

Morphological, Electrophoretic, and Fecundity Characteristics of Atlantic Snow Crab, *Chionoecetes opilio*, and Implications for Fisheries Management

K. Davidson,¹ J. C. Roff,² and R. W. Elner

Invertebrates and Marine Plants Division, Fisheries Research Branch, Department of Fisheries and Oceans, Biological Station, St. Andrews, N.B. E0G 2X0

Davidson, K., J. C. Roff, and R. W. Elner. 1985. Morphological, electrophoretic, and fecundity characteristics of Atlantic snow crab, *Chionoecetes opilio*, and implications for fisheries management. Can. J. Fish. Aquat. Sci. 42: 474-482.

For adult snow crabs (*Chionoecetes opilio*), from the western Gulf of St. Lawrence, eastern and western Cape Breton Island, and eastern Newfoundland, we compared morphometric, meristic, electrophoretic, and fecundity characteristics. Our morphometric, meristic, and fecundity data indicated that snow crabs from the four areas are morphologically and biologically distinct; therefore, they represent four "phenotypic" or "biological" stocks. We propose that the differences in morphology are due largely to environmental effects on growth during juvenile stages. The electrophoretic data indicate that Newfoundland and western Gulf of St. Lawrence snow crabs differ genetically from each other and from the Cape Breton Island snow crabs; therefore, they represent two different "genetic" stocks. Eastern and western Cape Breton Island snow crabs did not exhibit electrophoretic differences and, thus, they represent a single genetic stock. Genetic exchange between Atlantic Canadian snow crab populations appears possible through larval dispersal. There is a widely different degree of resilience to exploitation and response to the same management strategy between eastern and western Cape Breton Island snow crab populations; hence, a phenotypically and/or genotypically defined stock is not necessarily a useful management tool. Stocks may be subdivided into more meaningful management units that reflect intra-stock factors such as growth and recruitment patterns.

On compare les caractères morphométriques, méristiques et électrophorétiques et les données sur la fertilité du crabe des neiges, *Chionoecetes opilio*, adulte peuplant l'ouest du golfe du Saint-Laurent, les eaux à l'est et à l'ouest de l'île du Cap-Breton et les eaux à l'est de Terre-Neuve. Les caractères morphométriques et méristiques et les données sur la fécondité révèlent que les crabes des neiges présents dans ces quatre régions sont morphologiquement et biologiquement différents; ils représentent donc quatre stocks « phénotypiques » ou « biologiques ». On formule l'hypothèse que les variations morphologiques sont principalement causées par l'incidence environnementale sur la croissance au cours des stades juvéniles. Les données électrophorétiques révèlent que le crabe des neiges des eaux de Terre-Neuve et celui de l'ouest du golfe du Saint-Laurent sont génétiquement différents, en plus d'être différents de celui des eaux de l'île du Cap-Breton; on est donc en présence de deux différents stocks « génétiques ». Les individus capturés à l'est et à l'ouest de l'île du Cap-Breton n'ont pas montré de variations électrophorétiques; ils constituent donc un seul stock génétique. Un échange génétique entre les populations de crabe des neiges peuplant les eaux canadiennes de l'Atlantique semble possible par la dispersion de larves. Il existe un degré très variable d'adaptation à l'exploitation et de réaction à la même stratégie de gestion entre les populations présentes à l'est et à l'ouest de l'île du Cap-Breton. En conséquence, un stock phénotypiquement défini n'est pas nécessairement un outil de gestion utile. Les stocks peuvent être subdivisés en unités de gestion plus représentatives qui traduisent des facteurs propres au stock comme les régimes de croissance et de recrutement.

Received July 24, 1984
Accepted November 27, 1984
(J7881)

Reçu le 24 juillet 1984
Accepté le 27 novembre 1984

The snow crab, *Chionoecetes opilio* (O. Fabricius), is a large spider crab (Majidae, Oregoniinae) that inhabits deep, cold waters in the Northwest Atlantic and North Pacific oceans and the Sea of Japan. In Atlantic Canada,

commercial concentrations of snow crab occur in the Gulf of St. Lawrence, around Cape Breton Island, and off the coasts of Labrador and Newfoundland (Elner 1982a).

Adult snow crabs in the Northwest Atlantic are most abundant at depths of 60–200 m on mud or mud–sand–gravel bottoms where temperatures remain between -1°C and 4°C (Brunel 1960; Squires 1966; Powles 1968; Watson 1969). Female snow crabs undergo a terminal molt to maturity and reach a maximum size of 47–95 mm carapace width (CW) (Ito 1963; Watson 1970a; Elner and Robichaud 1983a). Males continue to molt

¹Present address: Freshwater and Anadromous Division, Fisheries Research Branch, Department of Fisheries and Oceans, P.O. Box 5030, Moncton, N.B. E1C 9B6.

²Present address: Department of Zoology, College of Biological Science, University of Guelph, Guelph, Ont. N1G 2W1.

TABLE 1. Sample sites and collection details for adult male and female snow crabs collected for morphometric, meristic, and fecundity analyses.

Sample site	No. collected		Location		Depth (m)	Date
	Males	Females	Lat.	Long.		
Newfoundland (Port-de-Grave)	50	51	47°46'	52°46'	68–189	Aug. 23, 1980
Eastern Cape Breton Island (Gabarus)	101	98	45°45'	59°56'	109–155	Aug. 25, 1980
Western Cape Breton Island (Pleasant Bay – Cheticamp)	34	85	46°55'	61°00'	50–159	July 8, 1980
	77	34	46°53'	59°58'	124–135	July 23, 1980
Western Gulf of St. Lawrence (Anticosti)	174	99	50°07'	64°44'	65–207	Aug. 25–30, 1980

after attaining maturity at 51–80 mm CW and can reach a size of approximately 160 mm CW (Watson 1969, 1970a).

Since its inception in 1960, the snow crab fishery has increased steadily in importance to its present status as the most valuable crab species fished in Canadian waters (Elner 1982a) and the fourth most valuable fishery in Atlantic Canada. Female snow crabs are not commercially fished and the reproductive potential of the resource appears unaffected by the commercial harvesting of mature males ≥ 95 mm CW (Elner and Robichaud 1983a). However, as the unpredictable trends in the Atlantic snow crab fishery demonstrate, the relationships between stock and recruitment are not clear (Bailey 1982; Elner 1982a, 1982b; Waiwood and Elner 1982). The wide variation in the response and resilience of various snow crab populations to fishing pressure and management strategies (Elner 1982a, 1982b) leads to the hypothesis that Gulf of St. Lawrence, Cape Breton Island, and Newfoundland snow crab populations³ represent different stocks⁴ whose integrity depends on the amount of interaction (probably in the form of larval exchange) with other stocks. Mark-recapture studies off Cape Breton Island and Newfoundland have not revealed either extensive or clear patterns of movement by male snow crabs (Elner 1982a; D. M. Taylor, Department of Fisheries and Oceans, St. John's, Nfld., unpubl. data). In the Gulf of St. Lawrence, the majority of marked snow crabs have been recaptured within 15 km of the release point (Watson 1970b; Watson and Wells 1972).

The delineation of stocks has remained an important concern in fisheries management (Ihssen et al. 1981a). Although various approaches have been applied to the problem of stock delineation, the use of multivariate statistical comparisons of morphological characteristics and electrophoresis has gained acceptance among fisheries scientists (Saila and Flowers 1969; Messieh and Tibbo 1971; Parsons and Hodder 1971; Johnson et al. 1972, 1973, 1974; Messieh 1975; Smith et al. 1980; Lindsey 1981; Mulley and Latter 1981a, 1981b). Using such techniques, differences in morphometric, meristic, and/or electrophoretic characteristics are used to infer phenotypic and/or genotypic differences between individuals. To date, these types of studies on decapod crustaceans in the Northwest Atlantic have been restricted to the American lobster, *Homarus americanus* (Milne-

Edwards), and have met with limited success (Barlow 1969; Saila and Flowers 1969; Barlow and Ridgway 1971; Tracey et al. 1975; Campbell and Mohn 1982).

In this paper, we document the morphometric, meristic, fecundity, and electrophoretic characteristics of four Northwest Atlantic snow crab populations. In addition, we reared snow crab larvae in the laboratory to elucidate the possibility for current-mediated larval exchange between Atlantic snow crab populations. Given the existence of phenotypic and genotypic differences between the populations, we investigated whether they provide a viable means of delineating snow crab stocks for management purposes.

Materials and Methods

A total of 813 mature male and female snow crabs were collected for morphometric and meristic analyses from sample areas off St. John's, Nfld.; eastern Cape Breton Island (off Gabarus); western Cape Breton Island (off Pleasant Bay and Cheticamp); and in the western Gulf of St. Lawrence (off northwestern Anticosti Island) (Table 1; Fig. 1). Crabs were captured with commercial crab traps (1.5 × 1.5 × 0.6 m steel frames covered by 90-mm mesh). The crabs were then killed by exposure at air temperature, preserved in 10% formalin-seawater, and transported to the Department of Fisheries and Oceans, Biological Station, St. Andrews, N.B. (SABS), for dissection and measurement. The sex, 40 morphometric, and 8 meristic (discrete or discontinuous) characters were recorded for each crab (Fig. 2, 3, 4). Carapace and appendage measurements (Fig. 2, 3) were taken to the nearest 0.1 mm, using dial read-out calipers. Gill measurements were made by using a dissecting microscope and precalibrated ocular micrometers, to the nearest 0.1 mm. All appendages and gills counted were from the right side of the body.

Two partitioning regimes were applied to the data. The first regime consisted simply of separating the data according to sex before analysis. In the second regime, crabs of each sex were arranged into small (males ≤ 80 mm CW; females ≤ 60 mm CW), medium (males 80.1–100.0 mm CW; females 60.1–70.0 mm CW), and large (males > 100.0 mm CW; females > 70.1 mm CW) and each size group was analysed. The analysis utilized was the SPSS version of discriminant function analysis (Klecka 1975), using no a priori probabilities of membership or weighting procedures, and seeking to maximize the minimum Mahalanobis distance between the two closest groups.

³“Population” refers to any spatially, temporally, or artificially (i.e. by management unit) delineated intraspecific group of organisms.

⁴For the purpose of this paper, “stock” will refer to an intraspecific group of individuals exhibiting unique phenotypic, genotypic, or biological attributes.

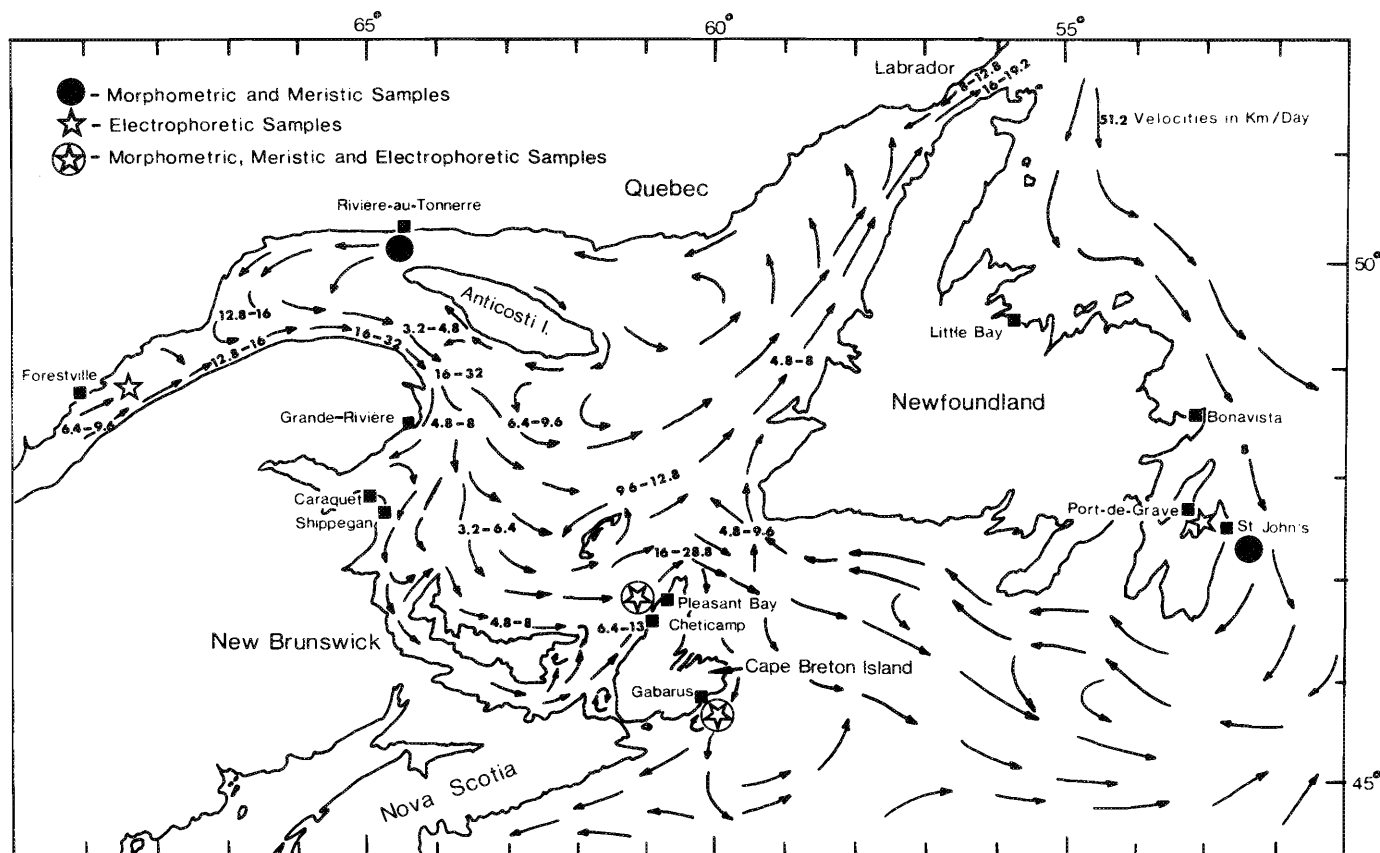


FIG. 1. Typical Atlantic summer surface circulation patterns (after Hachey 1961; Bumpus and Lauzier 1965; Trites 1970; Kudlo and Burmakin 1972; Sutcliffe et al. 1976) in relation to snow crab sample sites.

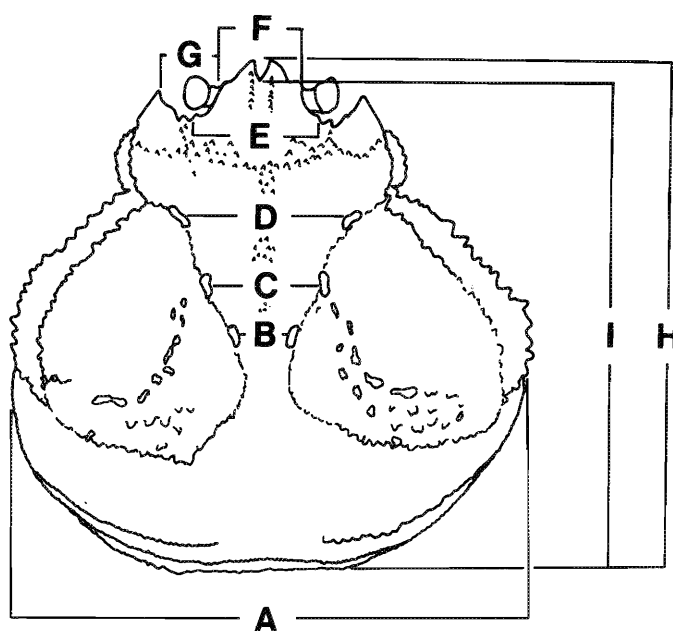


FIG. 2. Carapace measurements made during the morphometric analyses of four Atlantic snow crab populations. A, carapace width; B, distance between third dorsal tubercles; C, distance between second dorsal tubercles; D, distance between first dorsal tubercles; E, rostrum width at base; F, rostrum width at tip; G, orbit width; H, carapace length; I, notch length.

Estimates of fecundity were made for all females from each sample area. The egg-mass from each female was carefully removed from the pleopods and dried to constant weight at approximately 70°C. The dry weight of each egg-mass (total weight of the egg-mass, TWEM) was recorded to the nearest milligram. From each area, a subsample of 10 females was taken. From each of these females, four samples of 30 dried eggs were weighed to the nearest microgram, using a Cahn electrobalance. The mean weight of an egg (WE) was then calculated as follows:

$$(1) \text{ Mean weight per egg (WE)} = \frac{\sum \text{Weights 1-4}}{120}$$

where weights 1-4 are the weights of each 30-egg sample.

Mean weight per egg (WE) was regressed against carapace width, using a geometric mean regression as outlined by Haynes et al. (1976), and was compared between areas, using a one-way analysis of variance.

Fecundity estimates were made as follows:

$$(2) \text{ Fecundity of female}_{AN} = \frac{\text{TWEM}_{AN}}{\text{WE}_A}$$

where A = area and N = sample number of the female.

An analysis of covariance was used to compare TWEM, as it covaries with carapace width, between areas.

Samples for electrophoretic analysis, consisting of the right

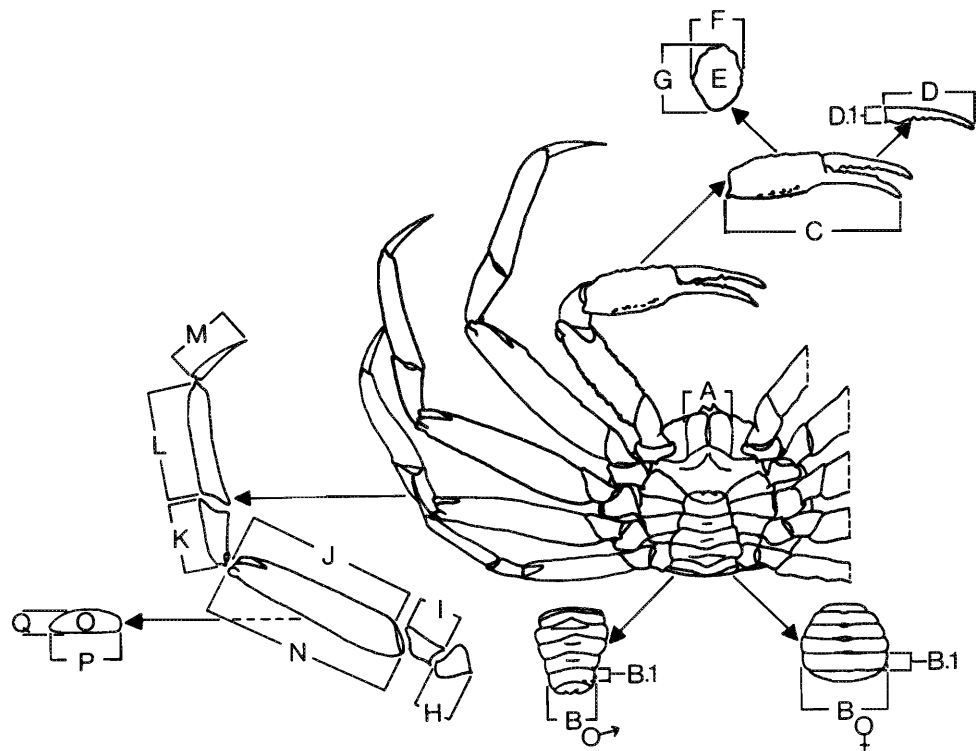


FIG. 3. Appendage, abdomen, and ventral carapace measurements made during the morphometric analysis of four Atlantic snow crab populations. A, pterygostomium width; B, width of the fifth abdominal segment; B.1, length of the fifth abdominal segment; C, length of the first propodus; D, length of the first dactylus; D.1, width of the first dactylus; E, cross-section of the first propodus at its widest point; F, width of the first propodus; G, depth of the first propodus; H, length of coxa of cheliped and pereopods; I, length of basis of cheliped and pereopods; J, inside length of merus of cheliped and pereopods; K, length of carpus of cheliped and pereopods; L, length of propodus of pereopods; M, length of dactylus of pereopods; N, length of merus of cheliped and pereopods; O, cross-section of merus of cheliped and pereopods at the widest point; P, width of merus of cheliped and pereopods; Q, thickness of merus of cheliped and pereopods.

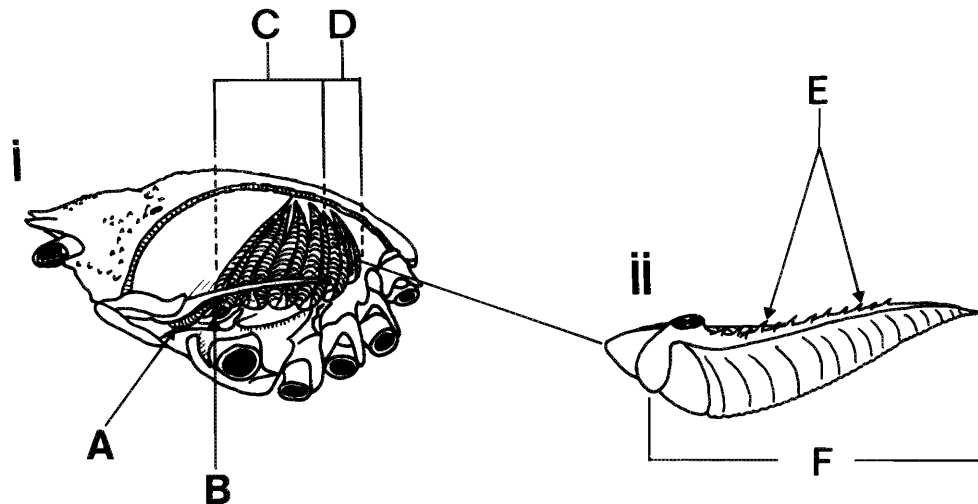


FIG. 4. Gills, method of gill measurement, and location of gill spines for morphometric and meristic analysis of four Atlantic snow crab populations. (i) Thorax of *C. opilio* dissected from the left side to show (A) first podobranch, (B) second podobranch, (C) arthrobranchs, and (D) pleurobranchs. (ii) Isolated pleurobranch of *C. opilio* showing (E) gill spines and (F) gill length dimension.

cheliped of hard-shelled males of legal size (≥ 95 mm CW), were collected from the western Gulf of St. Lawrence off Forestville, Que. (August 19, 1982; depth 55–146 m); western Cape Breton Island off Pleasant Bay (July 28, 1982; depth 100–146 m); eastern Cape Breton Island off Gabarus (July 29,

1982; depth 132–183 m); and Newfoundland off Port-de-Grave (November 11, 1982; depth 271 m) (Fig. 1). The samples were stored in dry ice or in freezers at -35°C until transported to the University of Windsor, Windsor, Ont., where a disc polyacrylamide electrophoretic survey (Ornstein 1964) of 10 enzyme

TABLE 2. Enzymes surveyed during electrophoretic examination of cheliped muscles from snow crab collected from sites off Newfoundland, eastern Cape Breton Island, western Cape Breton Island, and the western Gulf of St. Lawrence.

Enzyme	Abbreviation	Type of gel used	
		Starch	Polyacrylamide
α -Esterase	EST (EC 3.1.1.2)	×	×
Glucose-6-phosphate dehydrogenase	G-6-PDH (EC 1.1.1.49)	—	×
Glutamate oxaloacetic transaminase	GOT (EC 2.6.1.1)	×	×
Phosphoglucose isomerase	PGI (EC 5.3.1.9)	—	×
Lactate dehydrogenase	LDH (EC 1.1.1.27)	×	×
Leucine amino peptidase	LAP (EC 3.4.11.1)	—	×
Phosphoglucomutase	PGM (EC 2.7.5.1)	—	×
Fumarase	FUM (EC 4.2.1.2)	×	×
Xanthine dehydrogenase	XDH (EC 1.2.1.37)	—	×
Malate dehydrogenase	MDH (EC 1.1.1.37)	×	×
General protein	GP	×	—
Aconitase	Acon (EC 4.2.1.3)	×	—
Malic enzyme	ME (EC 1.1.1.40)	×	—
Isocitrate dehydrogenase	IDH (EC 1.1.1.42)	×	—

TABLE 3. Frequency of esterase phenotypes for four Atlantic populations of snow crabs (S_1 – S_3 = slow bands; M = medium band; F = fast band).

Phenotypes	Sample population			
	Newfoundland	Eastern Cape Breton Island	Western Cape Breton Island	Western Gulf of St. Lawrence
MF	30 (48.4%)	0 (—)	0 (—)	11 (20.0%)
S_3 MF	5 (8.1%)	60 (96.8%)	54 (93.1%)	33 (60.0%)
S_2 S_3 MF	4 (6.4%)	1 (1.6%)	3 (5.2%)	5 (9.5%)
S_1 S_2 S_3 MF	11 (17.7%)	0 (—)	0 (—)	3 (5.4%)
S_1 S_2 MF	6 (9.8%)	0 (—)	0 (—)	1 (1.8%)
S_1 MF	1 (1.6%)	0 (—)	0 (—)	0 (—)
S_2 MF	4 (6.4%)	0 (—)	0 (—)	2 (3.7%)
S_1 S_3 MF	1 (1.6%)	1 (1.6%)	1 (1.7%)	0 (—)
Total	62	62	58	55

systems (Table 2) was made for merus and propodus muscles from 10 sample chelipeds from each of the four sample areas. Esterases were surveyed for all sample chelipeds (55–62 per area, Table 3).

To obtain larvae for laboratory rearing, five ovigerous *C. opilio* females were collected off Cheticamp, Cape Breton Island (46°43'N, 61°12'W), on November 25, 1980. The females were transported to SABS where they were held individually in 68- to 91-L aquaria at 3–5°C until the hatching of their larvae had been completed. Upon hatching, larvae were transferred to individual rearing containers in a flow-through rearing system modelled after that utilized by D. E. Aiken for American lobster culture at SABS. Water temperature in the rearing system was maintained at a mean temperature of 11°C (range: 10.0–12.5°C) and salinity of 27.9–31.9‰ throughout the rearing period. The larvae were fed daily with freshly hatched brine shrimp, *Artemia salina* (Linnaeus), nauplii. The numbers of larvae molting or dying were recorded daily. Dead larvae and exuviae were removed daily along with excess *A. salina* from the previous feeding.

Results

Morphometrics and Meristics

With all 48 morphometric and meristic characters, the proportion of both males and females of all sizes (the first partitioning regime) properly classified by discriminant function analysis (i.e. their predicted group membership coincides with their actual group membership) exceeds 83% for all areas (Table 4). A higher percentage of females than males was properly classified for areas other than western Cape Breton Island (Table 4). Newfoundland exceeded the other areas in the percentage of both males and females properly classified (Table 4).

The mean percentage of males and females properly classified according to area in small, medium, and large size groups (the second partitioning regime) was 87.9, 79.4, and 75.2, respectively, for males and 93.3, 69.1, and 68.1, respectively, for females.

A comparison of the percentage of individuals properly classified versus the number of variables used for classification in the discriminant function analysis (Fig. 5) indicates that the

TABLE 4. Results of a discriminant function classification (based on 48 morphometric and meristic characters) of four Atlantic snow crab populations. Females from all areas correctly classified = 89.9%; males from all areas correctly classified = 85.4%.

Actual group	No. of cases		Predicted group membership (%)							
			Newfoundland		Eastern Cape Breton Island		Western Cape Breton Island		Western Gulf of St. Lawrence	
	Males	Females	Males	Females	Males	Females	Males	Females	Males	Females
Newfoundland	50	51	90.0	94.1	2.0	0.0	0.0	2.0	8.0	3.9
Eastern Cape Breton Island	101	98	0.0	2.0	83.2	90.8	5.9	4.1	10.9	3.1
Western Cape Breton Island	121	119	3.3	4.2	7.4	4.2	87.6	86.6	1.7	5.0
Western Gulf of St. Lawrence	174	99	4.0	3.0	11.5	3.0	0.6	3.0	83.9	90.9

TABLE 5. Estimates of total fecundity and regressions of fecundity (Y) with carapace width (X in mm) for female snow crabs from four Atlantic snow crab populations (R = correlation coefficient).

	No. of females sampled	Fecundity regression	R	Mean fecundity	Fecundity range
Newfoundland	51	$Y = 6.4080X^{2.1690}$	0.777	52 000	37 900 – 81 200
Eastern Cape Breton Island	115	$Y = 14.8371X^{1.9859}$	0.660	80 100	42 300 – 120 400
Western Cape Breton Island	98	$Y = 38.4554X^{1.7649}$	0.635	74 500	32 600 – 128 400
Western Gulf of St. Lawrence	98	$Y = 13.2530X^{1.9922}$	0.747	58 800	12 100 – 122 900

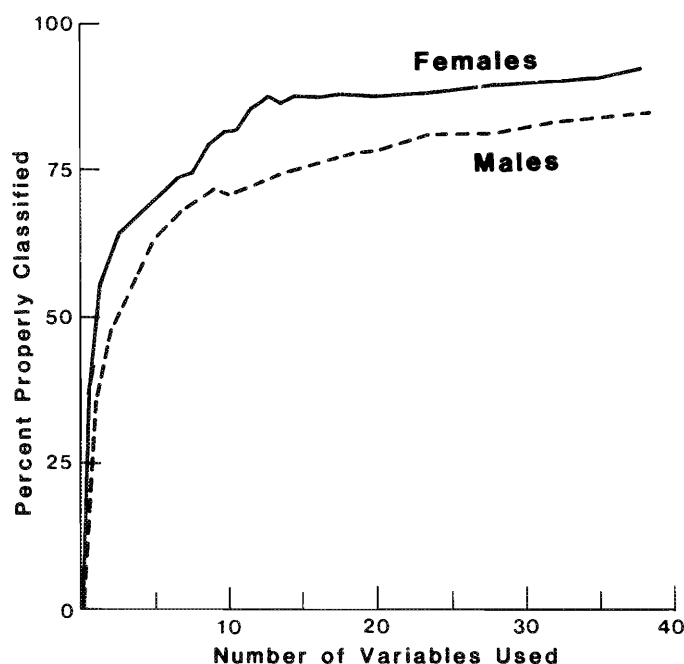


FIG. 5. Percentage of male and female snow crabs properly classified during discriminant function analysis versus the number of variables used during the analysis.

use of 12–15 discriminating variables would provide at least 70% proper classification and be logistically more effective than the 48 variables we used.

Fecundity

The mean weight per egg (WE) did not correlate with female size (CW) for any of the areas. In addition, analysis of variance results indicated a greater variance in WE within areas than between them. For this reason, WE for all females were pooled

to give an overall mean of 5.81×10^{-15} g per egg (WE_A in Equation 2), which was used in calculating fecundity. Fecundity estimates ranged from 12 100 to 128 400 eggs per female (Table 5). The total weight of the egg mass (TWEM), as it covaries with carapace width, was found to vary significantly ($p < 0.0001$) between areas with Duncan's multiple range test grouping each area separately ($p < 0.05$). The areas were grouped from highest to lowest TWEM as follows: eastern Cape Breton Island, western Cape Breton Island, western Gulf of St. Lawrence, Newfoundland.

Electrophoresis

Of those enzymes that resolved well (LDH, MDH, fumerase, G-6-PDH, and esterases) only esterases exhibited polymorphisms. Eight phenotypes (banding patterns) were observed (Table 3). Only the Newfoundland snow crabs exhibited all eight esterase phenotypes (Table 3). Six phenotypes were present in the western Gulf of St. Lawrence snow crabs and only three phenotypes were present in the eastern and western Cape Breton Island snow crabs (Table 3). A chi-square comparison of phenotype frequencies between areas (Table 6) shows that eastern and western Cape Breton Island snow crabs do not differ

TABLE 6. Comparison of esterase phenotypes for four Atlantic snow crab populations. H_0 : phenotype frequencies do not differ significantly between areas; *significantly different, $p < 0.05$ (calculated χ^2 values).

	Western Gulf of St. Lawrence	Western Cape Breton Island	Eastern Cape Breton Island
Newfoundland	(40.8)*	(92.8)*	(100.3)*
Western Gulf of St. Lawrence	—	(23.5)*	(28.2)*
Western Cape Breton Island	—	—	(1.2)

significantly from each other, while both the Newfoundland and western Gulf of St. Lawrence snow crabs differ significantly from each of the other areas.

Larval Rearing

Snow crab larvae hatched from March 25 to late April and exhibited high mortality rates in the flow-through rearing system we used. Only three larvae reached the megalopa stage and only one attained the first crab stage. The mean length of time (days after hatching) required to attain the second zoea, megalopa, and first crab stages was 25.7 d ($n = 15$, range: 16–29), 36.7 d ($n = 3$, range: 35–38), and 71 d ($n = 1$), respectively.

Discussion

Morphometrics and Meristics

Invertebrates, such as crustaceans, generally exhibit little morphological change in response to short-term changes in their environments. In addition, their rigid exoskeleton often allows for more precise morphometric measurements compared with “softer bodied” vertebrates. Such characteristics suggest that morphological comparisons of crustacean populations may provide useful evidence for delineating stocks. This contention is supported by the results of the present study (Table 4), which meet or exceed those of previous similar studies (Saila and Flowers 1969; Messieh 1975; Footitt and Mackauer 1980; Ihssen et al. 1981b; Almeida 1982; Campbell and Mohn 1982) and indicate a high degree of phenotypic distinctness between the four snow crab populations sampled.

If a “stock” is considered to be an intraspecific group of individuals that exhibit specific phenotypic attributes in response to environmental and/or genetic factors, then from our results of the morphometric, meristic, and fecundity comparisons we propose that the four snow crab populations sampled represent four distinct stocks. As discussed by Boone (1981), it is often difficult to distinguish between genetic and environmental effects on phenotypic characteristics. The physical characteristics of the adult snow crab environment in all four sample areas are similar and temporally homogeneous; therefore, one might assume that the majority of the phenotypic variability observed between areas would be due to genetic dissimilarities. However, such an assumption fails to consider the effect of the environment on early life history stages.

We hypothesize that the phenotypic differences observed between snow crab populations are due to morphological differentiation in response to environmental factors during the juvenile stages when the crabs are in relatively heterogeneous environments (Miller 1975; Adams 1979; Desrosiers et al. 1982; D. A. Robichaud, Biological Station, St. Andrews, N.B., unpubl. data). As the crabs grow larger and move to their relatively homogeneous adult environments, they tend to converge in their morphological attributes. This convergence would be cut short in females due to the terminal molt at maturity, but should extend on through the life of the adult males. The hypothesis is supported by our results which indicate that females and small crabs are phenotypically more distinct between areas than large male crabs.

Fecundity

The results of the fecundity against CW comparisons indicate that the four populations studied are distinct. Thus, the

fecundity data support the morphometric and meristic results in suggesting that the four populations represent separate stocks.

Electrophoresis and Larval Duration

Previous authors (Horrall 1981; Boone 1981; Kutkuhn 1981) have implied that for the formation and maintenance of stocks “a moderately high degree of reproductive isolation is necessary” (Horrall 1981). Such a view implies a need for genetic isolation, and that stocks should be defined as intraspecific groups of individuals exhibiting similar genetic attributes.

From electrophoretic studies it was inferred that decapod crustaceans, especially large, mobile species, exhibit low levels of genetic variability (Nelson and Hedgecock 1980). Esterases are often found to exhibit the greatest amount of polymorphism and have been genetically interpreted for some decapods (Smith et al. 1980; Turner and Lyster 1980). However, esterases are often weak and unstable and there is evidence that their isozymes may change due to nongenetic causes, such as ontogenetic or physiological state (McWhinnie and Corkill 1964; Manwell and Baker 1970; Johnson et al. 1974; Kannupandi 1980).

The differences in esterase patterns we observed were not amenable to genetic interpretation (such as deviations from Hardy–Weinberg equilibria) due to our inability to describe their genetic basis; therefore, for this reason and those mentioned previously, they were interpreted as phenotypic expressions of probable genotypic differences. Our results indicate that the snow crabs from Newfoundland and the western Gulf of St. Lawrence possibly differ genetically from each other and from those of eastern and western Cape Breton Island, and represent separate genetic stocks. The results also indicate that eastern and western Cape Breton Island snow crabs represent a single genetic stock.

If genetic characteristics of populations (as opposed to phenotypic and/or biological characteristics) are accepted as the basis for delineating stocks, then a reason for these characteristics should be postulated. All of the snow crab areas sampled are geographically separated (Fig. 1). This fact, coupled with the observation from tagging studies that adult snow crab movements are limited, implies a lack of interbreeding between adults from different areas, and provides an explanation for the genotypic differences we inferred. Why then do the eastern Cape Breton Island and western Cape Breton Island populations appear genetically similar? The answer may lie in the exchange of pelagic larvae.

Kon (1970) derived estimates of larval duration in relation to water temperature. His estimate for total duration at 11°C of 69–73 d corresponds well to the 71-d estimate we obtained. The median surface water temperature in the Gulf of St. Lawrence, Cape Breton Island, and southern Newfoundland regions for the period of May through August (the period when *C. opilio* larvae are most likely to be present in surface waters) is 11°C (Lauzier and Hull 1969). Assuming a pelagic larval duration of 71 d for the areas studied, and given surface current velocities of 3.2–32.0 km/d (2–20 mi/d; Trites 1970; Fig. 1), distances of 227–2272 km can be estimated for the passive transport of snow crab larvae in surface currents. These estimates assume straight-line movements and may not be entirely realistic; however, they do serve to illustrate the potential for transport and exchange of snow crab larvae. When the estimates of larval transport by surface currents are considered in conjunction with typical summer surface circulation patterns (Fig. 1), it is possible for

genetic exchange through larval recruitment to occur between all Atlantic snow crab grounds. The magnitude of larval exchange between areas would be affected by oceanographic patterns and should be directly proportional to the distance between areas, the velocity of surface currents, and larval duration. Eastern and western Cape Breton Island snow crab grounds are close geographically with strong currents running between them (Fig. 1); thus, larval recruitment to the eastern Cape Breton Island snow crab grounds possibly originates from snow crab populations off western Cape Breton Island. Such a scenario would account for the apparent genetic similarity of the eastern (Gabarus) and western (Pleasant Bay) Cape Breton Island snow crab stocks as inferred by our electrophoresis results.

The Commercial Fishery

The results of the morphometric, meristic, fecundity, and electrophoretic studies indicate that Newfoundland and western Gulf of St. Lawrence snow crab populations represent separate phenotypic and genotypic stocks differing significantly from each other and from Cape Breton Island snow crab populations. With respect to the eastern and western Cape Breton Island snow crab populations, the electrophoretic results conflict with those of the morphometric, meristic, and fecundity studies by indicating that they form a single "genetic" stock.

Given that stock definition is frequently attempted to define management units, we can review the applicability of the "single-stock-management-unit" concept, by comparing the history of the two areas within the Cape Breton Island "genetic" snow crab stock. Since 1978, the management strategy for eastern and western Cape Breton Island snow crab grounds has been to develop a stable, supplementary fishery with a large number of participants (Elner 1982b). Consequently, total allowable catch restrictions in these areas were based on a strategy of permitting only the harvest of biomass equivalent to the calculated growth and recruitment additions for the previous year, in an attempt to maintain a large, stable stock (Elner 1982b). Both areas were expected to respond similarly to this management strategy. However, within four fishing seasons, catch rates and the commercial biomass in eastern Cape Breton Island collapsed (Elner 1982b; Elner and Robichaud 1983b). In contrast, catch rates and commercial biomass have remained relatively stable in western Cape Breton Island (Elner 1982b). The substantial differences in historical landings between these two snow crab grounds appear more remarkable given that the areas are of approximately equal size (2750 km² vs. 2059 km²), have similar numbers of fishermen (27 vs. 26), and are separated by less than 160 km of landmass. Furthermore, the number of snow crab females in the Atlantic can be assumed to approximate prefishery levels and, hence, decreases in egg production are unlikely to be a factor in the collapse.

Evidence accrued from stock assessments (Elner and Robichaud 1983b) indicates that eastern Cape Breton Island snow crab grounds are unproductive in terms of growth and recruitment. Possibly, the eastern areas, being at the southern edge of known commercial snow crab concentrations in the Atlantic, represent marginal grounds in terms of habitat. Thus, although comparisons of biomass, catch rates, and size frequencies for eastern Cape Breton Island reveal apparent recruitment failures, it may be that the situation represents the normal pattern of production.

Probably there is little endemic recruitment within the eastern Cape Breton Island snow crab population. Larvae released from

this population may become entrained in local gyres or swept northeast toward Newfoundland (Fig. 1), but the predominant surface currents in the area would tend to disperse pelagic larvae south, down the coast of Nova Scotia or out into the Atlantic (Fig. 1). *Chionoecetes opilio* larvae are present throughout the Scotian Shelf, with early larval stages more abundant in the north, and the megalopa stage found only in the south (Roff et al. 1984). This type of larval distribution, plus the presence of small numbers of snow crab off Grand Manan Island in the Bay of Fundy, and in the Gulf of Maine (M. J. Dadswell, Biological Station, St. Andrews, N.B. pers. comm.), supports the possibility of a large, southward loss of *C. opilio* larvae from eastern Cape Breton Island. Thus, the eastern Cape Breton Island snow crab population was probably built up over time through trickles of larval recruitment largely from western Cape Breton Island. Such a scenario would account for the initially high catch rates and landings on the grounds, the lack of resilience of the stocks to exploitation, and the subsequent devastation of biomass and catch rates after only a few fishing seasons.

In contrast with the east coast, the management by "stable-stock" policy appears to have succeeded in western Cape Breton Island. Overall annual biomass additions, although variable in periodicity, have appeared relatively large and consistent since 1978 (Elner 1982b). This consistency, despite exploitation rates of 47–64%, has conferred resilience to the western Cape Breton Island stock and has facilitated management.

The experiences of the Cape Breton Island snow crab fishery indicate that the "stock" per se, as defined by genetic and/or phenotypic characteristics, is not necessarily a meaningful management unit. Stocks may be more usefully subdivided into management units that reflect intra-stock factors such as growth and recruitment patterns. Thus, unique phenotypic and/or genotypic characteristics of intraspecific groups of individuals may be useful in the delineation of stocks, but should not be accepted as a basis for management strategies until the biotic and abiotic factors governing these characteristics are elucidated.

Acknowledgments

We are grateful to P. Herbert, University of Windsor, for assistance with electrophoresis and P. Fanning, University of Guelph, for assistance with analyses. R. F. J. Bailey and D. M. Taylor were instrumental in providing snow crab samples from the Gulf of St. Lawrence and Newfoundland, respectively. Drs. M. J. Dadswell and P. Lawton gave helpful reviews of earlier drafts of the manuscript.

References

- ADAMS, A. E. 1979. The life history of the snow crab, *Chionoecetes opilio*, a literature review. Alaska Sea Grant Program, University of Alaska, Alaska Sea Grant Rep. 78-13: 141 p.
- ALMEIDA, F. P. 1982. An analysis of the stock structure of silver hake, *Merluccius bilinearis*, in NAFO Subareas 5 and 6. Northwest Atlantic Fisheries Organization SCR Doc. 82/IX/81, Ser. No. N587: 36 p.
- BAILEY, R. 1982. Relationship between catches of snow crab, *C. opilio* (O. Fabricius), and abundance of cod (*Gadus morhua* L.) in the southwestern Gulf of St. Lawrence, p. 485–497. In Proceedings of the International Symposium on the Genus *Chionoecetes*. Lowell Wakefield Fisheries Symposia Series, University of Alaska, Alaska Sea Grant Rep. 82-10.
- BARLOW, J. 1969. Studies of molecular polymorphisms in the American lobster (*Homarus americanus*). Ph.D. thesis, University of Maine, Orono, ME.
- BARLOW, J., AND G. J. RIDGWAY. 1971. Polymorphisms of esterase isozymes in the American lobster (*Homarus americanus*). J. Fish. Res. Board Can. 28: 15–21.
- BOOKE, H. E. 1981. The conundrum of the stock concept — are nature and nurture definable in fishery science? Can. J. Fish. Aquat. Sci. 38: 1479–1480.

- BRUNEL, P. 1960. Observations sur la biologie et al biométrie du crabe-araignée, *Chionoecetes opilio* (Fabr.). Rapp. Annu. 1960, Dép. Pêcheries Québec, Stn. Biol. Mar. Grande-Rivière, P.Q. p. 59-67.
- BUMPUS, D. F., AND L. M. LAUZIER. 1965. Surface circulation on the Continental Shelf off eastern North America between Newfoundland and Florida. Ser. Atlas Mar. Environ., Am. Geogr. Soc. Folio 7.
- CAMPBELL, A., AND R. MOHN. 1982. The quest for lobster stock boundaries in the Canadian Maritimes. Northwest Atlantic Fisheries Organization SCR Doc. 82/IX/107, Ser. No. N615: 45 p.
- DESROSIER, G., J.-C. F. BRÊTHES, AND F. COULOMBE. 1982. Edaphic segregation within a population of *C. opilio* in the southwestern part of the Gulf of St. Lawrence (Chaleur Bay area), p. 353-379. In Proceedings of the International Symposium on the Genus *Chionoecetes*. Lowell Wakefield Fisheries Symposia Series, University of Alaska, Alaska Sea Grant Rep. 82-10.
- ELNER, R. W. 1982a. An overview of the snow crab, *Chionoecetes opilio*, fishery in Atlantic Canada, p. 5-19. In Proceedings of the International Symposium on the Genus *Chionoecetes*. Lowell Wakefield Fisheries Symposia Series, University of Alaska, Alaska Sea Grant Rep. 82-10.
- 1982b. Characteristics of the snow crab, *Chionoecetes opilio*, fishery off Cape Breton Island, p. 657-680. In Proceedings of the International Symposium on the Genus *Chionoecetes*. Lowell Wakefield Fisheries Symposia Series, University of Alaska, Alaska Sea Grant Rep. 82-10.
- ELNER, R. W., AND D. A. ROBICHAUD. 1983a. Observations on the efficacy of the minimum legal size for Atlantic snow crab, *Chionoecetes opilio*. Can. Atl. Fish. Sci. Adv. Comm. Res. Doc. 83/63: 26 p.
- 1983b. Status of the snow crab resource off the Atlantic coast of Cape Breton Island, 1982. Can. Atl. Fish. Sci. Adv. Comm. Res. Doc. 83/5: 27 p.
- FOOTITT, R. G., AND M. MACKAUER. 1980. Morphometric variation between populations of the balsam woolly aphid, *Adelges piceae* (Ratzeburg) (Homoptera: Adelgidae), in North America. Can. J. Zool. 58: 1494-1503.
- HACHEY, H. B. 1961. Oceanography and Canadian Atlantic waters. Bull. Fish. Res. Board Can. 134: 120 p.
- HAYNES, E., J. F. KARINEN, J. WATSON, AND D. J. HOPSON. 1976. Relation of number of eggs and egg length to carapace width in the brachyuran crabs *Chionoecetes bairdi* and *C. opilio* from the southeastern Bering Sea and *C. opilio* from the Gulf of St. Lawrence. J. Fish. Res. Board Can. 33: 2592-2595.
- HORRALL, R. M. 1981. Behavioral stock-isolating mechanisms in Great Lakes fishes with special reference to homing and site imprinting. Can. J. Fish. Aquat. Sci. 38: 1481-1496.
- IHSSEN, P. E., H. E. BOOKE, J. CASSELMAN, J. M. MCGLADE, N. R. PAYNE, AND F. M. UTTER. 1981a. Stock identification: materials and methods. Can. J. Fish. Aquat. Sci. 38: 1838-1855.
- IHSSEN, P. E., D. O. EVANS, W. J. CHRISTIE, J. A. RECKAHN, AND R. L. DESJARDINE. 1981b. Life history, morphology, and electrophoretic characteristics of five allopatric stocks of lake whitefish (*Coregonis clupeaformis*) in the Great Lakes region. Can. J. Fish. Aquat. Sci. 38: 1790-1807.
- ITO, K. 1963. Some observations on the degree of ripeness of the eggs of the snow crab (*Chionoecetes opilio*). Bull. Jpn. Sea Reg. Fish. Res. Lab. 11: 1-12.
- JOHNSON, A. G., F. M. UTTER, AND H. O. HODGINS. 1972. Electrophoretic investigation of the family Scorpaenidae. Fish. Bull. 70: 403-413.
1973. Estimate of genetic polymorphism and heterozygosity in three species of rockfish (genus *Sebastes*). Comp. Biochem. Physiol. 44B: 397-406.
1974. Electrophoretic comparison of five species of pandalid shrimp from the northeastern Pacific ocean. Fish. Bull. 72: 799-803.
- KANNUPANDI, T. 1980. Protein patterns during ontogeny of the Xanthid crab, *Rhithropanopeus harrisi*. Indian J. Mar. Sci. 9: 127-131.
- KLECKA, W. R. 1975. Discriminant analysis, p. 434-467. In N. H. Nie, C. H. Hull, J. G. Jenkins, K. Steinbrenner and D. H. Brent [ed.] Statistical Package for the Social Sciences. 2nd ed. McGraw-Hill Co., Montreal, Que.
- KON, T. 1970. Fisheries biology of the Tanner crab — IV. The duration of planktonic stages estimated by rearing experiments of larvae. Bull. Jpn. Soc. Sci. Fish. 36: 219-224. (English translation by Fish. Res. Board Can., Transl. Ser. 1603)
- KUDLO, B. P., AND V. V. BURMAKIN. 1972. Water circulation in the South Labrador and Newfoundland areas in 1970-1971. International Commission for the Northwest Atlantic Fisheries Res. Doc. 72/104.
- KUTKUHN, J. H. 1981. Stock definition as a necessary basis for cooperative management of Great Lakes fish resources. Can. J. Fish. Aquat. Sci. 38: 1476-1478.
- LAUZIER, L. M., AND J. H. HULL. 1969. Coastal station data temperatures along the Canadian Atlantic coast, 1921-1969. Fish. Res. Board Can. Tech. Rep. 150: 25 p.
- LINDSEY, C. C. 1981. Stocks are chameleons: plasticity in gill rakers of coregonid fishes. Can. J. Fish. Aquat. Sci. 38: 1497-1506.
- MANWELL, C., AND C. M. A. BAKER. 1970. Molecular biology and the origin of species. University of Washington Press, Seattle, WA. 394 p.
- MCWHINNIE, M. A., AND A. J. CORKILL. 1964. The hexosemonophosphate pathway and its variation in the intermolt cycle in crayfish. Comp. Biochem. Physiol. 12: 81-93.
- MESSIEH, S. N. 1975. Delineating spring and autumn herring populations in the southern Gulf of St. Lawrence by discriminant function analysis. J. Fish. Res. Board Can. 32: 471-477.
- MESSIEH, S. N., AND S. N. TIBBO. 1971. Discreteness of Atlantic herring (*Clupea harengus harengus*) populations in spring and autumn fisheries in the southern Gulf of St. Lawrence. J. Fish. Res. Board Can. 28: 1009-1014.
- MILLER, R. J. 1975. Density of the commercial spider crab, *Chionoecetes opilio*, and calibration of effective area fished per trap using bottom photography. J. Fish. Res. Board Can. 32: 761-768.
- MULLEY, J. C., AND B. D. H. LATTER. 1981a. Geographic differentiation of eastern Australian penaeid prawn populations. Aust. J. Mar. Freshwater Res. 32: 889-895.
- 1981b. Geographic differentiation of tropical Australian penaeid prawn populations. Aust. J. Mar. Freshwater Res. 32: 897-906.
- NELSON, K., AND D. HEDGECOCK. 1980. Enzyme polymorphism and adaptive strategy in the decapod Crustacea. Am. Nat. 116: 238-280.
- ORNSTEIN, N. 1964. Disc electrophoresis Part I: Background and theory. Ann. N.Y. Acad. Sci. 121: 321-349.
- PARSONS, L. S., AND V. M. HODDER. 1971. Meristic differences between spring- and autumn-spawning Atlantic herring (*Clupea harengus harengus*) from southwestern Newfoundland. J. Fish. Res. Board Can. 28: 553-558.
- POWLES, H. 1968. Distribution and biology of the spider crab, *Chionoecetes opilio*, in the Magdalen Shallows, Gulf of St. Lawrence. Fish. Res. Board Can. MS Rep. 997: 106 p.
- ROFF, J. C., L. P. FANNING, AND A. B. STASKO. 1984. Larval crabs (Decapoda, Brachyura) zoeas and megalopas of the Scotian Shelf. Can. Tech. Rep. Fish. Aquat. Sci. 1264: 22 p.
- SAILA, S. B., AND J. M. FLOWERS. 1969. Geographic morphometric variation in the American lobster. Syst. Zool. 18: 330-338.
- SMITH, P. J., J. L. MCKAY, AND P. J. MACHIN. 1980. Genetic variation in the rock lobsters *Jasus edwardsii* and *Jasus novaehollandiae*. N. Z. J. Mar. Freshwater Res. 14: 55-63.
- SQUIRES, H. J. 1966. Distribution of decapod Crustacea in the northwest Atlantic. Ser. Atlas Mar. Environ., Am. Geogr. Soc. Folio 12.
- SUTCLIFFE, W. H. JR., R. H. LOUCKS, AND K. F. DRINKWATER. 1976. Coastal circulation and physical oceanography of the Scotian Shelf and the Gulf of Maine. J. Fish. Res. Board Can. 33: 98-115.
- TRACEY, M. L., K. NELSON, D. HEDGECOCK, R. A. SHLESER, AND M. L. PRESSICK. 1975. Biochemical genetics of lobsters: genetic variation and the structure of American lobster (*Homarus americanus*) populations. J. Fish. Res. Board Can. 32: 2091-2101.
- TRITES, R. W. 1970. The Gulf of St. Lawrence from a pollution viewpoint. FAO Tech. Conf. Mar. Pollut. FIR:MP/70/R-16: 23 p.
- TURNER, K., AND T. A. LYERLA. 1980. Electrophoretic variation in sympatric mud crabs from North Inlet, South Carolina. Biol. Bull. 159: 418-427.
- WATWOOD, K. G., AND R. W. ELNER. 1982. Cod predation of snow crab (*Chionoecetes opilio*) in the Gulf of St. Lawrence, p. 499-520. In Proceedings of the International Symposium on the Genus *Chionoecetes*. Lowell Wakefield Fisheries Symposia Series, University of Alaska, Alaska Sea Grant Rep. 82-10.
- WATSON, J. 1969. Biological investigations on the spider crab *Chionoecetes opilio*. Can. Fish. Rep. 13: 24-47.
- 1970a. Maturity, mating, and egg laying in the spider crab, *Chionoecetes opilio*. J. Fish. Res. Board Can. 27: 1607-1616.
- 1970b. Tag recaptures and movements of adult male snow crabs, *Chionoecetes opilio* (O. Fabricius), in the Gaspé region of the Gulf of St. Lawrence. Fish. Res. Board Can. Tech. Rep. 204: 16 p.
- WATSON, J., AND P. G. WELLS. 1972. Recaptures and movements of tagged snow crabs (*Chionoecetes opilio*) in 1970 from the Gulf of St. Lawrence. Fish. Res. Board Can. Tech. Rep. 349: 12 p.