Reproductive Cycle and Fecundity of Primiparous and Multiparous Female Snow Crab, *Chionoecetes opilio*, in the Northwest Gulf of Saint Lawrence

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A total of 1 691 mature female *Chionoecetes opilio* was collected by beam trawl in Baie Sainte-Marguerite on seven occasions from April 1991 to May 1992. Quantitative analyses of ovaries, brood, eggs, and spermathecal contents were performed on a subsample of 318 females. Females moulted to maturity in March and April. Development of ovaries and brood were phased and lasted 24–27 mo. Eggs hatched mainly from April to June. Spermathecae contained zero to three ejaculates, and the mean blotted weight of freshly deposited ejaculates was significantly greater in primiparous (0.513 g) than in multiparous (0.249 g) females. The weight of stored ejaculates decreased over time independently of spawning events. Fecundity was correlated positively with carapace width and negatively with mean egg diameter. Eggs of primiparous females were on average 1.4–2.7% larger, but 16.4–22.7% fewer per brood, than those of multiparous females. Some large multiparous females had small broods, due possibly to lesser fertility. Females probably hatch only two broods in a lifetime and produce a total of 81 630 to 83 143 larvae at 57.4 mm carapace width. Primiparous females apparently contribute >40% of larvae produced by the population.

Un total de 1 691 femelles matures de *Chionoecetes opilio* a été capturé à l'aide d'un chalut à perche au cours de sept campagnes effectuées dans la baie Sainte-Marguerite d'avril 1991 à mai 1992. L'analyse quantitative des ovaires, de la portée, des oeufs et du contenu des spermathèques a été réalisée sur un sous-échantillon de 318 femelles. Les femelles deviennent matures en mars et avril. Les ovaires et la portée se développent de façon synchrone sur une période de 24 à 27 mo. L'éclosion des oeufs a lieu surtout d'avril à juin. Les spermathèques contiennent de zero à trois éjaculats et le poids humide moyen des éjaculats récemment déposés est significativement plus élevé chez les femelles primipares (0,513 g) que chez les femelles multipares (0,249 g). Le poids des éjaculats entreposés décroit avec le temps et ce, indépendamment de la ponte. La fécondité était corrélée positivement avec la largeur de la carapace et négativement avec le diamètre moyen des oeufs. Les oeufs des femelles primipares sont 1,4 à 2,7 % plus gros, mais 16,4 à 22,7 % moins nombreux par portée, que ceux des femelles multipares. Quelques femelles multipares de grande taille ont de petites portées, possiblement pour cause d'infertilité partielle. Les femelles ne libèrent probablement que deux portées au cours de leur vie et une femelle de 57,4 mm de largeur de carapace produirait au total entre 81 630 et 83 143 larves. Les femelles primipares produiraient >40 % des larves de la population.

emales of the genus *Chionoecetes* (Brachyura: Majidae) have paired spermathecae and are iteroparous. Four types of females may be recognized (Sainte-Marie and Hazel 1992). Immature and pubescent females have narrow abdomens indicating a nonreproductive state. Pubescent females, however, have ripe ovaries and are committed to maturity at the next moult. Mature females are characterized by a broad abdomen and include primary (primiparous) and repeat (multiparous) spawners.

Pubescent females moult to maturity, generally with the help of a male (Watson 1970, 1972; Donaldson and Adams 1989; Sainte-Marie and Hazel 1992), and must be fertilized within days in order to produce a viable brood (Paul et al. 1983; Paul and Adams 1984). The moult to maturity is considered to be the last (Yoshida 1941; Ito 1963; Watson 1972; Hilsinger 1976), so females subsequently mate in the hard-shell condition (Somerton 1981; Adams 1982; Taylor et al. 1985). However, like

other majids, female *Chionoecetes* may produce more than one viable brood from sperm deposited in the spermathecae (e.g., Hartnoll 1965; 1969; Watson 1970, 1972; Adams and Paul 1983; Paul et al. 1983; Paul 1984; Diesel 1989).

Primiparous and multiparous *Chionoecetes* may differ in fecundity and in quality of progeny. Development of ovaries in brachyuran crabs is limited by the volume of the body cavity (Hines 1982, 1992). In Tanner crab, *C. bairdi*, primiparous females are less fecund than multiparous females for a constant carapace width, possibly because brood size of primiparous females depends on premoult body size (Somerton and Meyers 1983). However, pubescent females must also allocate energy simultaneously to somatic and gonadic growth, with unknown effects on broods (Somerton and Meyers 1983; Hartnoll 1985; Elner and Beninger 1992). Finally, for *C. bairdi* and snow crab, *C. opilio*, there is evidence that mates of pubescent females are smaller than those of multiparous females (Somerton 1982;

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TABLE 1. Criteria used for rating exoskeleton condition, apparent age, and brood development of mature female *C. opilio*.

Female characteristic	Criteria
Exoskeleton condition	
Clean soft	Exoskeleton soft and immaculate; carapace devoid of epizoites; chelae iridescent
Clean hard	Exoskeleton hard and immaculate; carapace devoid of epizoites; chelae iridescent
Intermediate	Exoskeleton hard and marked or lightly scarred; carapace with small epizoites; chelae more or less iridescent
Dirty hard	Exoskeleton hard, dirty, and heavily scarred; carapace with extensive bryozoan mats and other numerous and often large epizoites; chelae dull
Dirty soft	Exoskeleton soft, dirty, and heavily scarred; carapace with extensive bryozoan mats and other numerous, large, and often dead epizoites; chelae dirty
Apparent age	
New recruit	Exoskeleton in clean soft, clean hard, or intermediate condition; no mating scars on pereiopods
Old recruit	Exoskeleton in intermediate, dirty hard, or dirty soft condition; generally with mating scars on pereiopods
Brood development	
Stage 1	No brood
Stage 2	Orange eggs
Stage 3	Dark-orange eggs with developing eyespots
Stage 4	Dark-brown or purple, eyed eggs
Stage 5	Empty egg shells, possibly mixed with dark, eyed eggs
Stage 6	Degenerating eggs

Sainte-Marie and Hazel 1992; Stevens et al. 1993). The vast majority of males that mate with both types of females are morphometrically mature (Conan and Comeau 1986; Ennis et al. 1988, 1990; Sainte-Marie and Hazel 1992; Stevens et al. 1993) and the size at which this condition is achieved might be an inheritable trait (Conan 1986; Elner et al. 1986; Bailey and Elner 1989). Consequently, primiparous and multiparous females may produce genetically different progenies.

Commercial exploitation could lead to increased participation of small males in reproduction. Male competition for females and size dimorphism in favour of males in mating pairs are common features of breeding Brachyura (Christy 1987), and specifically of *Chionoecetes* (Brown and Powell 1972; Taylor et al. 1985; Conan and Comeau 1986; Ennis et al. 1988, 1990; Sainte-Marie and Hazel 1992). *Chionoecetes* fisheries in North America target only the largest males because of a minimum size regulation that excludes all females and small males (Miller 1976). A possible consequence is a reduction of competition and increase of the breeding activity of small males, as suggested for *Chionoecetes* (Bailey and Elner 1989) and other brachyurans (Butler 1960). Alternatively, if suitable male mates are unavailable, large primary spawners may extrude and carry nonviable broods, while large repeat spawners may rely on stored sperm acquired from small males at the first mating.

In the present work, I compared the reproductive cycle and fecundity of primiparous and multiparous *C. opilio* in light of the above hypotheses. A prime objective was to determine the relative contribution of primiparous and multiparous females to population reproductive output. This study also serves as a backdrop for experiments on reproduction and heritability in *C. opilio*.

Materials and Methods

Collection and Treatment of Females

Snow crab were collected from Baie Sainte-Marguerite (~50°06′N, 66°35′W), in the northwest Gulf of Saint Lawrence (for maps and site description, see Sainte-Marie et al. 1988; Sainte-Marie and Hazel 1992). The Bay is intensively fished and despite an area of only ~270 km² shoreward of the 150-m isobath, it yielded ~218 t of snow crab in 1992, which represented the highest catches per unit area on the north shore of the Gulf.

Sampling was conducted on April 11–15, June 19–24, August 22–29, October 23–29, and December 11–12, 1991, and on March 19–21 and May 12–14, 1992. Snow crab were collected with a 3-m beam trawl during 15- to 20-min tows at three randomly selected locations in each of three depth strata: 4 to ≤20 m, >20 to ≤80 m, and >80 to 140 m. Ship speed was 2.5–3 kn. Trawl contents were sorted onboard. Mature females were recognized by their large and rounded abdomen which almost completely covers the cephalothoracic sternites. These females were measured and their exoskeleton condition, apparent age, and brood development determined as described below and in Table 1.

On the first six dates, a sample of mature females was fixed by injection of, and immersion in, 4% buffered formalin in seawater. In the laboratory, preserved females were again rated for exoskeleton condition, apparent age, and brood development according to criteria in Table 1. The widths of carapace (CW) and fifth abdominal segment (AW) at their broadest points were measured with a vernier caliper to the nearest 0.01 mm. The numbers of missing and of regenerated pereiopods were recorded.

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The weight of blotted females was determined to the nearest 0.01 g. Weights of blotted brood and ovaries, along with two subsamples each of 20 eggs, were measured to the nearest 10^{-5} g. Fecundity was determined as the ratio of brood weight to mean egg weight. Diameters of 10 randomly chosen eggs from each female were measured to the nearest 0.01 mm with an eyepiece micrometer. When the egg was ovoid, as occasionally was the case, diameter was calculated as the mean of the long and short axes. The spermathecae were sectioned longitudinally and the discretely layered ejaculates were counted. Recent ejaculate was whiter than old ejaculate, as reported for *C. bairdi* (Adams and Paul 1983), and was located in the ventral part of the spermatheca. The weight of blotted recent ejaculates from both spermathecae was determined to the nearest 10^{-5} g.

Analysis of Data

Data were $\log_{10}$ transformed to account for the known allometric relationships between reproductive traits (e.g., Hines 1982). The resulting multivariate data set, exclusive of ejaculate weight, was explored using partial correlation analysis to measure the degree of association between two variables while the effects of other specified variables were held constant (Sokal and Rohlf 1981). Simple or multiple linear regression was used to describe relationships between variables. Comparison of significant regressions proceeded in two steps. First, the slopes were tested for equality by analysis of variance. Second, when slopes were equal, elevations were tested for equality by analysis of covariance (Sokal and Rolf 1981). Statistics used for univariate data are the mean and standard error.

Results

Seasonal Changes in Exoskeleton Condition and Brood

A total of 1691 mature females, ranging from 40 to 77 mm CW, were sampled from March 1991 to May 1992. Clean soft females were captured only in April 1991 and in March 1992 in shallow waters, coincident with diver observations of moulting pubescent females on bottoms <35 m deep (Sainte-Marie and Hazel 1992, and unpublished data). The 1991 new recruits were distinguished from other females with a high degree of confidence until December 1991. Thereafter, accumulated fouling and scarring rendered categorization uncertain. For the March 1992 sample, a conservative approach was adopted and only the least fouled and least scarred females with hard exoskeletons were categorized as 1991 new recruits. Thus, I was able to distinguish new from old recruits for 9 mo after the moult to maturity; Ito (1967) separated these two types of females for 6 mo by shell hardness alone.

Females with Stage 2 broods (orange eggs) dominated samples at all times of the year, but there was obvious seasonal variation (Fig. 1). All but one female had Stage 2 broods in August 1991. Thereafter, the proportion of females with Stage 3 and Stage 4 broods increased gradually to a maximum of 24.3% in March 1992, similar to the observed 22.7% in April 1991. Females with Stage 5 (hatching) broods were found most frequently in June 1991 and in May 1992. Barren females were very scarce throughout the year.

Ovary and Brood Development

None of the 318 mature females dissected in the laboratory had a second carapace, nor incidentally did any of the 1691
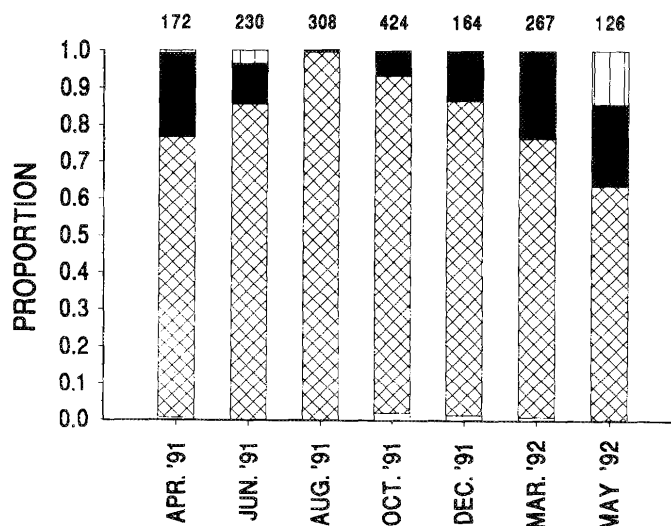

FIG. 1. Proportions of female *C. opilio* with broods at different stages of development in Baie Sainte-Marguerite from April 1991 to May 1992. Sample size appears above the bars. The white part of the bars represents barren females, cross-hatching represents females with Stage 2 broods (orange eggs), black represents females with Stage 3 and 4 broods (eyed eggs), and vertical hatching represents females with Stage 5 broods (empty egg shells present).

females from field samples have a visible second shell. These features normally characterize individuals that are committed to moulting (Sainte-Marie and Hazel 1992).

Females represented in scattergrams of weight of ovaries on carapace width were separated into groups with different spawning histories, on the basis of apparent age and brood development (Fig. 2). In each scattergram, an oblique line was traced to separate 1991 new recruits from old recruits higher on the ordinate. Another oblique line in the March scattergram separated 1992 new recruits from 1991 new recruits. In the April, June, and August scattergrams, an additional oblique line separated females with Stage 3–5 broods from those with Stage 2 broods. The groups formed by these lines were numbered I–IV. All lines had a slope of 2.9, which was determined by trial and error to be the only slope that consistently allowed separation of females according to the above criteria. Work by B. Sainte-Marie and G.A. Lovrich (in preparation) provided a posteriori justification for the slope value and parallelism of separating lines. First, the 2.9 slope value fell within the 95% confidence interval of the regression coefficient of weight of ovaries on carapace width determined for 84 primiparous females sacrificed in formalin ≤ 12 h after extrusion of eggs. Second, at various fixed times before or after brood extrusion by primiparous females, the slopes of regressions of weight of ovaries on carapace width were found to be constant, while ordinates (y-intercepts) increased with ovary (or brood) development.

The weight of ovaries of 1991 new recruits increased from April 1991 to March 1992 but broods remained in Stage 2. In June 1991, the presence of females with Stage 5 (hatching) broods and an influx of many old recruits to Group II indicated that larval release and egg extrusion were underway for Group IV females. The 1991 recruits thus served as "tracers" for old recruits that respawned in 1991. Weight of ovaries in Group III also increased from April 1991 to March 1992, while broods remained in Stage 2 until August 1991 and from thereon
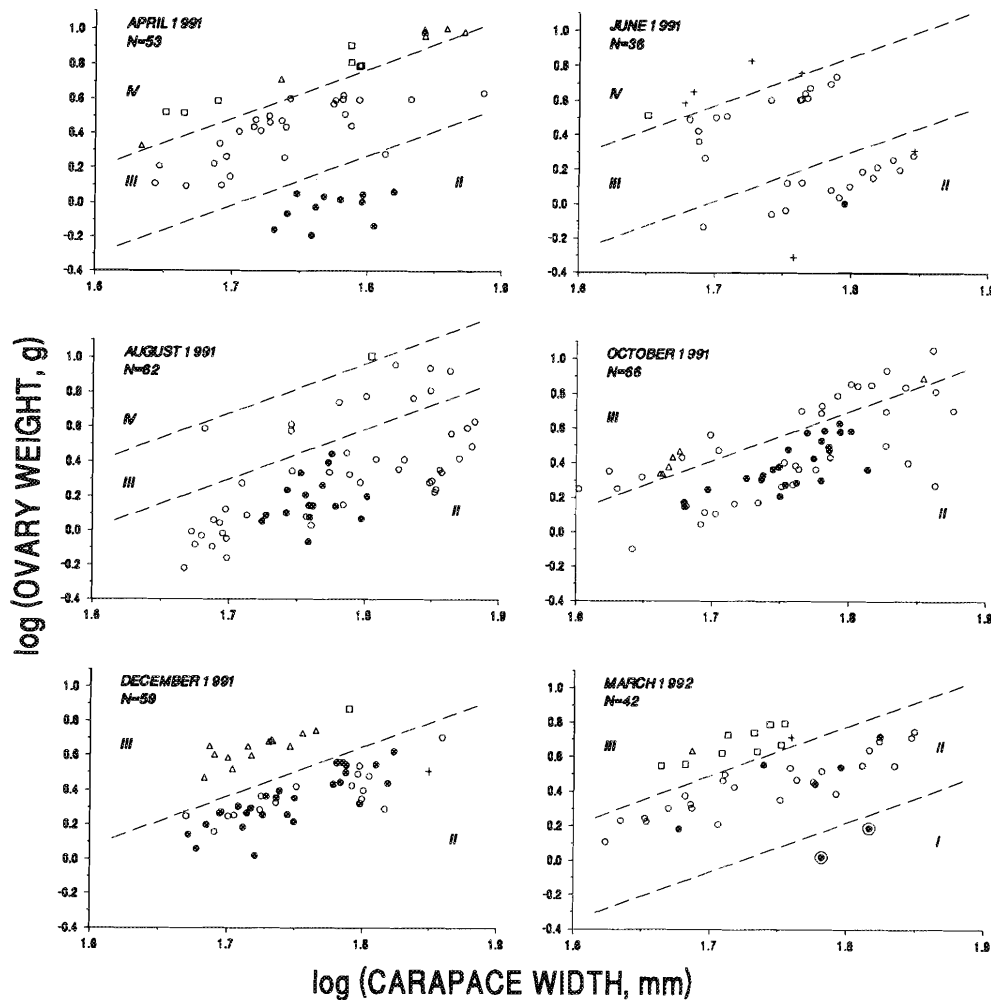
FIG. 2. Scattergrams of weight of ovaries on carapace width for mature female *C. opilio* collected in Baie Sainte-Marguerite from April 1991 to March 1992. Broken lines were fitted by eye and all have the same slope; they separate female Groups I–IV on the basis of apparent age and brood development. Group II females in April 1991 and Group I females in March 1992 had clean soft exoskeletons. Note that the broken line separating Group IV from Group III in April 1991 is in exactly the same position as the line separating Group III from Group II in March 1992. ◉; 1992 new recruit with Stage 2 brood (orange eggs); ●, 1991 new recruit with Stage 2 brood; ○, old recruit with Stage 2 brood (orange eggs); △, old recruit with Stage 3 brood (eyed eggs); □, old recruit with Stage 4 brood (dark, eyed eggs); +, old recruit with Stage 5 (hatching) or no brood; *N*, sample size.

gradually changed to Stage 4.

Group II females marked by plus signs in June and December scattergrams were barren or had degenerating broods. One of these females (1.76 log CW, June) was senescent, judging from the dirty soft exoskeleton and necrosing gills. The scarcity of 1991 new recruits in June may be an artefact of sampling: in May and June, females moving offshore away from the shallow moulting ground (Sainte-Marie and Hazel 1992) cross relatively steep terrain which is not adequately sampled by our beam trawl.

The slopes of regressions of weight of ovaries on carapace width did not vary across female groups and sampling times ($P = 0.816$, June Group IV and March Group I excluded), but analysis of covariance pointed to significant differences in elevation ($P < 0.001$). For each combination of female group and sampling period, the weight of ovaries was adjusted (Fig. 3) to the overall mean carapace width of females (57.4 mm). Adjusted weight of ovaries increased between April 1991 and March 1992 from −0.065 (i.e., 0.86 g) to 0.470 (i.e., 2.95 g) in Group II and

from 0.458 (i.e., 2.87 g) to 0.762 (i.e., 5.78 g) in Group III. Adjusted weight of ovaries did not differ between Group I in March 1992 and Group II in April 1991 ($P = 0.434$), between Group II in March 1992 and Group III in April 1991 ($P = 0.636$), and between Group III in March 1992 and Group IV in April 1991 ($P = 0.483$). Adjusted weight of ovaries in Group IV varied from 0.735 (i.e., 5.44 g) in April 1991 to 0.875 (i.e., 7.51 g) in August 1991, but differences for any pair of sampling dates (April, June, or August 1991) were not significant ($P \geq 0.125$). Incidentally, the log weight of ovaries ≤12 h after extrusion of eggs was estimated by regression to be −0.08 ± 0.07 for a 57.4 mm CW primiparous female sacrificed in formalin (B. Sainte-Marie and G.A. Lovrich, in preparation), a value very close to the −0.06 ± 0.03 obtained for Group II females in March 1991 (Fig. 2). This confirms that new recruits sampled in March 1991 were beginning their reproductive cycle.

The weight of ripe ovaries of females in Group IV was comparable with the weight of recently extruded broods in old
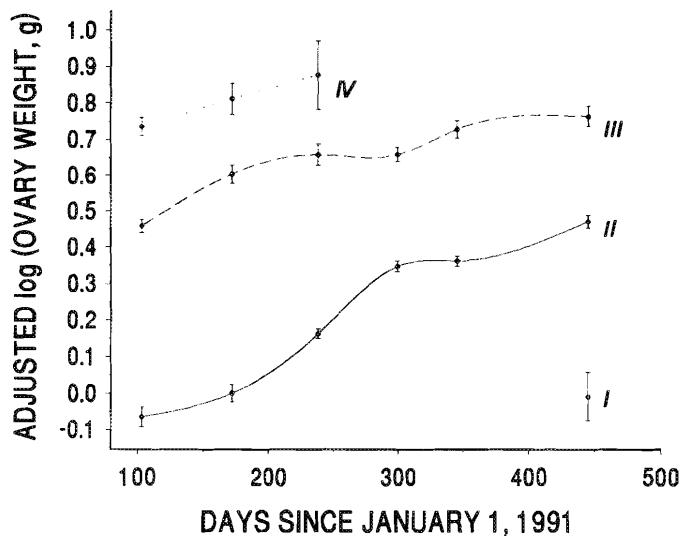
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FIG. 3. Adjusted log weight ± 1 SE of ovaries as a function of elapsed time for Groups I–IV of mature female *C. opilio* collected in Baie Sainte-Marguerite from April 1991 to March 1992. Weight of ovaries was standardized for a constant 57.4 mm CW by analysis of covariance.
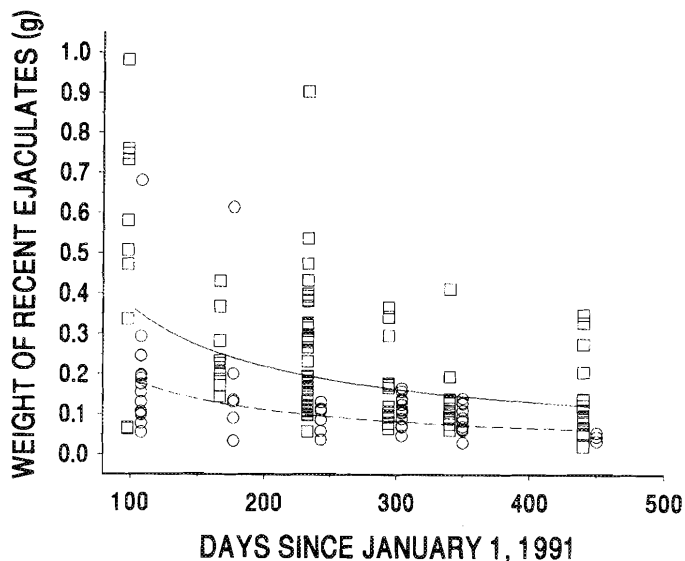

FIG. 4. Weight of recent ejaculates in spermathecae as a function of elapsed time for Groups II and III of mature female *C. opilio* collected in Baie Sainte-Marguerite from April 1991 to March 1992. Squares and solid line ($Y = 11.455 \cdot X^{-0.745}$) represent Group II females; circles and broken line ($Y = 5.794 \cdot X^{-0.745}$) represent Group III females. Adjusted equations were fitted to the data after equality of slopes was demonstrated. Data points are staggered by −10 d (□) and +10 d (○) about sampling time.

recruits from Group II. The predictive regression of brood weight (BW, in grams) on carapace width (CW, in millimetres) for the June 1991 sample of Group II old recruits was

(1) $\log BW = 1.967 \log CW - 2.513$

$$N = 14, \, r^2 = 0.714, \, F = 27.41, \, P < 0.001.$$

From this regression, the weight of a recently extruded brood estimated for a 57.4 mm CW female was 0.948 ± 0.055 (i.e., 8.87 g), a value close to the adjusted weight of ovaries of Group IV (i.e., ripe) females in June (0.811 ± 0.042) and August (0.875 ± 0.094) of 1991.

Female maturity indices used so far with *Chionoecetes* species were based on the ratio of weight of ovaries to body weight exclusive of ovaries and, sometimes, of brood. These indices are biased if the female is not whole (Hilsinger 1976). For my sample of females, regression of total body weight (FW, in grams) on carapace width (CW, in millimetres) and on numbers of missing (MP) and of regenerated (RP) pereiopods gave

(2) $\log FW = 2.773 \log CW - 0.023 MP - 0.022 RP - 3.020$

$$N = 318, \, R^2 = 0.939, \, F = 1622.79, \, P < 0.001.$$

The three coefficients were highly significant ($P < 0.001$). Each pereiopod thus accounted for about 5.1% of total body weight. Since only 55% of the females were whole, with the remaining females each missing up to five pereiopods or having up to two regenerated pereiopods, weight of ovaries adjusted for carapace width is a more appropriate index of maturity than indices based on weight ratios. Another advantage is that carapace width does not change after the moult, while body weight exclusive of ovaries and brood is subject to temporal variation due to somatic growth and fouling.

Number and Weight of Ejaculates

Females judged to be new recruits ($N = 84$) had zero (1.2% of

84) or one (98.8%) ejaculate per spermatheca, while females judged to be old recruits ($N = 234$) had one (10.3%), two (88.0%), or three (1.7%) ejaculates per spermatheca. In four females, one spermatheca contained an ejaculate, while the other was empty. The weight of recent ejaculates was not correlated with female carapace width ($r = 0.073, P > 0.33$).

The total quantity of ejaculate remaining in spermathecae, shortly after brood extrusion, was greater in new than in old recruits. Twelve of 13 new recruits from April 1991 and March 1992, compared with 10 of 15 old recruits in Group II from April and June 1991, had recent ejaculates in their spermathecae. The weight of recent ejaculates was 0.513 ± 0.079 g in new recruits and 0.249 ± 0.028 g in old recruits (*t*-test: $t = 2.91, P = 0.009$). Up to 0.982 g of recent ejaculate was found in one female (Fig. 4), a primary spawner sampled in April 1991.

Recent ejaculates in the spermathecae gradually darkened and decreased in weight over time ($P < 0.001$) in Group II and Group III females (Fig. 4). Slopes of regressions of ejaculate weight on time were similar for both groups of females ($F = 1.79, P = 0.183$), but elevations differed significantly ($F = 49.44, P < 0.001$). Adjusted ejaculate weight was −0.705 ± 0.026 (i.e., 0.197 g) in Group II females and −1.001 ± 0.035 (i.e., 0.099 g) in Group III females. The presence of large quantities (>0.3 g) of recent ejaculate in the spermathecae of a few ovigerous females in Groups III (Fig. 4) and IV (not shown) indicates that females may occasionally be inseminated during the spring breeding period, prior to hatching of their eggs.

Differences in Fecundity and Egg Diameter

Some females were excluded from analyses of fecundity and egg diameter (Fig. 5) because they were barren ($N = 6$), had begun to release their larvae ($N = 2$), or had unusually small

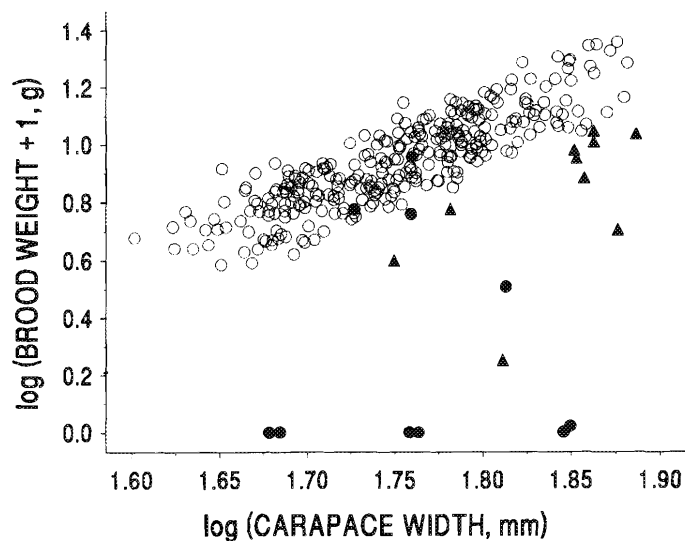*Can. J. Fish. Aquat. Sci., Vol. 50, 1993*

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FIG. 5. Scattergram of brood weight on carapace width for 318 female *C. opilio* collected in Baie Sainte-Marguerite from April 1991 to March 1992. ○, female considered in analyses of brood weight, fecundity, and egg size; ●, female with hatching, degenerating, or no brood; ▲, female with normal-looking but undersized brood.

TABLE 2. Partial correlations between weight of ovaries (OW), carapace width (CW), abdomen width (AW), egg diameter (ED), and brood weight (BW) above diagonal or fecundity (FEC) below diagonal for 298 female *C. opilio* collected in Baie Sainte-Marguerite from April 1991 to March 1992. Note underlined coefficients (P < 0.01). All data were log transformed.

	OW	CW	AW	FEC\BW	ED
OW	—	0.08	−0.09	_0.29_	_0.27_
CW	0.12	—	_0.92_	_0.26_	−0.07
AW	−0.08	_0.94_	—	0.06	0.03
FEC\BW	0.17	_0.22_	0.03	—	0.08
ED	_0.35_	0.00	0.04	_−0.23_	—

broods ($N = 12$). In the last category, two females had degenerating Stage 2 broods; one was a 1991 new recruit with empty spermathecae. Ten other females, including seven old recruits from Group II representing 36.8% of all females ≥71 mm CW, had undersized but otherwise apparently normal broods (Fig. 5).

Partial correlations between weight of ovaries, carapace width, abdomen width, egg diameter, and brood weight or fecundity appear in Table 2. Two separate analyses were performed because fecundity was not measured independently of brood weight. Besides the obvious correlation between widths of carapace and abdomen, five strong partial correlations were of interest. Brood weight and fecundity were positively correlated with carapace width, egg diameter was negatively correlated with fecundity, and brood weight and egg diameter were positively correlated with weight of ovaries, Thus, although there was no change in the appearance of eggs in Group II females with time (Fig. 2), individual eggs increased in volume as ovaries increased in weight.

Two different approaches were taken to contrast fecundity and egg diameter between primiparous and multiparous females. In the first, females with one ejaculate in at least one spermatheca were considered to be primiparous, while females with two or more ejaculates in at least one spermatheca were considered to be multiparous. In the second approach, new and old recruits in Group II from the April–December 1991 period were considered to be primiparous and multiparous, respectively. Both approaches led to the same conclusions, but the definition based on apparent age always produced greater contrasts between reproductive traits of primiparous and multiparous females. The relative differences in brood weight, fecundity, and egg diameter between primiparous and multiparous females are presented below as ranges that reflect the two approaches.

There was no significant difference between the slopes of regressions of log body weight and of log brood weight on log carapace width for whole (i.e., no missing or regenerated pereiopods) primiparous and multiparous females ($P > 0.15$). This was expected, since brood weight scales isometrically to body weight in a variety of other brachyuran crabs (Hines 1982). Elevations of regressions differed significantly ($P < 0.001$). Using values of body weight and brood weight adjusted for a constant carapace width by analysis of covariance, I calculated that brood weight averaged 10.0–10.8 and 11.8–11.9% of body weight in primiparous and multiparous females, respectively.

Multiple regression performed separately on Group II and Group III females showed that fecundity varied with carapace width but was independent of weight of ovaries, as expected from Table 2. Because weight of ovaries increased with time since extrusion (Fig. 3), this observation strongly suggested that fecundity did not change over time. This conclusion was confirmed for Group II and Group III females by multiple regression of log fecundity on log carapace width and on log time elapsed since January 1, 1991. In both cases, fecundity varied positively with carapace width ($P < 0.001$) but independently of elapsed time ($P > 0.390$). Therefore, further comparisons of fecundity did not take into account the temporal component.

Overall predictive regressions of fecundity on carapace width appear in Table 3. The fecundity estimates for primiparous and multiparous females of 57.4 mm CW were, respectively, 37 870 and 45 273 eggs when female type was defined by number of ejaculates and, respectively, 35 597 and 46 033 eggs when female type was defined by apparent age. Thus, primiparous females were about 77.3–83.6% as fecund as multiparous females.

Egg diameter increased with time (see above), from a minimum of 0.58 mm for recently extruded, bright-orange eggs to a maximum of 0.83 mm for ripe, dark-purple eggs. Additionally, multiple regression performed separately on Group II and Group III females showed that log egg diameter varied positively with log time elapsed since January 1, 1991 ($P < 0.006$), and independently of log carapace width ($P > 0.05$). Slopes of regressions of log egg diameter on log weight of ovaries were not significantly different ($P > 0.25$) between primiparous and multiparous females, but elevations differed significantly ($P < 0.015$). For a constant weight of ovaries, egg diameter of primiparous females was 1.4–2.7% greater than that of multiparous females. Incidentally, using the weight of ovaries in lieu of elapsed time can account for variability in the timing of individual reproductive cycles.

Discussion

Reproductive Cycle

Several lines of evidence support the conclusion that females of *C. opilio* in Baie Sainte-Marguerite have a biennial repro-

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TABLE 3. Mature female *C. opilio* from Baie Sainte-Marguerite. Regressions of fecundity (FEC, number of eggs per brood) on carapace width (CW, in mm) for females with one or more ejaculates in at least one spermatheca and for Group II new and old recruits sampled from April to December 1991. Slopes and elevations were compared by analyses of variance and covariance, respectively. Adjusted equations were fitted to the data after equality of slopes was demonstrated. r^2, coefficient of determination; F, F-statistic; ns, $P > 0.2$; ***$P < 0.001$; N, sample size.

Female	Regression equation	r^2	F	N
1 ejaculate	log FEC = 2.407 log CW + 0.342	0.508	104.37***	103
>1 ejaculate	log FEC = 2.725 log CW − 0.136	0.707	465.72***	195
Slopes			1.39 ns	
Elevations			32.64***	
Adjusted equations				
1 ejaculate	log FEC = 2.656 log CW − 0.094			
>1 ejaculate	log FEC = 2.656 log CW − 0.016			
New recruit	log FEC = 2.948 log CW − 0.633	0.612	115.30***	75
Old recruit	log FEC = 2.506 log CW − 0.255	0.690	176.14***	81
Slopes			1.58 ns	
Elevations			51.78***	
Adjusted equations				
New recruit	log FEC = 2.616 log CW − 0.050			
Old recruit	log FEC = 2.616 log CW + 0.062			

ductive cycle. First, in April 1991 and in March 1992, about 2 mo before the peak hatching time, most females and in particular old recruits carried eggs without eyespots (Fig. 1 and 2). Second, after 11 mo of development from April 1991 to March 1992, new recruits had ovaries that were less than half the weight of ovaries of females with mature broods and eggs that had not yet developed eyespots (Fig. 2). Third, at any given time, up to two or three groups of females could be separated on the basis of apparent age and egg development (Fig. 2). The progression of adjusted weight of ovaries and of brood stage for these groups of females produced a coherent, biennial pattern (Fig. 2 and 3). Finally, spermathecae of Group II females contained twice as much recent ejaculate as those of Group III females, whereas both groups exhibited a significant trend of decreasing ejaculate weight from April 1991 to March 1992 (Fig. 4). This observation independently supports the separation between Group II and Group III females and implies that the latter were inseminated at a much earlier time than the former.

The reproductive cycle inferred for female *C. opilio* in Baie Sainte-Marguerite is the following. The main period for egg extrusion is February–April for primary spawners (this study; Sainte-Marie and Hazel 1992, and unpublished data) and April–June for repeat spawners. Brood and ovary development are phased, as indicated by the positive partial correlation between egg diameter and weight of ovaries (Table 2) and scarcity of barren females (Fig. 1). Since egg hatching occurs from April to June (Fig. 1), maturation of ovaries and brood lasts approximately 27 mo in primiparous and approximately 24 mo in multiparous females (Fig. 2 and 3). Thus, primiparous females in Groups I, II, III, and IV spawned in 1992, 1991, 1990 and 1989, respectively. Eggs remain without eyespots for approximately 16–19 mo; eyespots appear only in the fall of the second year of brooding. This protracted development may result from diapause early in the incubation period, such as documented for two other majid species by Wear (1974). The times for egg extrusion and hatching in Baie Sainte-Marguerite are the same as those inferred or observed for other localities of the Gulf of Saint Lawrence (Brunel 1962; Powles 1968; Watson 1969, 1970, 1972; Elner and Robichaud 1983; Elner and Gass 1984; Taylor et al. 1985; Conan

and Comeau 1986; Hooper 1986; Moriyasu et al. 1987; Ennis et al. 1988, 1990; Comeau et al. 1991). However, the 2-yr development period of eggs in Baie Sainte-Marguerite is much longer than the previously estimated 18 mo for primiparous and 12 mo for multiparous females, a pattern often surmised to be general (e.g., Adams 1979; Elner and Beninger 1992).

Field evidence in support of an annual reproductive cycle for *C. opilio* in eastern Canada is not overwhelming. It revolves around Watson's (1969) time series of egg development in females from unspecified localities in the Gulf of Saint Lawrence, presumably Baie des Chaleurs and the Gaspé coast. Watson (1969) reported that all mature females carried eyed or hatching eggs from January to April inclusively, which admittedly implies annual breeding and contrasts sharply with my observations (Fig. 1 and 2); however, the proportion of females with eyed eggs in January and February was guessed, and sample sizes and collection depths and methods were not specified. This is important because females segregate spatially by reproductive experience (Sainte-Marie and Hazel 1992), and catchability in traps may change with brood development. Other authors have simply inferred a 1-yr cycle because there are annual, synchronous periods of egg extrusion and hatching (e.g., Powles 1968; Elner and Robichaud 1983; Coulombe 1984). Brunel (1962) also noted this, but cautiously offered that whether egg development lasts 1 yr or more cannot be settled on the basis of knowledge of extrusion and hatching periods alone. A major influence on Canadian scientific opinion, undoubtedly, was the early Japanese literature which reported an approximately 1-yr reproductive cycle (e.g., Ito 1963, 1967; Kon and Nanba 1968; Kon and Honma 1970; Kon 1980). However, there is now convincing data in support of a 2-yr cycle for *C. opilio* in the southwest Okhotsk Sea (Kanno 1987) as well as for queen crab, *C. japonica* in the Japan Sea (Ito 1976).

This is the first study to have considered a year-long time series of ovary and brood development for *C. opilio* in eastern Canada. However, Elner and Gass (1984) qualitatively investigated the degree of ovary and egg development for a population off northwest Cape Breton in November 1983. They found that some females had large ovaries and eggs with eyespots, while others

had small ovaries and eggs without eyespots. This difference in development was tentatively explained by the presence of primiparous and multiparous females with 18- and 12-mo spawning cycles, respectively. But this seems unlikely, since all females had dark exoskeletons, similar wear patterns, and widespread bryozoan mats. The pattern observed by Elner and Gass (1984) is similar to that seen in Baie Sainte-Marguerite in December 1991 (Fig. 2). In my opinion, more investigations of *C. opilio* in eastern Canada are necessary to ascertain the existence of the 1-yr reproductive cycle, and if it indeed does exist, to measure the scope of annual and biennial reproductive patterns with respect to oceanographic and demographic features.

Brood Characteristics and Reproductive Status

Fecundity and egg size of female *C. opilio* in Baie Sainte-Marguerite were comparable with those reported in previous investigations of Gulf of Saint Lawrence populations (e.g., Brunel 1962; Watson 1969; Haynes et al. 1976; Davidson et al. 1985). Only limited comparisons are possible, however, because earlier work did not discriminate between primiparous and multiparous females.

A high proportion of the largest females, all multiparous, carried broods that were abnormally small (Fig. 5). Similarly, Kon (1974) reported that egg loss was greater in large than in small females of *C. opilio* from the Japan Sea. Reduced fecundity and/or brood mortality may result from a variety of processes (Kuris 1991). However, only failure to extrude and egg loss by abortion are know to selectively affect large females of decapod species (Kuris 1991), and infertility is their most probable cause. Female infertility could result from a reduction in the availability of suitable mates in crustacean populations subjected to high male fishing mortality (McMullen and Yoshihara 1971; Smith and Jamieson 1991). Paul (1984) showed that multiparous females of *C. bairdi* that were forced to use stored sperm to produce second and third clutches were less fecund than similar females that were allowed to mate prior to extrusion. In the northwest Gulf of Saint Lawrence, fishing mortality of large *C. opilio* males is estimated at 60–70% (Dufour and Coutu 1989).

Two novel observations on sperm transfer and storage reported herein require some discussion. First, the weight of recent ejaculate remaining in spermathecae shortly after brood extrusion was twice as great in primiparous as in multiparous females. This may be due to the fact that the spermathecae have more room to expand (Diesel 1989) in the vacuous body cavity of recently moulted, mature females than in the tightly filled body cavity of hard-shelled, repeat spawners. Complementary or alternative explanations are (1) reduced use of sperm by primiparous females due to their relatively smaller broods, (2) limited room in the spermathecae of multiparous females due to previously stored ejaculatory products, and (3) assortative mating with males with different reproductive potentials. Second, my data indicate that the quantity of ejaculate in spermathecae decreases over time, independently of spawning events. This observation may have implications for Paul's (1984) estimates of sperm required to fertilize broods in *C. bairdi*. Those estimates were based on the decrease in volume of stored ejaculate, assuming that number of sperm per unit volume of ejaculate was constant and that changes in the volume of ejaculate resulted only from expenditure of sperm at time of extrusion. The presently observed decrease in weight of recent ejaculate may be due only to reduction of seminal fluids, although the fate of spermatophores and sperm remains unknown.

Excluding females with abnormally small broods, my data indicate no significant brood mortality over time for primiparous and multiparous females of *C. opilio* in Baie Sainte-Marguerite. Indeed, fecundity in both types of females was independent of weight of ovaries or of elapsed time for a standard carapace width. This finding contrasts with an earlier report of ~54% brood mortality in *C. opilio* females from the Japan Sea (Kon 1974). This latter estimate, however, was based on one comparison in time of the fecundity of females in two different year classes, one sampled prior to and the other soon after extrusion, and the proportions of primiparous and multiparous females in samples were not determined. In the western Gulf of Saint Lawrence, Brunel (1962) found that females ~65–80 mm CW carried about 30 000 to 85 000 orange eggs but only 10 000 to 30 000 ripe, eyed eggs (see his fig. 1). However, he stated that hatching had already started in many of the females with eyed eggs; thus, no brood mortality can be inferred from his data.

Brood size and fecundity were less in primiparous than in multiparous females for a constant carapace width (Table 3). Such a difference was suspected for *C. opilio* (Haynes et al. 1976; Jewett 1981; Elner and Robichaud 1983), but never demonstrated. Brood size and fecundity of females are constrained by the volume of body cavity available for development of ovaries (Hines 1982, 1992; Somerton and Meyers 1983), which obviously is less before than after the moult to maturity. Therefore, knowing that brood weight and fecundity scale isometrically to body weight (this study; Hines 1982, 1992) and that the increment in carapace width at terminal moult of female *C. opilio* in Baie Sainte-Marguerite is ~16–18% (Sainte-Marie and Hazel 1992, and unpublished data), one may predict from Eq. 2 that primiparous females should be ~63–66% as fecund as multiparous females. The estimated differences from my field samples, however, were much less: adjusted fecundity of primiparous females was 77.3–83.6% that of multiparous females. By comparison, Somerton and Meyers (1983) reported that primiparous females of *C. bairdi* were ~70% as fecund as equal-sized multiparous females.

For *C. opilio* there may be at least two reasons for the difference between predicted and observed ratios of primiparous to multiparous fecundity. One is that some females were misclassified, a particularly acute problem when female type was defined by number of ejaculates in spermathecae. Misclassified females were those that (1) extruded a second brood without mating or (2) remated before releasing their first brood. Such cases occur in *C. opilio* and are documented for other majids as well (Hinsch 1968; Schöne 1968; Diesel 1989). Furthermore, if males curette spermathecae prior to insemination, as proposed (Beninger et al. 1991; Elner and Beninger 1992), the number of stored ejaculates may not reflect the number of matings. Errors in classification were less likely to occur when apparent age was used to discriminate between primiparous and multiparous females, hence the greater contrasts in reproductive traits. The second reason, a biological one, is that some multiparous females do not realize their full reproductive potential due to fertility problems (see above).

Eggs of primiparous females were slightly, albeit significantly, larger than those of multiparous females. This novel observation is consistent with the approximately 3-mo longer development period of eggs in primiparous compared with multiparous females. Indeed, development period is known to depend on egg

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size for a variety of crustaceans (e.g., Wear 1974; Steele 1977). The consequences of this size difference for larval development and survival are unknown. Interestingly, Roff et al. (1984) noted that *C. opilio* zoeae II on the Scotian Shelf had a bimodal size distribution.

Number of Broods and Lifetime Fecundity

Females of *C. opilio* in Baie Sainte-Marguerite probably carry only two broods in a lifetime. Because mature females are terminally moulted (this study; Yoshida 1941; Ito 1963; Watson 1970), the number of broods produced by a female depends on life expectancy following the moult to maturity. Comeau et al. (1991) reported that mature females in Bonne Bay, Newfoundland, live for a maximum of 4 yr after the terminal moult, and the oldest exoskeletons in the Saguenay Fjord (Sainte-Marie et al. 1992) are ~5 yr (G. Y. Conan, Department of Fisheries and Oceans, Gulf Region, Moncton, N.B., personal communication), based in both cases on ageing by radioelements. If this is also the case for Baie Sainte-Marguerite females, then a 4- to 5-yr life span after maturity and a 2-yr reproductive cycle allow hatching of only two broods. The number of ejaculates in spermathecae appears to bear out this conclusion: only a small minority of females had two or more ejaculates per spermatheca. However, counting of ejaculates to determine maximum number of broods may be unreliable, for reasons detailed above.

Biennial breeding and biparity have important implications. Lifetime fecundity for *C. opilio* in Baie Sainte-Marguerite averages 81 630 to 83 143 eggs for a standard 57.4 mm CW female. Assuming conservatively that primiparous females are only 63–66% as fecund as multiparous females, and that there is no brood mortality, primiparous females would account for >40% of larvae from the Baie Sainte-Marguerite population. This estimate, however, assumes that there is no mortality of mature females. My findings also imply that small males contribute extensively to reproduction. Indeed, 88.3% of pubescent females in Baie Sainte-Marguerite mated with morphometrically mature males smaller than the minimum legal size of 95 mm CW (Sainte-Marie and Hazel 1992). Moreover, a substantial proportion of repeat spawners apparently relied on stored sperm from the pubescent mating (this study), and an additional unknown proportion may have remated with small morphometrically mature males (e.g., Ennis et al. 1990). This is disquieting, since morphometric maturity is achieved only at the terminal moult of males (Conan and Comeau 1986; Sainte-Marie and Hazel 1992) and might be genetically determined (Conan 1986; Elner et al. 1986; Bailey and Elner 1989).

Acknowledgements

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