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GROWTH AND SURVIVAL OF *SPISULA SOLIDISSIMA SIMILIS* LARVAE FED DIFFERENT RATIONS OF TAHITIAN STRAIN ISOCHRYSIS SPECIES

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ABSTRACT Laboratory-spawned veliger-stage larvae of the southern Atlantic surfclam, *Spisula solidissima similis* (Say 1822), were reared to late pediveliger stage on five different cell concentrations of Tahitian strain *Isochrysis* species (T-Iso) to determine an optimal food ration for this subspecies. Larvae were fed daily 0, 50,000, 100,000, 200,000, or 300,000 cells/mL of T-Iso. Day-old veliger larvae were stocked in 150 (1-L) replicate flasks at mean densities of 0.7 or 0.8 larvae/mL for trials A and B, respectively. Larval growth and survival were assessed every 2 days over the 14-day trial periods. Significantly greater growth and survival of larvae occurred in both trials in the lower food rations of 50,000 and 100,000 cells/mL. A reduction in larval growth rate and survival was observed at the higher ration treatments. A decline in overall larval health may be associated with the deliterious effects of surplus ration degradation.

KEY WORDS: *Spisula*, larvae, aquaculture, food ration, growth, survival

INTRODUCTION

The economic importance of the Atlantic surfclam, *Spisula solidissima solidissima* (Dillwyn 1817), fishery has been recognized for decades (Ropes 1968). The surfclam fishery, the second leading clam fishery in terms of dollars earned in the United States, produced 73.9 million pounds of meat valued at 34 million dollars in 1993 (O'Bannon 1994). The southern subspecies, *Spisula solidissima similis* (Say 1822), which occurs from Massachusetts to Florida and through the Gulf of Mexico to Texas (Abbott 1974), is not commercially harvested. In contrast to *S. s. solidissima*, which has been extensively studied in terms of its natural history (Ropes 1968) and fishery (Merrill and Ropes 1969) and aquacultural potential (Goldberg 1980, Goldberg and Walker 1990, Walker and Heffernan 1991), far less economic or natural history information is available on *S. s. similis*.

Growth and longevity studies (Walker and Heffernan 1994) indicate that *S. s. similis* individuals from inshore populations in Georgia reach a mean maximum shell length of 47–48 mm, with a mean longevity of 1.5 y. Also, in Georgia, *S. s. similis* mature sexually by January to February and spawn from March until May (Kanti et al. 1993). Coupled, these studies would seem to indicate that *S. s. similis* has good aquacultural potential for the lucrative raw, fried, and steamer markets, as well as the pasta clam market.

Optimal salinity and temperature regimens for *S. s. similis* embryo-to-larval metamorphosis in a laboratory have also been documented (Walker et al. 1995). The effect of food ration quality and quantity is an important aspect of bivalve larval husbandry (Loosanoff et al. 1955, Pratt and Campbell 1956, Epifanio et al. 1976, Goldberg 1980, Rhodes et al. 1984) and in this case needs to be addressed on the subspecies level. Therefore, the objective of this study was the determination of the optimal feeding ration based on cell numbers for hatchery-reared *S. s. similis* larvae fed Tahitian strain *Isochrysis* species (T-Iso) through metamorphosis.

METHODS

Adult southern Atlantic surfclams, *S. s. similis*, were captured as broodstock from St. Catherines Sound, GA, in early February 1993. After acquisition, clams (n = 272 total) were equally divided into two, 6-mm mesh, 70 × 70 × 20 cm, vinyl-coated wire cages placed below mean-low water, on a sandy-tidal flat at the mouth of House Creek in Wassaw Sound, GA. On March 8, the broodstock were returned to the laboratory and placed in 400-L conditioning tanks maintained at 13°C and 26 ppt salinity. The broodstock were randomly divided into three equal size groups (n = 87), and placed in separate conditioning tanks. Clams were acclimated to temperatures of 15, 20, and 25°C in preparation for another experiment (Walker and Hurley 1995), by increasing the water temperature by 1°C daily. Unsolicited mass spawning occurred on April 3 and 4 from broodstock held in the 15 and 20°C conditioning tanks, respectively. Each resulting larval cohort was held in separate tanks maintained at 20°C and allowed to develop into veligers before the commencement of the experimental trials.

On April 4, Feeding Trial A was initiated from the 1-day-old veliger larvae of the 15°C conditioned broodstock. Larvae were stocked in nonaerated, 1-L flasks (n = 160 total) at a concentration of 0.7 larvae/mL. Water salinity of 25 ppt and temperature of 20 ± 1°C were maintained constant throughout the trial for all larval treatments. Larval treatments consisted of a ration of T-Iso at concentrations of 0, 50,000, 100,000, 200,000, and 300,000 cells/mL delivered once daily. All replicate flasks received a water exchange and a thorough rinse through a 20-μm-pore-size sieve on alternate days. On each alternate day, immediately before the water exchange, the contents of each of four flasks per treatment were sieved through a 20-μm-pore-size screen, fixed in a 10% buffered Formalin and Rose Bengal stain solution (v:v) and concentrated to a 50-mL suspension. Initial stocking density validation was based on three replicate 1-mL counts for each of four flasks per treatment at Time 0. Survival estimates were based on Sedgewick-Rafter

slide counts of three 1-mL subsamples per replicate suspension per treatment per sample period. All survival data were proportionally adjusted to the original replicate flask culturing volume (1 L) before statistical analysis. Shell length measurements (maximum anterior-posterior distance) were taken for 30 animals per treatment per sample date (see Heffernan et al. 1991).

On April 5, Trial B was initiated with 1-day-old veliger larvae from the 20°C conditioned broodstock spawning. Larvae were stocked at a density of 0.8 larvae/mL in 1-L flasks (n = 150 total) with treatments consisting of a daily deliverance of 0, 50,000, 100,000, 200,000, and 300,000 cells/mL of T-Iso. Larval treatments in Trial B were fed, maintained, and sampled as described above for Trial A.

Differences in growth and survival among treatments were determined by analysis of variance ($\alpha = 0.05$) and Tukey's Studentized Range Test ($\alpha = 0.05$). All percent survival data were arcsine transformed before statistical analysis. Statistical analysis was performed on SAS for PC (SAS Institute Inc. 1989).

RESULTS

Statistically, greater stocking densities of veligers ($p = 0.0178$) occurred in the 200,000 cells/mL treatment at the initiation of the study; thus, the 200,000 cells/mL treatment was eliminated from Experimental Trial A. No significant differences in larval stocking size existed among the remaining treatments ($p = 0.1732$) at Time 0 (Table 1). On Day 2, the larvae from treatments given no food and 50,000 cells/mL were equal in size, but significantly smaller than the two higher density ration treatments ($p < 0.0001$). Days 4, 6, and 8 exhibited the same trends with significantly greater larval size in all fed treatments compared with the unfed treatment (all $p < 0.0001$). By Day 10, the unfed treatment had no surviving larvae and was discontinued. Also, by Day 10 ($p < 0.0001$) and on subsequent Days 12 ($p = 0.0005$) and 14 ($p = 0.0060$), larvae from the 50,000 and 100,000 cells/mL ration treatments were not significantly different from each other but were significantly larger than those from the 300,000 cells/mL treatment ($p < 0.0001$).

No significant differences in larval stocking densities existed among the remaining treatments of Trial A at Time 0 ($p = 0.1433$; Table 2). Significantly lower larval survival occurred on Day 2 for the 50,000 cells/mL treatment ($p < 0.0001$), whereas significantly lower survival occurred for both the unfed and 50,000 cells/mL treatments ($p < 0.0004$) on Day 4. No significant differences in survival occurred among fed treatments on Day 8 ($p = 0.2463$) or 10 ($p = 0.0871$). Significantly lower survival occurred in the 300,000 cells/mL treatment on both Days 12 ($p = 0.0017$) and 14 ($p = 0.0002$) as compared with the lower food ration treatments of 50,000 and 100,000 cells/mL.

In Trial B, statistically higher larval stocking densities occurred at Time 0 in the 300,000 cells/mL ration treatment ($p = 0.0283$), and this treatment was thus eliminated from the trial. No significant differences in larval size existed among the remaining treatments at Time 0 ($p = 0.4749$) or Day 2 ($p = 0.2251$) (Table 3). By Day 4 and on subsequent days, all fed treatments exhibited significantly larger larval size (all $p < 0.0001$) compared with the unfed treatment. On Days 6 and 10, larvae from the 50,000 and 100,000 cells/mL treatments were not significantly different in size; however, larvae in both treatments were significantly smaller than those in the 200,000 cells/mL treatment ($p < 0.0001$ and $p = 0.0081$, respectively). Additionally, the unfed treatment had no surviving larvae by Day 10 and was discontinued. On Days 12 and 14, larvae in the 50,000 and 100,000 cells/mL treatments were significantly larger than the 200,000 cells/mL treatment larvae ($p < 0.0001$ for both days).

No significant differences in larval density existed between treatments in Trial B at Time 0 or Day 2 ($p = 0.9811$ and $p = 0.1757$, respectively) (Table 4). On Day 4, no significant differences in larval survival existed between the 50,000 cells/mL and the unfed treatments; however, both treatments had significantly lower survival than the higher ration treatments of 100,000 and 200,000 cells/mL ($p < 0.0001$). On Days 6 ($p = 0.7504$) and 8 ($p = 0.4924$), no significant differences in larval survival existed among treatments. By Day 10, the unfed treatment exhibited total

TABLE 1.

Trial A mean size (μm) of *S. s. similis* larvae (±SE) fed four different food rations (cells/mL) of T-Iso.

	Treatment (Cells/mL per Day)			
Sample Day and Tukey's Ranking	**300,000**	**100,000**	**50,000**	**0**
Day 0 ($p = 0.1732$)	73.6 ± 0.4(a)*	73.4 ± 0.3(a)	74.3 ± 0.4(a)	73.3 ± 0.3(a)
Day 2 ($p < 0.0001$)	83.3 ± 0.7(a)	81.4 ± 0.4(a)	75.5 ± 3.3(b)	78.3 ± 0.2(b)
Day 4 ($p < 0.0001$)	91.4 ± 0.9(a)	90.1 ± 0.8(a)	88.8 ± 0.9(a)	78.6 ± 0.3(b)
Day 6 ($p < 0.0001$)	112.9 ± 1.5(a)	108.2 ± 1.7(a)	108.7 ± 1.8(a)	81.2 ± 0.6(b)
Day 8 ($p < 0.0001$)	130.0 ± 2.1(a)	133.3 ± 2.4(a)	131.5 ± 2.3(a)	84.0 ± 0.7(b)
Day 10 ($p < 0.0001$)	136.1 ± 2.5(b)	161.0 ± 3.6(a)	151.9 ± 4.4(a)	†
Day 12 ($p = 0.0005$)	147.9 ± 4.0(b)	179.6 ± 4.9(a)	191.4 ± 7.1(a)	†
Day 14 ($p = 0.0060$)	125.0 ± 20.9(b)	193.4 ± 8.0(a)	172.3 ± 6.7(a)	†

* Letters in parentheses adjacent to mean larval size identify the Tukey's ranking.

† Total mortality observed.

TABLE 2.

Trial A percent mean survival (±SE) (larvae/mL) of *S. s. similis* larvae fed four different food rations (cells/mL) of T-Iso.

	Treatment (Cells/mL per Day)			
Sample Day and Tukey's Ranking	**300,000**	**100,000**	**50,000**	**0**
Day 0				
(p = 0.1433)	0.741 ± .038(a)*	0.600 ± .084(a)	0.562 ± .060(a)	0.642 ± .073(a)
Day 2				
(p < 0.0001)	0.558 ± .046(a)	0.518 ± .048(a)	0.050 ± .014(b)	0.579 ± .026(a)
Day 4				
(p = 0.0004)	0.863 ± .051(a)	0.879 ± .095(a)	0.463 ± .079(b)	0.513 ± .0963(b)
Day 6				
(p = 0.0037)	0.704 ± .070(a)	0.738 ± .070(a)	0.792 ± .062(a)	0.463 ± .050(b)
Day 8				
(p = 0.2463)	0.679 ± .046(a)	0.692 ± .053(a)	0.613 ± .083(a)	0.521 ± .073(a)
Day 10				
(p = 0.0871)	0.479 ± .057(a)	0.575 ± .032(a)	0.446 ± .030(a)	†
Day 12				
(p = 0.0017)	0.142 ± .015(b)	0.433 ± .044(a)	0.500 ± .093(a)	†
Day 14				
(p = 0.0002)	0.042 ± .088(b)	0.283 ± .046(a)	0.366 ± .056(a)	†

* Letters in parentheses adjacent to larval count identify Tukey's rankings.
† Total mortality observed.

mortality and was discontinued. On Days 10 (p = 0.1117), 12 (p = 0.3673), and 14 (p = 0.0837), no significant differences in larval survival existed among the remaining treatments.

DISCUSSION

Food ration is an important consideration of bivalve larval culture and has been demonstrated to affect larval survival and growth in cultured *Mercenaria mercenaria* (Loosanoff and Davis 1963, Castagna and Kraeuter 1981, Riisgard 1988), *Ostrea edulis* (Helm and Laing 1987), *Crassostrea gigas* (Nascimento 1980), *Mytilus edulis* (Riisgard 1991), and *S. s. solidissima* (Goldberg 1985). In our study, *S. s. similis* larvae had significantly greater growth and survival at food rations of 50,000 and 100,000 cells of T-Iso/mL than at higher cell concentrations. Consequently, these food ration treatments are interpreted by us as the optimal treatments, among those tested, for larval culture of *S. s. similis*. The observed developmental time of *S. s. similis* larvae fed the flagellate T-Iso to late pediveliger stage in this study (14 days) also approximates that of *S. s. solidissima* reared under similar temperatures and salinities, given a mixed daily ration of 100,000 cells/mL of *Pavlovi lutheri* and *Isochrysis galbana* (Goldberg 1980).

TABLE 3.

Trial B mean size (μm) of *S. s. similis* larvae (±SE) fed four different food rations (cells/mL) of T-Iso.

	Treatment (Cells/mL per Day)			
Sample Day and Tukey's Ranking	**200,000**	**100,000**	**50,000**	**0**
Day 0				
(p = 0.4749)	73.9 ± 0.2(a)*	73.6 ± 0.3(a)	73.5 ± 0.3(a)	73.3 ± 0.2(a)
Day 2				
(p = 0.2251)	78.2 ± 0.4(a)	77.4 ± 0.3(a)	77.4 ± 0.3(a)	77.6 ± 0.3(a)
Day 4				
(p < 0.0001)	87.6 ± 0.7(a)	90.4 ± 0.8(a)	83.6 ± 0.6(a)	82.0 ± 0.5(b)
Day 6				
(p < 0.0001)	122.1 ± 1.6(a)	113.7 ± 1.6(b)	115.7 ± 1.3(b)	87.1 ± 0.6(c)
Day 8				
(p < 0.0001)	138.0 ± 1.8(a)	138.4 ± 2.0(a)	132.5 ± 1.8(a)	95.5 ± 0.8(b)
Day 10				
(p = 0.0081)	174.0 ± 3.0(a)	161.1 ± 2.8(b)	163.2 ± 3.0(b)	†
Day 12				
(p < 0.0001)	179.4 ± 3.6(b)	212.0 ± 4.1(a)	218.7 ± 4.3(a)	†
Day 14				
(p < 0.0001)	157.3 ± 5.9(b)	224.3 ± 4.2(a)	209.4 ± 5.8(a)	†

* Letters in parentheses adjacent to mean larval size identify the Tukey's ranking.
† Total mortality observed.

TABLE 4.

Trial B percent mean survival (±SE) (larvae/mL) of *S. s. similis* fed four different food rations of T-Iso.

	Treatment (Cells/mL per Day)			
Sample Day and Tukey's Ranking	**200,000**	**100,000**	**50,000**	**0**
Day 0 ($p = 0.9811$)	0.896 ± .042(a)*	0.892 ± .029(a)	0.900 ± .068(a)	0.883 ± .032(a)
Day 2 ($p = 0.1757$)	0.988 ± .058(a)	0.829 ± .048(a)	0.846 ± .077(a)	0.921 ± .033(a)
Day 4 ($p < 0.0001$)	0.758 ± .094(a)	0.771 ± .119(a)	0.183 ± .067(b)	0.325 ± .074(b)
Day 6 ($p = 0.7504$)	0.770 ± .061(a)	0.839 ± .031(a)	0.796 ± .055(a)	0.780 ± .029(a)
Day 8 ($p = 0.4924$)	0.750 ± .036(a)	0.621 ± .102(a)	0.729 ± .058(a)	0.713 ± .061(a)
Day 10 ($p = 0.1117$)	0.829 ± .046(a)	0.700 ± .041(a)	0.792 ± .036(a)	†
Day 12 ($p = 0.3673$)	0.634 ± .025(a)	0.733 ± .021(a)	0.733 ± .091(a)	†
Day 14 ($p = 0.837$)	0.333 ± .085(a)	0.625 ± .119(a)	0.550 ± .045(a)	†

* Letters in parentheses adjacent to larval count identify the Tukey's rankings.
† Total mortality observed.

Similar results were obtained in other laboratory studies using comparable cell concentrations with *M. mercenaria* larvae (40,000–60,000 cells/mL) fed T-Iso (Riisgard 1988) and *M. edulis* larvae (40,000–50,000 cells/mL) fed *I. galbana* (Jespersen and Olsen 1982). However, optimal bivalve growth rates in laboratory conditions may vary considerably from maximal growth rates in nature (Kiørboe et al. 1981; Jorgensen 1990). It is presumed that these growth rate differences may be attributed to the adaptive responses of bivalves to laboratory conditions and the difficulty in creating optimal conditions such as feeding regimes and algal concentrations to which a bivalve species is adapted in the wild (Riisgard 1991). In veligers of both *M. mercenaria* (Riisgard 1988) and *M. edulis* (Jespersen and Olsen 1982), a reduction in the filtration rate due to higher algal concentrations was associated with reaching maximum gut retention, leading to valve closure, reduced metabolism, and reduced biosyntheses/growth (Riisgard 1991). Conversely, Perez-Camacho et al. (1994) found a direct relationship between ration cell numbers and larval clearance, ingestion, and growth in *Ruditapes decussatus* fed up to 300,000 cells/mL for short-time exposure (hours). The maricultural application of these results, however, may be misleading, because factors associated with prolonged exposure to higher cell densities could negatively affect larval survivability, as demonstrated in this study.

The consistency of the results for both larval size (Tables 1 and 3) and survival (Tables 2 and 4) further validates the finding that rations greater than 200,000 cells/mL are excessive and yield inferior larval production. Consideration of broodstock conditioning temperature is important in interpreting these results. Broodstock, embryo, and subsequent larval cohorts were subjected to different pre-experimental temperature treatments of 15 and 20°C (Trials A and B, respectively). Higher larval survival (33–63%; Table 4) occurred in Trial B, in which larvae were spawned in 20°C conditioning tanks and were reared at 20°C. Lower larval survival (4–37%; Table 2) occurred in Trial A, in which animals were conditioned in 15°C tanks but reared at 20°C. Thermal conditioning temperatures of broodstock and its effect on subsequent larval cohorts, therefore, may have confounded the results between the optimal ration treatments; however, it played an apparently minor role in elucidating an optimal versus a suboptimal ration. Both trials demonstrated optimal larval growth and survival at food rations of 50,000 and 100,000 cells/mL. Previous work of broodstock conditioning effects on *S. s. similis* larvae (Walker and Hurley 1995) noted similar results, with 15°C conditioned broodstock yielding larvae of equal size and higher survivability as compared with larvae from 20°C conditioned broodstock. It is important to note that Walker and Hurley (1995) found the optimal conditioning temperature for *S. s. similis* broodstock to be 25°C, based on larval survival and size at 48 h.

Survival data (Tables 2 and 4) displayed no consistent trends among treatments until Days 10 (Trial A) and 12 (Trial B). Survival for Days 2 through 8 gave ambiguous results, fluctuating among the treatments and sample periods. By Days 10, 12, and 14, however, the lower food ration treatments of 50,000 and 100,000 cells/mL in both Trials A and B displayed greater survival than the higher ration treatments of 200,000 cells/mL (Trial B), or 300,000 cells/mL (Trial A). These increases suggest that ration densities approaching or exceeding 200,000 cells/mL are excessive.

The increased mortality and lower growth rates in the higher ration density treatments could be explained in part by an increase in deleterious microbial activity and contamination in the culture chambers (Loosanoff and Davis 1963). The decomposition of nonutilized algal cells promotes microbial activity, which can directly affect larval survival via exposure to harmful bacterial and fungal pathogens (Loosanoff and Davis 1963). Additionally, an increase in larval size results in an increase in larval oxygen demand (Riisgard et al. 1981). Prolonged hypoxia has been demonstrated to reduce both larval development and growth in *M. mercenaria* (Morrison 1971) and *M. edulis* (Wang and Widdows 1991). Excess food decomposition and increases in secondary production, coupled with an increase in oxygen demand as the larvae grow, could result in an overall decrease in available dissolved oxygen in the culture chambers. Suboptimal oxygen content in the rearing chambers would have created additional stress on the larvae. This oxygen stress coupled with contamination effects could reduce

larval vigor, which in turn could affect larval foraging ability and size. Metamorphosis is accountable for the primary loss of lipid reserves in developing larvae (Waldock and Holland 1978). The lack of an adequate accumulation of nutritional reserves necessary for the successful completion of "set" is frequently manifested as mortality associated with the final metamorphic stage (Loosanoff and Davis 1963). The lower growth rate of larvae in the higher ration treatments could be explained by an increase in the mortality of the larger, metamorphically competent individuals during this latter, physiologically stressful stage of their development.

Two primary culturing applications are evident from the results of this study. First, the cost benefits of reducing food ration cell density to approximately 75,000 cells/mL, as opposed to 150,000 cells/mL or greater, are significant. The algal production of T-Iso could be reduced by half, resulting in a concomitant reduction in necessary labor and expense. Second, both larval survival and growth benefits associated with appropriate ration treatments will result in higher yields to the aquaculturalist.

In conclusion, this study has determined that the optimal food ration for developing *S. s. similis* larvae fed T-Iso is between 50,000 and 100,000 cells/mL in stocking densities of 0.7–0.8 larvae/mL. Increases in the food ration beyond 200,000 cells/mL result in both increased mortality and reduced growth rates.

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LITERATURE CITED

Abbott, R. T. 1974. American Seashells. 2nd ed. Van Nostrand Reinhold, New York. 633 pp.

Castagna, M. & J. N. Kraeuter. 1981. Manual for Growing the Hard Clam *Mercenaria*. Special Report in Applied Marine Science and Ocean Engineering. No. 249, Virginia Institute of Marine Science, Gloucester Point, VA. 110 pp.

Epifanio, C. E., C. M. Logan & C. Turk. 1976. Culture of six species of bivalves in a recirculating seawater system. pp. 97–108. *In:* G. Persoone and E. Jaspers (eds.). Proceedings of the 10th European Symposium on Marine Biology. vol. 1. Institute of Marine Science Research, Bredene.

Goldberg, R. 1980. Biological and technological studies on the aquaculture of yearling surf clams. Part I. Aquaculture production. *Proc. Natl. Shellfish. Assoc.* 70:55–60.

Goldberg, R. 1985. Growth and energetics of the surf clam, *Spisula solidissima,* (Dillwyn), at different algal concentrations. Masters Thesis, Southern Connecticut State University, Groton, CT.

Goldberg, R. & R. L. Walker. 1990. Cage culture of yearling surf clams *Spisula solidissima* (Dillwyn, 1817), in coastal Georgia. *J. Shellfish Res.* 9:187–193.

Heffernan, P. B., R. L. Walker & J. W. Crenshaw, Jr. 1991. Negative larval response to selection for increased growth rate in northern quahogs, *Mercenaria mercenaria* (Linnaeus, 1758). *J. Shellfish Res.* 10:199–202.

Helm, M. M. & I. Laing. 1987. Preliminary observations on the nutritional value of 'Tahitian *Isochrysis*' to bivalve larvae. *Aquaculture* 62:281–288.

Jespersen, H. & K. Olsen. 1982. Bioenergetics in veliger larvae of *Mytilus edulis*. (L.). *Ophelia* 21:101–113.

Jorgensen, C. B. 1990. Bivalve Feeding: Hydrodynamics, Bioenergetics, Physiology and Ecology. Olsen and Olsen, Fredensborg, Denmark.

Kanti, A., P. B. Heffernan & R. L. Walker. 1993. Gametogenic cycle of the southern surf clam, *Spisula solidissima similis* from St. Catherines Sound, Georgia. *J. Shellfish Res.* 12:255–261.

Kiørboe, T., F. Møhlenberg & O. Nøhr. 1981. Effect of suspended bottom material on growth and energetics in *Mytilus edulis*. *Mar. Biol.* 61: 283–288.

Loosanoff, V. L. & H. C. Davis. 1963. Rearing of bivalve mollusks. *Adv. Mar. Biol.* 1:1–136.

Loosanoff, V. L., H. C. Davis & P. E. Chanley. 1955. Food requirements of some bivalve larvae. *Proc. Natl. Shellfish. Assoc.* 45:66–83.

Merrill, A. S. & J. W. Ropes. 1969. The general distribution of the surf clam and ocean quahog. *Proc. Natl. Shellfish. Assoc.* 59:40–45.

Morrison, G. 1971. Dissolved oxygen requirements for embryonic and larval development of the hardshell clam, *Mercenaria mercenaria*. *J. Fish. Res. Bd. Can.* 28:379–381.

Nascimento, I. A. 1980. Growth of larvae of *Crassostrea gigas* Thurnberg, fed with different algal species at high cell concentrations. *J. Cons. Int. Explor. Mer.* 39:134–139.

O'Bannon, B. K. 1994. Fisheries of the United States, 1993. Current Fisheries Statistics No. 9300. U. S. Department of Commerce, NOAA, National Marine Fisheries Service, Washington, DC. p. 121.

Perez-Camacho, A., R. Beiras & M. Albentosa. 1994. Effects of algal food concentration and body size on the ingestion rates of *Ruditapes decussatus* (Bivalvia) veliger larvae. *Mar. Ecol. Prog. Ser.* 15:87–92.

Pratt, D. M. & D. C. Campbell. 1956. Environmental factors affecting growth in *Venus mercenaria*. *Limnol. Oceanogr.* 1:2–17.

Rhodes, E. W., J. C. Widman & E. L. Grinsburgs. 1984. Optimal algal concentrations and algal consumption rates for bivalve larvae in culture, and some implications for some feeding protocols. *J. Shellfish Res.* 4:99 (abstract).

Riisgard, H. U. 1988. Feeding rates in the hard clam (*Mercenaria mercenaria*) veliger larvae as a function of (*Isochrysis galbana*) algal concentration. *J. Shellfish Res.* 7:377–378.

Riisgard, H. U. 1991. Filtration rate and growth in the blue mussel, *Mytilus edulis,* Linnaeus, 1758: dependance on algal concentration. *J. Shellfish Res.* 10:29–35.

Riisgard, H. U., A. Randlov & K. Hamburger. 1981. Oxygen consumption and clearance as a function of size in *Mytilus edulis* L. veliger larvae. *Ophelia* 20:179–183.

Ropes, J. W. 1968. Reproductive cycle of the surf clam, *Spisula solidissima,* in offshore New Jersey. *Biol. Bull.* 135:349–365.

SAS Institute Inc. 1989. SAS Users Guide: statistics. Version 6. SAS Institute Inc., Cary, NC. 846 pp.

Waldock, M. J. & D. L. Holland. 1978. Fatty acid composition of the triacylglycerols of the cypris larva of the barnacle *Balanus balanoides* during metamorphosis. *Mar. Biol.* 46:163–166.

Walker, R. L. & P. B. Hefferman. 1991. Mariculture potential of the Atlantic surf clam, *Spisula solidissima* (Dillwyn 1817), in the coastal waters of Georgia. *Ga. J. Sci.* 49:168–176.

Walker, R. L. & P. B. Heffernan. 1994. Age, growth rate, and size of the southern surf clam, *Spisula solidissima similis* (Say 1822). *J. Shellfish Res.* 13:433–441.

Walker, R. L. & D. H. Hurley. 1995. Optimum hatchery conditioning temperature for egg production in *Spisula solidissima similis* (Say 1822) (Bivalvia: Mactridae). *Ga. J. Sci.* 53:127–136.

Walker, R. L., F. X. O'Beirn & D. H. Hurley. 1995. Embryonic and larval development of the southern surf clam, *Spisula solidissima similis,* (Say 1822). *J. Shellfish Res.* 14:281 (abstract).

Wang, W. X. & J. W. Widdows. 1991. Physiological responces of mussel larvae, *Mytilus edulis* to environmental hypoxia and anoxia. *Mar. Ecol. Prog. Ser.* 70:223–236.