

Morphometry and Gonad Maturity of Male Snow Crab, *Chionoecetes opilio*

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Comeau, M., and G. Y. Conan. 1992. Morphometry and gonad maturity of male snow crab, *Chionoecetes opilio*. Can. J. Fish. Aquat. Sci. 49: 2460–2468.

The relationship between chela height (CH) and carapace width (CW) of male snow crab, *Chionoecetes opilio*, goes through three allometric stages. The "immature stage" (mostly <34 mm CW) evolves into a "juvenile stage" (34–120 mm CW) through a "juvenile molt" defining a change in allometry marked by an angular point around 34 mm CW. Fifty percent of males reach gonad maturity, defined by the presence of spermatophores inside the vasa deferentia, at an estimated size of 34 mm CW. The third allometric stage, "morphometrically mature," is separated from the juvenile stage by a "molt to morphometric maturity" at sizes ranging from 50 to 120 mm CW. Juvenile males have smaller claws than morphometrically mature males of the same size. This secondary sexual character is justified by a specific behavior of the males holding the pereopods of the female in one chela during precopulatory embrace. Male snow crab efficiently mate in nature with intermolt multiparous females only after reaching morphometric maturity. Therefore, the presence of spermatophores is not the sole determinant factor necessary for male copulation. Juvenile males larger than the minimum legal size of 95 mm CW are harvestable before they may efficiently mate.

La relation morphométrique entre la hauteur de la pince (CH) et la largeur de la carapace (CW) des mâles chez le crabe des neiges, *Chionoecetes opilio*, évolue selon trois phases d'allométrie. La phase « immature » (<34 mm CW) évolue en phase « juvénile » (34 à 120 mm CW) après une « mue juvénile » représentée sur la relation d'allométrie par un point anguleux à 34 mm CW. Cinquante pourcent des crabes mâles atteignent la maturité gonadique, établie par la présence de spermatophores dans les vasa deferentia, à une taille estimée à 34 mm CW. La troisième phase, « morphométriquement matures », est séparée de la phase juvénile par la « mue de maturité morphométrique » à des tailles variant entre 50 et 120 mm CW. Les mâles juvéniles ont, à taille égale, une plus petite pince que les mâles morphométriquement matures. Ce caractère sexuel secondaire est justifié par le comportement du mâle qui tient les péréopodes de la femelle dans ses pinces durant l'étreinte pré-nuptiale. Les crabes des neiges mâles observés dans le milieu naturel ne s'accouplent qu'après différenciation de leur pince (maturité morphométrique). Ainsi, la présence de spermatophores n'est pas le seul facteur déterminant permettant aux mâles de s'accoupler. Les mâles juvéniles de taille supérieure à la taille minimale légale de 95 mm CW sont actuellement légalement pêchables avant d'avoir eu l'opportunité de s'accoupler.

Received February 5, 1992

Accepted June 8, 1992

(JB396)

Reçu le 5 février 1992

Accepté le 8 juin 1992

The snow crab, *Chionoecetes opilio* (Brachyura, Majidae), fishery in Atlantic Canada is regulated by a minimum legal size of 95 mm carapace width (CW). The minimum legal size was thought to protect the reproductive potential of the stock (Watson 1970) because female snow crab never grew larger than 95 mm CW and all male snow crab were thought to reach full maturity between 51 and 72 mm CW. Recent works have suggested that the minimum legal size may not protect the reproductive potential of the stock as efficiently as it was once believed (Comeau 1985; Conan and Comeau 1986; Comeau et al. 1991). Conan and Comeau (1986) indicated that in commercial fisheries, as many as 40% of harvested males could be juvenile, i.e. not fully mature individuals.

The terminology dealing with maturity of majid crabs varies between authors (Table 1). For clarity, the terminology proposed by Conan et al. (1986b) will be used in this paper.

The criteria used for identifying maturity of male *C. opilio* differ between authors and imply distinct interpretations of the life cycle. Watson (1970) mentioned that male *C. opilio* simul-

taneously reach morphometric maturity (defined as a differentiation of the shape of chela) and gonad maturity (production of spermatophores) and that all males larger than 60 mm CW were mature. Conan and Comeau (1986) also reported that spermatophores are present in the vasa deferentia of all males larger than 60 mm CW. However, they further showed that differentiation of a secondary sexual character, the shape of the chela, defined as a molt to "morphometric maturity" occurs at CW ranging from 60 to 120 mm for different individuals. They suggested that the differentiation of the shape of the chela is an adaptation to hold the female during precopulatory embrace (Fig. 1). They observed in aquaria that juvenile males, of identical or larger sizes than their mature counterparts, would not develop precopulatory behavior when confronted with multiparous females, i.e. hard-shell females having already mated and spawned at least once (Paul 1984).

The observations made by Conan and Comeau (1986), Conan et al. (1988a), and Comeau et al. (1989, 1991) provide an updated interpretation of the life cycle of *C. opilio* that is consistent with the interpretation most generally provided by other authors on other species of majid crabs. Huxley (1924, 1932), Teissier (1928, 1935, 1948, 1955, 1960), Huxley and Teissier

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TABLE 1. Equivalent terminology used to describe morphometric maturity, critical molts, and gonad maturity for the snow crab (*C. opilio*) and other majids.

	<i>Chionoecetes opilio</i>			Other majids
Morphometric maturity	Conan and Comeau (1986)	Conan et al. (1988b)	Teissier (1935)	Vernet-Cornubert (1958)
Stage 1	Morphometrically immature	Immature	Immature (1st phase)	Juvenile
2	Morphometrically immature	Juvenile	Immature (2nd phase)	Prepubertal
3	Morphometrically mature	Morphometrically mature	Mature	Pubertal
Critical molts				
Stage 1		Juvenile molt	Prepuberty molt	Prepuberty molt
2	Molt to maturity (terminal molt)	Molt to maturity	Puberty molt	Puberty molt
Gonad maturity	Powles (1968)	Watson (1970)		
Stage 1	Immature	Immature		
2	Mature (undeveloped gonad)	Immature		
3	Mature (developing)	Mature (developing)		
4	Mature (ripe)	Mature (ripe)		



FIG. 1. Snow crab (*C. opilio*) mating couple in precopulatory embrace. Underwater photography taken by Gérard Conan at a depth of 30 m in Bonne Bay, 1984.

(1936), and Hartnoll (1963, 1974, 1978, 1982) have shown that a constant allometric relationship appears as a straight line on a logarithmic plot of chela height (CH) versus CW. Starting from the ordinate, three segments can be identified for majid males. The first segment models the immature stage of small crabs and leads, without discontinuity, to an angular point marking a transition to a second segment which models the juvenile stage. The immature and juvenile stages are separated by a "juvenile" molt. Neither Teissier nor Hartnoll provided a functional interpretation of the juvenile stage. The third line segment, identified as representing a morphometrically mature

stage, is parallel to the second, but shifted in ordinate. Watson (1970) implicitly assumed that morphometric maturity is directly associated with gonad maturity for *C. opilio*, although Hartnoll (1965) indicated that some large juvenile males of related majid crabs (*Microphrys bicornutus* and *Mithrax sculpus*) may carry spermatophores before morphometric differentiation of the claw. The discontinuity between the second and the third segments originates from a "molt to maturity" identified by Teissier (1935) as a terminal molt during which the chela increases considerably in volume by one abrupt step and in certain species changes considerably in shape and ornamentation.

tations (Vernet-Cornubert 1958). The molt to maturity may occur over a two- to threefold range in carapace size.

For male *C. opilio* from the southern Gulf of St. Lawrence, Conan and Comeau (1986) demonstrated the existence of a molt functionally equivalent to the "molt to maturity" and identified it as a terminal molt, but did not at the time identify the "juvenile" molt or infer its biological function.

The objectives of the present work are to demonstrate the existence of a juvenile molt in male *C. opilio* and to interpret its biological function in the reproductive process. Further, we interpret the morphometric, gonadal, and behavioral processes leading to maturity of male *C. opilio* in the perspective of fisheries management.

Material and Methods

Sampling Sites and Gear

Male snow crabs were collected using a Bay of Biscay "Bigouden" *Nephrops* 20-m head rope otter trawl with 2.5-cm-mesh cod end in Bonne Bay, Newfoundland (49°32'N, 57°56'W; Fig. 2), at depths ranging from 120 to 140 m in October 1985 and June–July 1990. Bonne Bay is a deep fjord consisting of two basins. The 140-m outer basin, which extends into South Arm, is connected easterly by a narrow and shallow strait to a second 220-m-deep basin, the East Arm. The Bonne Bay snow crab population remains below the thermocline and is geographically isolated from the Gulf of St. Lawrence fishing grounds by a shallow 50-m glacial sill at the entrance of the bay. Snow crabs are not commercially exploited in Bonne Bay (Taylor et al. 1985) and may show characteristics of a population in its initial state, prior to any commercial fishing. Snow crabs were sampled from the outer basin (Fig. 2). A reference sample was also taken for observation of vasa deferentia on the fishing grounds of baie des Chaleurs (48°03'N, 65°05'W) at a depth of 80 m on November 28, 1984.

Biological Observations

Biometric measurements on CW and CH were made to the nearest 0.1 mm using a modified vernier caliper (Watson and Wells 1970). CW and CH were used respectively as an index for size and for secondary sexual character development, as recommended by Conan and Comeau (1986).

All males measured in 1985 were dissected, and squashes of their right vas deferens were examined under light transmission microscope, at magnifications of 100× and 250×, for presence of spermatophores.

In order to quantitatively study the vasa deferentia condition, a vaso-somatic index (VSI) was defined as the ratio of the wet weight of the vasa deferentia to the wet weight of the whole animal. A total of 23 new-shell (shell not fouled by epizootes) morphometrically mature males (65–144 mm CW), 26 old-shell (shell heavily fouled by numerous epizootes) morphometrically mature males (62–85 mm CW), and 12 juvenile males (76–101 mm CW) in intermolt (molt stage C determined by the observation of the maxilla; Moriyasu and Mallet 1986) with no missing or regenerated limbs were sampled in November 1984. VSI versus CW were plotted on natural logarithmic (log) scales.

Statistical Analysis of Data

To identify morphometric maturity, we used a bivariate discriminant function calculated by Comeau et al. (1991), as described in Conan and Comeau (1986), from a sample of males taken during the 1989 Bonne Bay trawl survey.

The individuals identified as nonmorphometrically mature in the 1985 survey were reexamined to detect possible immature and juvenile stages. All crabs were independently classified into two categories using a criterion of presence or absence of spermatophores in the vasa deferentia. The size frequency histograms specific to each category were examined. In order to

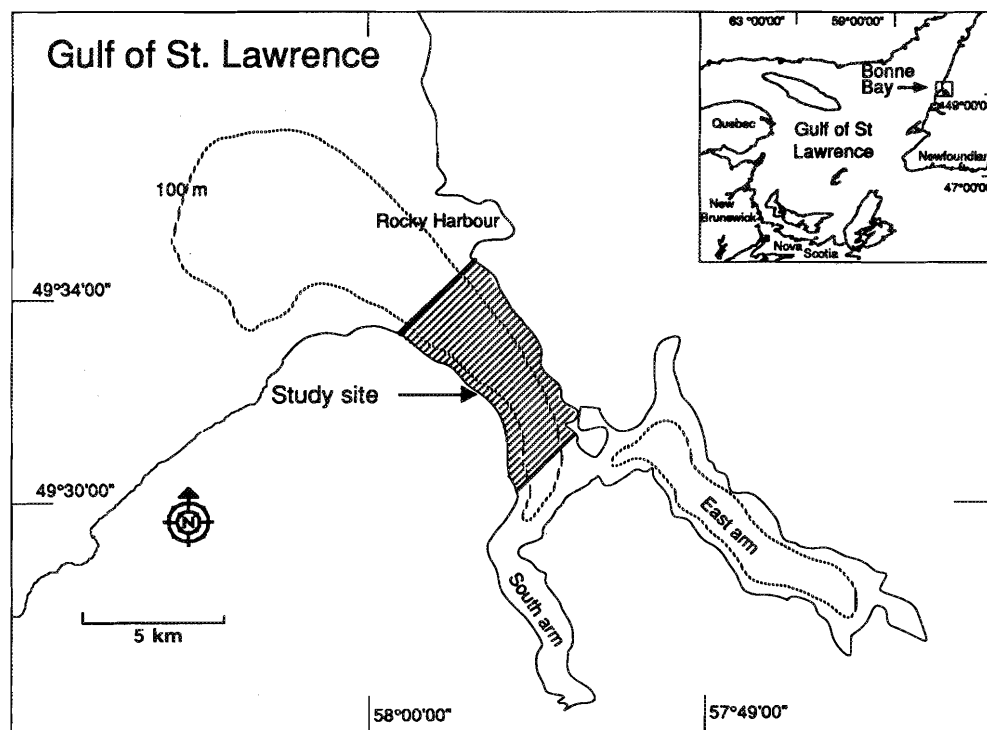


FIG. 2. Map of the fjord of Bonne Bay, Newfoundland, with 100-m depth contour and indicating the site (hatched) where snow crab (*C. opilio*) were collected.

facilitate statistical analysis and conform with standard techniques of comparison of regression lines (Snedecor and Cochran 1980; Gaertner and Laloé 1986), predictive regression lines were fitted by least squares to the log-transformed data separately for each group contrasted, as a substitute for functional regression lines. The estimate of the point of intersection for two regression lines calculated from predictive regression lines would, in this case, differ only slightly from the intersection of equivalent functional regression lines due to high correlations (>0.97) in the allometric relationships of log CH versus log CW. An analysis of variance (ANOVA) was used to test for differences between the regression lines (Snedecor and Cochran 1980), if the residual mean squares were homogeneous (F -test). The point of intersection for the two regression lines was calculated, if the ANOVA showed a significant difference between the slopes, using the equation

$$K_{CW} = \frac{b_2 - b_1}{a_2 - a_1}$$

where K_{CW} is the carapace width at the point of intersection, b_1 and a_1 are, respectively, the y -intercept and the slope of group 1, and b_2 and a_2 are, respectively, the y -intercept and the slope of group 2. The differences between regression lines were tested and the position of the angular point was calculated by the method described by Gaertner and Laloé (1986).

The proportion of individuals bearing mature gonads among the males at a given size was modelled by a logistic curve. Mature gonads are identified by the presence of spermatophores in the vasa deferentia. Data were regrouped into 1-mm CW size-classes. The logistic equation reparameterized as in Conan (1987) is

$$P = \frac{1}{1 + \exp(-4S(CW - CW_{50}))}$$

where P is the proportion of individuals with mature gonads, CW is the carapace width, CW_{50} is the abscissa of the inflection point or size at which 50% of crabs have spermatophores in their vasa deferentia, and S is the slope of the tangent to the maturity curve at the inflection point

$$S = \left(\frac{dP}{dCW} \right)_{CW_{50}}$$

The equations were fitted on untransformed data using Marquadt's iterative nonlinear least square algorithm. The initial estimates were obtained from a regression using the linear transformed equation $y = \log(1/P - 1)$.

Results

Morphometric Maturity

A total of 605 and 1354 male snow crabs were collected by trawl in Bonne Bay in 1985 and 1990, respectively (Fig. 3). Two swarms of points with parallel major axes are identifiable in the graphs of log CH versus log CW (Fig. 4). In 1985, the upper swarm of points, representing the morphometrically mature males (Conan and Comeau 1986), overlaps only slightly (from 57.1 mm CW to 59.5 mm CW) with the lower swarm of points, representing immature and juvenile males (Fig. 4A). In 1990, the two swarms widely overlap (from 51.0 mm CW to 116.6 mm CW; Fig. 4B).

A cutting line based on a bivariate discriminant function is considerably more efficient (99%; Comeau et al. 1991) than a

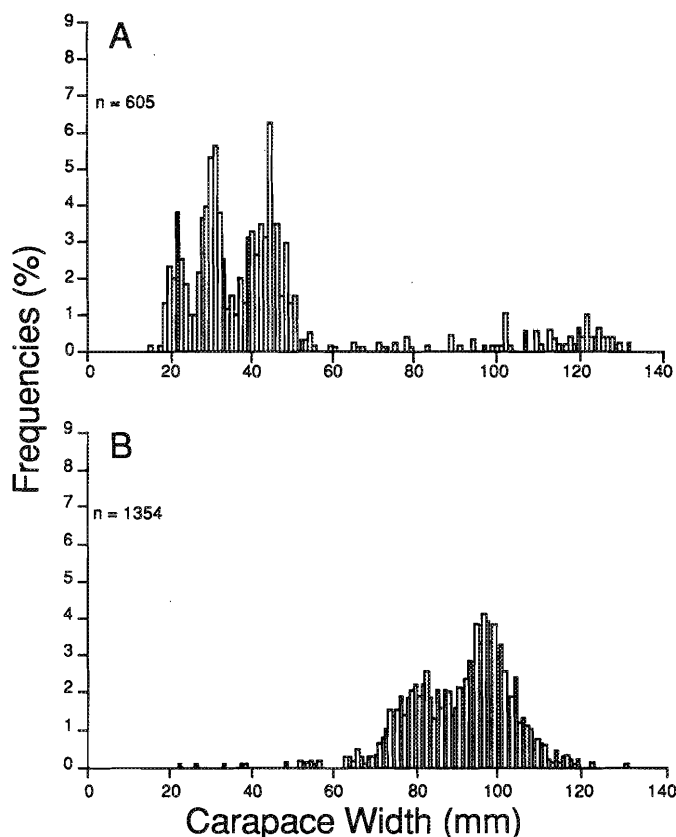


FIG. 3. Size frequency distributions for male snow crab (*C. opilio*) caught by *Nephrops* trawl in Bonne Bay in (A) 1985 and (B) 1990. Total number of individuals (n) collected in both years is indicated.

discriminant technique based on a univariate cutting point criteria. However, CH is more efficient than CW for separating males into juvenile males and morphometrically mature males, as shown in Fig. 4B. By switching from the existing minimum legal size of 95 mm CW to a corresponding 20 mm CH, the proportion of juvenile males retained for sale would have decreased by 26% (from 36 to 10%), while the proportion of morphometrically mature males would have increased by 15% (from 53 to 68%).

Observation of the Vasa Deferentia

Three stages of vasa deferentia development were observed for males: (1) stage I — the vasa deferentia are not morphologically differentiated. (2) stage II — the vasa deferentia are morphologically differentiated, but no spermatophores are observed. The vasa deferentia are translucent and appear as straight tubes. (3) stage III — the vasa deferentia are opaque and their shape varies from a straight tube to a strongly coiled mass. Spermatophores are present in the vasa deferentia.

The size distribution of stage I ranged from 15.1 mm CW to 33.6 mm CW (Fig. 5A) and generated a mode at 22 mm CW in the overall size distribution (Fig. 3A). The size distribution of stage II ranged from 23.4 mm CW to 37.4 mm CW (Fig. 5B) and generated a mode at 31 mm CW in the overall size distribution (Fig. 3A). The size distribution of stage III ranged from 31.3 mm CW to 59.5 mm CW (Fig. 5C) for the nonmorphometrically mature males and generated a mode at 44 mm CW in the overall size distribution (Fig. 3A). All morphometrically mature males determined by the discriminant analysis had stage III vasa deferentia.

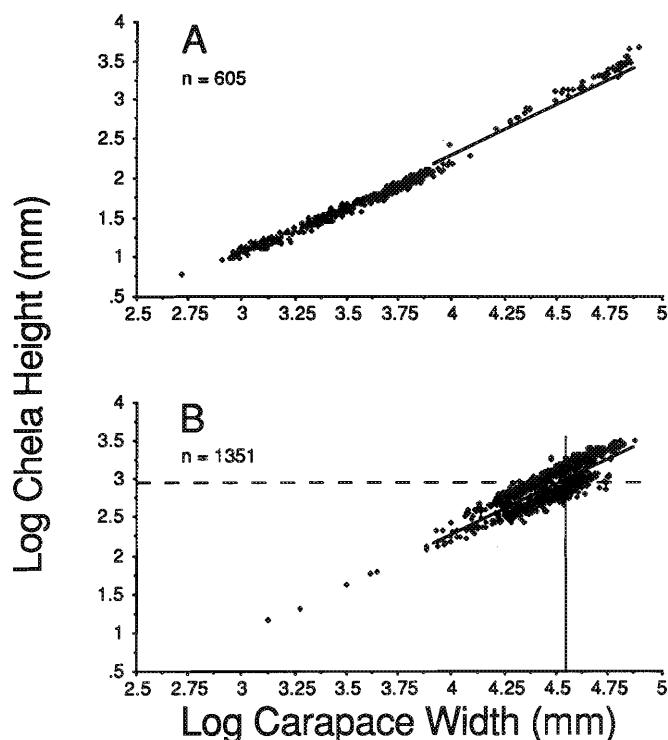


FIG. 4. Relationship between log chela height and log carapace width for male snow crab (*C. opilio*) collected by trawl in Bonne Bay in (A) 1985 and (B) 1990. The cutting line ($\log CH = -2.94 + 1.3 \log CW$) is from a discriminant analysis calculated by Comeau et al. (1991); the upper swarm of points represent the morphometrically mature males and the lower swarm of points represent the immature–juvenile males. In 1990, by switching from the existing minimum legal size of 95 mm CW to an equivalent 20 mm CH, the proportion of juvenile males retained would have decreased by 26% (from 36 to 10%), while the proportion of morphometrically mature males would have increased by 15% (from 53 to 68%).

The morphometrically mature males' VSI was inversely correlated with CW (Fig. 6). Although the size range is small for the old-shell males and the inverse relationship less obvious, the relationships between VSI and CW do not differ significantly ($p = 0.2$) between new-shell and old-shell morphometrically mature individuals. The VSI was significantly ($p < 0.05$) lower for juvenile males compared with morphometrically mature males and was not correlated with CW (Fig. 6).

Gonad Maturity

The logistic maturity curve (Fig. 7) indicates that 50% of male individuals reach gonad maturity as defined by the presence of spermatophores, at 34.2 mm CW.

The plot of log CH versus log CW for immature–juvenile males (Fig. 8) reveals that two distinct intersecting allometric lines may provide a better fit than a single one. A regression line was fitted to each of the sets of points identified by the criterion absence (stages I and II; Fig. 5A and 5B) or presence (stage III; Fig. 5C) of spermatophores in the vasa deferentia. These regression lines differ in slope ($p < 0.05$) when compared by ANOVA. A single regression does not provide as good a fit as $p < 0.05$ when tested by Gaertner and Lalo  s (1986) method. The two regression lines intersect at a CW value $K_{CW} = 34.0$ mm, thus separating an immature from a juvenile stage (Fig. 8).

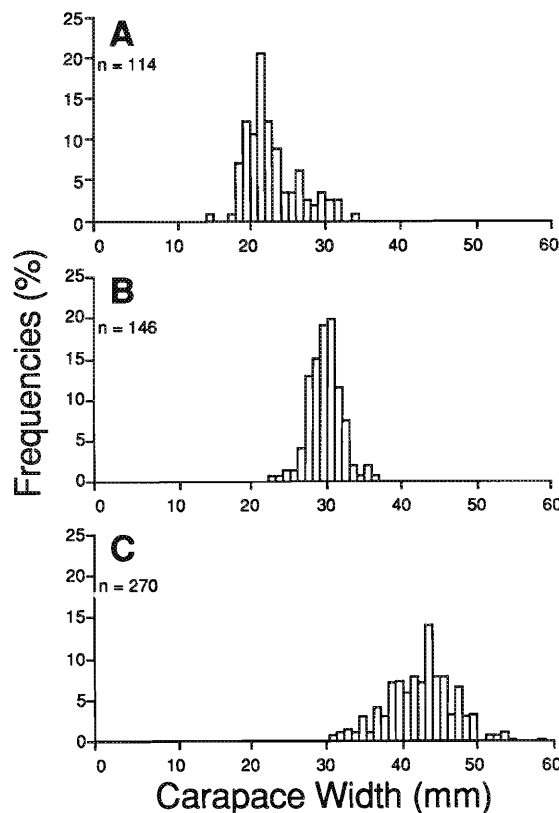


FIG. 5. Size frequency distributions for immature and juvenile male snow crab (*C. opilio*) of the three stages of vasa deferentia development observed in Bonne Bay in 1985: (A) stage I (vasa deferentia not differentiated), (B) stage II (vasa deferentia morphologically differentiated, but no spermatophores are observed), and (C) stage III (spermatophores inside the vasa deferentia).

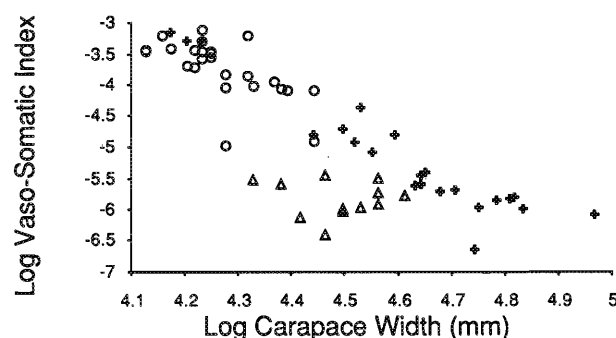


FIG. 6. Relationship between log vaso-somatic index (wet weight of the vasa deferentia/total wet weight of the animal) and log carapace width for juvenile (Δ ; $n = 12$), new-shell ($+$; $n = 23$), and old-shell (\circ ; $n = 26$) morphometrically mature snow crab (*C. opilio*) males.

Discussion

Gonad Maturity

The three morphological stages of vasa deferentia development we observed in 1985 by macroscopic and microscopic observations appear to be equivalent to the first three of the four stages defined by Powles (1968) and by Watson (1970) (Table 1). The stages I and II define, respectively, males with undifferentiated vasa deferentia and males with differentiated vasa deferentia but no spermatophores. The third

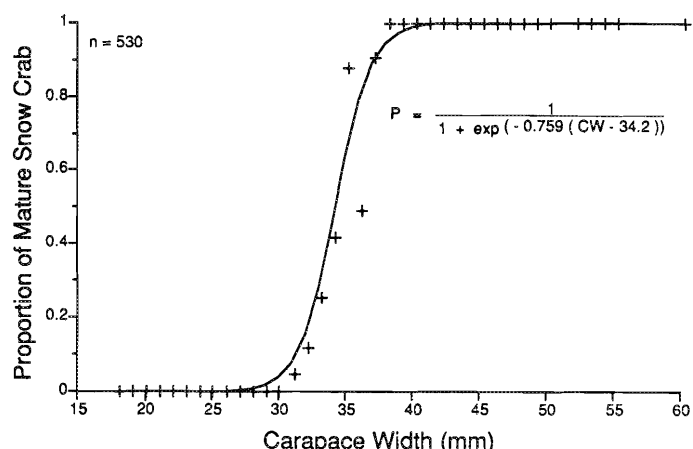


FIG. 7. Relationship between the proportion of males reaching gonad maturity (as defined by the presence of spermatophore in the vasa deferentia) and carapace width of snow crab (*C. opilio*) in Bonne Bay. Fifty percent of male snow crab reached gonad maturity at 34.2 mm CW.

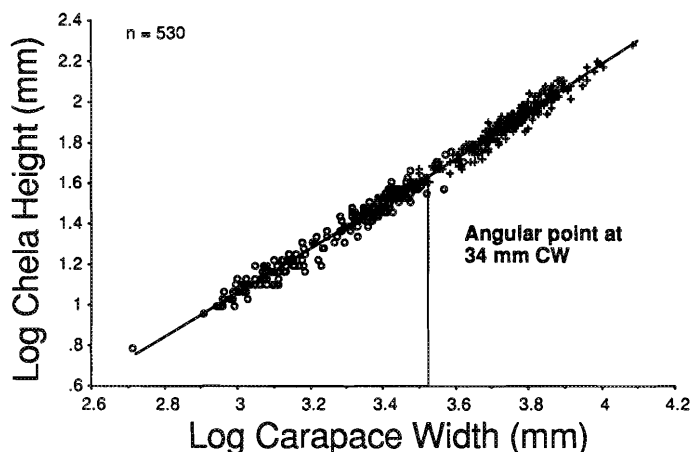


FIG. 8. Relationship between log chela height and log carapace width for male snow crab (*C. opilio*): ○, immature males (stages I and II of the gonad maturity); +, juvenile males (stage III of the gonad maturity). Immature males: $\log CW = -2.23 + 1.09 \log CH$, $n = 260$; juvenile males: $\log CW = -2.52 + 1.18 \log CH$, $n = 270$.

stage regroups males with mature (functional) gonads, and with well-developed, opaque, and convoluted vasa deferentia containing spermatophores.

Powles (1968) and Watson (1970) described the first two stages of vasa deferentia development as "immature," the third as "mature developing," and a fourth stage as "mature ripe" with convoluted, opaque, coiled vasa deferentia extending to fill most of body cavity. Stage 4 "mature ripe" was not observed on morphometrically mature or juvenile males from Bonne Bay in 1985. As shown in Fig. 6, the VSI (wet weight of vasa deferentia/wet total weight) of morphometrically mature males varies inversely in a harvested reference stock with the overall size of the individuals. Powles (1968) and Watson (1970) defined stage 4 solely on the qualitative basis of appearance and volume of the vasa deferentia relative to body cavity. Conan and Elner (R. W. Elner, Environment Canada, P.O. Box 340, Delta, B.C. V4K 3Y3), while diving in Bonne Bay in 1984, observed on the mating grounds a proportion of 1/3 bachelor males to 2/3 males in couples (only

morphometrically mature males were considered) and no solitary females. Stage 4 males were abundant in the Bonne Bay population at that time (pers. obs.). Since 1985, as the population structure evolved, the sex ratio of morphometrically mature males and mature females became unbalanced in favor of females (1:7 in 1985; Comeau et al. 1991) and morphometrically mature male bachelors have been scarce or absent on the Bonne Bay mating grounds (pers. obs.). In a population containing a high proportion of morphometrically mature males, such as in the Gulf of St. Lawrence prior to the present intensive fishing activity (Chiasson et al. 1992), the sex ratio was not unbalanced in favor of females (Brunel 1962, 1963) and stage 4 males were frequently found (Watson 1970). Conversely, in a population intensively harvested, such as presently in the Gulf of St. Lawrence, the number of mature females widely exceeds the number of large morphometrically mature males (Chiasson et al. 1991) and stage 4 males can no longer be found except for very small old-shell males (Y. Chiasson, DFO, P.O. 5030, Moncton, N.B. E1C 9B6). Thus, our interpretation is that Powles' (1968) and Watson's (1970) stage 4 is not a state of maturity of the males, but a state of depletion of the vasa deferentia by spermatophores in small males which are less successful in mating due to competition. Consequently, their vasa deferentia appear more replete than those of larger males.

The three stages of vasa deferentia development are successive and appear to correspond to three successive molt-groups. We suggest that males from stages I and II generate, respectively, modes at 22 mm CW and 31 mm CW in the CW frequency distribution. Males generating a mode at 44 mm CW in the frequency distribution pertain to the first molt-group of stage III. The molt increments presented in this study were approximately 41–42%, which is similar to the percentages of increase between instars found by Robichaud et al. (1989) for small crab caught off Cape Breton in the Gulf of St. Lawrence.

The size at which 50% of males reached their gonad maturity in Bonne Bay (34.24 mm) is much lower than the 57 mm CW observed by Watson (1970), on the basis of the presence of spermatophores in the vasa deferentia in the Gulf of St. Lawrence. A relationship between the development of the vasa deferentia and the presence of molt-groups is given in Kon and Honma (1970) for *C. opilio* in Japan. Male snow crab from Japan reach gonad maturity at instar IX (49.2 mm CW). Spermatophores were not observed by these authors in the vasa deferentia of males during instar VIII (36.8 mm CW). The carapace sizes corresponding to the appearance of spermatophores in the vasa deferentia indicated by Kon and Honma (1970) are somewhat larger than in the Bonne Bay data. Geographical or year-to-year variations may explain the differences in our results.

Relationship between Morphometric Maturity and Gonad Maturity

The allometric relationship between CH and CW for male snow crab is characterized by a shift in ordinate generating a discontinuity between two parallel segments representing immature–juvenile males and morphometrically mature males. These two stages of development are separated by a molt to maturity which is reached over a wide range of sizes for distinct individuals. Watson (1970) observed a small overlap of the two swarms of points from 51 mm CW to 71 mm CW for male snow crab collected from the Gulf of St. Lawrence in 1968 and 1969 prior to the opening of the snow crab fishery. Our data showed that the small overlap of the swarms in the allometric

TABLE 2. Biological characteristics of the terminology used in this paper to describe gonadal, vasa deferentia, and morphometric maturity suggested for snow crab (*C. opilio*) based on Conan et al. (1988b).

Stage of morphometry	Critical molt marking transition to next stage	Size range	Stage of gonad maturity	Vasa deferentia morphology	Presence of spermatophores	Size range
Immature	The "juvenile molt" is reached at a common size for all individuals; it is marked by an angular point separating two distinct allometric relationships	Males <34 mm CW	I	Not morphologically differentiated	No	Males <33 mm CW; major mode at 22 mm CW
			II	Morphologically differentiated as translucent straight tubes	No	22–37 mm CW; major mode at 31 mm CW
Juvenile	The "molt to maturity" is reached at sizes specific to each individual; it is marked by a discontinuity between two distinct allometric relationships	34–120 mm CW (chela nondifferentiated)	III	Opaque with shape varying from straight tube to a strongly coiled mass	Yes	50% maturity at 34 mm CW; all males >37 mm CW
Morphometrically mature	N/A (terminal molt males)	Males >50 mm CW with differentiated chela				

relationship (Fig. 4A) observed in Bonne Bay in 1985 changed into a wide overlap (Fig. 4B) over a period of 5 yr. During that time in Bonne Bay, Comeau et al. (1991) observed a decrease in the number of large morphometrically mature males (due to natural mortality) from 1985 to 1988 followed by the appearance for the first time in 1990 of large juvenile males with carapaces older than 1 yr, i.e. having skipped the spring molt period. The present pattern in Bonne Bay (1990) is quite similar to the pattern of the exploited population in the Gulf of St. Lawrence observed by Conan and Comeau (1986) in 1984. These observations corroborate Waiwood and Elner's (1982) suggestion that the removal of large old crabs would release the snow crab population from a "stagnant" phase into a "dynamic," high-growth phase. Thus, we hypothesize that the removal by fishing, as seen in the Gulf of St. Lawrence, and/or natural mortality, as seen in Bonne Bay, of large morphometrically mature males from the accumulated biomass reduces the mortality of juvenile males, therefore allowing for survival and growth within the lower swarm of points of immature and juvenile morphometric stages. A possible explanation is that at the nonoverlapping swarms stage in the dynamics of a natural population, the structure is maintained in equilibrium by cannibalism of large terminal molt males on juvenile males of similar sizes at the time of their molt.

The shift in ordinate of CH versus CW allometry lines defining two types of male snow crab had been observed but not satisfactorily interpreted by previous authors (Powles 1968; Watson 1970; Coulombe et al. 1985), who associated the "maturity" of gonads with morphometric maturity. Conan and Comeau (1986) provided the functional interpretation of the molt to maturity and its identity with a terminal molt that we presently use. In the present study, we now have shown for *C. opilio* the presence of a third allometric stage at sizes smaller than 34 mm CW prior to gonad development. In other majid

crab species, Teissier (1935) had also detected an "immature" to "juvenile" transition on the basis of morphometry, but had not identified a biological "raison d'être" for this angular point between allometric lines, although he (Teissier 1948, 1960) suspected this transition to correspond to important physiological changes. Hartnoll (1982) mentioned that "the molt to maturity need not coincide with the maturation of the gonads, but it almost invariably indicates entry into the instar in which sexual activity will commence."

We now conclude that maturity of male *C. opilio* is reached through three allometric steps (Table 2) coinciding firstly with differentiation of primary sexual characters (functional gonads) and secondly with differentiation of secondary sexual characters (claw morphometry), related to behavioral (Conan and Comeau 1986) and hormonal changes, as documented by Cormier et al. (1992) on *C. opilio* and indirectly by Homola et al. (1991) on *Libinia emarginata*. These modifications are required by the males to efficiently mate with multiparous females (Conan and Comeau 1986; Ennis et al. 1990; Comeau et al. 1991; Sainte-Marie and Hazel 1992).

Implication for the Fishery

The peculiar majid growth pattern of *C. opilio* has important implications for fishery management. The benefits of setting a minimum legal size should be reconsidered due to the presence of a terminal molt reached by males over a wide range of carapace sizes. The Gulf of St. Lawrence snow crab fishery presently harvests indiscriminately juvenile and morphometrically mature males larger than 95 mm CW (Elner and Robichaud 1986; Comeau and Davidson 1987; Chiasson et al. 1991). In terms of yield-per-recruit, a large proportion of individuals will never grow to the minimum legal size and will never become harvestable. It is advisable for both conservation of stocks (allowing males to reproduce before being caught) and

enhancement of yield (allowing the juvenile males to grow until they reach the terminal molt) to minimize harvesting of juvenile males and maximize harvesting of morphometrically mature males. Due to the particular morphometry of juvenile versus morphometrically mature males, if the minimum harvestable size were defined as a function of chela size rather than the present carapace width, more terminal molt (morphometrically mature) and less preterminal molt (juvenile) crab would be selectively retained as commercial catch (Fig. 4B). An even more efficient, but possibly less practical, alternative would be to use a minimum legal "size" based on two measurements and a bivariate discriminant function (Conan and Comeau 1986). A specially designed electronic gauge allowing direct calculation of a discriminant score CH versus CW would be 99% efficient.

An alternative to a minimum size of either chela or carapace, in order to achieve maximal yield-per-recruit and protect the reproductive potential of the stock, would be to design, as suggested by Conan and Comeau (1986), a type of fishing gear to catch or selectively retain only morphometrically mature animals.

The effects of heavy exploitation of males larger than 95 mm CW on the stock reproductive potential are not yet fully understood. The selective harvesting of large terminal molt males potentially increases efficiency of small terminal molt males to mate by reducing competition pressure from larger dominant terminal molt males. As mentioned by Elner et al. (1986) and by Conan et al. (1988b), this could result in an artificial genetic selection in favor of males reaching terminal molt at small sizes, if an early propensity to molt to morphometric maturity were a genetically inherited character. Fortunately, the storage of spermatophores from large males in the spermatheca of females (Watson 1970) may partially compensate for the depletion of large terminal molt males by fishing.

A detailed knowledge of growth, including the probability for crabs to reach terminal molt as a function of size or age, is required prior to developing a sound yield-per-recruit model. Such a model would allow calculation of parameters such as minimum claw size, effort, catch/biomass ratio, and period for rotation of fishing grounds, optimizing the fishery yield.

Acknowledgments

The authors wish to thank Drs. T. W. Sephton and M. Starr, Mr. G. Chaput, R. Cormier, and F. Maynou for their critical comments on an earlier version of this manuscript as well as Mr. P. Mallet for his laboratory assistance.

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