacement scheme (Table 4). Juveniles with an initial shell length of 8.5 mm reached between 45.6 and 49.6 mm (Fig. 4B), exhibiting monthly growth rates from 0.21 to 0.24 mm d^{-1}. The greatest growth was observed in animals cultured at a depth of 6 m and with bimonthly net replacement (Table 4). From August to December of 2012, the water temperature oscillated between 25 and 29°C (Fig. 5A), with the lowest values at depths of 9 and 12 m in December and the highest values at 6 m in November (Table 2). Salinity fluctuated between 35 and 38 ppt (Fig. 5B), being significantly higher in December and lower in September at a depth of 6 and 9 m (Table 2). Seston concentration varied between 1.8 and 4.3 mg l^{-1} (Fig. 5C), with no significant differences found in different months and culture depths (Table 2). Seston organic content fluctuated between 31 and 65% (Fig. 5D), with no significant differences found between different months (Table 2), but with values significantly higher at a depth of 12 m (Table 2). A significant, positive correlation was found between the growth rate of *N. nodosus* and water temperature (Table 3).

The frequency of presence of cymatid snails in the pearl nets fluctuated between 0 and 8 ind. m^{-2}, while their size varied between 8 and 40 mm (Fig. 6A), and their growth rates were between 0 and 40 mm mo^{-1}. Similarly, the frequency of presence of portunid crabs oscillated between 0 and 16 ind. m^{-2}, and their carapace width presented values between 7 and 25 mm mo^{-1} (Fig. 6B), and their growth rates were between 0 and 15 mm mo^{-1}. No significant differences were found in the frequency of presence or growth rate of predators between different months, culture depths or different net replacement frequencies (Table 4) during the experiment. Biofouling dry biomass fluctuated between 73.7 and 1083.3 g m^{-2} (Fig. 6C). Significantly higher values were registered under bimonthly net replacement, especially in August and at 6 or 9 m of depth (Table 4). There was no significant correlation between predators or biofouling variables and the growth or survival of *N. nodosus* (Table 3).

4. DISCUSSION

The present study demonstrates how survival and growth of the 2 Caribbean pectinid species studied

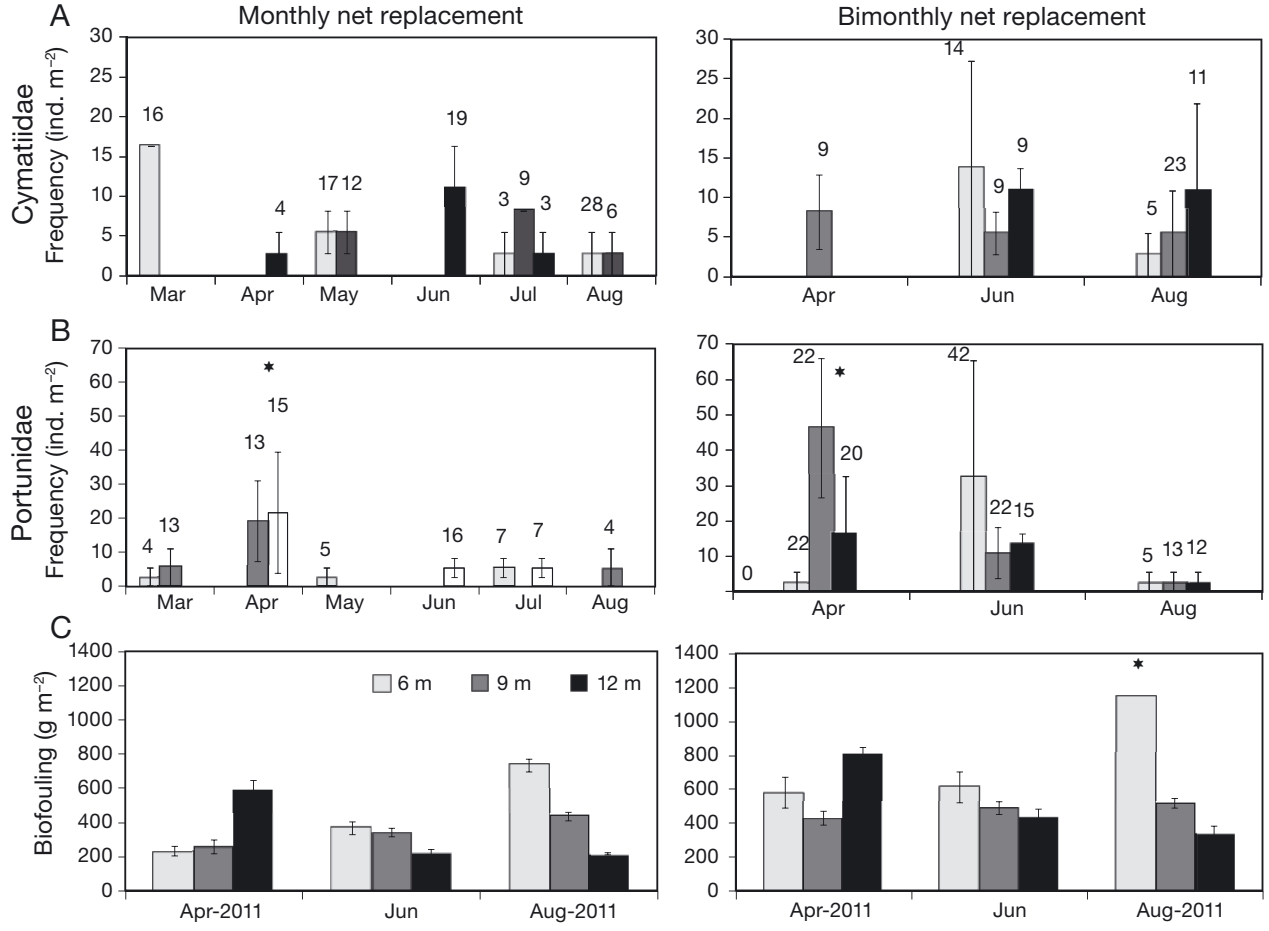

Fig. 3. Mean ± SE frequency of presence and size of the predators (A) Cymatiidae and (B) Portunidae inside the pearl nets with *Argopecten nucleus* and (C) biofouling dry biomass in the nets under different conditions (i.e. culture depths and net replacement frequencies). Numbers above bars represent the predator size means in mm (shell length for cymatid snails and carapace width for portunid crabs). *$p < 0.05$

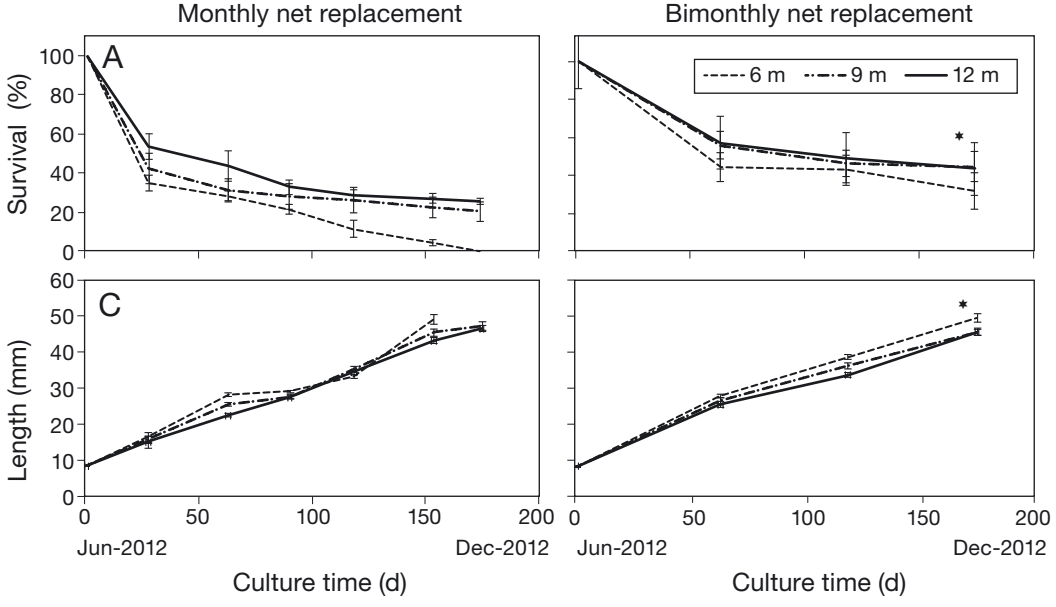

Fig. 4. Mean ± SE (A) survival and (B) growth in shell length of *Nodipecten nodosus* maintained at different conditions (i.e. culture depths and net replacement frequencies). *$p < 0.05$

Table 4. ANCOVAs and ANOVAs of the survival and shell length of *Nodipecten nodosus* maintained at different suspended culture conditions (i.e. culture depths and net replacement frequencies)

Variable	Source of variation	SS	df	Square means	*F*	p
Survival	Covariable: Culture time	47 523.10	1	47523.10	172.36	0.0000
	A: Depth	2232.20	2	1116.10	4.05	0.0207
	B: Net replacement	11 450.90	1	11450.90	41.53	0.0000
	A × B Interaction	256.60	2	128.30	0.47	0.6294
Shell length	Covariable: Culture time	374 641 000.00	1	374 641 000.00	5467.62	0.0000
	A: Depth	3 172 850.00	2	1 586 420.00	23.15	0.0000
	B: Net replacement	827 432.00	1	827 432.00	12.08	0.0005
	A × B Interaction	405 746.00	2	202 873.00	2.96	0.0520
Cymatid frequency	A: Culture time	0.28	2	0.14	1.78	0.1835
	B: Depth	0.07	2	0.04	0.44	0.6447
	C: Net replacement	0.14	1	0.14	1.78	0.1908
	A × B Interaction	0.06	2	0.03	0.24	0.7885
	A × C Interaction	0.36	4	0.09	1.11	0.3664
	B × C Interaction	0.07	2	0.04	0.44	0.6447
	A × B × C Interaction	0.07	2	0.04	0.44	0.6447
Cymatid size	A: Culture time	241.25	2	120.63	1.75	0.1875
	B: Depth	102.98	2	51.49	0.75	0.4801
	C: Net replacement	63.74	1	63.74	0.93	0.3421
	A × B Interaction	96.04	4	24.01	0.35	0.8428
	A × C Interaction	70.58	2	35.29	0.51	0.6028
	B × C Interaction	82.24	2	41.12	0.6	0.5552
	A × B × C Interaction	466.71	4	116.68	1.7	0.1721
Portunid frequency	A: Culture time	0.48	2	0.24	0.37	0.6924
	B: Depth	2.48	2	1.24	1.91	0.1622
	C: Net replacement	1.19	1	1.19	1.83	0.1847
	A × B Interaction	0.19	2	0.09	0.48	0.6233
	A × C Interaction	4.74	4	1.19	1.83	0.1447
	B × C Interaction	1.37	2	0.69	1.06	0.358
	A × B × C Interaction	0.26	2	0.13	0.2	0.8196
Portunid size	A: Culture time	99.81	2	49.90	0.87	0.4256
	B: Depth	457.25	2	228.62	4.01	0.0568
	C: Net replacement	346.39	1	346.39	6.07	0.0586
	A × B Interaction	723.30	4	180.82	3.17	0.0549
	A × C Interaction	90.39	2	45.19	0.79	0.4606
	B × C Interaction	114.75	2	57.37	1.01	0.3758
	A × B × C Interaction	389.16	4	97.29	1.71	0.1702
Fouling	A: Culture time	1838.53	2	919.26	20.95	0.0000
	B: Depth	4139.53	2	2069.76	47.16	0.0000
	C: Net replacement	20 126.00	1	20 126.00	458.6	0.0000
	A × B Interaction	7768.61	4	1942.15	44.25	0.0562
	A × C Interaction	1025.53	2	512.76	11.68	0.0001
	B × C Interaction	2861.08	2	1430.54	32.6	0.0698
	A × B × C Interaction	7970.39	4	1992.60	45.4	0.0745

are affected by culture depth and net replacement frequency, in addition to environmental variables such as water temperature, biofouling biomass and the size of portunid predators. These results facilitate a better understanding of the complex dynamics between environmental and operational variables inherent to scallop aquaculture in suspended systems and productive traits, which can support better management practices to improve productivity.

4.1. Effect of depth

The high survival of *Argopecten nucleus* and *Nodipecten nodosus* cultured at the greatest depth tested (12 m), as well as the highest growth of *A. nucleus* under such conditions, are similar to results previously reported for the survival of *N. nodosus* (Lodeiros et al. 1998), the growth and survival of *Euvola ziczac* (Lodeiros & Himmelman 2000), and the

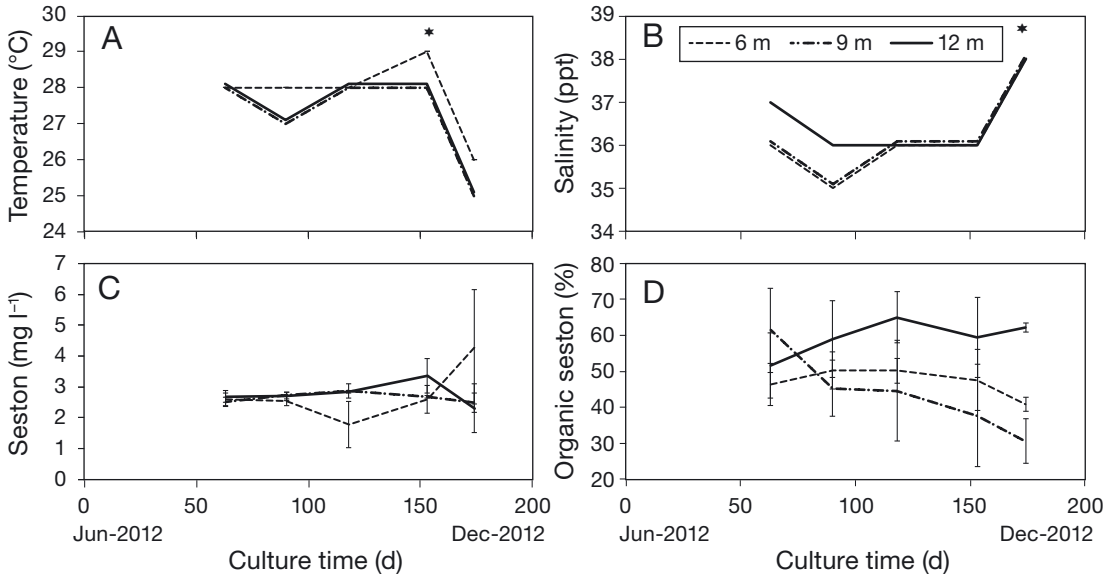

Fig. 5. Mean ± SE (A) temperature, (B) salinity, (C) seston concentration and (D) seston organic content in Taganga Bay during the experimental culture of *Nodipecten nodosus* (August to December of 2012). *p < 0.05

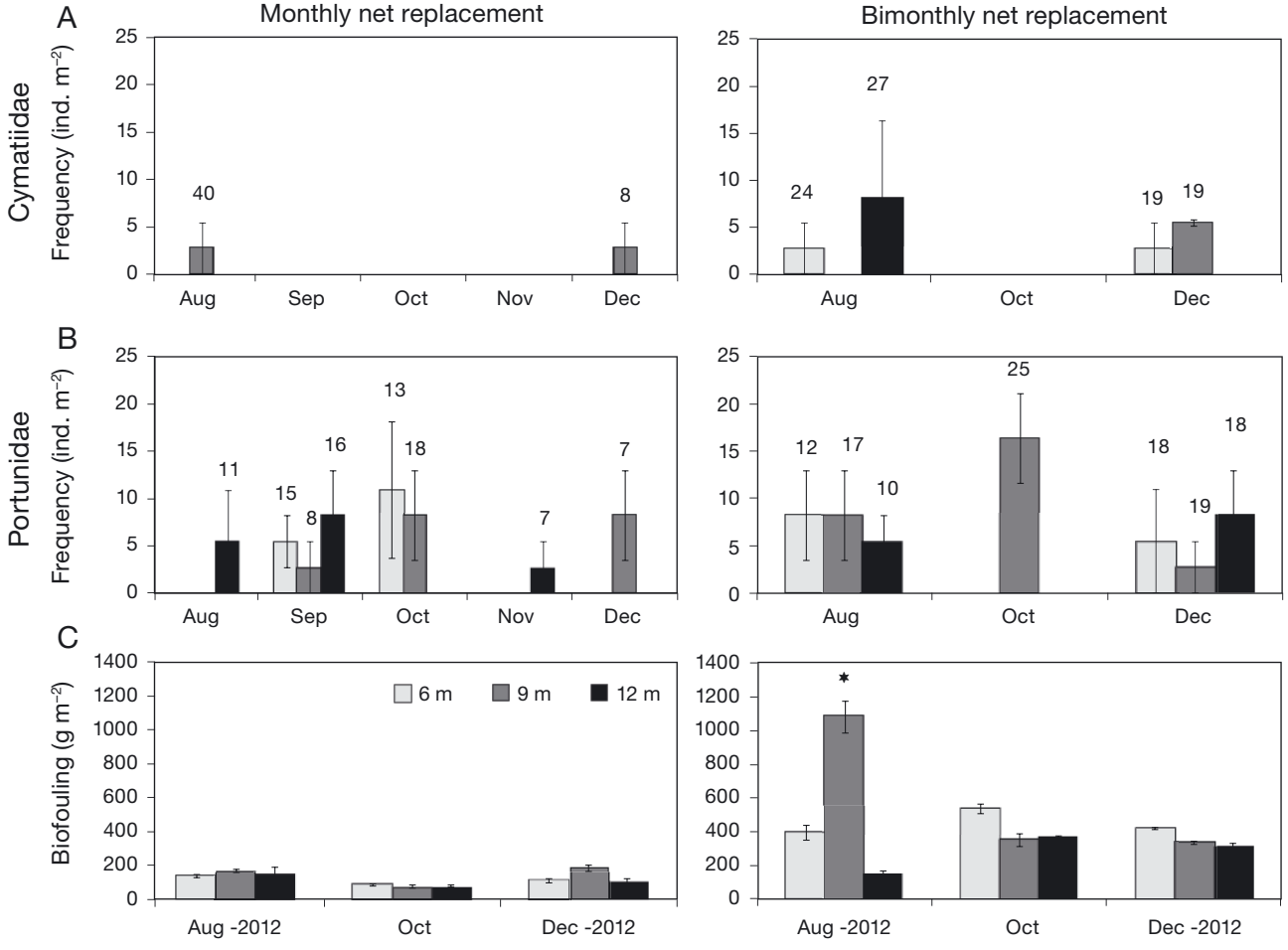

Fig. 6. Mean ± SE frequency of presence and size of the predators (A) Cymatiidae and (B) Portunidae inside the pearl nets with *Nodipecten nodosus* and (C) biofouling dry biomass in the nets under different conditions (i.e. culture depths and net replacement frequencies). Numbers above bars represent the predator size means in mm (shell length for cymatid snails and carapace width for portunid crabs). *p < 0.05

growth of *Aequipecten opercularis* (Román et al. 1999) and *Pecten maximus* (Román et al. 2003). The lower temperatures as well as the lower values of biofouling dry biomass found in the pearl nets maintained at greater depths in most of the months suggest that these factors promoted survival in both pectinid species studied and the growth in *A. nucleus*. High temperatures (28°C) can cause a decrease in food intake and an increase in metabolic demands, resulting in less energy available for growth and reproduction of these 2 species (Velasco 2006). Similarly, the presence of a larger biofouling biomass in the pearl nets maintained in shallow waters most of the months probably exerted additional stress in the scallops, thus increasing their susceptibility to death. Some of the main causes of stress on scallops related to the presence of biofouling are (1) toxic nitrogenous waste products released to the water, (2) competition for resources such as food, oxygen and space, and (3) energetic costs related to repair of shell damage caused by shell-boring organisms (Lesser et al. 1992, LeBlanc et al. 2002, Fitridge et al. 2012). In contrast, the highest growth of *N. nodosus* cultured at 6 m suggests that this species had large energetic reserves to support its growth and/or that it had low energetic demands for shell reparation under high temperature and biofouling abundance conditions. It has been shown that *N. nodosus* is capable of storing, transferring and using nutrients from the muscle and digestive gland to support somatic and gonadic growth, respectively (Lodeiros et al. 2001), especially under suboptimal conditions (Velasco & Barros 2008). The suspension of the culture systems at greater depths, especially in August, was able to decrease the settlement of larval stages of biofouling species in the nets, thus promoting a positive effect on the survival of the 2 pectinid species studied and on the growth of *A. nuleus*.

4.2. Effect of net replacement frequency

The higher values of survival and growth in individuals of *A. nucleus* cultured under a monthly net replacement scheme, in comparison to those under a bimonthly scheme, are similar to those found for *E. ziczac* (Lodeiros & Himmelman 1996), *Placopecten magellanicus* (Claereboudt et al. 1994) and *Pinctada margaritifera* (Pit & Southgate 2003) cultured in systems with monthly and bimonthly net cleaning. These results are related to the higher values of biofouling biomass size and frequency of portunid crabs found in the pearl nets with bimonthly replacement. Indeed, crabs of larger size are able to predate on a greater number of cultured scallops, which has been previously reported for *Carcinus maenas* (Klein-Breteler 1975). Additionally, the positive correlation found between the size of portunid crabs and growth of *A. nucleus* suggests that portunids of larger size consumed a greater number of small scallops within the culture systems, which exhibited slower growth, therefore indirectly selecting larger scallops with a faster growth rate. Similar results have been reported in oysters *Crassostrea virginica* predated by crabs *Callinectes sapidus* (Eggleston 1990). It seems likely that a monthly net replacement contributes towards minimizing the settlement of larval stages of biofouling species in the nets as well as towards hindering the growth of portunid crabs, thus preventing them from reaching a critical body size within the pearl nets. These 2 aspects should explain the higher survival and growth of *A. nucleus* under a monthly net replacement scheme.

The high values of survival and growth observed in individuals of *N. nodosus* cultured under a bimonthly net replacement scheme suggest this species has low sensitivity to the deleterious effects of biofouling but high sensitivity to handling during net replacement. A lack of a significant relationship between the amount of biofouling and survival and growth has been previously documented for this species (Rupp 2007, Carraro et al. 2012) and other bivalves like *Mytilus galloprovincialis* and *Ostrea edulis* (Perera et al. 1999). The greater biofouling resistance of *N. nodosus* than of *A. nucleus* could be related to its higher shell thickness (1.5 mm vs. 1 mm in adults, respectively). Apparently, in *N. nodosus*, a monthly net replacement negatively affects survival and growth, which might be related to the stress inflicted by handling and manipulating the animals more frequently.

Higher mortality of *A. nucleus* and *N. nodosus* during the first period of experimental culture, immediately after seeding the scallops in the pearl nets (54 and 44% on average for *A. nucleus* and *N. nodosus,* respectively), suggest that the exposure to air, handling and manipulation during the detachment of juveniles from the artificial collectors, grading and seeding represent important stress factors that ultimately increase mortality rates. Usually these activities are performed for long periods of time (4 to 6 h) in the beach at high water temperatures (28 to 32°C) and in limited shade, where the scallops are placed in containers at high densities with small volumes of seawater (20 to 50 l) and low water renewal. To increase survival and growth in this species, it is highly recommended to reduce the duration of the

detachment, grading and seeding activities, in addition to implementing a system with flow-through tanks containing larger volumes of seawater.

4.3. Predation and biofouling

The maximum frequencies of presence of cymatid and portunid predators found in the pearl nets with *A. nucleus* and *N. nodosus* in Bahía Taganga (16 cymatids m^{-2} mo^{-1} and 24 portunids m^{-2} mo^{-1}) are similar to those reported for *A. nucleus* in the same geographical area (22 cymatids m^{-2} mo^{-1} and 11 portunids m^{-2} mo^{-1}; Velasco et al. 2009) but lower than those found in the protected area Parque Natural Nacional Tayrona in other bivalve species like *Pinna carnea* (45 cymatids m^{-2} mo^{-1} and 33 portunids m^{-2} mo^{-1}; Velasco & Borrero 2004), *Pteria colymbus* (41 cymatids m^{-2} and 6 portunids m^{-2} mo^{-1}; Velasco & Borrero 1996) and *Pinctada imbricata* (33 cymatids m^{-2} mo^{-1} and 55 portunids m^{-2} mo^{-1}; Velasco & Barros 2010). These results suggest that scallops are less appetizing or more difficult to predate than other Caribbean marine bivalves. This could also be indicative of a higher abundance of predators of bivalves inside protected areas. The growth rates of cymatids and portunids found in this study (40 and 42 mm mo^{-1}, respectively) are high in relation to those estimated under suspended culture conditions of *P. colymbus* (12 to 26 mm mo^{-1}, respectively; Velasco & Borrero 1996) and *P. imbricata* (23 to 25 mm mo^{-1}, respectively; Velasco & Barros 2010). These differences could be related to temporal and spatial variations in water physicochemical conditions, changes in the species composition of the predator groups or differences in the nutritive value of the scallops and pearl oysters.

A decrease in the biofouling biomass in most culture systems at greater depths has been reported in other studies (Claereboudt et al. 1994, Rupp 2007). This decrease has been associated with the reduction of the supply of food for the biofouling biota, mainly composed of filter feeders or phototrophic organisms. This pattern was maintained under stratified conditions, but it was lost when upwelling or strong wind events took place, such as those verified in April 2011 as well as in August to October 2012, respectively. The lower average rate of biofouling formation in the pearl nets suspended in Taganga found in the present study (190 g m^{-2} mo^{-1}), in comparison to those reported in Chile for *Argopecten purpuratus* (620 g m^{-2} mo^{-1}, Uribe et al. 2001), Venezuela for *E. ziczac* (384 g m^{-2} mo^{-1}, Lodeiros & Himmelman 2000) and *P. imbricata* (963 g m^{-2} mo^{-1}, Lodeiros & García 2004) and Canada for *P. magellanicus* (1900 g m^{-2} mo^{-1}; Claereboudt et al. 1994), indicate that Bahía Taganga might offer favorable conditions for local bivalves aquaculture, given the relatively low incidence levels of predators and biofouling in the culture systems. The impact of biofouling in tropical zones has been considered negligible in comparison to the high biofouling biomass reported in temperate regions (Dürr & Watson 2010). However, the lower survival of both scallops studied as well as the biofouling biomass obtained in shallow waters do not support this hypothesis. Also, although the level of biofouling in this study is lower (1.8 to 7.7 mg l^{-1}) than in temperate waters, the same trend is also true for the seston concentration (63.1 to 77.8 mg l^{-1}; Grizzle & Morin 1989). So, even a low level of competition or flow obstruction of biofouling organisms could affect the tropical scallop performances. Considering that biofouling on the culture nets is one of the problems facing both scallop species studied, the use of cylindrical nets might be worthwhile as these may well have a lower surface area:volume ratio than pyramidal nets.

5. CONCLUSIONS

In summary, the suspension of culture systems at greater depths (12 m) is a suitable practice for reducing the settlement of larval stages of biofouling species and protecting the scallops from high temperatures, increasing survival in *N. nodosus* and *A. nucleus* as well as promoting growth in *A. nucleus*. A higher frequency of net replacement (i.e. monthly) reduces biofouling formation, thus increasing survival and growth in *A. nucleus* but not in *N. nodosus*, which seems to be affected to a greater degree by more frequent manipulation. However, considering that the low survival values obtained in this study were not mainly due to the environmental factors studied (i.e. predators, biofouling and physicochemical parameters) but instead due to the high mortality of juveniles at the beginning of the culture, it is recommended to carry out additional research to optimize the practices related to the operations of seed detachment from the artificial collectors, grading and seeding.

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LITERATURE CITED

Acosta V, Freites L, Lodeiros C (2000) Densidad, crecimiento y supervivencia de juveniles de *Lyropecten* (*Nodipecten*) *nodosus* (Pteroida: Pectinidae) en cultivo suspendido en el golfo de Cariaco, Venezuela. Rev Biol Trop 48:799–806

Adams CM, Shumway SE, Whitlatch RB, Getchis T (2011) Biofouling in marine molluscan shellfish aquaculture: a survey assessing the business and economic implications of mitigation. J World Aquacult Soc 42:242–252

Barros J, Velasco LA, Winkler FM (2018) Heritability, genetic correlations and genotype by environment interactions in productive traits of the Caribbean scallop, *Argopecten nucleus* (Mollusca: Bivalvia). Aquaculture 488:39–48

Carraro JL, Rupp GS, Mothes B, Lerner C, Würdig NL (2012) Characterization of the fouling community of macroinvertebrates on the scallop *Nodipecten nodosus* (Mollusca, Pectinidae) farmed in Santa Catarina, Brazil. Cienc Mar 38:577–588

Ciocco NF, Orensanz JM (2001) Depredación. In: Maeda-Martinez A (ed) Los moluscos pectinidos de Iberoamerica: ciencia y acuicultura. LIMUSA, Mexico City, p 267–284

Claereboudt MR, Bureau D, Coté J, Himmelman JH (1994) Fouling development and its effect on the growth of juvenile giant scallops (*Placopecten magellanicus*) in suspended culture. Aquaculture 121:327–342

Cortés-Useche C, Gomez-León J, Santos-Acevedo M (2011) Erizos de mar como control biológico del 'fouling' en un cultivo de *Nodipecten nodosus* en el área de Santa Marta, Caribe colombiano. Bol Investig Mar Costeras 40:233–247

Díaz JM, Puyana M (1994) Moluscos del Caribe Colombiano, un catálogo ilustrado. Colciencias, Fundación Natura y Universidad del Magdalena, Bogotá

Dürr S, Watson DI (2010) Biofouling and anti-fouling in aquaculture. In: Dürr S, Thomason JC (eds) Biofouling. Wiley-Blackwell, Singapore, p 267–287

Eggleston DB (1990) Functional responses of blue crabs *Callinectes sapidus* Rathbun feeding on juvenile oysters *Crassostrea virginica* (Gmelin): effects of predator sex and size, and prey size. J Exp Mar Biol Ecol 143:73–90

Fitridge I, Dempster T, Guenther J, de Nys R (2012) The impact and control of biofouling in marine aquaculture: a review. Biofouling 28:649–669

Freedman K, Bell JD (1996) Effects of different substrata and protective mesh bags on collection of spat of the pearl oysters, *Pinctada margaritifera* (Linnaeus, 1758) and *Pinctada maculata* (Gould, 1850). J Shellfish Res 15:535–541

Freites L, Núñez M (2001) Cultivo suspendido de *Lyropecten* (*Nodipecten*) *nodosus* (L., 1758) mediante los métodos de bolsa y aurícula 'ear hanging'. Bol Inst Oceanogr 4:21–29

Freites L, Hilmmelman J, Lodeiros C (2000) Impact of predation by gastropods and crabs recruiting onto culture enclosures on the survival of the scallop *Euvola ziczac* (L.) in suspended culture. J Exp Mar Biol Ecol 244: 297–303

Gómez-León J, Acosta E, Castellanos C, Santos-Acevedo M (2010) Cultivo de Pectínidos en el Caribe colombiano. Proyecto. Optimización de la producción de postlarvas del ostión *N. nodosus* y la conchuela *A. nucleus* en el Caribe colombiano código 2105-09-17982. Serie de Publicaciones Generales No. 40, INVEMAR, Santa Marta

Grizzle RE, Morin PJ (1989) Effect of tidal currents, seston, and bottom sediments on growth of *Mercenaria mercenaria*: results of a field experiment. Mar Biol 102:85–93

Klein-Breteler WCM (1975) Food consumption, growth and energy metabolism of juvenile shore crabs, *Carcinus maenas.* Neth J Sea Res 9:255–272

LeBlanc A, Landry T, Miron G (2002) Fouling organisms in a mussel cultivated bay: their effect on nutrient uptake and release. Can Tech Rep Fish Aquat Sci 2431

Lesser MP, Shumway SE, Cuccia T, Smith J (1992) Impact of fouling organisms on mussel rope culture: interspecific competition for food among suspension-feeding invertebrates. J Exp Mar Biol Ecol 165:91–102

Lodeiros C, García N (2004) The use of sea urchins to control fouling during suspended culture of bivalves. Aquaculture 231:293–298

Lodeiros CJ, Himmelman JH (1996) Influence of fouling on the growth and survival of the tropical scallop, *Euvola* (*Pecten*) *ziczac* L. 1758 in suspended culture. Aquacult Res 27:749–756

Lodeiros C, Himmelman JH (2000) Identification of factors affecting growth and survival of the tropical scallop *Euvola* (*Pecten*) *ziczac* in the Golfo de Cariaco, Venezuela. Aquaculture 182:91–114

Lodeiros C, Freites L, Nuñez M, Himmelman JH (1993) Growth of the Caribbean scallop *Argopecten nucleus* (Born, 1970) in suspended culture. J Shellfish Res 12: 291–294

Lodeiros C, Rengel J, Freites L, Morales F, Hilmmelman JH (1998) Growth and survival of the tropical scallop *Lyropecten* (*Nodipecten*) *nodosus* maintained in suspended culture at three depths. Aquaculture 165:41–50

Lodeiros C, Rengel JJ, Himmelman JH (1999) Growth of *Pteria colymbus* (Röding, 1798) in the Golfo de Cariaco, Venezuela. J Shellfish Res 18:155–158

Lodeiros C, Rengel J, Guderley HE, Nusetti O, Hilmmelman JH (2001) Biochemical composition and energy allocation in the tropical scallop *Lyropecten* (*Nodipecten*) *nodosus* during the months leading up to and following the development of gonads. Aquaculture 199:63–72

Mendoza Y, Freites L, Lodeiros CJ, López JA, Himmelman JH (2003) Evaluation of biological and economical aspects of the culture of the scallop *Lyropecten nodosus* in suspended and bottom culture. Aquaculture 221:207–219

Pacheco A, Garate A (2005) Bioincrustantes en estructuras de cultivo de *Argopecten purpuratus* en Bahía Samanco, Perú. Ecol Apl 4:149–152

Perera M, Ballesteros M, Turon X (1999) Estudio de los organismos epibiontes en un cultivo de bivalvos marinos del delta del Ebro. Cah Biol Mar 31:385–399

Pérez E, Lodeiros C, Semidey D, Uribe E, Freites L (2016) Crecimiento, supervivencia e influencia de factores ambientales en tres cohortes de la ostra perla *Pinctada imbricata*, en cultivo suspendido en el Golfo de Cariaco, Venezuela. Lat Am J Aquat Res 44:99–112

Pit JH, Southgate PC (2003) Fouling and predation; how do they affect growth and survival of the blacklip pearl oyster, *Pinctada margaritifera*, during nursery culture? Aquacult Int 11:545–555

Roma RPCR, de Almeida-Marques HL, Stojanov-Bueno R (2009) Controle biológico de organismos incrustantes em um cultivo de vieiras *Nodipecten nodosus* (Linnaeus, 1758) em Ubatuba, SP, Brasil. Biotemas 22:107–115

Román G, Campos MJ, Acosta CP, Cano J (1999) Growth of the queen scallop (*Aequipecten opercularis*) in suspended culture: influence of density and depth. Aquaculture 178:43–62

Román G, Louro A, De La Roche JP (2003) Intermediate culture of king scallop (*Pecten maximus*) in suspension in cages: effect of stocking density and depth. J Shellfish Res 22:647–654

Rupp GS (2007) Cultivo de vieira *Nodipecten nodosus* em Santa Catarina: influência da profundidade, densidade e freqüência de limpeza. Bol Téc Epagri Santa Catarina 135:1–82

Strickland JDH, Parsons TR (1972) A practical handbook of seawater analysis, 2nd edn. Bull Fish Res Board Can 167

Uribe E, Lodeiros C, Felix-Pico E, Etchepare I 2001 Epibiontes en pectínidos de Iberoamérica. In: Maeda-Martínez AN (ed) Los moluscos pectínidos de Iberoamérica: ciencia y acuicultura. LIMUSA, Mexico City, p 249–266

Valderrama D, Velasco LA, Quiroz N (2016) Economic assessment of hatchery production of *Argopecten nucleus* spat to support the development of scallop aquaculture in the Wider Caribbean. Aquacult Rep 4:169–177

Velasco LA (2006) Effect of microalgal concentration and water temperature on the physiology of the Caribbean scallops *Argopecten nucleus* and *Nodipecten nodosus.* J Shellfish Res 25:823–831

Velasco LA (2008) Biología y cultivo de los pectínidos de interés comercial de Colombia. Fondo de Publicaciones de la Universidad del Magdalena, Santa Marta

Velasco LA, Barros J (2007) Potential of hatchery broodstock conditioning of the Caribbean scallops *Argopecten nucleus* and *Nodipecten nodosus.* Aquaculture 272:767–773

Velasco LA, Barros J (2008) Experimental larval culture of the Caribbean scallops *Argopecten nucleus* and *Nodipecten nodosus*. Aquacult Res 39:603–618

Velasco LA, Barros J (2009) Survival and growth of hatchery-produced postlarvae and spat of the Caribbean scallops *Argopecten nucleus* and *Nodipecten nodosus.* Aquacult Res 40:362–375

Velasco LA, Barros J (2010) Spat collection and experimental culture of the Atlantic pearl oyster, *Pinctada imbricata* (Bivalvia: Pteriidae), under suspended conditions in the Caribbean. J World Aquacult Soc 41:281–297

Velasco LA, Borrero FJ (1996) Cultivo experimental de la ostra perlífera alada *Pteria colymbus* (Bivalvia: Pteriidae) en el Caribe colombiano. In: Silva A, Merino G (ed) Acuicultura en Latinoamérica, comunicaciones cortas IX Congreso Latinoamericano de Acuicultura, Coquimbo, 15–18 October 1996, Asociación Latinoamerica de Acuicultura, p 224–231

Velasco LA, Borrero FJ (2004) Captación de semilla y cultivo experimental del hacha *Pinna carnea* (Mollusca: Bivalvia) en el Parque Nacional Natural Tayrona, Caribe colombiano. Intropica 1:75–83

Velasco LA, Barros J, Acosta E (2007) Spawning induction and early development of the Caribbean scallops *Argopecten nucleus* and *Nodipecten nodosus.* Aquaculture 266:153–165

Velasco LA, Barros J, Guerrero A (2009) Growth and survival of the Caribbean scallops *Argopecten nucleus* and *Nodipecten nodosus* in suspended culture at the Taganga Bay, Colombia. Aquacult Res 40:687–695

Velasco LA, Barros J, Trujillo C, Gómez J, Arias LM, Hernández R, Rojas J (2011) State of shellfish aquaculture on the Caribbean coast of Colombia and potential site for a regional hatchery facility. In: Lovatelli A, Sarkis S (eds) A regional shellfish hatchery for the Wider Caribbean: assessing its feasibility and sustainability. FAO Regional Technical Workshop, Kingston. FAO Fish Aquacult Proc No. 19. FAO, Rome, p 119–132

Velasco LA, Barros JM, Carrera S, Barbosa W, Barreto A (2013) Alliance between university and artisanal fishermen: a model for Caribbean scallops culture in Colombia. In: 19th Int Pectnid Workshop, Florianápolis

Ventilla RF (1982) The scallop industry in Japan. Adv Mar Biol 20:310–382

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