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Hard clam, *Mercenaria mercenaria*, broodstocks: growth of selected hatchery stocks and their reciprocal crosses*

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ABSTRACT

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Crosses between and within two hatchery stocks of hard clams, *Mercenaria mercenaria*, were created in three independent experiments and the offspring reared to 2 years of age. Environmental variation between experiments strongly influenced early growth, but mean sizes at 2 years were similar for the three experiments. Offspring from all crosses had above-average growth rates. Offspring were assessed electrophoretically at seven enzyme loci, and gene frequencies and overall heterozygosities were compared to parental stocks. There was no correlation between heterozygosity and size at 2 years, nor between heterozygosity and variance of mean size. Reciprocal crosses were not consistently faster growing nor more heterozygous than purebred lines, nor was any relationship apparent between cross and variance of mean size. However, offspring from the reciprocal crosses were genetically distinct from each other and from the purebred lines and possessed the desirable traits of the parental stocks.

INTRODUCTION

The commercial culture of hard clams, *Mercenaria mercenaria*, in North America has made considerable progress since its rather modest beginnings in 1939 with the first hatchery production of seed clams. Today, it is estimated that approximately 19 commercial hatcheries have hard clam production capabilities (Manzi and Castagna, 1989) and that approximately 100 growout operations exist in 14 states, 80 in Florida alone (David Vaughan, Harbor Branch Oceanographic Institution, pers. commun.). Most of this growth has occurred in the last 10 years as the major technical obstacles to culture have been overcome.

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One area that has resisted significant progress is the production of improved stocks for commercial culture, despite considerable interest in genetic improvement of bivalve broodstocks (Newkirk, 1980, 1983; Wilkins, 1981; Dillon and Manzi, 1987). Hard clams are relatively slow growing (2–5 years to market size of 45–50 mm, longest dimension) and exhibit a highly variable growth rate. The development of commercial broodstocks with improved growth rates and/or decreased variability could dramatically increase the economic attractiveness of commercial culture.

There has been evidence of a positive correlation between growth rate and multiple-locus enzyme heterozygosity in wild populations of marine bivalves (Zouros et al., 1980; Garton et al., 1984; Koehn and Gaffney, 1984). The same relationship has not been established, however, in hatchery populations (Adamkewicz et al., 1984; Gaffney and Scott, 1984; Foltz and Chatry, 1986). Hybridization is a common technique for improving stocks and its success is often attributed to increased heterozygosity (Frankel, 1983; Mitton and Grant, 1984). Hybridization of the hard clam, *Mercenaria mercenaria,* with its sister species *M. campechiensis* has been reported to result in improved growth rates and tolerance to a wider range of environmental variables (Menzel, 1962, 1989). In practice, however, it has proven difficult to hybridize the two species in South Carolina, possibly because of differing requirements for maturation. The heterotic effects of hybridization, however, can theoretically be achieved by crossbreeding inbred stocks (Wilkins, 1981; Frankel, 1983).

A project in South Carolina to develop hard clam stocks with improved growth rates included experiments crossing individuals from two lines developed and maintained by two commercial-scale hatcheries, Aquaculture Research Corporation (ARC) in Dennis, Massachusetts, and the Virgina Institute of Marine Science (VIMS) in Wachapreague, Virginia. An analysis of isozyme frequencies in the two hatchery stocks was performed and results compared to wild populations (Dillon and Manzi, 1987). While neither stock exhibited any reduction in heterozygosity, both stocks showed evidence of genetic drift and loss of rare alleles, suggesting that a cross between the two might produce genetically distinct offspring. Isozyme frequencies have also been compared in faster- and slower-growing F_1 offspring from some ARC and VIMS crosses after 1 year of culture (Dillon and Manzi, 1988). Results indicated that loose linkage disequilibrium was the most likely explanation of differences in gene frequencies between clams of different sizes. Alleles seemed to be marking the entire genomes of their parents, such that any relationship between growth and overall heterozygosity was obscured. In this report, we compare the growth of a more complete sample of these ARC and VIMS lines with that of their reciprocal crosses over a 2-year period.

METHODS

Hard clam stocks were obtained from Aquaculture Research Corporation (ARC), Dennis, Massachusetts, and the Virginia Institute of Marine Science

(VIMS), Wachapreague, Virginia. Both stocks have been selected for fast growth for three to five generations, but rigorous inbreeding has not been performed and some wild clams have been included in some generations (Dillon and Manzi, 1987).

Three experiments were performed (October 1984; February and April 1985). In each experiment, adults of each hatchery stock were stimulated to spawn in individual containers. As spawning occurred, gametes were pooled within each sex and stock. After all gametes were pooled in this manner, eggs of each stock were separated into two portions and half were fertilized with sperm from the like stock, the rest with sperm from the other stock. The actual numbers of spawners for each experiment are listed in Table 1. In most cases, different individuals were involved in each cross, but there was some overlap. One ARC male, three ARC females, and 2 VIMS females spawned in both Experiments 1 and 2. One ARC male, 1 ARC female and 1 VIMS male spawned in both Experiments 1 and 3. One ARC male, 1 ARC female, and 3 ARC males were involved in both Experiments 2 and 3. No individuals spawned in all three experiments.

Offspring were reared using standard hatchery and nursery techniques (Manzi, 1985) and were deployed in intertidal field cages when all seed reached a minimum size of 7 mm. No culling of small individuals was performed and each entire population was retained in the hatchery or nursery until the smallest individuals were ready for transfer. Shell length was measured at regular intervals over a 2-year period (Table 2).

Mean shell lengths were compared at 2 years of age. Within each experiment, the four crosses were compared by analysis of variance followed by the Student-Neuman-Keuls step-wise comparison among means (Sokal and Rohlf, 1969). All twelve crosses were compared by two-way analysis of variance (Sokal and Rohlf, 1969).

At 1 year of age, offspring were sampled for determination of allelic frequencies at seven enzyme loci and overall heterozygosity (Dillon and Manzi, 1988). Lists of the enzyme loci examined and the buffer systems employed,

TABLE 1

Number of females (F) and males (M) spawning to produce pure lines (ARC, VIMS) and reciprocal crosses (A×V, V×A) and the effective breeding number (EN = [4F×M]/[F+M]). In reciprocal crosses the female parent is designated first

Experiment	ARC			VIMS			A×V			V×A		
	F	M	EN	F	M	EN	F	M	EN	F	M	EN
1	10	7	16	5	5	10	10	5	13	5	7	12
2	8	18	22	7	8	15	8	8	16	7	18	20
3	3	8	9	2	8	6	3	8	9	2	8	6

TABLE 2

Mean size (shell length, mm) at different ages (months) and growth rate over the subsequent sampling period (Δ, mm/month) for four crosses produced in three experiments

Exp.	Age	ARC			A×V			VIMS			V×A		
		SL	N	Δ	SL	N	Δ	SL	N	Δ	SL	N	Δ
1	3	4.31	100	1.01	5.54	100	1.84	3.06	100	1.45	4.04	100	1.51
	6	7.35	57	3.23	11.05	37	2.37	7.40	55	2.00	8.58	31	2.24
	9	17.03	30	3.47	18.15	40	5.29	13.41	32	3.52	15.29	48	3.35
	12	27.45	100	1.35	34.02	50	0.67	23.96	50	0.89	25.33	150	1.09
	18	35.57	101	1.61	38.01	100	0.96	29.31	112	0.64	31.88	108	1.23
	24	45.20	100		43.74	100		33.14	100		39.25	100	
				1.88*			1.82*			1.38*			1.64*
2	3	5.56	87	3.16	6.49	60	3.07	6.74	50	3.12	6.48	50	3.47
	6	15.03	33	−0.13	15.71	31	−0.28	16.11	45	0.14	16.89	38	0.36
	9	14.64	50	0.25	14.88	50	0.46	16.52	50	0.44	17.97	30	0.55
	12	15.40	50	2.80	16.26	50	2.93	17.84	50	2.63	19.62	50	2.75
	18	32.17	102	0.85	33.83	102	0.89	33.62	100	1.41	36.11	100	1.22
	24	37.29	100		39.15	100		42.10	101		43.40	100	
				1.55*			1.63*			1.75*			1.81*
3	3	8.29	60	0.92	8.87	38	1.09	5.91	60	1.24	6.49	91	0.44
	6	11.04	50	0.35	12.14	50	0.35	9.63	51	0.40	7.82	52	0.33
	9	12.08	51	1.21	13.20	50	1.85	10.82	50	0.84	8.80	51	1.87
	12	15.72	50	2.53	18.76	50	2.94	13.34	50	2.87	14.43	50	3.13
	18	30.91	100	1.25	36.42	100	1.46	30.53	109	1.55	33.19	100	1.40
	24	38.14	101		45.19	101		39.84	98		41.59	99	
				1.59*			1.88*			1.66*			1.73*

*Average growth rate over entire experiment.

TABLE 3

Mean (Size) and variance (S^2) of 24-month size (shell length, mm) and mean overall heterozygosity ($\bar{H}$) of four crosses produced in three experiments. Superscript letters indicate no significant difference in mean size within experiments ($P<0.05$). Superscript numerals indicate no significant difference in heterozygosity within experiments (X^2, $\alpha=0.05$)

Exp.	ARC			A×V			VIMS			V×A		
	Size	S^2	$\bar{H}$	Size	S^2	$\bar{H}$	Size	S^2	$\bar{H}$	Size	S^2	$\bar{H}$
1	45.20[a]	47.43	0.381	43.74[a]	37.20	0.528	33.14	43.52	0.446[1]	39.36	28.37	0.470[1]
2	37.29	39.22	0.382[2]	39.15	39.32	0.410[2,3]	42.10[b]	48.11	0.396[2]	43.40[b]	42.30	0.471[3]
3	38.40	36.12	0.460[4]	45.19	35.61	0.476[4]	39.84	26.80	0.345[5]	41.59	27.02	0.288[5]

together with references for sample preparation, electrophoresis and stain recipes, are available in Dillon and Manzi (1987, 1988). A total of 120 individuals were analysed from each cross in Experiment 1 and from the pure lines of Experiment 2; 60 individuals were analysed from each of the other six crosses. Equal numbers of large and small individuals were sampled to avoid size bias. Mean observed heterozygosity, correcting for unequal sample sizes at some loci, was calculated for each of the twelve crosses. Comparisons between crosses were made using Yates-corrected chi-square tests. Heterozygosities were compared with mean size at 24 months and with variance of mean size, using Spearman's rank-correlation coefficient (Table 3).

RESULTS

Experiment 1 was initiated in late fall and juveniles were held in the hatchery until almost 6 months of age, during which time growth rates ranged from 1.0 to 1.8 mm/month (Table 2). After transfer to the nursery, these crosses grew rapidly (2.0–3.2 mm/month). Rapid growth continued after transfer to field culture but slowed down during the winter months (Fig. 1). The average growth rates over 15 months of field culture were 1.2–1.7 mm/month, and the average growth rates for the entire 2 years of the experiment were 1.4–1.8 mm/month (Table 2).

Experiments 2 and 3 were initiated in early and late spring, respectively, and populations reached nursery size rapidly. However, experimental protocols required retaining populations in the nursery until the smallest individuals had reached 7 mm. Thus, although the average growth rate in the nursery was initially quite high (>3 mm/month in Experiment 2), the seed were held in the nursery through the summer, and very high water temperatures resulted in little growth during that period (Fig. 1). After transfer to the field, growth was very rapid, and average growth rates in field culture were 1.8–2.0 mm/month and 1.9–2.2 mm/month for Experiments 2 and 3, respectively (Table 2). Growth rates over the entire 24 months averaged 1.5–1.8 mm/month for Experiment 2 and 1.6–1.9 mm/month for Experiment 3.

Within experiments, significant differences in mean size at 2 years were observed (Table 3). In general, the offspring of the reciprocal crosses were more similar in size and general appearance to the maternal than the paternal stock. In Experiment 1, ARC and A×V did not differ significantly in size but were significantly larger than V×A, which was larger than VIMS (Table 3). In Experiment 2, VIMS and V×A were not significantly different from each other but were significantly larger than A×V which was significantly larger than ARC. In the third experiment, all crosses were significantly different at 24 months, with the two reciprocal crosses being the largest. Two-way analysis of variance could not demonstrate any significant differences in mean size among the twelve crosses.

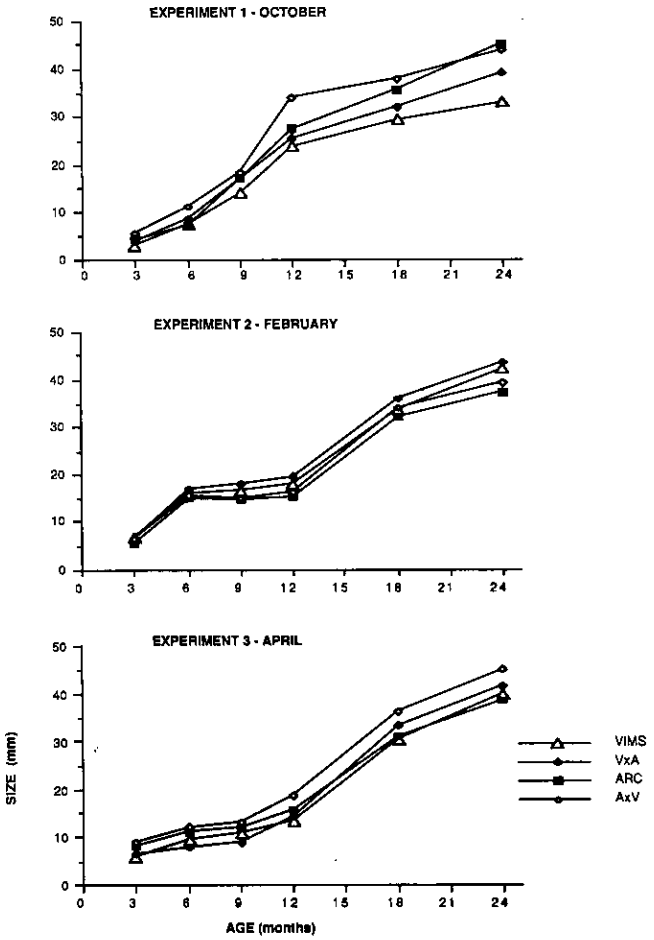

Fig. 1. Growth of four experimental stocks of hard clams in three 24-month experiments.

The reciprocal crosses did not exhibit any consistent difference in variance of mean size relative to the pure lines, nor did they show any consistent increase in heterozygosity (Table 3). There was no correlation between heterozygosity and mean size at 24 months ($r_s = 0.06$, $P > 0.05$) or variance of mean size ($r_s = 0.22$, $P > 0.05$). It appears that in hatchery experiments involving relatively few individuals (effective breeding number < 20), variation in the growth rates of offspring from individual parents may obscure any relationship with overall heterozygosity (Dillon and Manzi, 1988).

Significant differences in allele frequencies were commonly noted among lines, as illustrated in Table 4 with data from Experiment 2 at the 6 PGD locus. This locus is one at which the ARC and VIMS hatchery stocks are most distinct, and thus the striking difference between the two pure crosses is ex-

TABLE 4

Number of individuals (N), frequency of alleles (110, 100, 90) and observed heterozygosity (H) for the 6 PGD locus among offspring from Experiment 2

	ARC	VIMS	A×V	V×A
N	114	123	59	56
110	0.00	0.09	0.00	0.03
100	0.86	0.63	0.85	0.73
90	0.14	0.28	0.15	0.24
H	0.26	0.57	0.27	0.36

TABLE 5

Expected and observed size/age relationships of hard clams in three separate grow-out experiments

Age (months)	Expected* size (mm)	Observed size (mm)			Gain ⟨Loss⟩ (mm)		
		Exp. 1	Exp. 2	Exp. 3	Exp. 1	Exp. 2	Exp. 3
12	16	24–34	15–20	13–19	8–18	⟨1⟩–4	⟨3⟩–3
24	32	33–45	37–43	38–45	1–13	5–11	6–13
Size (mm)	**Expected* age (months)**	**Observed age (months)**			**Gain (months)**		
		Exp. 1	Exp. 2	Exp. 3	Exp. 1	Exp. 2	Exp. 3
20	15	9–11	12–14	12–14	4–6	1–3	1–3
35	27	14–27	18–22	18–21	0–13	5–9	6–9
45**	36	24–33	25–34	24–32	3–12	2–10	4–12

*Expectations based on unpublished data collected over 5 years of operation of a commercial-scale clam facility (Trident Seafarms, Inc., 1980–1983; Folly Field Station 1984–1985) in South Carolina.
**For lines which did not reach this size during the experiment, projections are based on average growth rate over 12–15 months of field culture.

pected. The offspring from the V×A cross had allele frequencies intermediate between the two pure crosses, but allele frequencies in the A×V cross are almost indistinguishable from the pure ARC line. This is almost certainly an accidental consequence of the smaller effective number of parents (Table 1).

Environmental conditions strongly affected growth rates of all twelve crosses (Fig. 1). Growth rates of different crosses within an experiment (e.g., ARC and A×V in Experiment 1) were more similar than growth rates of the same cross between experiments (e.g., ARC in Experiments 1, 2, and 3). Within experiments, early growth appears to be correlated with growth to market size, but if the data from all experiments are combined, no correlation is evident until 18 months of age (Table 2). There is no correlation between size and growth over the subsequent sampling period within experiments, but when

considered all together, a negative correlation is observed between size at 12 months and growth over the next 6 months.

At 2 years of age (from spawning), the twelve crosses averaged 33–45 mm in length (Table 3). This size compares favorably with previous reports for clam growth in South Carolina (Eldridge et al., 1976; Manzi et al., 1980, 1981, 1982). At 2 years of age, the crosses produced in these experiments were as much as 13 mm larger than expected (Table 5). In terms of growout time, the populations reached (or were projected to reach) 45 mm 2–12 months earlier than expected.

DISCUSSION

The hatchery stocks used as parental lines for these experiments have been selected for several generations, but are not demonstrably inbred (Dillon and Manzi, 1987). The overall heterozygosities of the twelve crosses produced for this study were not markedly different from the parental lines. The lowest heterozygosity observed was 0.381 and the highest was 0.476 (Table 3), compared with 0.46 for VIMS stocks and 0.48 for ARC stocks (Dillon and Manzi, 1987, 1988). We would hesitate to draw any conclusions about the relationship between heterozygosity and growth from these data. However, it is apparent that these hatchery stocks, although selected for rapid growth in Virginia and Massachusetts, perform very well in the warmer waters of South Carolina.

Crossbred offspring were not consistently faster growing than purebred offspring. Growth rates of all crosses, both pure and outbred, were better than expected, based on 5 years of unpublished data from commercial-scale clam culture in South Carolina (Table 5). Based on those data, we expect average nursery growth rates of 1.8 mm/month, varying from 0.2 mm/month in winter and summer to 4 mm/month in late spring and fall. Expected field growth rates average 1.2 mm/month over the growout cycle, gradually decreasing from an initial rate of 1.5 to about 1 mm/month as the clams approach market size. Thus, assuming a 1–2-month hatchery residence, we expect to have planting size seed in about 5–6 months and market size clams (45–50 mm) 30 months after that, thus having a total growout period, from spawning to market of 35–36 months, and an average growth rate over this period of 1.25 mm/month. In these experiments, growth rates over 2 years averaged 1.4–1.9 mm/month and populations reached, or were projected to reach, a mean of 45 mm in 24–34 months. Thus the fastest growing crosses reached market size a year sooner than anticipated, and the slower growers were projected to reach market size in average time.

Eldridge and Eversole (1982) reported that hard clams exhibited compensatory growth. Clams which had been held at extremely high densities compensated, after density reduction, by growing more rapidly than individuals

which had been at low densities throughout. Eversole et al. (1986) also reported compensatory growth, but found that, after an initial rapid growth period, relative sizes of clams remained fairly constant. They suggested that any selection for rapid growth should be postponed until clams had completed this rapid growth period and reached 45 mm. In our experiments, seed were held for unusually long periods in either the hatchery (Experiment 1) or nursery (Experiments 2 and 3) during which time little growth occurred. The rapid growth in the first 3 to 6 months of field culture suggests that some compensatory growth was occurring. This appeared to taper off as the clams reached 30 mm (Fig. 1). In Experiment 1, offspring averaged 30 mm at about 1 year of age, but in other experiments this size was not achieved until almost 18 months. Yet, at 24 months the mean sizes in Experiments 2 and 3 were similar to those in Experiment 1. Thus it would appear that selection for fast-growing stocks could be performed at 18 months of age, or at 30 mm length, whichever is earlier.

In summary, crossbred offspring were not consistently more heterozygous nor less variable than parental lines or purebred offspring. However, reciprocal crosses were genetically distinct from each other and their parental lines and retained the rapid growth characteristic of the parental stocks. Crossbreeding of hatchery stocks may, therefore, be a useful way of increasing or maintaining genetic variation without loss of desirable traits.

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