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Possible effects of changes in CIL temperature and thickness on population dynamics of snow crab, *Chionoecetes opilio*, in the Gulf of Saint Lawrence

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ABSTRACT

The cold intermediate layer (CIL) of the Gulf of Saint Lawrence is subject to interannual changes in core temperature and thickness, which are superimposed on persistent west-east and north-south gradients for these same variables. Since the mid 1980's, the CIL has been thicker and colder than normal. This cold period has lasted for more than one generation of snow crab (*Chionoecetes opilio*) and may have had major effects on the spatial distribution and population dynamics of this species. The extent of the spatial distribution of snow crab apparently increased during the cold period, while egg production may have declined owing to a shift from a 1 year to a 2 year duration for egg incubation. Furthermore, we propose that the size threshold for the onset of gonad development and the size at terminal molt in both sexes are partly temperature-dependent. Cohorts with immature individuals subjected to the recent cold period are currently expressing precocious maturity, and a large fraction of males are undergoing terminal molt to sublegal sizes. These changes may have important consequences for reproductive processes and may directly affect fishery performance in the next years.

RÉSUMÉ

L'épaisseur et la température minimale de la couche intermédiaire froide (CIF) du golfe du Saint-Laurent varient interannuellement, ces variations étant surimposées à des gradients spatiaux persistants d'ouest en est et de nord en sud pour ces deux mêmes variables. Depuis le milieu des années 1980, la CIF a été plus épaisse et plus froide que la normale. Cette période de froid dure depuis plus d'une génération de crabe des neiges (*Chionoecetes opilio*) et a pu avoir des effets importants sur la distribution spatiale et la dynamique de population de cette espèce. L'étendue de la distribution spatiale du crabe des neiges a apparemment augmenté au cours de cette période froide, alors que la production d'oeufs aurait décru parce que la durée d'incubation des oeufs est passée d'un à deux ans. De plus, nous proposons que la taille à laquelle les gonades commencent à se développer et la taille à la mue terminale chez les deux sexes sont en partie dépendantes de la température. Les cohortes dont les individus immatures ont été exposés à la récente période froide manifestent présentement une maturité précoce et une fraction importante des mâles effectue la mue terminale sans atteindre la taille légale. Ces changements pourraient avoir des conséquences importantes pour les processus reproducteurs et pourraient directement affecter la performance des pêcheries au cours des prochaines années.

Introduction

Notwithstanding the problem of overfishing, the demise of cod (*Gadus morhua*) in eastern Canada has drawn attention to the deleterious effects of decreased water temperature for production of exploited species (Mann and Drinkwater, 1994). Poor condition indices and reduced growth and fecundity rates for cod, leading to greater natural mortality and decreased egg production and recruitment, have been linked to below average temperatures that have prevailed in the Gulf of Saint Lawrence since the mid 1980's (Lambert and Dutil, 1997; Dutil et al., 1998). The cod population in the northern Gulf may have been particularly vulnerable, because water temperature from the outset of this cold period was close to the species' lower bound for temperature tolerance.

Intuitively, it might be thought that species with affinities for low temperature in the Gulf of Saint Lawrence were little affected by the cold period. The snow crab (*Chionoecetes opilio*), in particular, reportedly prefers waters < 3-4 °C (Rathbun, 1925; Somerton, 1981a; Brêthes et al., 1987; Slizkin, 1990) and is closely associated with the cold intermediate layer (CIL). However, the metabolism of snow crab may be sensitive to very slight changes in temperature, of only a few tenths of one degree (Foyle et al., 1989; Thompson and Hawryluk, 1990; Maynard, 1991). Although the CIL is often perceived as being a rather stable environment, retrospective analyses indicate that its core temperature has varied interdecadally by up to 2 °C (Gilbert and Pettigrew, 1997, Figure 1 herein). Snow crab might therefore respond sharply to climatological change, as well as to regional differences, affecting temperature of water masses and of the CIL specifically.

Snow crab populations are characterized by discontinuous recruitment patterns (Somerton, 1981a; Comeau et al., 1991, 1998; Robichaud et al., 1991; Elner and Beninger, 1995; Sainte-Marie and Dufour, 1995). In the Gulf of Saint Lawrence, populations apparently cycle in abundance with a period of about 8 years, a group of at most 5 moderate to strong year-classes (called a recruitment wave) alternating with a group of at least 3 weak year-classes (called a recruitment trough, Sainte-Marie et al., 1996). The ups and downs of the Gulf fisheries reflect to a large extent the passage of recruitment waves and troughs: current declines in catch rates and landings are due to weak 1985-87 year classes. Because both sexes undergo a terminal molt to adulthood and have a limited lifespan thereafter, the population cycle also causes profound changes in the abundance and size structure of adult crabs, the adult sex ratio, the representation of the various female reproductive types, and population egg production (Sainte-Marie and Dufour, 1995; Sainte-Marie et al., 1996). The cycle is apparently endogenous and may be caused by density-dependent processes affecting survivorship of the early benthic instars (Lovrich et al., 1995; Sainte-Marie et al., 1995; Conan et al., 1996; Lovrich and Sainte-Marie, 1997), that may be reinforced and phased on broad geographical scales through large fluctuations in egg/larvae production and dispersal (Sainte-Marie and Dufour, 1995; Sainte-Marie et al., 1996). Thus, environmental processes that modify the spatial distribution, growth and reproductive output of snow crab might have significant effects on stock productivity and the fortunes of fisheries.

Based on preliminary analyses of contemporaneous and historical data, the present paper outlines some of the possible effects of differences in CIL temperature and thickness on spatial distribution, growth, size at terminal molt (adulthood), and egg production of snow crab. These hypotheses constitute the frame of a proposed Strategic Research Program entitled "*Changes in the reproduction and distribution of snow crab due to CIL interannual variability in the Gulf of Saint Lawrence*" aiming to investigate the impact of CIL variability on productivity of snow crab populations by way of empirical and experimental approaches.

Methods

Temperature data used to study the interannual changes in CIL core temperature, thickness and volume from the mid-1940's until now are primarily from the AFAP (Atlantic Fisheries Adjustment Program) database of temperature and salinity. Biological observations come from long-term monitoring programs of snow crab pilot populations in Baie Sainte-Marguerite, northwest Gulf of Saint Lawrence, and in the Saguenay Fjord. The Baie Sainte-Marguerite population is commercially exploited (Sainte-Marie et al., 1996). The Saguenay Fjord, which opens into the Gulf system through the north shore of the Saint Lawrence Estuary, harbors a small unexploited population of snow crab (Sainte-Marie et al., 1992). Benthic stages of snow crab in the Fjord are confined by a succession of sills and low salinity surface waters to the deep layer of the upstream basin, where temperature ranges over the year from about +0.5 to +3 °C (Schafer et al., 1990; DFO, Laurentian Region, unpubl. data). This is roughly 1 to 2 °C warmer than the core temperature of the CIL in the nearby Estuary and northwest Gulf of the Saint Lawrence.

The terminology used herein to describe the various snow crab developmental stages and categories of maturity comes from Sainte-Marie et al. (1995) and Alunno-Bruscia and Sainte-Marie (1998). Briefly, benthic stages of snow crab are called immature from settlement time until they undergo a critical molt after which their gonads begin to develop. This critical molt is called the prepuberty molt in females and the puberty molt in males, and its occurrence can be detected externally by changes in the growth allometry of the abdomen or the chelae. In males, the production of spermatophores starts soon after the puberty molt. Sperm-producing males are called adolescent until they undergo a terminal molt to adulthood, during which their chelae become fully differentiated. Adolescent males are capable of mating, but are less competitive than adult males. In females, ovary development proceeds through a series of prepubertal molt instars but the onset of reproductive life occurs only at the terminal molt to adulthood, during which their abdomen becomes greatly enlarged and modified to accomodate eggs. In the present paper, for convenience, we use the term preadult crab to collectively designate prepubertal females and adolescent males.

Spatio-temporal variations in CIL core temperature and thickness

Recent overviews of oceanographic conditions in the Gulf of Saint Lawrence (e.g., Gilbert et al., 1997) have drawn attention to the interannual variations of a Gulf-wide index of CIL core temperature (Figure 1). However, very little or nothing was said of the spatial variations in CIL core temperature. In the Gulf of Saint Lawrence, the CIL core temperature increases from east to west along Québec's North Shore, and also increases from north to south. These temperature gradients are observed not only in the climatology (Figure 2), but are also repeatably observed from year to year, as can be seen during the 1995 and 1997 summers (Figure 3) for instance. The northeast Gulf always has the coldest values of CIL core temperature, whereas the warmest values are generally observed in the Cabot Strait region and the Estuary. As might be expected, the CIL ($T < 0°C$) is also thicker in the northeast Gulf than in the Cabot Strait and the Estuary (Figure 4).

Below normal CIL core temperature and above normal CIL thickness have now been observed for a period of time approaching or surpassing the generation time for snow crab, i.e., about 8 to 12 years (Figure 1), and this could have major biological implications. A slow return to warmer conditions began in 1995 (Figure 1) and has been accompanied by a thinning of the CIL, as can readily be seen by comparing the 1995 CIL thickness with that of 1997 (Figure 4). Accordingly, for the southern Gulf, the areal index of bottom covered by waters < 1°C peaked in 1995 and has since been declining (Drinkwater et al., 1997).

Possible effects of CIL variability

1. Spatial distribution

There is evidence that the bathymetric and geographical range of adult snow crab expanded through the late 1980's and into the early 1990's. On small spatial scales within traditional snow crab habitat, this expansion coincided with large increases in the density of adult crab in core habitat as a recruitment wave unfurled (Lovrich et al., 1995). Thus, the increase in spatial distribution may to a certain extent represent a density-dependent response to increasing population size. However, anecdotal accounts by fishers and the recent extension or intensification of harvest on non traditional snow crab fishing grounds suggest that areal expansion may have been linked at least in part to colder and more pervasive CIL waters that contributed to open new snow crab habitat. This has been particularly striking at the species southern limit, on the Scotian Shelf, where expanding cold-water grounds (Drinkwater et al., 1997 and earlier reports cited therein) may have been a major factor in the range extension of snow crab (Tremblay, 1997). Nonetheless, there is evidence that expansion of cold water habitat occurred all throughout the Gulf of Saint Lawrence (e.g., Swain, 1993). Although they made no reference to interannual changes in CIL core temperature and thickness, Conan et al. (1996) noted that any interannual fluctuation in the depth of the upper and lower boundary of the CIL could modify the location and extent of habitat available to immature, preadult and adult snow crab. The effects would be more perceptible in bottom areas with gentle slopes, such as the Scotian Shelf, than in bottom areas with steep slopes.

Range extension leading to new or improved fisheries may occur through the immigration of preadult and adult crabs to new habitat, or through the colonization of new settlement grounds by postlarvae and the subsequent emergence of a local population. This second possibility could occur only if temperature conditions remained favorable for a period of time sufficiently long to allow for postlarvae to grow to legal size, such as has been the case during the recent cold period. The immature stages of snow crab up to molt instar IV are apparently of a more cryptic and a more sedentary habit than the later immature stages and especially than the preadult and adult stages, and these early benthic stages tend to concentrate in a narrow nursery habitat localized below the surface mixed layer (Kon, 1980; Slizkin, 1990; Lovrich et al., 1995; Conan et al., 1996; Comeau et al., 1998). The physiological capability for extended and sustained movements in males may be intimately linked to activitation of a specific enzyme that is associated with gonad development (Angers et al., 1994). Therefore, the early benthic stages probably have little or no refuge against extreme environmental conditions resulting from winter and CIL temperature anomalies, and may represent the weak link in the emergence of a local population.

2. Growth and size at terminal molt

Interannual changes in CIL temperature may directly affect growth of snow crab. There is experimental evidence from controlled laboratory experiments with immature snow crab that the relative molt increment decreases slightly and the duration of intermolt decreases markedly with increasing temperature over the range –1 to 4 °C (Sainte-Marie, unpubl. data). Consequently at a given molt instar snow crab are slightly smaller, while at a given post-hatching age they are notably larger, in warmer than in colder water. Judging from preliminary comparative analyses of growth patterns in the "warm" Saguenay Fjord and in the "cold" Baie Sainte-Marguerite (Sainte-Marie et al., 1995 and unpubl. data), the net result of differential growth appears to be that males can reach legal size (i.e., 95 mm carapace width, CW) about 1 or 2 years sooner (i.e., at 6.7 or 7.7 years post-settlement age) at warmer than at colder temperatures.

The size at terminal molt (adulthood) for snow crab is notoriously variable and elucidation of the factor(s) that determine(s) the onset of terminal molt represents one of the important challenges to snow crab science. In the Gulf of Saint Lawrence, adult females may range from 34 to 95 mm CW and adult males from 38 to 162 mm CW (Sainte-Marie et al., 1995 and unpubl. data; Alunno-Bruscia and Sainte-Marie, 1998; Dufour and Sainte-Marie, 1998). Hypotheses invoked to date to explain variability within and among cohorts in the size at which individuals reach terminal molt have focused on males and have revolved around the concepts of heritability of size, which might be adversely affected by fishing pressure (e.g., Bailey and Elner, 1989), and of density-dependent triggers related to competition for reproductive resources (i.e., receptive females) or nonreproductive resources such as food or space (e.g., Comeau et al., 1991, 1998; Elner and Beninger, 1995). If the factors that determine the onset of terminal molt are the same for females and males, the former gender may be the most interesting candidate for investigation of temporal trends in size at terminal molt because they are unmistakably recognizable as adults and are not subject to exploitation. To the contrary, determination of adult status in males is subject to error and males may experience size-selective (95 mm CW legal size) fishing mortality, leading to truncated or otherwise modified size distributions.

There is strong evidence that the size at terminal molt (adulthood) in females is in part temperature-dependent. The existence of geographical differences in size at terminal molt for female snow crab has been known for some time (e.g., Haynes et al., 1976; Jewett, 1981; Paul et al., 1997). In the North Pacific, the average body size of adult females decreases from south to north coincident with a declining gradient of summer bottom temperature of about +3 to –1 °C, and a direct link between temperature and average size of adult females has been posited (Somerton, 1981a, 1981b; J.M. Orensanz, School of Fisheries, University of Washington, pers. comm.). A similarly striking geographic disparity in size of adult females is also seen in the Gulf of Saint Lawrence. Adult females that recruited to populations in 1997 were much larger in the "warm" Saguenay Fjord than in the "cold" Baie Sainte-Marguerite (Figure 5), albeit differential gear selectivity might explain a small measure of the difference in female size structure between the two habitats. Alunno-Bruscia and Sainte-Marie (1998) noted that adult females in the northern Gulf of Saint Lawrence are currently of a smaller average size than in the late 1970's and the middle 1980's, and proposed that the below normal temperature of the CIL was responsible for this size shift. Given that fecundity is highly correlated with female body size in snow crab (Figure 6), changes in the size structure of females would have important effects on population egg production.

It is only recently that the idea of a terminal molt to adulthood for males was proposed, validated and became widely accepted (Conan and Comeau, 1986; Sainte-Marie and Hazel, 1992). The resulting short history of investigation into the factors that might trigger terminal molt for males, and lack of dependable and extended datasets on interannual size variations for adult males, may perhaps explain why the possibility of an environmental cotribution to determinism of male size at terminal molt has not hitherto been considered. Fortunately, however, several authors have investigated the size for onset of gonad development in males and the pattern that emerges from these data is evocative. In each specific case, the transition from immature to adolescent occurs over a very narrow range of body sizes (e.g., Powles, 1969; Watson, 1970; Comeau et al., 1992; Sainte-Marie et al., 1995), suggesting that there is little intracohort variability in the size threshold for onset of puberty. This contrasts sharply with the large intracohort variability that characterizes the size threshold for onset of terminal molt. However, there is also good evidence of interdecadal or geographical differences in the size threshold for onset of gonad development that might be correlated with temperature. For example, in the Gulf of Saint Lawrence the size at which 50 % of males carried spermatophores was 57 mm CW in 1968-69 (Watson, 1970) after 5-6 years of slightly colder or warmer than average CIL core temperature (Figure 1), compared to 34-38 mm CW in 1991-92 (Comeau and Conan, 1992; Sainte-Marie et al., 1995) after several successive years of below average CIL core temperature (Figure 1). These changes in size at puberty appear to have been paralleled by changes in the size at adulthood for males (see discussion in Sainte-Marie et al., 1995). Moreover, the minimum, mean and maximum sizes for terminal molt of males are much larger in the "warm" Saguenay Fjord than in the "cold" Baie Sainte-Marguerite (Sainte-Marie et al., 1992 and unpubl. data), while year-classes born and grown in the northern Gulf of Saint Lawrence during the current cold period produced record small adult males in 1995-97 (Dufour and Sainte-Marie, 1998). Thus, the scant data for males seem to suggest the existence of temporal and spatial patterns for size at terminal molt similar to those observed for females and that may be linked to temperature.

The mechanism that we propose to explain temperature-driven variability in the size of adult snow crab invokes a change in the size threshold for the onset of gonad development, which is a physiological prerequisite for the terminal molt to occur in both sexes. We hypothesize that the time elapsed from hatching or settlement until the onset of gonad development is approximately constant, irregardless of temperature. As a consequence, the prepuberty molt of females and the puberty molt of males would occur at larger sizes in warmer than in colder waters owing to shorter intermolt periods (see above). A constant, temperature-independent time trigger for the onset of gonad development seems to be the only mechanism that can explain (*i*) why individuals in given cohort begin to develop their gonads over a very narrow range of sizes and (*ii*) why individuals that apparently belong to the same year-class, but that occur in different habitats with different temperatures regimes (e.g., Saguenay Fjord and Baie Sainte-Marguerite), concurrently develop gonads at different sizes. The phenotypic size constraint on the process of terminal molt being set by the onset of gonad development, one or more intrinsic factors (reviewed above) might then largely be responsible for the triggering of the terminal molt. Temperature may have a much lesser impact on preadult than on immature stages because the former are locked into an annual molt cycle and may to some extent avoid temperature extremes through active movement. Thus, temperature would act on size at terminal molt in an indirect manner, by modifying growth of immature crab and shifting the size range of individuals that can undergo terminal molt to smaller or to larger sizes.

3. Egg incubation time

Adult female snow crab extrude their eggs beneath their abdomen, where they become attached to the pleopods and are incubated until hatching. Studies of reproductive patterns of female snow crab conducted in Baie des Chaleurs in 1989-90 (Mallet et al., 1993) and in Baie Sainte-Marguerite in 1991-92 (Sainte-Marie, 1993) led to the conclusion that eggs are incubated for about 24 months. However, cursory investigations in the same general geographical regions conducted circa 1969 and in 1982-83 had previously lead to the conclusion that eggs were incubated for only one year (e.g., Watson, 1969; Coulombe, 1984), although data were not very conclusive. Similarly, in the northwest Pacific female snow crab were reported to incubate their eggs for one year (Kon, 1980) or for two years (Kanno, 1987) depending on locality.

Mallet et al. (1993) suggested that egg development time for snow crab was temperature-dependent and that both the 12- and 24-month incubation times could co-occur within a population. These authors postulated that this would happen if some females resided in surface waters at spring warming, while others remained within the CIL. Petersen (1995) demonstrated experimentally for the related cold-water majid crab *Hyas araneus* that egg incubation time was temperature-dependent and that switching from incubation times of one to two years can occur, and that it is achieved through a variably long diapause initiated very early in embryo ontogeny. Snow crab embryos also have a diapause which begins soon after gamete fusion (Sainte-Marie, 1993). Since primiparous female snow crab extrude their eggs during winter on shallow bottoms bathed by the cold surface waters (Sainte-Marie and Hazel, 1992; Lovrich et al., 1995) and most multiparous females extrude eggs in spring on bottoms bathed by the CIL (Comeau et al., 1991; Starr et al., 1994; Lovrich et al., 1995), we propose that the duration of egg incubation time should passively reflect prevailing temperature for surface waters in winter and for CIL in spring. There may be a rather strong correlation between these two last variables, as winter temperature has a direct bearing on CIL core temperature and thickness. Accordingly, continuous monitoring since 1990 of egg development patterns for adult female snow crab in Baie Sainte-Marguerite revealed a massive shift from a two- to a one-year incubatory cycle in 1996-97 (Sainte-Marie, unpubl. data), coincident with a warmer winter than in previous years and initiation of a marked warming trend for the CIL (Figure 1; Gilbert et al., 1997).

Potential implications for population dynamics and fishery

If snow crab populations do indeed react to variability in CIL core temperature and thickness in the ways we have postulated above, there are many important effects on population dynamics that may be reflected in the fisheries:

(*i*) If the current warming trend for the CIL persists, present-day populations of snow crab in marginal areas of the species' distribution range, such as the Scotian Shelf, may collapse or become quite diminished through emigration of preadults and adults to colder areas, attrition of postlarval settlement, and/or local mortality.

(*ii*) Population egg production will vary extensively owing not only to recruitment cycles, but also to the possibly concomitant changes in female size (i.e., fecundity) and in egg incubation time. Egg production and consequently sperm requirements for the female population will be higher at warmer than at lower temperatures. This represents a major concern for a species in which there is a strong potential for sperm limitation to occur due to selective exploitation of males (Sainte-Marie et al., 1996).

(*iii*) The proportion of males in a cohort that becomes vulnerable to fishing may increase when immature crabs have been exposed to warmer temperatures, because fewer males undergo terminal molt to sublegal size. Conversely, commercial yield of populations may be less when immature crabs have been exposed to colder temperatures.

(*iv*) In spite of variability in the rates of egg production, growth, and terminal molt to legal size in response to temperature, the period for snow crab population cycling may remain quite stable because it reflects density-dependent interactions among the immature stages. Faster growth rates for immature crabs at warmer temperatures, which could conceivably give rise to shorter periods for population cycles (Lovrich et al., 1997), would be offset by a larger size threshold for initiation of gonad development at colder temperatures.

Given that there are persistent spatial gradients in CIL core temperature and thickness, irregardless of interannual variations in climatology (Figures 3 and 4), the last three effects could also explain a large measure of the geographical variability in the dynamics and productivity of snow crab populations. In particular, the observed west-east gradient of decreasing temperature along the north shore of the estuary and gulf of the Saint Lawrence in conjunction with narrower recruitment waves to the east could explain the lesser productivity of snow crab populations along the Lower North Shore.

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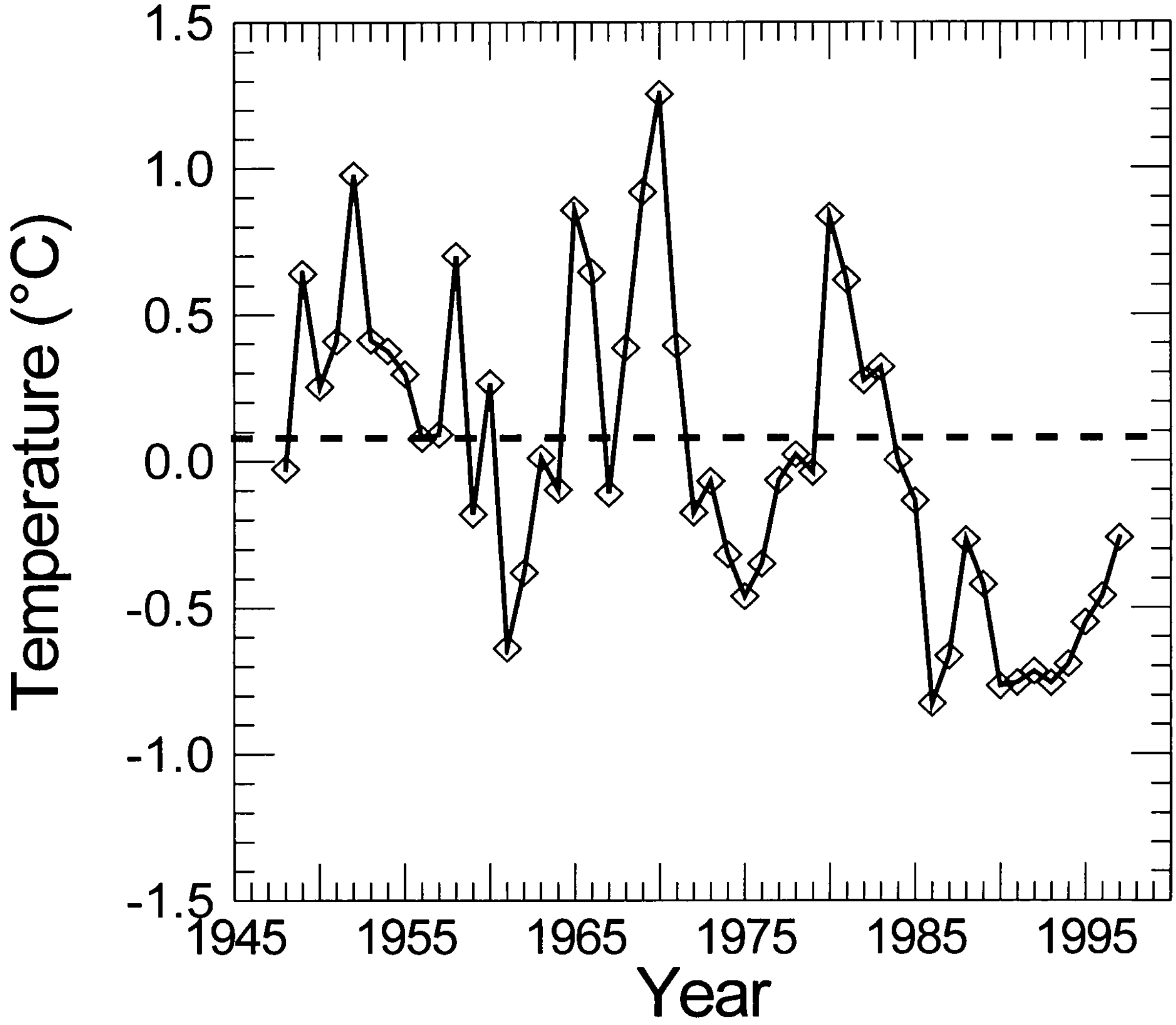

Figure 1. Time series of the CIL core temperature in the Gulf of Saint Lawrence.

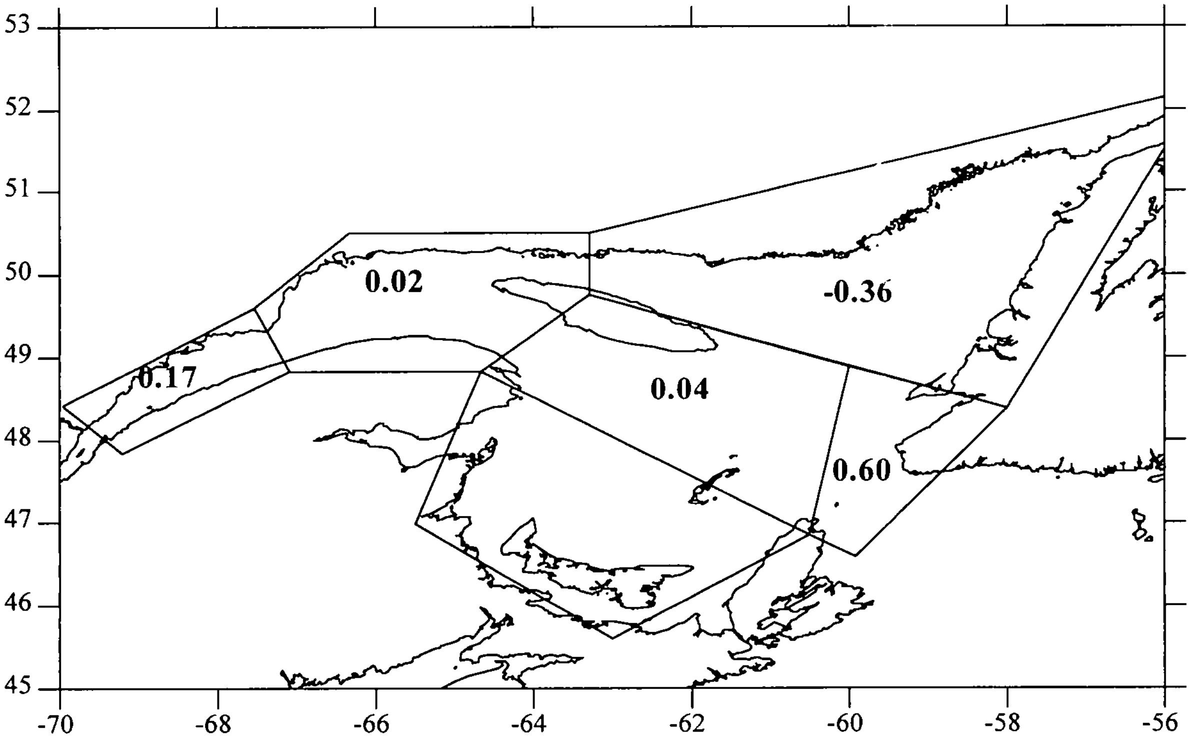

Figure 2. Climatological (1948-1994) CIL core temperature in the five deep subregions of the Gulf of Saint Lawrence (based on Table 2 in Gilbert and Pettigrew, 1997).

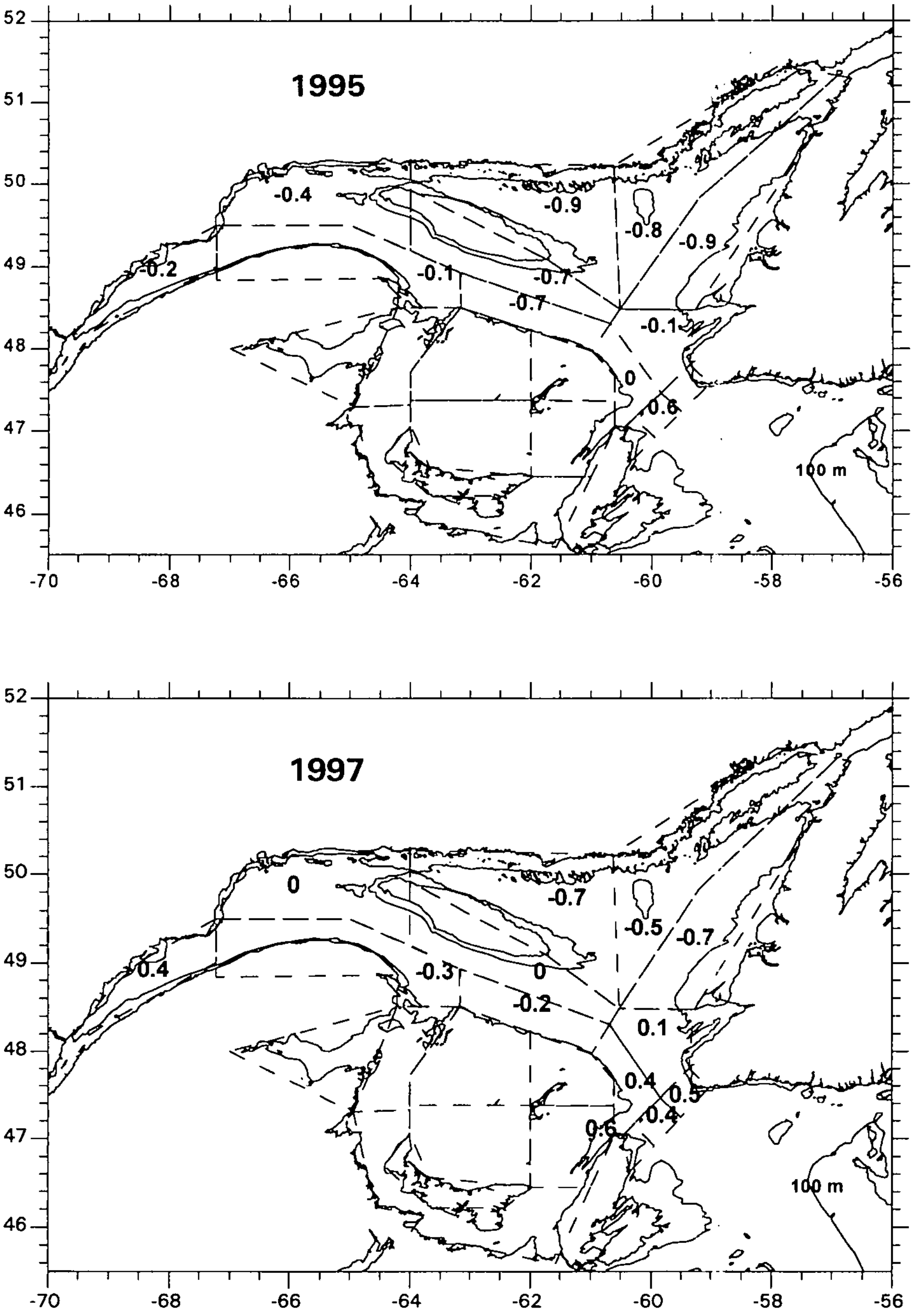

Figure 3. CIL core temperature in the Gulf of Saint Lawrence during August-September 1995 and 1997, based on CTD data from the Needler surveys.

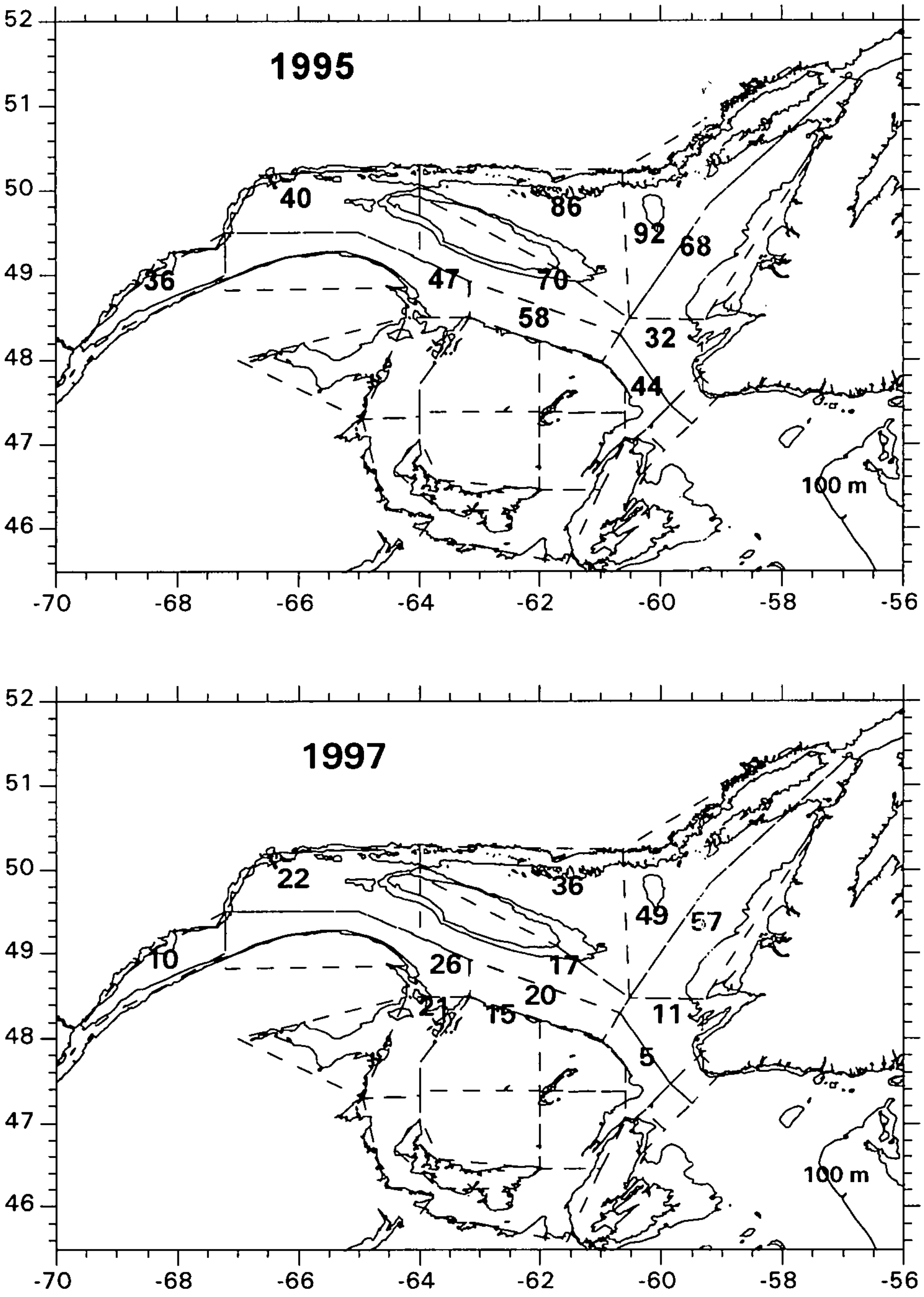

Figure 4. Thickness (m) of the layer with T < 0°C in August-September 1995 and 1997, based on CTD data from the Needler surveys.

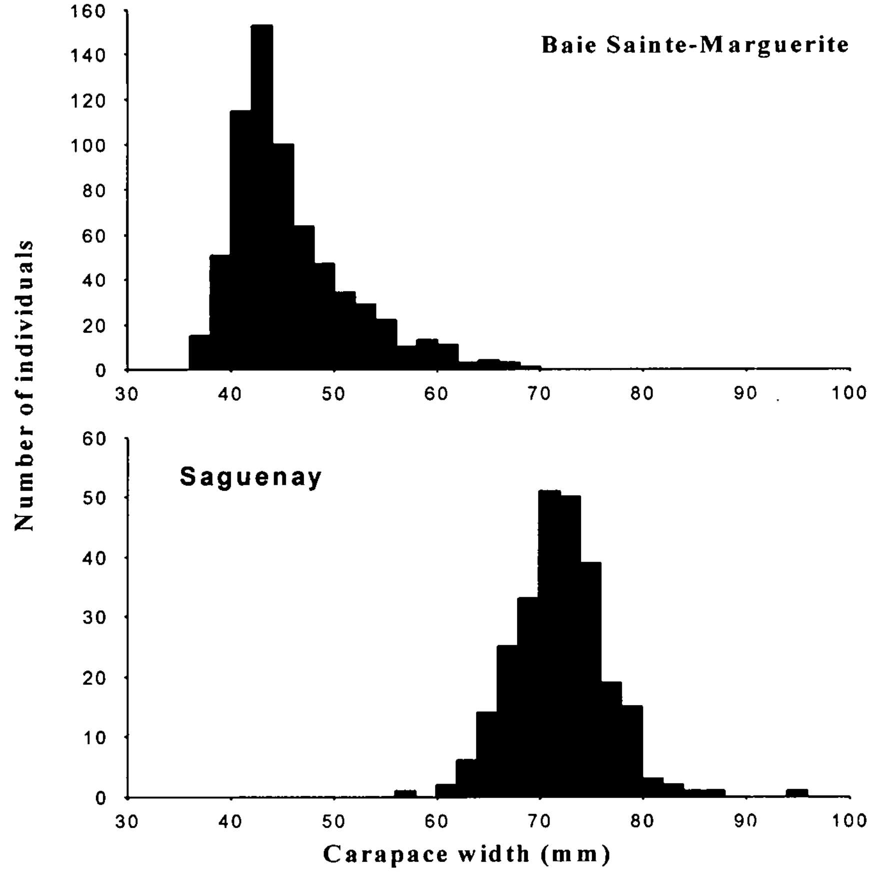

Figure 5. Size frequency distribution of primiparous females in Baie Sainte-Marguerite (trawl samples) and in the Saguenay Fjord (small-mesh trap samples) in May 1997.

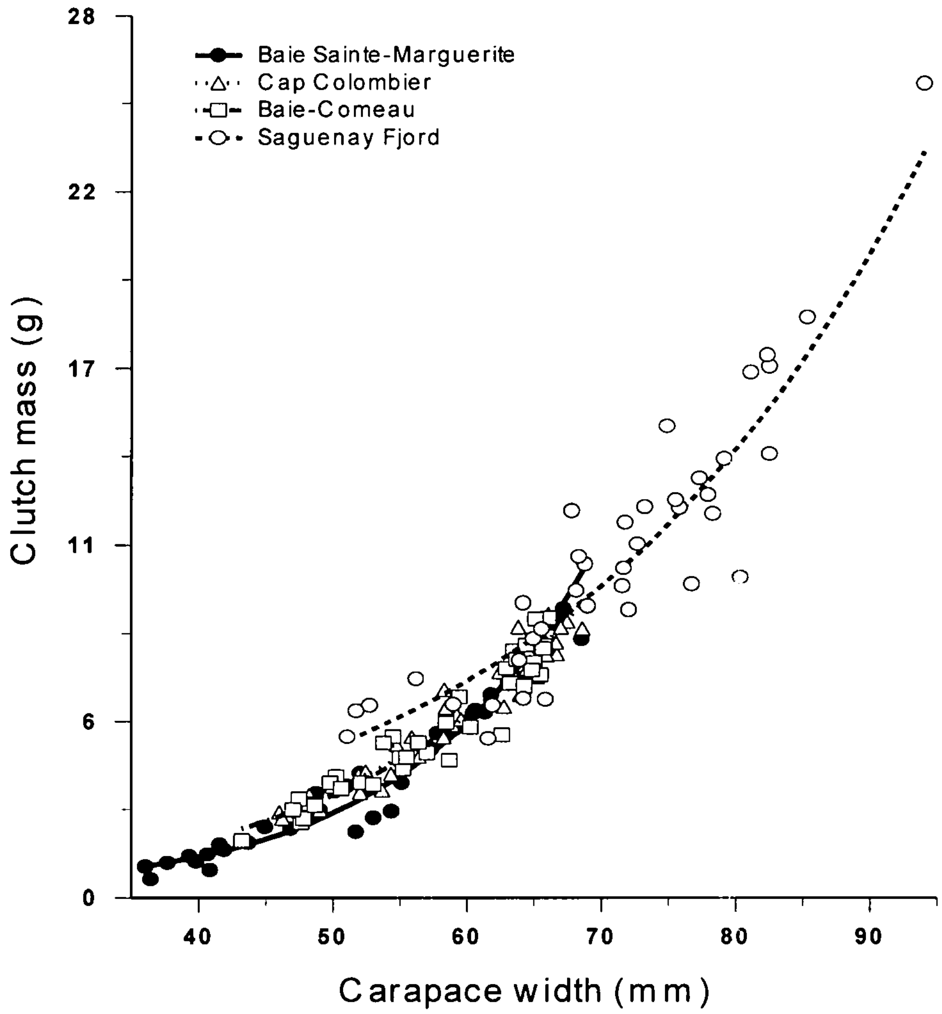

Figure 6. Index of fecundity for 1997 primiparous females in Baie Sainte-Marguerite, the Saint Lawrence Estuary (Baie Comeau and Cap Colombier) and the Saguenay Fjord.