BIOMETRY AND POPULATION GENETICS OF DEEP- AND SHALLOW-WATER POPULATIONS OF THE SEA SEALLOP *PLACOPECTEN MAGELLANICUS* (GMELIN, 1791) FROM THE GULF OF MAINE

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ABSTRACT

Growth phenotype and genotype of the sea scallop *Placopecten magellanicus* (Gmelin) were compared between populations in the Damariscotta River (Maine, USA) (at 13 to 20 m depth) and the Gulf of Maine (at 170 to 180 m depth) in 1986. The deep-water population differed more from the shallow water population in shell weight, wet adductor weight, gonad wet weight, total wet weight, condition index and age than could be expected from differences in shell height. The Gulf of Maine scallops were considerably more stressed than their inshore conspecifics, which was most likely due to nutritional deficiency. Allelic and genotypic variation (measured at 6 polymorphic loci) was limited; the deep-water population differed significantly in allele frequency at the octopine dehydrogenase locus. We conclude that there is no evidence of two genetically different populations. The extensive morphological and physiological differences between both populations are likely due to environmental factors, although they might have a small genetic component.

INTRODUCTION

The sea scallop *Placopecten magellanicus* (Gmelin) is widely distributed inshore and offshore between the Northern Gulf of St. Lawrence and North Carolina (Cape Hatteras). The most productive and extensive population lives on Georges Bank (NW Atlantic) and sustains an economically important fishery. Secondary populations are located, among others, in the Bay of Fundy, in the southern part of the Scotian Shelf and in the Gulf of Maine. A synopsis of the general biology, including the distribution, ecology and genetics of the sea scallop is given in Shumway et al. (in prep.).

In recent years, populations growing in the Gulf of Maine have drawn special scientific interest because of the occurrence of apparently healthy and marginal populations living at short distances from each other at different depths (Langton et al. 1987, Shumway and Schick 1987, Shumway et al. 1987, Barber et al. 1988, Shumway and Schick 1988, Schumway et al. 1988, Schick et al. 1989). A comparison of the morphology, biometry, repro-

Table I. *Placopecten magellanicus*. Average value (with 95 min. and max. value) of biological characteristics comparing a standard scallop of 100 mm shell height living at a shallow-water site (Damariscorta River, Maine, USA) and a deep-water site (Gulf of Maine, USA)

	Reference	Shallow-water	Deep-water
Shell height (mm)	b	100.00	100.00
Shell length (mm)	b	102.07 (97.47-106.88)	99.90 (91.11 - 109.53)
Shell width (mm)	b	28.83 (23.98-34.66)	21.19 (14.00-32.07)
Shell weight (g)	b	95.30 (75.70-119.97)	36.07 (18.08-71.96)
Whole animal weight (g)	b	164.16 (136.54-197.37)	91.93 (60.74-139.14)
Adductor wet weight (g)	b	19.79 (15.72-24.91)	11.63 (6.39-21.16)
Adductor dry weight (g)	b	4.78 (3.62-6.30)	2.32(1.22-4.42)
Tissue wet weight (g)	b	48.97 (38.90-61.65)	32.97 (21.78-49.90)
Tissue dry weight (g)	b	10.12 (7.68-13.34)	5.27 (3.32-8.35)
Condition of soft tissue(10^3)	-	16.6	15.6
Oocyte diameter	a	41	40
Average age (yr)	b	4.15	7.05
Food	c	equal proportion of benthic and pelagic food species	more benthic than pelagic food species

a Barber et al. 1988
b Schick et al. 1989 (values were obtained by regression analysis)
c Shumway et al. 1987

ductive ecology, physiology, feeding ecology and fishery between both populations pointed to remarkable differences in many respects (Table 1). The deep-water scallops showed a reduced growth rate and fertility; scallops of similar shell height were on average younger at the shallow water site, had a greater somatic and gonadal tissue weight, showed a higher reproductive output and fed more on equal proportions of planktonic and benthic food species.

These strong phenotypic variations raise the question whether there are also genotypic variations between both populations. So far, genetic similarity between sea scallop populations has proven to be large. Scallops on the Scotian Shelf and in the Bay of Fundy showed little electrophoretically scored protein variation (Foltz and Zouros 1984, Gartner-Kepkay and Zouros 1985, Volckaert and Zouros 1989, J. Worms, DFO, pers. comm). Frequencies of most polymorphic loci were similar between these populations. Although variation at the locus octopine dehydrogenase was higher, its impact on the overall genetic variation of the population was small. In general within population variation tended to vary predictably (the older the scallops, the higher the average degree of heterozygosity), while variation between populations was small. The small geographic variation has been confirmed in a study of mitochondrial genome size variants in the Bay of Fundy and the Scotian Shelf (Snyder et al. 1987, K Fuller, Dalhousie University: pers. comm.).

The principal aim of this study is the comparison of the genotypic variation relative to the phenotypic variation between a shallow-water and a deep-water population of the sea scallop *Placopecten magellanicus*. It remains a standing question whether the latter population is locally recruited (recruitment at the deep-water site seems small, highly variable and cyclical (Shumway and Schick 1987), and whether selection is different from the shallow water site. Scallops at 180 m depth produce apparently viable eggs, although in smaller quantities than those at shallower depths (Barber et al. 1988).

We sampled a shallow water population in spring (pre-spawning) and fall (post-spawning), and a deep-water population in fall. Biometric characteristics were compared and related to genetic traits. We conclude that the phenotypic differences between both populations are rather environmental than genetic in origin.

MATERIALS AND METHODS

Specimens of the sea scallop *Placopecten magellanicus* (Gmelin) were collected from the lower Damariscotta River (43° 51.26'N; 69° 34.00'W) and the Gulf of Maine (43° 26.50'N; 69° 33.30'W), 35 km south of Boothbay Harbor (Maine, USA). At the former site, 150 scallops were haphazardly collected by divers from a depth of approximately 20 m on 12 March 1986 and on 7 and 8 October 1986. At the latter site, 150 scallops were collected by scallop dredge at a depth of approximately 180 m on 16 October 1986. Further information on the hydrography of both sites is available from Bigelow (1927).

Scallops were brought to the Fisheries Research Laboratory in West Boothbay Harbor (Maine, USA) and kept for a few days in running seawater. The following variables were measured : sex, shell height (i.e., the distance measured between umbo and ventral edge of the shell in a straight line), shell width and whole animal wet weight (after draining the water and blotting the shell dry). Upon careful dissection of each scallop, shell wet weight, gonad wet weight, adductor wet weight and wet weight of the remaining soft body tissue were measured. Ages were estimated according to the von Bertalanffy growth equation specific to the Damariscotta River (Langton et al. 1987) and the deepwater site (Schick et al. 1989) (Table 2). The condition index was calculated as I = (soft tissue wet weight/shell volume) x 100. We chose volume (height x width x length) as nominator because of the fairly conservative behavior of the shell dimensions (compared to the highly variable shell weight).

A small piece of adductor muscle (phasic part) was collected, immediately frozen at -70°C and stored at this temperature prior to analysis. This material was used to measure the allele and genotype frequencies at six polymorphic loci : 6-phosphogluconate dehydrogenase (Pgd, EC 1.1.1.44), octopine dehydrogenase (Odh, EC 1.5.1.11), aspartate aminotransferase (Aat, EC 2.6.1.1.), phosphoglucomutase (Pgm, EC 2.7.5.1), mannosephosphate isomerase (Mpi, EC 5.3.1.8) and glucosephosphate isomerase (Pgi, EC 5.3.1.9.). Nomenclature of all six alleles and assay conditions are similar to Foltz and Zouros (1984) and Volckaert and Zouros (1989). Extract of soluble muscle protein was put on a buffered horizontal starch gel and run anodally at a given voltage for 3 to 12 h (specific to the buffer chosen). Proteins were stained with enzyme specific reactions according to Selander et al. (1971), Schaal and Anderson (1974) and Siebenaller (1979). Allele and genotype frequencies, heterozygote deficiency ($D = (H_e - H_o)/H_e$), G test for fit of genotypic frequencies to those expected from Hardy-Weinberg equilibrium, G_H test for gene frequency heterogeneity (Sokal and Rohlf 1981), Nei's genetic distance, regression analysis and analysis of variance were calculated.

Table 2. *Placopecten magellanicus*. Von Bertalanffy growth equation (H_∞ : mean asymptotic shell height; K: Brody growth coefficient; t_0: parameter representing time when shell height is 0)

	Year	H_∞	K	t_0	Reference
Damariscotta River	1984	207±32	0.14±0.05	-023±0.52	Langton et al. 1987
Gulf of Maine	1984	116±4	0.28±0.03	-0.01±0.10	Schick et al. 1989

Table 3. *Placopecten magellanicus*. General characteristics (mean and standard error) of the samples collected at the Damariscotta River (USA) in April and October 1986 and offshore Boothbay Harbor (Gulf of Maine, USA) in October 1986

	Inshore April	October	Offshore October
Shell height (mm)	102.10 ± 1.29	110.55 ± 1.33	112.67±0.77
Shell length (mm)	105.46± 1.46	111.57± 1.50	115.45±0.85
Shell width (mm)	31.05±0.47	33.62±0.55	26.69±0.21
Shell weight (g)	103.12± 4.11	139.17±5.47	54.79 ± 1.33
Adductor weight (g)	24.75 ± 0.98	22.08±0.84	14.15±0.26
Gonad weight (g)	6.80±0.42	5.15±0.33	1.90±0.06
Total weight (g)	59.87±2.43	58.14±2.08	43.00±0.78
Condition of soft tissue(10^{-3})	16.8±1.3	13.4±1.1	12.2±0.9
Condition of gonad (10^{-3})	1.8±0.6	1.1±0.5	0.5±0.1
Heterozygosity	2.35±0.10	2.18±0.10	2.04±0.09
Estimated age (yr)	4.71±0.10	5.30±0.10	7.49±0.07
Sample number	150	150	150

Table 4. *Placopecten magellanicus*. Allometric regressions relating adductor weight, gonad weight and total wet weight (g) to shell height (mm) and shell volume (mm^3); H: shell height; V: calculated shell volume = height x length x width; (r): correlation coefficient

	Inshore April	October	Offshore October
Adductor mass	$-4.339.H^{2.838}$ (0.946)	$-4.610.H^{2.898}$ (0.931)	$-3.529.H^{2.277}$ (0.824)
	$-3.610.V^{0.901}$ (0.970)	$-3.570.V^{0.870}$ (0.953)	$-2.988.V^{0.746}$ (0.844)
Gonad mass	$-7.197.H^{3.953}$ (0.824)	$-7.094.H^{3.770}$ (0.732)	$-6.972.H^{3.519}$ (0.745)
	$-6.212.V^{1.260}$ (0.848)	$-5.403.V^{1.071}$ (0.710)	$-5.904.V^{1.111}$ (0.736)
Total wet mass	$-4.261.H^{2.989}$ (0.960)	$-4.322.H^{2.965}$ (0.971)	$-3.843.H^{2.665}$ (0.940)
	$-3.469.V^{0.944}$ (0.980)	$-3.184.V^{0.876}$ (0.980)	$-3.126.V^{0.858}$ (0.946)

RESULTS

A comparison of the biometric characteristics between both populations shows that scallops living at the shallow-water site are larger and heavier, that they grow faster, that they develop bigger gonads and that they are in better condition than the deep-water scallops (Table 3). While there is variation in shell weight within the shallow-water population, shells are still twice as heavy as for deep-water samples. This points partially to the different distribution of estimated ages among the samples; Gulf of Maine scallops are, on average, much older than Damariscotta River scallops for a given height.

Allometric regressions between adductor wet weight, gonad wet weight, and total wet weight versus shell height or calculated shell volume show a tighter fit for total wet weight than for adductor weight or gonad weight (Table 4). The volume measurement gives a marginally better fit than the shell height measurement as an independent variable. Phenotypic traits of deep-water scallops tend to show more variation. The results are comparable to the findings of Schick et al. (1989) and Barber et al. (1988).

Total wet weight increases with age, although marginally so in the offshore population (Fig. 1). Scallops of 8 to 9 years old from the deep-water site are only as heavy as 4.5 and 5 year-old scallops from the Damariscotta River. Shell weights of both the shallow water samples show similar trends (bearing in mind that ages are estimated with the same von Bertalanffy growth equation) (Fig. 2). Shell weight accrues more slowly with age in the Gulf of Maine population. Adductor wet weight has a similar development with age as total wet weight (Fig. 3). The increase in gonad wet weight with age is very small in the in deep-water population (Fig. 4). Gonads of scallops collected in Spring in the Damariscotta River have a higher weight increase with age than those collected in fall (i.e. after spawning).

The genotype has the following characteristics. The average degree of multiple-locus heterozygosity is comparable among the Damariscotta River samples, among the October sample from the Damariscotta River and the deep-water sample, but is significantly different between the shallow-water and October deep-water samples (Table 3). There is a scant deviation from the Hardy-Weinberg equilibrium at several loci; this is a common

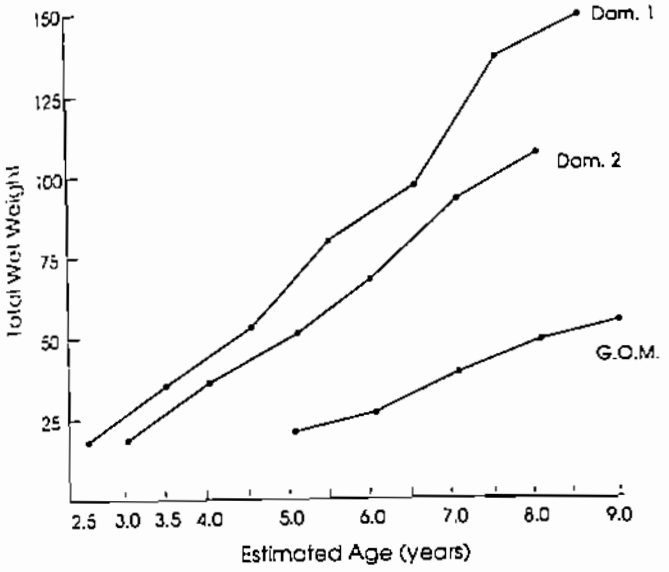

Figure 1. *Placopecten magellanicus*. Comparison of age specific total wet weight of two different populations (Damariscotta River (April (Dam.1) and October (Dam.2) 1986) and Gulf of Maine (October 1986) (G.o.M.)).

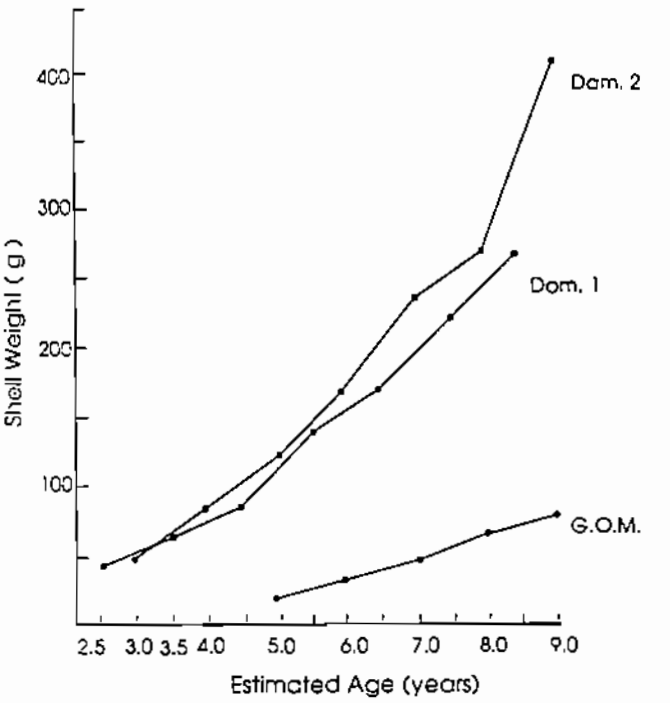

Figure 2. *Placopecten magellanicus*. Comparison of age specific shell weight. (See Fig. 1).

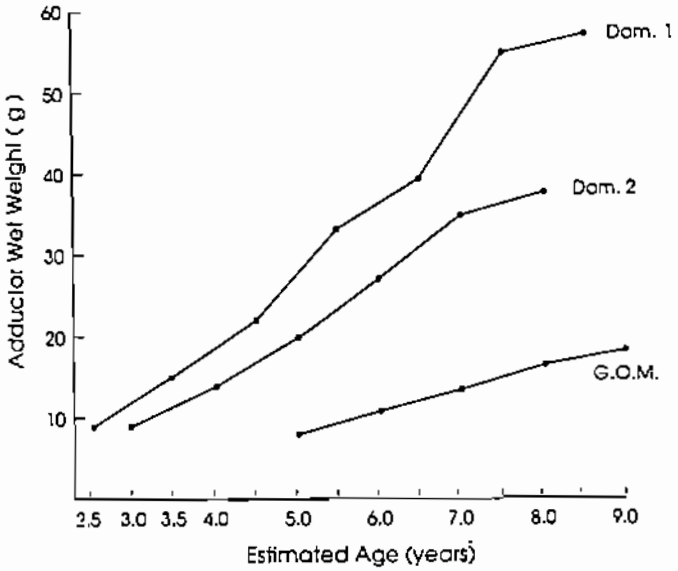

Figure 3. *Placopecten magellanicus*. Comparison of age specific adductor wet weight. (See Fig. 1).

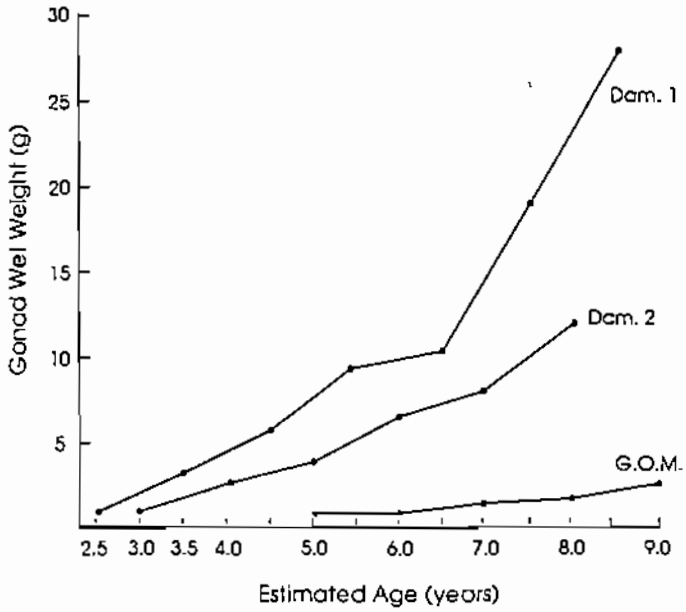

Figure 4. *Placopecten magellanicus*. Comparison of age specific gonad wet weight. (See Fig. 1).

feature in electrophoretic studies of bivalves (Foltz and Zouros 1984). The deep-water sample has the highest heterozygote deficiency (Table 5). The locus Pgd is the only one not in agreement with Hardy-Weinberg proportions in all 3 samples (Table 5). Allele frequencies do not differ much between populations and among samples, except at locus Odh (G_H test of gene frequency heterogeneity is significant at 95 %). The common alleles ^{100}Odh and ^{105}Odh show different frequencies between the sites (Table 5). We compared the genetic identity of all three samples with two other samples collected at the Eastern Shore (Ship Harbour, Nova Scotia, Canada) (Foltz and Zouros 1984) and from Passamaquoddy Bay (New Brunswick, Canada) (Volckaert and Zouros 1989) with Nei's genetic distance. Samples differ at most 0.0042 units (knowing that 0.0000 units represent total allelic similarity and 1.0000 units total dissimilarity) when

Table 5. *Placopecten magellonicus* Allele frequency estimates, D-values (with standard error), D (average heterozygote deficiency), G-test for fit to Hardy-Weinberg proportions, G_H test for gene frequency heterogeneity, degrees of freedom (DF) and number of samples (n); * scant at P <0.05, **significant at P < 0.005

		Inshore April	Inshore October	Offshore October	$\bar{D}$	G_H
Pgd	80	0.000	0.000	0.003		
	100	0.804	0.830	0.852		
	130	0.007	0.000	0.000		
	150	0.189	0.170	0.144		
	D	-0.279	-0.220	-0130	-0.243 (±0.018)	
	G	19.09**	6.22**	9.9O**		2.31
	DF	3	1	3		2
	n	136	150	149		
Odg	96	0.000	0.000	0.003		
	98	0.000	0.010	0.003		
	100	0.482	0.493	0393		
	105	0.518	0.497	0593		
	107	0.000	0.000	0.007		
	D	0.222	-0.202	-0.027	-0.0O2(±0.123)	
	G	6.78**	10.78**	3.17		6.13*
	DF	1	3	10		2
	n	136	150	150		
Aal	50	0.011	0.007	0.007		
	70	0.011	0.020	0.013		
	80	0.000	0.003	0.000		
	90	0.390	0.440	0.440		
	100	0.570	0.527	0.530		
	105	0.004	0.000	0.000		
	115	0.014	0.003	0.010		
	D	-0.002	0.123	-0.073	0.016 (±0.057)	
	G	10.29	14.26	14.36		2.14
	DF	15	15	10		4
	n	136	150	150		
Pgm	96	0.007	0.000	0.003		
	98	0.088	0.094	0.107		
	100	0.713	0.671	0.647		
	102	0.188	0.228	0.243		
	104	0.004	0.007	0.000		
	D	0.083	-0.052	-0.035	—0.001 (±0.042)	
	G	10.72	7.78	7.42		3.23
	DF	10	6	6		4
	n	136	149	150		
Mpi	75	0.004	0.003	0.000		
	87	0.228	0.287	0.267		
	100	0.765	0.710	0.730		
	108	0.004	0.000	0.003		
	D	0.012	-0.017	-0.310	-0.105 (±0.103)	
	G	1.07	0.72	14.36**		2.27
	DF	6	3	3		2
	n	136	150	150		
Pgi	87	0.007	0.000	0.000		
	100	0.927	0.940	0.940		
	115	0.066	0.060	0.060		
	D	-0.036	-0.173	-0.054	-0.088(±0.043)	
	G	13.02**	2.88	0.36		0.31
	DF	3	1	1		2
	n	136	150	150		
$\bar{D}$		0.000(±0.067)	-0.091(±0.054)		-0.122(±0.049)	

Table 6. *Placopecten magellanicus*. Nei's genetic distance ($D_x = -\ln \frac{J_{xy}}{\sqrt{J_x \cdot J_y}}$) averaged over 6 loci and at locus *Odh* at 5 sites (Damariscotta River (April (Dam.1), October (Dam.2)), Gulf of Maine (G.oM.), Ship Harbour (Sh.Harb.) and St. Andrews (St.And.); $J_{xy} = \Sigma P_{ix} P_{iy}$; $J_x = \Sigma P_{ix}^2$, $J_y = \Sigma P_{iy}^2$; $0.0 < D_x < 1.0$; P_{ix} and P_{iy}: frequency of the ith allozyme in population x andy; $\bar{D}_x$ average Nei's genetic distance.

6 loci:

	Dam.1	Dam.2	G.o.M.	St.Harb.	St.And.	$\bar{D}_x$
Dam.1	-	0.0023	0.00l0	0.0037	0.0011	0.0028
Dam1		-	0.0027	0.0018	0.0015	0.0020
G.o.M.			-	0.0042	0.0030	0.0036
Sh.Harb.				-	0.0020	0.0020
$\bar{D}_x$		0.0023	0.0034	0.0032	0.0019	

Locus *Odh*:

	Dam.1	Dam.2	G.o.M.	St.Harb.	St.And.	$\bar{D}_x$
Dam.1	-	0.0009	0.0109	0.0010	0.0000	0.0032
Dam1		-	0.0160	0.0000	0.0010	0.0057
G.o.M.			-	0.0180	0.0108	0.0144
Sh.Harb.				-	0.0008	0.0008
$\bar{D}_x$		0.0009	0.0135	0.0063	0.0032	

Nei's genetic distance is calculated at all six loci (Table 6). Variations in Odh allele frequency are prominent at the deep-water site where genetic distances are more than 10 times larger than at the other sites (Table 6).

Because gametogenesis is likely to be under genetic control (Rodhonse et al 1986, Volckaert and Zouros 1989), we checked whether gonad wet weight was related to sex and degree of multiple-locus heterozygosity after correcting for shell height (ANCOVA) (Table 7). Age was not included in the analysis because this represented an estimated and not a measured value. Heterozygosity was not related to gonad wet weight in any sample; sexual differentiation and gonad weight were correlated in the October samples (post-spawning).

DISCUSSION

This study again demonstrates that deep-water scallops are more stressed than shallow-water scallops living in the Gulf of Maine. Several phenotypic traits characterizing growth and reproduction indicate that scallops living at greater depth suffer from a limited availability of resources. In this respect, our study complements the study of Langton et al. (1987) (reproductive effort and fecundity), Shumway et al. (1987) (food resources) and Schick et al. (1989) (biometric traits).

Table 7.A. *Placopecten magellanicus*. Analysis of covariance of gonad wet weight and shell height (covariate), heterozygosity (factor 1), sex (factor 2) and the interaction factor heterozygosity by sex at the Damariscorta River site in April 1986; SS : sum of squares; DF: degrees of freedom; MS : mean sum of squares.

Gonad wet weight	SS	DF	MS	Significanee
Shell height	1531.35	1	1531.35	0.000
Heterozygosity	32.84	5	6.57	0.638
Sex	38.17	1	38.17	0.049
Heterozygosity by sex	17.64	5	3.53	0.871
Error	1031.06	107	9.64	
Total		119		

Table 7.B. *Placopecten magellanicus*. Analysis of covariance of gonad wet weight and shell height (covariate), heterozygosity (factor 1), sex (factor 2) and the interaction factor heterozygosity by sex at the Damariscotta River site in October 1986.

Gonad wet weight	SS	DF	MS	Significance
Shell height	729.84	1	729.84	0.000
Heterozygosity	16.15	5	3.23	0.696
Sex1	43.42	2	71.71	0.000
Heterozygosity by sex	116.83	8	14.60	0.008
Error	703.87	132	5.33	
Total		148		

Table 7.C. *Placopecten magellanicus* Analysis of covariance of gonad wet weight and shell height (covariate), heterozygosity (factor 1), sex (factor 2) and the interaction factor heterozygosity by sex at the offshore site (Gulf of Maine) in October 1986.

Gonad wet weight	SS	DF	MS	Significance
Shell height	37.37	1	37.37	0.000
Heterozygosity	0.98	4	0.24	0.394
Sex	4.77	2	2.38	0.000
Heterozygosity by sex	2.95	6	0.49	0.060
Error	31.77	134	0.24	
Total		149		

MacDonald and Thompson (1985a, b) observed that shells grew faster and that somatic production was higher in populations living in more shallow water (at 10 m versus 30 m). They attributed this phenomenon to the more favorable conditions of food and temperature associated with shallow water. This fits the general picture of decreasing biomass and production of organic matter with depth (Suess 1980, Rowe 1983). For similar reasons, gonad output, reproductive effort and residual reproductive value (representing the future reproductive potential of a female) were reduced in seallops living under less favorable conditions (deep-water) (MacDonald et al. 1987). Thus, gametogenesis represented a trade-off between growth and reproduction, with reproduction being scaled down under stressful conditions (see also Bayne et al. 1983). Adults from shallow water accumulated surplus energy which they shunted to gametogenesis; deep-water scallops do not enjoy such luxury. Moreover, the year to year variation in the above mentioned variables was clearly greater in shallow-water scallops (MacDonald et al. 1987) because of more variable environmental conditions. Shumway et al. (1988) identified food items in scallop guts as a measure of the availability of food resources. While shallow-water scallops apparently fed on an equal proportion of benthic and pelagic food items, deep-water scallops fed on a higher proportion of benthic species. The implications of this observation are not known.

Shumway et al. (1988) measured oxygen uptake in the Damariscotta River population and demonstrated a seasonal fluctuation. It is reasonable to expect that the weight-specific gross metabolic rate will be slowed down at the deep-water site and show less variation. This observation accompanies a decrease in gonad production with depth (see above), a lower food intake, less variable environmental conditions and colder average temperatures.

The apparently poor condition of deep-water scallops was also observed when enzymatic activity was measured at a site closely located to ours (E. Gould, NMFS, pers. comm.). The ratio of cellular enzyme levels of glutamate dehydrogenase, pyruvate kinase and malate dehydrogenase of sea scallops was significantly different in shallow-water scallops (which were supposedly less stressed) from deepwater scallops.

In addition to biometric variation we have used electrophoretically scored protein variation (which is entirely genetic in nature) to characterize both populations. Genetic geographic variation of *Placopecten magellanicus* and other pectinids have been documented in several cases. Wilkins (1978) noticed no significant difference in Gpi allele frequency between samples of *Pecten maximus* of the West and East Coast of Ireland. Pt-A genotypes of *Chlamys opercularis* were not so different from each other in the Irish Sea (Beaumont and Gruffydd 1975) but differed from the West Coast of Ireland (Mathers 1975). Beaumont (1982) measured significant geographic variation in the same species, especially at locus Pt-A, around the British Isles : at least 4 groups of populations could be distinguished. Genetic distances were such that one could distinguish "races" of *C. opercularis*. Populations of another scallop, *Chlamys varia*, living at the South and West Coast of Ireland, and the Irish Sea, differed from each other at two loci (Gosling and Burnell 1988). *Placopecten yessoensis*, which lives in bays on the North Coast of Hokkaido (Japan), showed an independent breeding structure with small genetic distances (calculated at 9 polymorphic loci) (Kijima et al 1984). P. *magellanicus* living between the Gulf of St. Lawrence and Cape Cod showed limited genetic variation (Foltz and Zouros 1984, Gartner-Kepkay and Zouros 1985, Volckaert and Zouros 1989). Our study corroborates the genetic homogeneity; allele frequency, genotype frequency, Nei's genetic distance and heterozygote deficiency do not differ much between the shallow-water and deep-water population. Locus Odh repre-

sents an exception; frequencies of Odh genotypes differ between sites. They are more variable when one compares the deep-water population (and a population living in the southern part of Georges Bank) (Gartner-Kepkay and Zouros 1985) with all other populations which have been evaluated so far in the Gulf of Maine, the Bay of Fundy, the Gulf of St.Lawrence and on the Scotian Shelf (including the Damariscotta River population of this study). The former samples represent the most southern sampling stations for genetic variation. Secondly, of all published records of allozyme variation in *P. magellanicus*, Odh is consistently not in Hardy-Weinberg equilibrium (except in the Damariscotta River sample of April). Other loci are, to variable degrees, deficient in heterozygotes. There are indications of strong selection pressures at locus Odh (Volckaert and Zouros 1989).

The small genetic variation observed limits the amount of information we can obtain from the samples. Several explanations may be presented for our observations : both populations may belong to the same population, they may be under selection pressures or their separation may be too recent for sufficient divergence. The latter explanation is hard to document. The Damariscotta River and Gulf of Maine sea scallops, however, clearly live in very different environments and may enjoy different selection pressures. Counteracting these divergent forces is the gene flow between the various local aggregations of sea scallops. Scallops live within an area dominated by the Labrador Current which slowly flows southward bordered by the East Coast and the Gulf Stream The dispersal of large numbers of tiny eggs and free-swimming larvae is somewhat confined by this current in the east-west direction, but is possible over a large area in the north-south direction. An average residual flow of 7.4 km/day to 9.7 km/day (Sutcliffe et al. 1975) means a dispersal of 296 to 388 km during the 40 days or so before settlement (Culliney 1974). Sinclair et al. (1985) noticed that the distribution of adult *Placopecten magellanicus* coincided with gyres, tidally induced features (frontal regions) and semi-enclosed bays. They suggest that the pattern is a self-sustaining one. Thus, eggs and larvae are dispersed, but ultimately juveniles settle in and move to geographically fragmented areas, each with its specific environmental conditions. We conclude that the shallow-water (inshore) and deep-water (offshore) populations sampled in the Gulf of Maine differ more so morphologically and physiologically than could be explained genetically. Contrasting environmental conditions explain some of these phenotypic differences, while the genotypic differences (due to above average variation at the Odh locus) are not so easily explained. A clear picture could emerge with inclusion of genetic information on mitochondrial DNA and nuclear DNA (restriction fragment length polymorphisms) variation.

ACKOWLEDGMENTS

We thank the diving team of the Department of Marine Resources and K. Pinkham for collecting the scallops. We also thank J. Barter and J. Stahlnecker for technical assistance. A. Beaumont, J. Grant, H. Hummel and two reviewers kindly provided valuable comments on the manuscript. Research was funded by a grant from the Natural Sciences and Engineering Research Council of Canada to E. Zouros and by the State of Maine. F.V. was supported by a scholarship from the Belgian-Canadian cultural Exchange Programme and is presently a researcher of the National Fund for Scientific Research (Belgium).

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The World Aquaculture Society
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Louisiana State University
Baton Rouge, LA 70803

Library of Congress Catalog Number: 91-58094

ISBN: 0-9624529-5-5

WORLD AQUACULTURE WORKSHOPS, NUMBER 1

Managing Editor, Paul A. Sandifer

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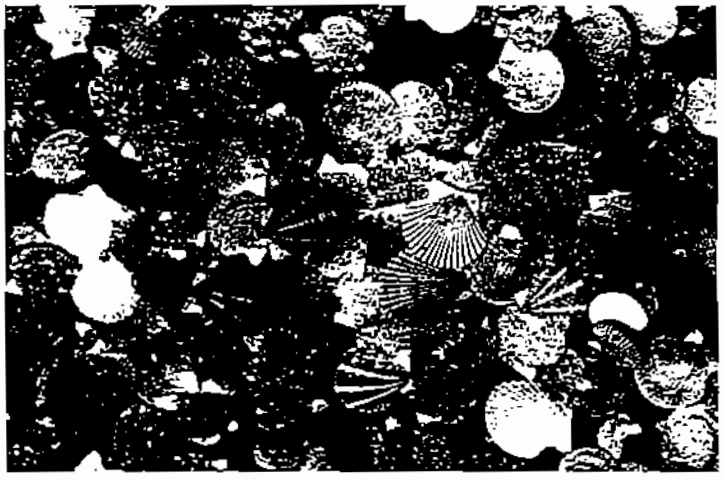

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