Growth and foraging behavior of hatchery propagated long-spined sea urchins, *Diadema antillarum*: Implications for aquaculture and restocking

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ABSTRACT

Stocking hatchery propagated long-spined sea urchins *Diadema antillarum* is a priority option for recovery of this keystone herbivore on Caribbean reefs. However, information on captive culture of *D. antillarum* is very limited due to historical lack of successful juvenile production from gametes in the hatchery. In this study, hatchery propagated *D. antillarum* juveniles were cultured using two diets, commercially available herbivore pellets and dried nori, with the presence/absence of stony coral *Acropora cervicornis* skeleton to understand how diet and habitat complexity affect growth and behavior of juveniles. Juvenile urchin growth, and the diel pattern of feeding and foraging behavior were significantly affected by diet type. Juveniles fed dried nori gained significantly higher live weight and test diameter than those fed herbivore pellets. Juvenile urchins displayed nocturnal feeding and foraging behavior irrespective of diet types and presence/absence of coral structure. Presence/absence of coral structure did not affect growth and diel pattern of feeding and foraging behavior, but modulated habitat usage patterns. Survival of juveniles was neither affected by diet types nor the presence/absence of coral structure. This study concludes that dried nori is a superior diet to herbivore pellets for juvenile urchin culture. Since the presence of coral structure influenced habitat usage patterns, provision of rugose structure in captivity has the potential to convey the innate shelter seeking behavior of juvenile urchins.

1. Introduction

Coral reef ecosystems are under severe threat due to multiple additive stressors including pollution, disease, recruitment failure, over harvesting of reef species and global climate change (Pandolfi et al., 2003). Caribbean coral reefs lost structural complexity with the demise of scleractinian corals because of bleaching, disease, and macroalgae overgrowth (Alvarez-Filip et al., 2009; Cabanillas-Terán et al., 2019). Recent local restoration paradigms include a set of wild collected corals propagated in an ocean-based nursery, and outplanted to degraded sites via "coral gardening" (Young et al., 2012; Lirman et al., 2016; Greer et al., 2020). While coral gardening is a viable option to increase local populations, a holistic ecological approach that also addresses the stressors leading to reef decline is necessary to attain long-term sustainability of reef ecosystems.

Restoration of a keystone herbivore, the long-spined sea urchin

Diadema antillarum, along with coral outplanting is considered as one of the potential approaches to improve long-term sustainability of Caribbean reefs (Francis et al., 2019). Coral cover and *D. antillarum* population recovery are interdependent as corals provide habitat for *D. antillarum* shelter, and in turn, *D. antillarum* graze upon macroalgae and reduce competitive interactions that inhibit coral recruitment (Lee, 2006; Idjadi et al., 2010; Clemente and Hernández, 2008). Recovery of *D. antillarum* populations within the reef ecosystem could alleviate the burden of macroalgal competition. Restocking a Pacific species of hatchery cultured sea urchins, *Tripneustes gratilla*, has been beneficial in controlling an invasive alga on the reefs of Hawaii, USA (Westbrook et al., 2015; Neilson et al., 2018). Large-scale culture and restocking efforts of *D. antillarum* could represent a viable aid to coral reef recovery due to the ecological services provided by this species (Moulding and Moore, 2015; Rogers and Lorenzen, 2016; Patterson, 2019).

Diadema antillarum, a large-bodied herbivore and bioeroder, was a

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highly abundant species for thousands of years throughout Caribbean and Western Atlantic reefs (Donovan, 2005; Lessios et al., 2001). This species experienced unprecedented mortalities in 1983–84 due to an unknown epizootic disease (Lessios et al., 1983, 1984), leading to a phase shift from coral dominated to macroalgae dominated Caribbean reefs (Hughes et al., 1987). Natural *D. antillarum* recovery has been very limited, and the recent population density was estimated to be only 12% compared to the density before the die-off event (Lessios, 2016). Due to the challenges of successful larval rearing to settlement, hatchery culture of *D. antillarum* at scales needed for restocking programs has been a challenge for decades (Eckert, 1998; Leber et al., 2010). Very limited information is currently available for *ex-situ* culture of *D. antillarum* juveniles, including basic information on the requirements of diets and structural complexity. *D. antillarum* predominantly feed on benthic algal turf and macroalgae (Sammarco, 1980), stay in a structurally complex area during daytime to avoid predation, and emerge at night to forage (Ogden et al., 1973). Captive culture has been shown to induce behavioral changes in juvenile *D. antillarum*, potentially reducing predator avoidance in the natural environment (Sharp et al., 2018). A novel recirculating system for *D. antillarum* larvae (Pilnick et al., 2021) and effective culture protocols (Pilnick et al., 2022) have been developed by our group, and recently produced over 500 juvenile urchins from a batch of fertilized eggs. This success in larval rearing has given us the unique opportunity to study growth and behavior of hatchery-propagated juvenile *D. antillarum*.

Sea urchin aquaculture is primarily focused on improving gonad quality, as this organ represents a high value seafood item (McBride, 2005). Provision of a suitable diet improves production efficiency, health status and survival of juveniles in grow-out systems. Although dietary requirements of juvenile sea urchins are available for some species (Kennedy et al., 2005; Cárcamo, 2015), information on *D. antillarum* juvenile culture is very limited. Insights on *D. antillarum* growth and behavior in captivity are limited to two studies (Idrisi et al., 2003; Sharp et al., 2018). Other studies have examined *D. antillarum* behavior in natural environments in response to habitat complexity, predators and conspecifics (Carpenter, 1984; Lee, 2006; Clemente and Hernández, 2008). In this study, we investigated growth and behavior of *D. antillarum* fed two commercial diets. Due to the cryptic nature of this species, we also tested the hypothesis that including structural habitat would affect growth and behavior of *D. antillarum* juveniles in captivity. Growth, survival, diel pattern of feeding and foraging behavior of *D. antillarum* juveniles were thus measured as response variables to the treatment effects of diet and presence/absence of supplemental coral skeleton structure.

2. Materials and methods

2.1. Source of juvenile urchins, diets, and coral skeletons

Diadema antillarum can be found in the shallow hard-bottom reefs in the Caribbean and Atlantic Ocean. This species is most abundant at temperatures $\leq 35\ °C$ and salinity ≥ 30 ppt within areas of low to moderate wave action (Ogden and Carpenter, 1987).

This experiment was conducted at The Florida Aquarium's Center for Conservation in Apollo Beach, Florida, USA. Competent *D. antillarum* larvae produced from broodstock obtained from the Florida Keys were settled in April 2021 and a subset of 204, post-settled juveniles (10 weeks old) were used in this study. At the beginning of the experiment, juvenile live weights (mean ± SE) and test diameters were 0.23 ± 0.05 g and 5.68 ± 0.53 mm, respectively.

Diadema antillarum juveniles were fed with either dried nori or herbivore pellet for six weeks. Dried nori was made of roasted seaweed of the genus *Pyropia* and distributed by One Organic (San Francisco, USA). Herbivore pellets (1 mm size) were made from a mix of chlorella algae, kelp, spirulina, ulva, krill and squid, and distributed by New Life Spectrum® (FL, USA). Triplicate samples of both diets were analyzed for

proximate composition (Table 1) based on AOAC (2005) procedures (moisture - procedure 930.15, protein - procedure 990.03, crude fat - procedure 920.39, fiber - procedure 962.09 and ash - procedure 942.05). Nitrogen-free extract (NFE) or carbohydrate was calculated as NFE = 100 – [%protein + %crude fat + %fiber + %ash].

Coral skeletons were obtained from nursery-propagated staghorn coral *Acropora cervicornis* colonies that had experienced natural mortality. All coral tissue was removed from the skeletons before they were bleached and stored for two years prior to use. Skeletons were cut and glued to create roughly dome-shaped structures with 15 cm length, 11 cm width and 9 cm height.

2.2. Juvenile culture system

A recirculating aquaculture system (RAS) with 605-liter capacity was built to culture juveniles. Life support system components in the RAS included foam fractionators, fluidized media reactors with activated carbon, granular ferric oxide, poly-filter, 25 μm mechanical cartridge filtration and bio-media biological filtration. Temperature was maintained at ~25.5 °C using a submersible 800 watt titanium heating element and a ¼ horsepower chiller (Aqualogic, Connecticut, USA). The system was integrated with a sump (dimension 225 × 36 × 53 cm) and a fiberglass culture tank (dimension 240 × 86 × 30 cm). A set of five Odyssea 91 cm dual marine aquarium lights (39 W wattage, 7000 initial lumen) was installed at 30 cm distance from each other and at ~76 cm above the water surface. The juvenile culture system was in a room with a large north-facing window that allowed ambient light for 13.5 hrs during the time of year at which the experiment was conducted. A total of twelve plastic containers (each with 30.5 × 24.1 × 20.3 cm dimension) were placed inside the culture tank (Fig. 1a). Each container was filled with 7.5 L saltwater and stocked with a total of 17 juveniles (43.2 square cm/juvenile). The containers were supplied continuous gravity-fed waterflow (0.4 L/min/container) from a 95 L capacity header tank. Saltwater then passed through a perforated T-bar PVC overflow (1 mm mesh attached) to allow continuous water exchange (Fig. 1b, c). The position of culture containers was rotated each fortnight to eliminate confounding effects of light and container position on response variables.

2.3. Experimental design

Experimental design is presented in Table 2.

2.4. Water quality parameters

Natural sea water (~35 ppt) was used to culture juveniles with a 40% total system water change weekly. The natural seawater was collected from the Gulf of Mexico, sand filtered, ozonated and passed through 0.35-micron cartridge filter before use. Temperature was recorded daily using the cloud-based Apex Fusion system (https://apexfusion.com/). Salinity and pH were measured with a portable Hach HQ30D meter. Ammonia, nitrite, nitrate, and phosphate were measured using a Hach DR6000 spectrophotometer. Alkalinity was measured using a Metrohm OMNIS titration system. Alkalinity data were generated using EPA method 310.1 and a Single Endpoint Titration (SET) with a titrant of 0.1 mol/L sulfuric acid. Hardness was measured using a Dual Endpoint Titration (DET) on a Metrohm dCa Ion Selective Electrode (ISE). An ammonia buffer was added to the sample, which was then titrated with 0.05 mol/L ethylenediaminetetraacetic acid (EDTA). Calcium and Magnesium values were calculated from the difference between the two titration endpoints.

2.5. Feeding

Diets were provided daily at 4:00 pm and the uneaten food and feces were siphoned out on the next day. Juveniles were fed to satiation with

Table 1
Proximate composition (mean ± SD, n = 3) of the diets used in this study.

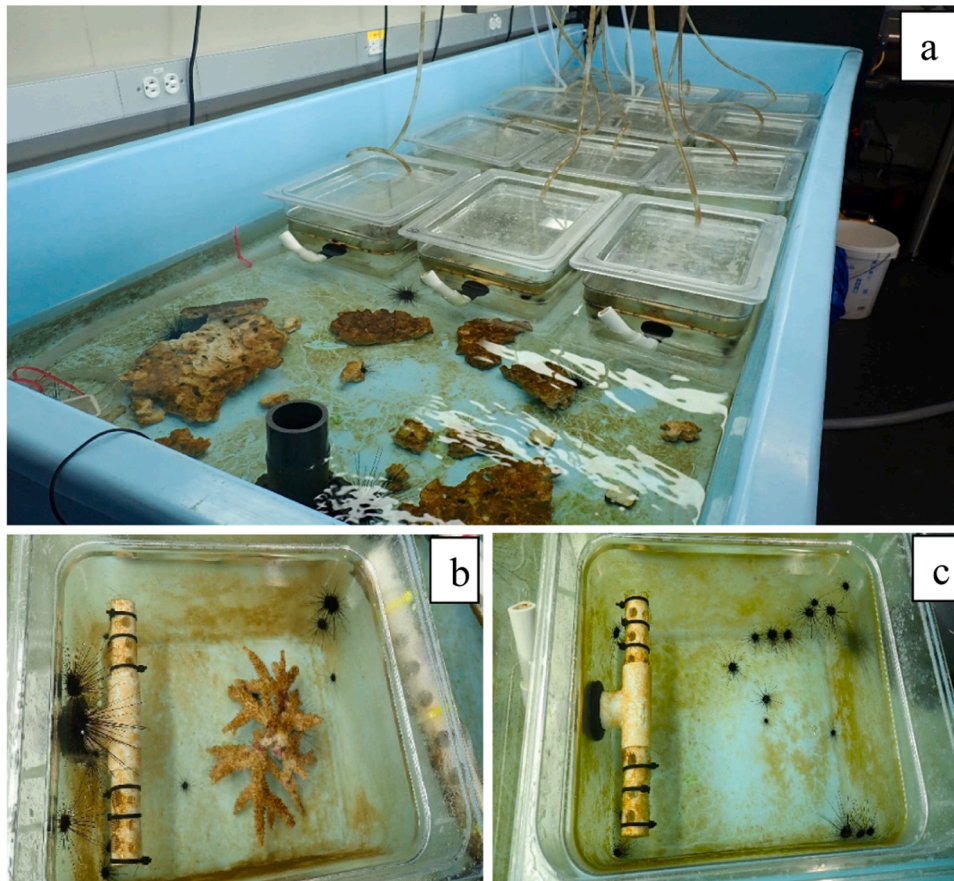| Diet type	Protein (% dry matter)	Crude fat (% dry matter)	Nitrogen free extract (% dry matter)	Crude fiber (% dry matter)	Ash (% dry matter)	Moisture (%)
Dried nori	44.54 ± 0.25	1.07 ± 0.04	38.41 ± 0.67	2.60 ± 0.70	10.32 ± 0.08	3.06 ± 0.26
Herbivore pellet	38.77 ± 0.07	4.98 ± 0.41	26.92 ± 0.75	5.63 ± 0.15	14.86 ± 0.01	8.83 ± 0.23

Fig. 1. Long-spined sea urchin, *Diadema antillarum* juvenile culture system, (a) top view of the fiberglass tank, (b) a representative container with supplemental coral structure (c) a representative container without supplemental structure.

an equivalent weight of dried nori and herbivore pellet. Feed ration was maintained within 4.5–8.0% of live body weight of juveniles.

2.6. Juvenile measurements

Live weight and test diameter of individual urchins were measured each fortnight. A transparent polystyrene container filled with saltwater was placed on laboratory scale (0.1 g readability). Juvenile urchins were dislodged and collected using curved forceps, gently shaken off to remove water, and were placed in the polystyrene container. Test diameter was measured by placing a ruler underneath the polystyrene container.

2.7. Observation of diel pattern in feeding, foraging, and habitat usage behavior

Feeding, foraging, and habitat usage behavior were observed once a week at 12:00 am, 6:00 am, 12:00 pm and 6:00 pm for six weeks. A juvenile found to be staying on the food was considered as feeding, while a juvenile away from food was considered as not feeding. A juvenile found to be staying on the bottom of the container was considered foraging. A juvenile found to be staying on/under the PVC outflow and

supplemental coral skeleton was considered as using structure, while a juvenile staying on the bottom/wall of the container was considered as not using structure.

2.8. Statistical analysis

Based on Shapiro-wilk and Levene's statistical test, data met the assumptions of normality and homogeneity of variance, respectively. All proportional behavior data were arcsine transformed. Initially, a factorial design was used to test interaction effect of diet and supplemental coral skeleton strucutre on growth and behavior. Due to the lack of an interaction effect, data were pooled by diet and structure treatments and were analyzed separately. The effects of diet or supplemental strucutre on growth and behavior were analysed using independent sample t-test. All data were analysed using IBM SPSS (v. 27).

3. Results

3.1. Water quality

All the water quality parameters were stable throughout the experiment except for ammonia, which reached 0.21 (mg/L) in week five.

Table 2

Diets and supplemental coral structure used to culture long-spined sea urchin, *Diadema antillarum* juveniles.

Treatment no	Container number	Treatment design	
		Diet type	Supplemental coral structure
1	1	Herbivore pellets	Present
	3	Herbivore pellets	Present
	5	Herbivore pellets	Present
2	7	Dried nori	Present
	9	Dried nori	Present
	11	Dried nori	Present
3	2	Herbivore pellets	Absent
	4	Herbivore pellets	Absent
	6	Herbivore pellets	Absent
4	8	Dried nori	Absent
	10	Dried nori	Absent
	12	Dried nori	Absent

Calcium and magnesium remained within the range of natural seawater. These divalent cations are indicators of hardness and an important component of skeletal structure in calcareous marine organisms. Data on water quality parameters are presented in Table 3.

3.2. Growth of juveniles

Juveniles fed with dried nori gained more live weight (mean $\pm$ SD) and test diameter than those fed herbivore pellet after six weeks (dried nori: 0.79 ± 0.07 g live weight and 11.71 ± 0.55 mm test diameter; herbivore pellet: 0.70 ± 0.20 g live weight and 10.24 ± 1.03 mm test diameter). No significant interaction effect of diet and supplemental structure was found on live weight ($F_{1,1} = 0.75$, $P = 0.39$) and test diameter size ($F_{1,1} = 0.48$, $P = 0.49$). When final growth data were compared at six weeks, significant differences were found in live weight ($t_{10} = 2.22$, $P < 0.05$) and test diameter ($t_{10} = 2.81$, $P < 0.05$) among juveniles fed herbivore pellet vs dried nori (Fig. 2). No significant difference in live weight ($t_{46} = 0.09$, $P = 0.93$) or test diameter ($t_{46} = 0.22$, $P = 0.83$) was found for juveniles cultured with the presence or absence of supplemental coral structure (Fig. 2).

The daily growth of juveniles fed dried nori was numerically faster than herbivore pellet (dried nori: 13.22 ± 1.9 mg/day increase in live weight and 0.27 ± 0.02 mm/day increase in test diameter; herbivore pellet: 11.46 ± 5.14 mg/day increase in live weight and 0.24 ± 0.03 mm/day increase in test diameter; Fig. 3).

3.3. Survival

Survival of juveniles was 99% at the end of the experiment, therefore

Table 3

Water quality parameters recorded throughout the juvenile culture period.

Water quality parameters	Value (mean $\pm$ SD)	n
Temperature (°C)	25.8 ± 0.2	46
Salinity (ppt)	35.4 ± 0.6	46
pH	8.1 ± 0.1	8
Alkalinity (mg/L)	123 ± 7	8
Ammonia (mg/L)	0.05 ± 0.08	8
Nitrite (mg/L)	0.008 ± 0.004	4
Nitrate (mg/L)	0.9 ± 0.1	4
Calcium (mg/L)	436 ± 12	8
Magnisium (mg/L)	1333 ± 44	4
Phosphate (mg/L)	0.03 ± 0.01	8

diet or supplemental structure did not affect survival. A total of 2 juveniles died in separate tanks fed with herbivore pellets and no death was recorded among juveniles fed with dried nori.

3.4. Diel pattern of feeding and foraging

A diel pattern of feeding and foraging behavior was found among juvenile urchins irrespective of diet type and presence/absence of supplemental coral structure. The highest percentage of juveniles fed and foraged at midnight, which gradually decreased in the morning and evening, and was lowest at noon (Fig. 4). In the factorial analysis, no significant interaction effect of diet and supplemental structure was found on the percentage of juveniles feeding ($F_{1,1} = 0.10$, $P=0.75$) or foraging ($F_{1,1} = 0.19$, $P=0.66$). When diets were compared in the diel cycle, significant statistical differences were found in percentage of juveniles feeding at 6 am ($t_{10} = 2.62$, $P<0.05$), 12 pm ($t_{10} = 3.27$, $P < 0.05$) and 6 pm ($t_{10} = 2.84$, $P < 0.05$), but no statistical difference was found at 12 am ($t_{10}= 0.09$, $P=0.93$). In addition, significant statistical differences were found in percentage of juveniles foraging at 6 am ($t_6 = 3.78$, $P < 0.05$), 12 pm ($t_6 = 2.73$, $P < 0.05$) and 6 pm ($t_6 = 2.39$, $P < 0.05$), but no statistical difference was found at 12 am ($t_6=0.95$, $P=0.38$). No significant difference was found in diel pattern of feeding ($t_{46}= 0.17$, $P=0.87$) and foraging ($t_{30}= 0.23$, $P=0.82$) in the presence/absence of supplemental coral structure.

3.5. Diel pattern of habitat structure usage

A similar diel pattern of habitat structure usage was observed irrespective of the presence or absence of supplemental coral structure. Higher proportions of juveniles used habitat structure during day-time compared to night-time (Fig. 5). A higher percentage of juveniles used habitat structure with the presence of supplemental coral structure than without coral structure ($t_{46} = 5.7$, $P < 0.05$).

4. Discussion

Information on captive culture of *D. antillarum* is very limited due to the historic lack of hatchery produced juveniles. This study fills out important knowledge gaps on captive culture of *D. antillarum* juveniles in response to commercial diets and structural complexity. Factors such as nutritional composition, food preference, palatability, and digestibility of the diets affect growth of sea urchins (Daggett et al., 2005; Kennedy et al. 2005; Dworjanyn et al., 2007; Zuo et al., 2017). The final live weight and test diameter of juveniles fed dried nori was significantly higher than those fed herbivore pellet. Among the elements of proximate composition – dried nori had higher protein content, but herbivore pellet had higher crude fat, crude fiber, ash and moisture content. Protein is the primary source of energy, therefore a diet high in protein spares energy for somatic growth. Direct assimilation of nitrogen from protein in *Ulva* macroalgae and a pelleted diet have been demonstrated in marine invertebrate culture (Sánchez et al., 2012). Higher protein content could increase nitrogen assimilation of dried nori versus herbivore pellets, leading to higher growth of juveniles. Juvenile sea urchin *S. intermedius* gained significantly higher weight when fed a 24% protein diet than a 12% protein diet (Zuo et al., 2017). Eddy et al. (2012) found that 22% protein was enough to support maximum growth of juvenile green sea urchins *S. droebachiensis* when the diet was formulated with high carbohydrate (40%). Compared to carnivorous species, the protein requirements of echinoderms are low (Bai et al., 2016). In this study, protein content of both dried nori and herbivore pellet was higher than the optimum protein level required in other urchin species (Eddy et al., 2012; Zuo et al., 2017), and thus protein was likely not the primary factor for the growth differences observed in this study.

Among other elements of proximate composition in the diets, crude fat is an important component for energy storage. Herbivore echinoderms have a low energy storage requirement except for gamete
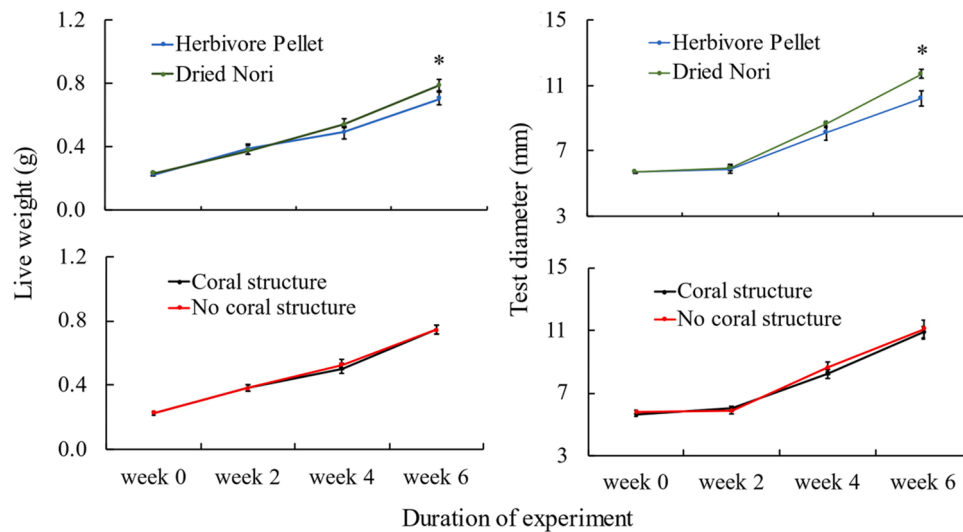
Fig. 2. Live weights (g) and test diameter size (mm) of long-spined sea urchin, *Diadema antillarum*, juveniles in response to diet and presence/absence of supplemental coral structure. Each data point represents mean ± SE of six replicates. Asterisks (*) denote significant statistical differences ($P < 0.05$) between treatments for a data point.
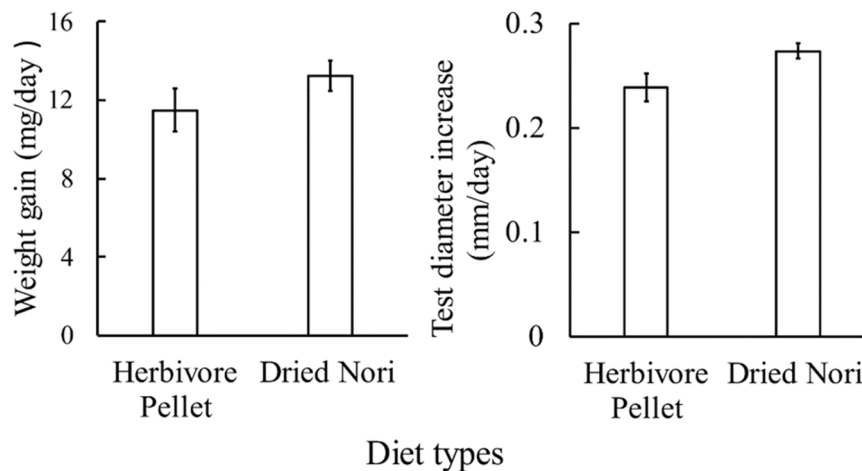

Fig. 3. Weight gain (mg/day) and test diameter increase (mm/day) in long-spined sea urchin, *Diadema antillarum*, juveniles fed herbivore pellet and dried nori diets. Each data point represents mean ± SE of six replicates.

production (Lawrence, 2020). Both diets used in this study contained a very low percentage of crude fat, which was feasibly enough to support energy storage requirements. Fiber and ash are the indigestible portion of the diet that contributes to production of solid waste or feces. Ash content is an indicator of minerals and inorganic residue that remains after water and organic matter are removed from a diet. Dried nori contained less crude fiber and ash, therefore, dried nori was theoretically more digestible than herbivore pellet, which might have contributed to higher growth of juveniles. One shortcoming of the present study was an inability to quantify total consumption of either diet. By the time excess diets and feces were siphoned out the day following feeding, diets had deteriorated and become mixed with feces to a point that drying and weighing uneaten food with precision was not possible. A future study could use more stable diets (e.g. a large block of food) or siphon more frequently to quantify total consumption for a more complete picture of the causes for differences in growth between treatments.

Naturally occurring biofilms that grew in the juvenile culture system cannot be ruled out as an important source of nutrition. Juveniles were found to scour biofilm from all culture containers irrespective of diet type or addition of structure. The type and extent of biofilm growth was qualitatively similar across the containers, likely due to continuous

water exchange, common lighting, and daily removal of waste. Thereby, biofilm intake likely did not contribute to the difference in juvenile growth observed between diet treatments.

Nocturnal behaviors evolved in echinoids to avoid predation by minimizing overlap of daily activity with potential predators (Nelson and Vance, 1979). In the natural environment, *D. antillarum* aggregate in reef crevices and forage at night within a short distance from shelter. The nocturnal behavior of diadematid species prioritizes protection against diurnal predators over food acquisition, which impacts their growth and survival negatively (Levitan, 1988, 1989). Propagation of *D. antillarum* juveniles in captive conditions without predation pressure is a key means of improving survival relative to wild urchins. Shelter homing behavior of *D. antillarum* improved with predation pressure (Carpenter, 1984), therefore simulation of captive predation pressure in future studies might consider potential tradeoffs between lower survival in captivity, but higher survival on the reef after restocking. In this study, we attempted to understand how the nocturnally active and day-time shelter seeking behaviors develop without the presence of potential predators. This study found no potential difference in feeding and foraging behavior due to the presence or absence of supplemental coral structure, suggesting that nocturnal feeding is an innate behavior
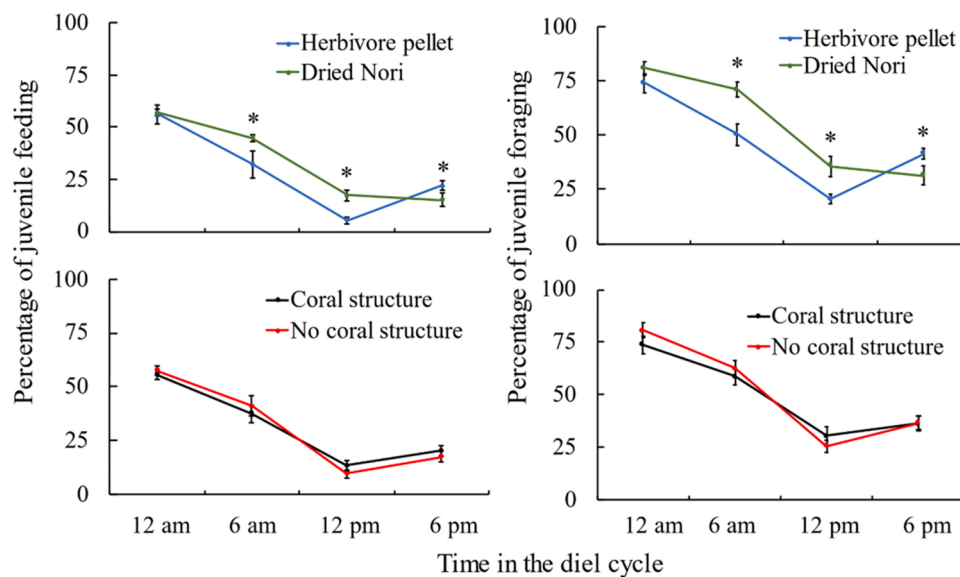
Fig. 4. Diel pattern of feeding and foraging in long-spined sea urchin, *Diadema antillarum*, juveniles in response to diets and presence/absence of supplemental coral structure. Each data point represent mean ± SE of six replicates. Asterisks (*) denotes significant statistical differences between treatments for a data point.
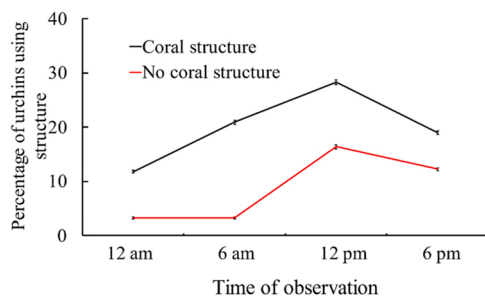

Fig. 5. Diel pattern of structure usage in long-spined sea urchin, *Diadema antillarum*, juveniles with the presence or absence of supplemental coral structure. Each data point represents mean ± SE of six replicates.

of *D. antillarum*. However, Sharp et al. (2018) found a lack of shelter seeking behavior in hatchery propagated *D. antillarum* relative to their wild conspecifics. During daytime, almost 90% of wild collected juveniles used shelters whereas less than 20% hatchery propagated juveniles exhibited this behavior. Sharp et al. (2018) noted that the discrepancy in diel activity pattern among hatchery propagated urchins was due to lack of crevice shelter in captive culture.

In this study, juvenile *D. antillarum* displayed a nocturnal feeding and foraging behavior, but diet type modulated the proportion of juveniles feeding and foraging. Given previous results and the understood importance of structural complexity to *D. antillarum* behavior (Sharp et al., 2018; Bodmer et al., 2021), it was surprising that this study revealed a greater influence of diet type on feeding and foraging behavior than the presence of supplemental structure. Empirical evidence suggests that foraging behavior can also be influenced by the nutritional status and food availability (Hart and Chia, 1990). In addition to proximate composition, texture and potentially palatability of herbivore pellets and dried nori were also different. Dried nori was observably less dense and thereby occupied more physical space than herbivore pellets. This might have contributed to higher nori accessibility during feeding, as the diets were fed on an equivalent weight basis. Further, dried nori was entirely plant-based, whereas herbivore pellet contained krill and squid meal. Since *D. antillarum* is primarily a macroalgae grazer, dried nori may have been more palatable, as evidenced in other sea urchin species such as *Tripneustes gratilla* (Dworjanyn et al., 2007). The palatability aspect could also be related to growth, as higher

proportions of juveniles fed on dried nori than herbivore pellet during the diel cycle, which may have led to relatively faster growth.

Habitat complexity has been found to affect nocturnal sheltering behavior of *D. antillarum*, whereby hatchery propagated urchins displayed less competence in predator avoidance than wild conspecifics (Sharp et al., 2018). In this study, we attempted to test whether the availability of rugose structure affected growth and behavior of juvenile urchins by providing supplemental coral structure in half of experimental replicate tanks. It is important to note that neither treatment was devoid of structure, as all replicate tanks contained a PVC outflow on the form of a T-bar (see Fig. 1). In addition, the beveled corners of the containers provided some degree of structure. This facilitated some use of structure by juvenile urchins even in the treatment that did not receive coral skeleton. Our results indicated that neither growth nor feeding/foraging behavior of juveniles was affected by the presence or absence of coral skeleton structure. However, a significantly higher percentage of juveniles used habitat structure when coral skeleton was present. Since provision of supplemental coral skeleton occupied more physical space within a tank, this could be partially due to the fact juveniles were simply more likely to find available hiding space when structure was more abundant. Laboratory experiments with wild origin animals revealed that *D. antillarum* are naturally attracted to shelters, but the chemical signals from conspecifics and predators modulate shelter usage pattern (Kintzing and Butler, 2014). Presence of conspecifics persuades against aggregation within shelters, but predation pressure persuades in favor of aggregation within shelter. In a natural environment, reductions in predation threat reduced shelter seeking behavior of reef dwelling echinoids (McClanahan and Muthiga, 1988; Clemente et al., 2010). Since juveniles propagated in the hatchery do not experience predation pressure, their predator avoidance behaviors could be less pronounced.

This study concludes that *D. antillarum* juveniles can be cultured in captivity using both herbivore pellets and dried nori, but macroalgae should be considered as the primary constituent of an optimal diet. We have observed a bottleneck in culture shortly after settlement when juveniles are yet to develop hardened mouthparts and appear to feed on benthic bacterial or algal biofilms. A similar shortcoming was also observed in *T. gratilla* with less than 1% post-settlement survival (Mos et al., 2011). A better understanding of the ontogeny of nutritional and physiological requirements of newly settled urchins should be investigated in future studies to improve survival of juveniles. Although

nocturnal behavior of juveniles did not disappear because of predator absence and captivity, some alterations of behavior could be expected due to diets and habitat complexity level. Dame (2008) indicated that the use of artificial crevice habitat in natural settings has potential to increase *D. antillarum* survival. Paradoxically, an increase in habitat complexity could also favor the abundance and diversity of other species including potential urchin predators, thereby a balance in habitat complexity should be taken into consideration when implementing coral reef restoration efforts (Mattila et al., 2008). In the next step, in-situ monitoring of survival of the hatchery propagated juveniles should be prioritized to evaluate restocking strategies.

Funding

CRediT authorship contribution statement

Conceptualization: MMH, ARP and JP; Formal analysis: MMH; Funding acquisition: KO and JP; Investigation: MMH, ARP, AMP, JH, CS and JP; Methodology: MMH, ARP, AMP, JH, CS and JP; Project administration: KO and JP; Resources: KO and JP; Supervision: KO and JP; Writing original draft: MMH; Review & editing: MMH, ARP, AMP and JP.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

All the data collected during this study are included in this manuscript. Raw data can be accessed from corresponding author upon reasonable request.

Acknowledgements

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