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A mesocosm system for ecological research with marine invertebrate larvae

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ABSTRACT: A unique flow-through mesocosm system powered by solar energy was developed for examining growth rates of marine invertebrate larvae in the field. The planktotrophic veligers of queen conch *Strombus gigas* were used as a test species. The mesocosm system was moored in a remote location in the oligotrophic waters of the Bahamas. Natural assemblages of phytoplankton (mean 160 ng chl *a* l^{-1}) were filtered with 5 µm and 50 µm filters to determine the growth rates of larvae fed 2 different assemblages. Initial stocking in each mesocosm was 20 veligers l^{-1}; and prior to metamorphosis, density was gradually reduced to 0.7 veligers l^{-1}. Growth rates from 0 to 9 d were identical for larvae fed 5 and 50 µm phytoplankton assemblages. The 5 µm treatment was discontinued on Day 9; the 50 µm treatment was continued through Day 16 when 95% of the veligers were competent for metamorphosis. The mesocosms provided good replication; growth rates for veligers fed 50 µm filtered phytoplankton were identical in Mesocosms 1 and 2. Routine sampling for chlorophyll *a* inside and outside the mesocosms showed no indication of phytoplankton biomass accumulation inside the mesocosm after 48 or 96 h of operation. This mesocosm system is an ideal apparatus for conducting ecological research with marine invertebrate larvae. Determination of larval growth and survival under field conditions can provide more accurate information on dispersal potential, and length of time and survival to metamorphosis compared to results achieved in the laboratory.

KEY WORDS: Gastropod · Growth · *In situ* · Larvae · Mesocosm · *Strombus gigas*

INTRODUCTION

Tracking organisms in the ocean to obtain direct assessment of larval life-span, development and survival is difficult, so most information about marine larval life has come from laboratory experiments. In the 1970s, large-volume enclosures or mesocosms were designed to be deployed in the field; these systems alleviate laboratory artifacts and simulate natural conditions of temperature, light and food (Øiestad 1982, 1990). Furthermore, mesocosms allow larvae and their prey to be stocked at natural densities, which provides more accurate *in situ* descriptions of growth and mortality, and behavioral responses than comparable experiments in small laboratory containers (de Lafontaine & Leggett 1987a, MacKenzie et al. 1990, Epifanio et al. 1991).

Mesocosms have been used to determine field growth and mortality rates in fish larvae (Rosenberg & Haugen 1982, de Lafontaine & Leggett 1987a, b, Cowan & Houde 1990, Duffy & Epifanio 1994, Houde et al. 1994), crab larvae (Epifanio et al. 1991), echinoderm larvae (Olson 1985, 1987), and copepods (Bollens & Stearns 1992). The effects of light and UV solar radiation on vertical migration of echinoid larvae (Pennington & Emlet 1986), gastropod larvae (Barile et al. 1994), and copepods (Bollens & Frost 1990) have been assessed in mesocosms. The vertical response of copepods to predatory fish has also been studied in large field enclosures (Bollens & Frost 1989, 1991).

Mesocosms differ in size and shape depending on their intended use and have been constructed from a variety of materials (de Lafontaine & Leggett 1987b, Øiestad 1990). Most mesocosms used today are conical bottom, cylindrical enclosures (volume 1.4 to 3.2 m^3) made from porous Nitex or Dacron mesh to allow diffusion of water from the outside (de Lafon-

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taine & Leggett 1987b, Cowan & Houde 1990, Duffy & Epifanio 1994). This exchange of water allows temperature, salinity, and oxygen to remain equal inside and outside the mesocosms; however, particle biomass and chlorophyll *a* (chl *a*) are usually lower inside the enclosures than in the surrounding water (de Lafontaine & Leggett 1987b). To accurately determine growth rates of invertebrate larvae which consume phytoplankton, it is necessary that biomass and chl *a* remain similar inside and outside of the mesocosm. The only *in situ* apparatus designed for this purpose was used to test growth rates of crown-of-thorns starfish *Ancanthaster planci* (Olson 1985, 1987). This novel system was comprised of small larval rearing chambers (<20 l) which were totally submerged in water and flushed periodically using pumps (Olson et al. 1987). The results were excellent; however, the size of containers limits stocking density and frequent maintenance on the system may be a constraint to long-term studies.

Our purpose was to develop a mesocosm system that could be used to examine field growth rates of planktotrophic invertebrate larvae fed natural phytoplankton. Veligers of queen conch *Strombus gigas* are planktotrophic for approximately 21 d (Davis 1994) and were used as a test species in this mesocosm system. The mesocosm system was designed to meet the following criteria: (1) to make chl *a* levels inside the mesocosm equal to ambient water, (2) to have large cylinders for stocking at experimentally meaningful numbers, (3) to require minimal system maintenance, (4) to operate the system continually for at least 3 wk, (5) to have a self-powered flow-through water pumping system for remote locations, and (6) to withstand 1 knot tidal currents, 15 to 20 knot winds, and 0.3 m seas. The system designed for this study incorporated ideas from field enclosures used for fish larvae (de Lafontaine & Leggett 1987b) and flow-through concepts developed by Olson (1985). However, our system is unique in that: (1) the mesocosm was made from nonporous material, (2) the mesocosm was supplied with a continuous flow of ambient filtered sea water, and (3) the water was pumped by solar energy. This paper provides details on the construction and operation of a new mesocosm system which was used for testing the effects of nutrition on the life-span of a marine invertebrate larva.

MATERIALS AND METHODS

Equipment and systems. A hexagonally shaped platform (3.6 m diameter) was built to support 6 mesocosms, solar array, batteries and pumping system (Fig. 1). It was constructed out of epoxy coated plywood (13 mm) and dimensional lumber (5 × 10 cm). The surface of the platform had a final coat of white enamel paint embedded with sand to provide a non-skid surface. It was built in 8 sections to facilitate transport, assembly and disassembly. The sections were bolted together with stainless steel bolts (13 mm diameter). For flotation, an airtight plywood box was built into each section, capped lengths of PVC pipe (10 cm diameter × 1.8 m length) were strapped to the outer edge of each section, and foam (15 cm thick) was fitted into empty spaces underneath the platform. With all equipment and 2 people working on the platform, the top of the platform remained approximately 5 cm above the water surface. The platform was secured on a 3 point mooring system in an anchorage (3 m deep) west of Lee Stocking Island, Bahamas, near the Caribbean Marine Research Center field station.

The 6 outer sections of the platform supported the mesocosms and the 2 middle sections were used as a work space (Fig. 1). Each mesocosm was a conical bottom (45°) cylinder (0.5 m diameter × 1.8 m length) (Fig. 1). The cylinders were manufactured by Solar Components Corp. (Manchester, NH) from Sun-Lite® fiberglass (1.5 mm thick), which is 90% transparent and allows 90% visual light transmission. They weigh only 8 kg each, therefore they were easily handled by 1 or 2 persons, depending upon the operation. Each mesocosm was submerged, except for 0.5 m, which remained above water to prevent sample loss and wave wash-over. To hold each mesocosm at the

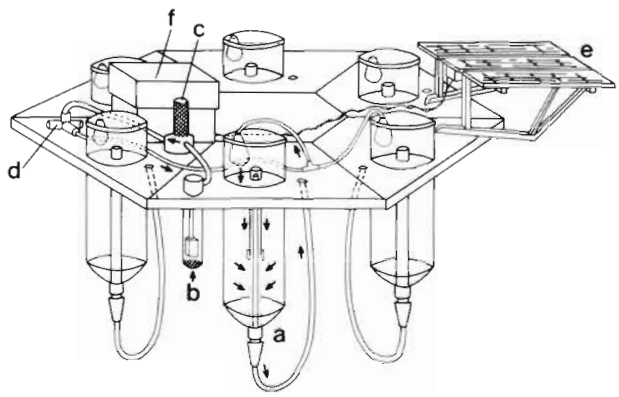

Fig. 1. Floating mesocosm system designed to test *in situ* growth rates of invertebrate larvae. (a) Mesocosm with standpipe and bag filter; (b) 12 V submersible pump with coarse filtration; (c) in-line filter; (d) manifold to divert water flow to 6 mesocosms; (e) solar array hooked up to batteries; and (f) battery box containing two 6 V batteries. Arrows indicate the incoming flow of water through the pump, in-line filter, manifold, bag filter and the discharge of water through the porous standpipe and tubing

desired height, a rubber dock bumper (8 cm width) was fastened around the cylinder with a hose clamp, and secured to the platform with 3 bolts and wooden braces. The mesocosms were reinforced with fiberglass cloth and resin in the area that was in constant contact with the platform. To avoid contamination, each mesocosm was covered with a transparent fiberglass top which was held in place by nylon line (6 mm diameter). The total working volume of each mesocosm was 0.2 m^3 (200 l).

A continuous flow of ambient water was pumped to each mesocosm at 1 l min^{-1}, allowing for 8 exchanges of water per day. For larval retention, a specially designed standpipe was threaded into a fitting (5 cm diameter) in the bottom of each mesocosm (Fig. 1). The top half of the standpipe (66 cm length) was made of PVC (5 cm diameter) and the bottom half (61 cm length) was made of porous tubing (Porex™) (65 µm pore size, 5 cm diameter). The porous tubing at the bottom forced water and phytoplankton to circulate through the mesocosm from surface to near-bottom (Fig. 1). A PVC pipe (2.5 cm diameter × 1.3 m length) was installed inside the standpipe to regulate water level (Fig. 1).

Ambient water was pumped from 1 m below the platform into each mesocosm using a Rule 12V, 2.5 amp bilge pump (23 l min^{-1}) (Fig. 1). The pump was powered by two 6V golf cart batteries (220 ampere hours each) which were connected in series to produce 12V. The batteries were housed inside a plywood box to avoid sea water intrusion (Fig. 1). They were kept charged with a solar array comprised of a rack of 3 Solarex VLX-53 solar modules (Fig. 1). Each panel produced 48W and 3.08 amp at 17.1V in full sunlight, an amount more than adequate to provide 24 h of continuous pumping. The solar panel surfaces were cleaned with fresh water every other day to avoid a decrease in power from salt crystal build-up.

The ambient water was initially filtered at the pump intake with a coarse mesh (2 mm) to exclude macroalgae and large debris (Fig. 1). It then passed through an in-line polyethylene filter (380 mm mesh) to remove potential predators and macrofaunal competitors of the cultured larvae (Fig. 1). This filter was cleaned daily. Next, the water was diverted through a manifold into 6 lengths of clear vinyl tubing (13 mm i.d.) that regulated flow into each of the 6 mesocosms through a valve attached to the end of each piece of tubing (Fig. 1). Depending on the experimental design, the water was further filtered prior to entering each mesocosm with a 5 or 50 µm flasked-shaped polyester felt bag fastened over the end of the supply valve (Fig. 1). These bag filters were changed daily and cleaned in fresh water between uses. The tubing and fittings were cleaned every 10 d with a mild solution of chlorine bleach (0.1%) to avoid larval mortality from potential bacterial infection and to remove accumulated debris (Davis 1994).

Test species. The large gastropod *Strombus gigas*, commonly known as queen conch, inhabits the shallow waters of Bermuda, Florida, Bahamas and the Caribbean region (Randall 1964). In the Bahamas, the reproductive season begins in late March and ends in October (Stoner et al. 1992), and the typical life-span of the planktotrophic larvae is 3 wk (Davis 1994). For this study, freshly laid egg masses were collected from the benthos at a reproductive site 1 km offshore from Lee Stocking Island (Stoner et al. 1992). They were incubated in the laboratory for 4 d in flow-through, upwelling containers (Davis 1994). The mesocosm experiments began with newly hatched veligers.

Experimental design. Preliminary mesocosm trials with veligers were conducted to test the 12V pumping system, and to determine optimal position of the mesocosms in the platform, how often to exchange the mesocosms based on standpipe clogging, exchange techniques, stocking density of veligers, and how to sub-sample veligers for observations. Once these details were known, the mesocosm system was ready for experimentation: (1) to determine the growth rates of *Strombus gigas* veligers fed 2 different natural assemblages of phytoplankton, and (2) to verify whether or not chl *a* levels were similar inside and outside the mesocosms.

To examine growth rates of veligers, 2 mesocosms were supplied with a flow-through of ambient sea water filtered to 5 µm and 2 mesocosms were supplied with sea water filtered to 50 µm. Newly hatched larvae were counted out for each mesocosm by averaging 6 aliquot samples from each egg mass hatching container and extrapolating the number of veligers per liter. The larvae were transported to the mesocosms in glass jars (2 l), which were immersed in a mesocosm until the temperature difference between the mesocosm and jar was <2°C. Initial stocking density was 20 veligers l^{-1} or 4000 mesocosm^{-1}. Although this initial density was higher than the highest reported in nature, 10 larvae m^{-3} (Stoner unpubl. data), it was 1 to 2 orders of magnitude lower than typical laboratory culture density for this species (Davis 1994). Assuming that filters would block the majority of zooplankton that would compete with the experimental veligers for food resources in the mesocosm, our experimental densities were appropriate. Every 4 d the density was lowered: from 20 to 4 veligers l^{-1} on Day 5; to 1.5 veligers l^{-1} on Day 9; and to 0.7 veligers l^{-1} on Day 13.

Larvae were grown in 5 µm filtered water for a total of 9 d and in 50 µm filtered water until they were metamorphically competent. Since 9 d provided

adequate growth data, the 5 µm treatment was discontinued to make space for other experiments. The larvae were transferred to a new mesocosm every 4 d to avoid standpipe clogging and microbe fouling on the interior walls of the mesocosm. Prior to a transfer, the number of veligers needed for the required new density were collected from the mesocosm with a screen ladle (15 cm diameter, 105 µm mesh), and placed in a clean mesocosm filled with fresh ambient sea water. The water in the original mesocosm was pumped out using a 12 V, 6.0 amp Shurflo pump (13 l min^{-1}) until approximately 10 l remained in the conical bottom of the mesocosm. A screen (105 µm mesh) was attached to the suction end of the pumping tube so larvae, zooplankton and debris in the mesocosm were not removed. After pumping was completed, 2 people lifted the mesocosm out of the platform and poured the contents into a 105 µm screen sieve that was partially submerged in a bucket of water. All macrofauna including veligers were later counted and identified.

Every 1 or 2 d, 15 larvae were removed from each mesocosm and observed, using a dissecting microscope, for changes in morphological development, feeding condition, activity level and growth. Larvae were removed using a ladle equipped with a screen bottom (15 cm diameter) and a long handle which allowed for sampling the entire water column. To determine growth rates and variability in individual sizes, shell length (SL) was measured for each larva by using a dissecting microscope equipped with an ocular micrometer.

Temperature was monitored only briefly, because it became apparent that water temperature inside and outside of the mesocosm were the same at all times and at any depth (surface to 1.5 m). The temperature fluctuated during the day from 28 to 30°C according to tidal stage.

To determine if phytoplankton biomass accumulated in the mesocosms over a 96 h period, chl *a* was monitored inside and outside the mesocosms 48 and 96 h after set-up. Ambient levels of chl *a* were also measured every other day to provide an overall indication of chl *a* concentrations over the experimental period. To measure chl *a*, 2 replicate samples of sea water (800 ml) were collected next to the platform and inside the mesocosm. In the laboratory, each sample was filtered through a Whatman GF/F filter (0.45 µm). The filter was frozen and later (<3 wk) submerged in 10 ml of dimethyl sulfoxide/acetone solution for 24 h (Shoaf & Lium 1976, K. Webb pers. comm.). After centrifuging for 2 min, the supernatant was analyzed on a Turner Model 112 fluorometer; fluorescence was converted to ng chl *a* l^{-1} according to the calibration of the fluorometer (Strickland & Parsons 1972).

RESULTS

Equipment and systems

The solar pumping system operated continuously throughout the 16 d experiment without any fluctuations in power or failure of the pump. Periodic checks with the volt meter confirmed the availability of 12 to 13 V from the batteries during both day and night. The solar panels produced between 12 and 17 V depending on the time of day and the amount of cloud cover.

All but 1 of the 6 mesocosms were used in the platform. The mesocosm exposed to the prevailing southeast wind was removed because constant vertical oscillation caused instability. The hexagonal shape of the platform protected the other 5 mesocosms from the typical 10 to 15 knot winds, and also during one occasion when the winds gusted to 40 knots. A slight water chop (0.2 to 0.5 m) in the anchorage occurred when wind and tidal current were against each other, but this condition did not cause vertical movement of the mesocosms. Water inside the mesocosms was always calm no matter what the conditions were outside.

Biological findings

There was no difference in growth rates (33 µm d^{-1}) from Day 0 to 9 for veligers fed 2 different phytoplankton assemblages (5 and 50 µm filtered water) (Fig. 2). Metamorphosis for veligers fed 50 µm filtered phytoplankton was first seen on Day 13, and, by Day 16, 95% of the veligers were either competent for metamorphosis or had completed metamorphosis with an

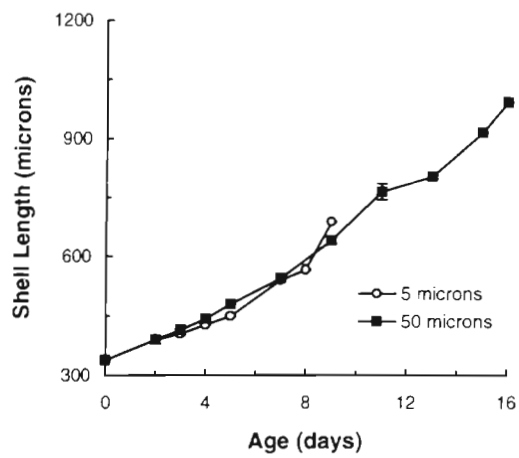

Fig. 2. *Strombus gigas*. Growth rates of veligers fed on 5 µm and 50 µm filtered phytoplankton from the ambient water. Values represent mean ± SD, n = 2 mesocosms per treatment

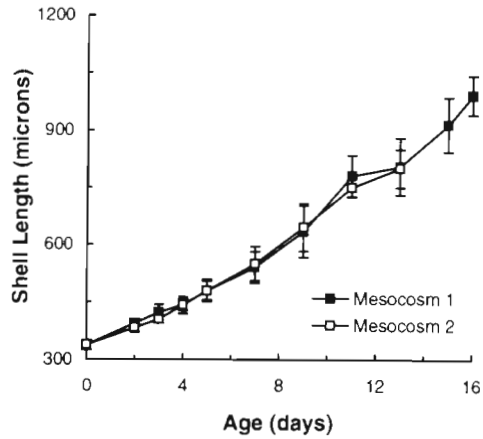

Fig. 3. *Strombus gigas*. Comparison of growth rates for 2 replicate mesocosms. Veligers were fed 50 µm filtered phytoplankton from the ambient water. Values are mean ± SD, n = 15 to 20 veligers

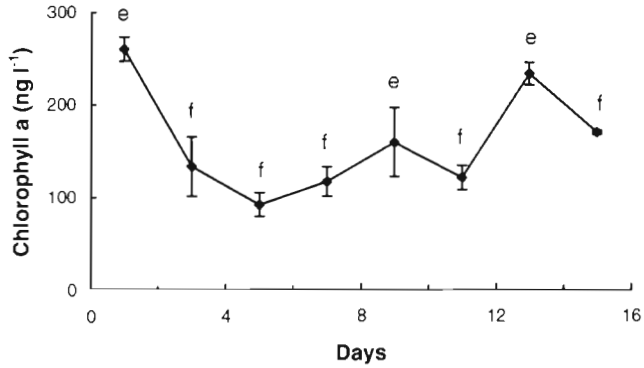

Fig. 4. Chlorophyll *a*. Ambient chl *a* (ng l^{-1}) concentrations throughout the 16 d experiment from water samples (50 µm filtered) collected next to the mesocosm platform; e: ebb tide; f: flood tide. Values are mean ± SD, n = 2 to 4 replicates d^{-1}

average shell length (SL) of 993 µm (±51 SD, n = 20). Overall growth rate for the veligers fed 50 µm filtered phytoplankton was 41 µm d^{-1}; however, variation in growth rates within the 50 µm treatment cohort was apparent. By Day 16, there was a difference of 200 µm SL between the smallest and largest veligers (min. 875 µm SL, max. 1075 µm SL) (Fig. 3). The mesocosms provided good replication; growth rates for veligers fed 50 µm filtered phytoplankton were identical in Mesocosms 1 and 2 (Fig. 3).

Although survival was not monitored on every transfer, 5 accurate counts indicated that survival was approximately 73% (±18 SD) of the total 77% (±16 SD) of veligers recovered after a transfer. Veligers in the mesocosm were distributed throughout the water column, except during the brightest time of the day when there was a slight migration away from the surface. Veligers were active and emerged from their shells almost immediately after disturbance, a sign of good condition. Phytoplankton was observed in the guts by Day 2 and guts were full by Day 3. The veliger shells were free of epiphytes, except for the occasional epiphytic bacteria *Vorcella* sp. or benthic diatom *Licmophora* sp.

Chl *a* concentration during the experiment ranged from 92 to 260 ng l^{-1} (mean 160 ± 59 SD) (Fig. 4). Concentrations fluctuated according to the tidal stage, and were higher on the ebb tide (1, 9, and 13 d) than on the flood tide (Fig. 4). Routine chl *a* sampling inside and outside the mesocosms showed that phytoplankton biomass did not accumulate inside the mesocosms after 48 h (Student $t_{(12)} = 1.65$, p = 0.12) or 96 h (Student $t_{(12)} = -0.757$, p = 0.464) of operation (Table 1). Therefore, a flow rate of 1 l min^{-1} or 8 exchanges of water per day in each mesocosm was satisfactory for maintaining similar chl *a* levels inside and outside the mesocosms.

Potential herbivorous competitors found in the mesocosms after 96 h of operation were divided into 5 categories (Table 2). Harpacticoid copepods and nauplii constituted the most abundant organisms. As expected, density of organisms in the 5 µm filtered water was 4 times lower than in the 50 µm filtered water. The 5 µm filter also excluded veligers (other than *Strombus gigas*) and polychaete larvae which were found in low numbers in the 50 µm filtered water. Variation in the density of organisms in each mesocosm was affected by weather, tide and condition of the bag filter.

Table 1. Chlorophyll *a*. There was no accumulation of phytoplankton biomass inside the mesocosms 48 or 96 h after the initial filling of water and stocking of veligers. All chl *a* comparisons were achieved by sampling water (50 µm filtered) inside and outside of the mesocosms. Values are mean ± SD (n = no. of trials, with 2 replicates per trial). Pairwise Student *t*-test was used for comparing chl *a* inside and outside the mesocosms

No. of hours after filling	Inside mesocosms chl *a* (ng l^{-1})	Outside mesocosms chl *a* (ng l^{-1})	Statistical values
48	150.6 ± 38.8 (14)	130.5 ± 27.7 (14)	$t(13) = 1.646$, p = 0.124
96	142.2 ± 41.1 (13)	149.7 ± 55.3 (13)	$t(12) = -0.757$, p = 0.464

Table 2. Organisms (other than veligers of *Strombus gigas*) found in the mesocosms after 96 h of operation

Organisms	% Composition			No. organisms l^{-1}		
	Mean ± SD	Min.	Max.	Mean ± SD	Min.	Max.
50 µm filter (n = 7)						
Calanoida	7.2 ± 3.9	3.1	13.1	0.22 ± 0.27	0.03	0.77
Harpacticoida	60.5 ± 13.2	36.1	72.3	1.47 ± 1.10	0.34	3.05
Nauplii	30.3 ± 13.1	13.1	49.5	1.03 ± 1.19	0.09	3.46
Polychaete larvae	1.7 ± 1.5	0	3.7	0.06 ± 0.09	0	0.24
Veligers (other)	0.2 ± 0.4	0	1.1	0.01 ± 0.01	0	0.01
Total				2.79	0.46	7.53
5 µm filter (n = 3)						
Calanoida	12.8 ± 4.2	8.1	16.1	0.06 ± 0.06	0.01	0.13
Harpacticoida	45.0 ± 15.0	28.6	58.1	0.33 ± 0.40	0.02	0.78
Nauplii	39.7 ± 12.5	25.8	50.0	0.27 ± 0.37	0.04	0.70
Polychaete larvae	2.5 ± 4.0	0	7.1	0 ± 0	0	0.01
Veligers (other)	0 ± 0	0	0	0 ± 0	0	0
Total				0.66	0.07	1.62

DISCUSSION

This unique mesocosm system was successful in providing data on growth rates of larvae of *Strombus gigas* in the field, and showed that a solar-powered flow-through system can work for extended periods in remote salt water locations. Although the design, equipment and operation of the mesocosm system were efficient, a few changes would improve the proficiency of the system. Since accumulation of phytoplankton did not pose a problem in this flow-through system, lengthening the time period (>4 d) between transfers of larvae from one mesocosm to another could be accomplished by increasing the filtration area of the standpipe and decreasing the flow of water (<1 l min^{-1}). The guts of *Strombus gigas* veligers were always full, indicating either that the zooplankton in the mesocosm may not be competitors for food or that sufficient amounts of food were available so that competition did not occur. In the future, we would reduce the number of organisms entering the mesocosm by always using 5 µm filters. The decision to use this filter size is also justified because growth rates of veligers in this mesocosm study and in recent laboratory experiments (Davis unpubl. data) were similar when they were fed 5 and 50 µm phytoplankton assemblages.

There are 5 constraints that must be considered when choosing an experimental site and designing an experiment for this mesocosm system. First, this system should be used in water of limited wave height (< 0.5 m) to avoid damage to the mesocosms. Second, larval transfers need to be carried out in calm water. Third, the rate of clogging for the flow-through standpipe depends on productivity of the water In the oligotrophic waters of the Bahamas standpipes began to clog after 4 to 5 d, but this period may be shorter in areas of higher productivity, such as in estuarine or coastal waters. Fourth, to achieve optimal flow rate, the size of the standpipe pore openings should vary according to the species being cultured. Fifth, potential competitors or predators may invade the system via the filters and produce a density-dependent effect, which must be considered when interpreting experimental results.

Up to this point, the larval life-span of *Strombus gigas* was unknown in the field. In the laboratory, veligers fed with cultured algae are typically competent for metamorphosis between 18 and 24 d (mean 21 d) (Brownell 1977, Davis et al. 1990, 1993, Weil & Laughlin 1994). In the mesocosm, metamorphosis was first observed on Day 13, and 95% of the veligers were competent for metamorphosis by Day 16. Veligers fed natural phytoplankton in the field not only demonstrated faster growth rates, but had more vigor than those raised in the laboratory (Davis pers. obs.). An *in situ* flow-through apparatus designed by Olson (1987) also showed that larvae of *Acanthaster planci* developed successfully and at near-maximal rates when compared with laboratory-cultured larvae. A properly designed mesocosm system may well be superior to laboratory systems in generating ecologically relevant growth data (de Lafontaine & Leggett 1987b, Epifanio et al. 1991).

A recent laboratory study compared growth rates of veligers of *Strombus gigas* fed diets of natural phytoplankton from the Bahamian waters and cultured algae (*Isochrysis* sp. and *Chaetoceros gracilis*) used in hatchery culture (Davis in press). Although the chl *a* level of the cultured algae was 50 times higher than that in the natural phytoplankton treatment (mean 176 ng chl *a* l^{-1}) growth rates were identical (Davis in press). These results suggest that quality of food may be more important than quantity, that nutritional value

of natural phytoplankton cells may be superior to cultured algae, and that natural food items must be used to establish growth rates likely to occur in the field.

Understanding factors affecting growth, development and survival rates of marine invertebrate larvae in the field will provide pertinent knowledge for determining dispersal and recruitment processes. Carefully designed mesocosms can achieve replication and manipulation of treatments, reproducibility of the natural physical, chemical, and biological conditions of the ambient water column, and observations on the behavioral characteristics of the organisms (de Lafontaine & Leggett 1987b). Furthermore, mesocosms are an ideal mechanism to experimentally determine what factors regulate larval life-span and survival, to test temporal and spatial variations in phytoplankton composition and biomass by placement in water masses where larvae are located, and to provide a controlled system for experiments in which predator quantity and type are manipulated. The mesocosm system designed in this study can accommodate these applications and can easily be used to test growth rates, observe behavior and estimate survival of a variety of marine invertebrate larvae.

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LITERATURE CITED

Barile PJ, Stoner AW, Young CM (1994) Phototaxis and vertical migration of the queen conch (*Strombus gigas* Linne) veliger larvae. J exp mar Biol Ecol 183:147–162

Bollens SM, Frost BW (1989) Predator-induced diel vertical migration in a marine planktonic copepods. J Plankton Res 11:1047–1065

Bollens SM, Frost BW (1990) UV light and vertical distribution of the marine planktonic copepod *Acartia hudsonica* Pihey. J exp mar Biol Ecol 137:89–93

Bollens SM, Frost BW (1991) Diel vertical migration in zooplankton: rapid individual response to predators. J Plankton Res 13:1359–1365

Bollens SM, Stearns DE (1992) Predator-induced changes in the diel feeding cycle of a planktonic copepod. J exp mar Biol Ecol 156:179–186

Brownell WN (1977) Reproduction, laboratory culture, and growth of *Strombus gigas, S. costatus* and *S. pugilus* in Los Roques, Venezuela. Bull mar Sci 27:668–680

Cowan JH Jr, Houde ED (1990) Growth and survival of bay anchovy *Anchoa mitchilli* larvae in mesocosm enclosures. Mar Ecol Prog Ser 68:47–57

Davis M (1994) Mariculture techniques for queen conch (*Strombus gigas* Linne): egg mass to juvenile stage. In: Appeldoorn RS, Rodriguez B (eds) Queen conch biology, fisheries, and mariculture. Fundacion Cientifica, Los Roques, Caracas, Venezuela, p 231–252

Davis M (in press) Differential growth rate influences dispersal potential of queen conch larvae. Proc Gulf Caribb Fish Inst 47

Davis M, Bolton CA, Stoner AW (1993) A comparison of larval development, growth, and shell morphology in three Caribbean *Strombus* species. Veliger 36:236–244

Davis M, Heyman WD, Harvey W, Withstandley CA (1990) A comparison of two inducers, KCl and *Laurencia* extracts, and techniques for the commercial scale induction of metamorphosis in queen conch *Strombus gigas* Linnaeus, 1758 larvae. J Shellfish Res 9:67–73

de Lafontaine Y, Leggett WC (1987a) Effect of container size on estimates of mortality and predation rates in experiments with macrozooplankton and larval fish. Can J Fish Aquat Sci 44:1534–1542

de Lafontaine Y, Leggett WC (1987b) Evaluation of *in situ* enclosures for larval fish studies. Can J Fish Aquat Sci 44: 54–65

Duffy JT, Epifanio CE (1994) Effects of larval density on the growth and survival of weakfish *Cynoscion regalis* in large-volume enclosures. Mar Ecol Prog Ser 104:227–233

Epifanio CE, Cope JS, Rowe PM, Jenkins FM (1991) Comparison of rates of development of Atlantic mud crab larvae in the laboratory and in field-deployed enclosures. J crust Biol 11:540–545

Houde ED, Gamble JC, Dorsey SE, Cowan JH Jr (1994) Drifting mesocosms: the influence of gelatinous zooplankton on mortality of bay anchovy, *Anchoa mitchilli*, eggs and yolk-sac larvae. ICES J mar Sci 51:383–394

MacKenzie BR, Leggett WC, Peters R (1990) Estimating larval fish ingestion rates: can laboratory derived values be reliably extrapolated to the wild? Mar Ecol Prog Ser 67:209–225

Øiestad V (1982) Application of enclosures to studies on the early life history of fishes. In: Grice GD, Reeve MR (eds) Marine mesocosms, biological and chemical research in experimental systems. Springer-Verlag, New York, p 49–62

Øiestad V (1990) Specific applications of meso- and macrocosms for solving problems in fisheries research. In: Lalli CM (ed) Enclosed experimental marine ecosystems: a review and recommendations. Coastal and Estuarine Studies 37, Springer-Verlag, New York, p 136–154

Olson RR (1985) *In situ* culturing of larvae of the crown-of-thorns starfish, *Acanthaster planci*. Mar Ecol Prog Ser 25: 207–210

Olson RR (1987) *In situ* culturing of larvae of the crown-of-thorns starfish, *Acanthaster planci*. Limnol Oceanogr 32: 895–904

Olson RR, Bosch I, Pearse JS (1987) The hypothesis of Antarctic larval starvation examined for the asteroid *Odontaster validus*. Limnol Oceanogr 32:686–690

Pennington JT, Emlet RB (1986) Ontogenetic and diel vertical migration of a planktonic echinoid larva, *Dendraster excentricus* (Eschscholtz): occurrence, causes and probable consequences. J exp mar Biol Ecol 104:69–95

Randall JE (1964) Contributions to the biology of the queen conch *Strombus gigas*. Bull mar Sci Gulf Caribb 14:246–295

Rosenberg AA, Haugen AS (1982) Individual growth and size-selective mortality of larval turbot (*Scophthalmus maximus*) reared in enclosures. Mar Biol 72:73–77

Shoaf WT, Lium BW (1976) Improved extraction of chlorophyll *a* and *b* from algae using dimethyl sulfoxide. Limnol Oceanogr 21:926–928

Stoner AW, Sandt VJ, Boidron-Metarion IF (1992) Seasonality of reproductive activity and abundance of veligers in queen conch, *Strombus gigas*. Fish Bull US 90:161–170

Strickland JDH, Parsons TR (1972) A practical handbook of seawater analysis, 2nd edn. Fisheries Research Board of Canada, Ottawa, p 201–202

Weil E, Laughlin RA (1994) Laboratory cultures of larvae of *Strombus gigas* Linne, in the Dos Mosquises Marine Station, Los Roques National Park, Venezuela. In: Appeldoorn RS, Rodriguez B (eds) Queen conch biology, fisheries, and mariculture. Fundacion Cientifica, Los Roques, Caracas, Venezuela, p 275–293

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