
**A Workshop on Mechanisms Affecting Year-Class Strength Formation
in Snow Crabs *Chionoectes opilio* in the Eastern Bering Sea**

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Reprinted from the Alaska Fishery Research Bulletin
Vol. 12 No. 2, Winter 2007

The Alaska Fisheries Research Bulletin can be found on the World Wide Web at URL:
<http://www.adfg.state.ak.us/pubs/afrb/afrbhome.php>

A Workshop on Mechanisms Affecting Year-Class Strength Formation in Snow Crabs *Chionoecetes opilio* in the Eastern Bering Sea

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ABSTRACT: A group of specialists on subarctic crab biology and fisheries participated in a workshop to discuss stage-specific recruitment processes of snow crab *Chionoecetes opilio* populations. The goal was to develop from experience with North Pacific and North Atlantic stocks a comprehensive set of hypotheses on the physical and biotic factors that may contribute to the variation in year-class success of the snow crab stock in the eastern Bering Sea. Participants identified 15 life history stages and associated survival and productivity processes. Some of the processes deemed to be most critical include match of hatching larvae with adequate densities of suitable prey, advection (or retention) of larvae to nursery areas suitable for settlement, predation by Pacific cod *Gadus macrocephalus* and other predators, and cannibalism of newly settled juveniles by older, larger snow crab juveniles. A comprehensive set of hypotheses is intended to serve as a vehicle by which to direct future field and laboratory research programs to better understand snow crab population and fishery dynamics.

INTRODUCTION

Our goal is to report on a comprehensive set of hypotheses about potential mechanisms affecting year-class success of snow crab *Chionoecetes opilio* in the eastern Bering Sea. Hypotheses were developed during a workshop involving crab scientists (Appendix 1) convened in Anchorage, Alaska, on January 21, 2001. Year-class success or recruitment strength is defined here as the relative abundance of crabs of a particular cohort resulting from one year of adult reproduction. Our approach was the events-time modeling procedure (Tyler 1992), which we applied previously during workshops for red king crab *Paralithodes camtschaticus* (Tyler and Kruse 1996a, b) and Tanner crab *Chionoecetes bairdi* (Tyler and Kruse 1997). This conceptual modeling procedure results in a defined set of biotic and abiotic factors, potentially affecting each life history stage, for subsequent statistical analysis and simulation modeling. Comparative information from different portions of the snow crab range in the eastern Bering Sea and northwest Atlantic Ocean allowed us to develop a comprehensive list of mechanisms operating under differing environmental conditions.

The eastern Bering Sea stock of snow crabs has undergone several large swings in abundance and

landings since the 1970s (Figure 1). During years of peak abundance, the stock supported one of the most valuable fisheries in the United States. Annual stock assessment trawl surveys have been conducted over the majority of the range of snow crabs in the eastern Bering Sea since 1978 (Otto 1981). Wide swings in abundance and landings in recent years have caused major difficulties for the Bering Sea crab fleet due to fishery closures associated with depressed crab abundance. By 1999 the spawning stock biomass had fallen below the minimum stock size threshold set for this stock in the Fishery Management Plan for Bering Sea and Aleutian Islands King and Tanner Crabs (NPFMC 1998). Poor stock status in 1999 prompted the Alaska Department of Fish and Game to propose more conservative rules to the Alaska Board of Fisheries for setting the guideline harvest level for the fishery in 2000, and work on a formal rebuilding plan was initiated. The Alaska Board of Fisheries adopted a more conservative harvest strategy starting in 2000 and the NPFMC adopted a rebuilding plan (NPFMC 2000).

Causes of recruitment successes and failures of eastern Bering Sea snow crabs remain topics of much speculation by scientists, fishery managers, and industry participants alike. This uncertainty may be costly

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Acknowledgments: We are grateful to all workshop participants for contributing their extensive knowledge about snow crabs. This paper benefited from helpful reviews by Robert Otto, Thomas Shirley and Shareef Siddeek. We dedicate this paper to Al Tyler, facilitator for this workshop, mentor and friend, who sadly passed away before this paper could be published.

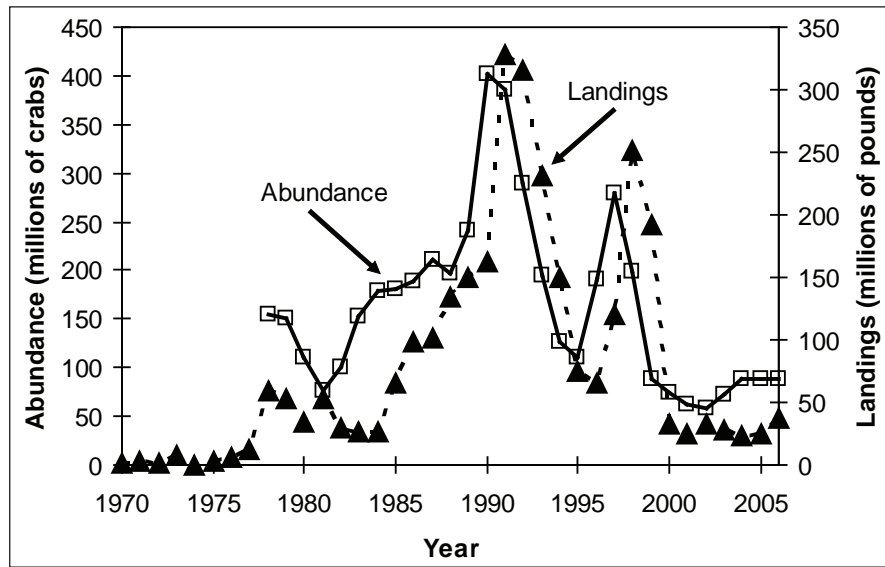


Figure 1. Summer abundance of large (≥ 102 mm carapace width) males (millions of crabs) estimated by a length-based assessment model from 1978–2006 (Turnock and Rugulo 2006) and subsequent winter commercial landings (millions of pounds) of snow crabs from the eastern Bering Sea from 1970–2006 (NPFMC 2006). Typically, landed crabs average 1.1 to 1.6 pounds each (Bowers et al. 2002).

owing to either foregone harvests associated with overly conservative management or lost productivity owing to unforeseen fishing effects. A motivation for our workshop was a strong desire to develop an understanding of potential mechanisms behind recruitment dynamics necessary to rebuild the eastern Bering Sea stock of snow crabs to serve as a basis for future research initiatives.

Development of Hypotheses by Life History Stage

The group began by identifying significant life history stages of snow crab in relation to reproduction and survival, then these stages were matched with the appropriate geographic areas and time of year. Using the chronologically ordered set of stages, seasons, and habitat characteristics, the group proceeded to articulate stage-by-stage hypotheses of processes that would likely be relevant to productivity and survival and be influenced by specific biotic and physical variables. The group characterized the season, locality, and habitat for snow crab life history stage in a stage-by-stage manner. Ecological relationships were discussed for each stage with the goal of developing a comprehensive set of process-oriented hypotheses. These testable hypotheses involved ecological relationships that, if true, would likely lead to observable variability in year-class strength indices.

The following 15 stages involving reproduction (stages 1–6) and survival (stages 7–15) were identified.

1. Ovary development and potential fecundity for prepubescent, pubescent and primiparous females
2. Ovary development and potential fecundity for multiparous females
3. Mating, egg fertilization and realized fecundity for primiparous females
4. Mating, egg fertilization and realized fecundity for multiparous females
5. Brooding of embryos for primiparous females
6. Brooding of embryos for multiparous females
7. Hatching of embryos
8. Zoeal larvae (two stages)
9. Megalops larvae
10. First-year benthic juveniles (age 0)
11. Later juveniles of ages 1 to 4 years
12. Adolescent males (ages 5 to 10 years) and prepubescent females (ages 3 to 7 years)
13. Adult (large-claw) males with new shells (sub-legal and legal size), ages 5 to 11 years
14. Adult (large-claw) males with old shells, up to maximum ages 11 to 17 years (i.e., up to 6 years post-molt to maturity)
15. Adult (large abdomen) females, up to maximum age 10 to 13 years (i.e., up to 6 years post-molt to maturity)

Description of Stages and Hypotheses

Workshop deliberations are described here and summarized in Table 1. While the following description includes all of the hypotheses in Table 1, they are arranged somewhat differently in the text for improved readability. We attempted to construct a comprehensive set of hypotheses deemed by the group to be sufficiently worthy to document for future investigation. By necessity, our workshop summary includes information and ideas, many of which are not citable in the peer-reviewed literature. Thus, the reader is cautioned not to confuse *hypotheses* as findings. In instances where some supportive evidence for the hypothesis exists for snow or Tanner crab, citations are provided. However, a full literature review and evaluations of the evidence for or against particular hypotheses were beyond the scope of the workshop. For a contemporary bibliography of snow crab research, the reader is directed to Paul (2000).

1. Ovary development and potential fecundity for pre-pubescent, pubescent and primiparous females

There is a point in the early life history of a cohort of crabs when relative year-class size is established. However, there is a significant lag between the time when ovary development and fecundity are determined and when year class strength can be detected. We distinguish between “potential fecundity” as the number of developing oocytes that could be subsequently fertilized and “realized fecundity” or clutch size as the number of developing embryos after successful fertilization. In the Gulf of St. Lawrence, year-class strength appears to be determined some time between ovary development and post-settlement age 1 to 2 years (Conan et al. 1996, Sainte-Marie et al. 1996) representing crabs of 5 to 10–15 mm carapace width (CW). In the eastern Bering Sea, annual stock assessment surveys (e.g., Stevens et al. 2002) provide rather reliable determinations of relative cohort size when crabs reach a size of approximately 50 mm CW. Hence, it may be questioned whether factors affecting ovary development can be detected as recruitment variability that can only be measured in later stages. Most likely, it is an accumulation of process effects through several life history stages that, acting in concert, result in the relative success of the cohort. Some factors may be inconsequential to recruitment variability in some years and highly influential in others.

At least 2 years are required for the ovaries to fully develop through the prepubescent stages. The last stage in the development of the ovary seems to occur in the shallowest part of the annual range of depths occupied by mature crabs, and from late December through

March, when temperatures are no higher than 2°C (Alunno-Bruscia and Sainte-Marie 1998). As is true for Tanner crabs (Somerton and Myers 1983), female snow crabs carrying their first clutch of fertilized eggs (termed “primiparous”) have a lower fecundity than females of the same size that brooded eggs at least once previously (termed “multiparous,” Sainte-Marie 1993). There may be more than one reason for this. First, fecundity of a primiparous female is probably constrained by its smaller body size prior to its molt to maturity (Hines 1982). Fecundity of a primiparous female may also be constrained by the energetic costs of growth and molting prior to the maturity molt. Indeed, once a female molts to first maturity, she does not molt again (i.e., so called “terminal molt”). Hence, the fecundity of a multiparous female is not constrained by the energetic costs of growth.

Oocyte size and numbers may depend on ration size. If there are many crabs in the habitat from the older year classes, then density-dependent competition may become a limiting factor on ration size and therefore ovarian development. Temperature influences the rate of development, either relative to the optimum temperature that maximizes developmental rate or with regard to an accumulation of degree days required to complete the maturation process. Also, temperature may have cumulative effects on fecundity through the life of the crab because crabs that inhabit environments with temperatures colder than optimum may experience slower growth rates and may achieve a smaller size at maturity than crabs experiencing more optimal temperatures (Alunno-Bruscia and Sainte-Marie 1998). Crabs maturing at smaller sizes produce fewer eggs (Sainte-Marie 1993).

2. Ovary development and potential fecundity for multiparous females

As discussed for stage 1, multiparous females have greater individual potential for producing more offspring than primiparous females. Oogenesis begins shortly after oviposition, which follows eclosion or hatching in May or June. The multiparous crabs are generally distributed in deeper water than are primiparous crabs and experience temperatures that are generally $\leq 3^{\circ}\text{C}$ in the eastern Bering Sea. Old multiparous crabs that have spawned 3 or 4 times show senescence, i.e., they likely have fewer oocytes than do younger multiparous crabs of the same size. The frequency and intensity of injury (limb loss and cuticle perforations) sustained after the maturity molt may be density-dependent (Sainte-Marie et al. 1999); lost chelae and other injuries may adversely affect potential fecundity of multiparous females, due to reduced foraging and

predator avoidance as evident in some other decapod crustacea (Juanes and Smith 1995). Other hypotheses in the primiparous stage (stage 1) pertaining to temperature, density-dependent effects, and constraints of body size apply to the multiparous stage as well (Table 1). In particular, very cold temperatures may increase reproductive cycles from 1 to 2 years, thereby halving potential fecundity of multiparous females.

3. Mating, egg fertilization, and realized fecundity for primiparous females

This stage occurs in the same habitats as the stage involving late development of oocytes (stage 1). Males are attracted to females as early as one month prior to the female molt when mating occurs. As in the case of Tanner crabs (Donaldson and Adams 1989), males hold the females (Watson 1972) and presumably afford them some protection from potential predators both prior to and after the maturity molt. Mating occurs within minutes to hours of the female's molt. The female retains sperm in seminal receptacles (spermathecae), and the eggs are fertilized internally in the ovary or as they are extruded onto the female's pleopods within approximately 6 hours of mating. Males often mate with more than one female, and vice versa (Urbani et al. 1998). If the abundance of mature males is insufficient, then some females may receive significantly less sperm and may not be able to fertilize all of their eggs; females that mate late in the season are particularly disadvantaged in this regard because dominant or preferred males may become sperm depleted (Rondeau and Sainte-Marie 2001). Larger males may have larger sperm volumes and mate preferentially with larger females. If large males are too sparse, then some portion of the egg clutch may go unfertilized. Mature males that are small or have very new (< 90 days old) or very old shells likely fertilize fewer females than do mature males that are large or have intermediate shells. It may be important to reduce fishing mortality on smaller sizes so that a sufficient number of large males survive and are able to mate for 2 to 4 years before being caught. Some females mate a second time after their molt to maturity, increasing the amount of sperm held for fertilization of future egg clutches. It is hypothesized that cool temperatures may be necessary for successful mating; if water temperatures are too warm in May and June, then mating may be disrupted.

4. Mating, egg fertilization and realized fecundity for multiparous females

The hypothesized mechanism stated in stage 3 (primiparous females) applies to stage 4 as well. The main

difference is that multiparous females tend to be spread over the Outer Domain (100–200 m) in the eastern Bering Sea, whereas the primiparous females occupy the Middle Domain (50–100 m) and shallow fringes of the Outer Domain (Ernst et al. 2005). Multiparous females may already have sperm in storage (therefore mating may be facultative), and, if they choose to re-mate, they mate 1 to 3 months later than primiparous females (Sainte-Marie and Hazel 1992). After the maturity molt and first mating, females can hold viable sperm for 2 to 3 years and continue to produce fertile eggs. Nonetheless, under laboratory conditions, the size of the second clutch of mature Tanner crabs was higher for females with access to males than for females relying on stored sperm (Paul and Paul 1992), however there was no difference in second clutch size for these same two groups of female snow crabs (Sainte-Marie and Carrière 1995). Also, in the laboratory, most multiparous Tanner crabs produced 2 but not 3 annual clutches with stored sperm only (Paul 1984).

5. Brooding of embryos for primiparous females

In the eastern Bering Sea, females undergo their maturity molt in the Middle Domain and mate in winter; in the subsequent year they migrate an average of 73.5 miles in a southwesterly direction toward the shelf edge, likely in response to temperature gradients (Ernst et al. 2005). In the Gulf of St. Lawrence, brooding females usually move from shallow mating grounds (4–20 m) to intermediate depths (20–80 m) as the surface waters warm and the thermocline forms (Lovrich et al. 1995). Completion of embryonic development depends on the accumulation of degree-days and takes 11 to 27 months following fertilization. Fertilized eggs sometimes hatch in spring, about 14 to 15 months after oviposition, but in areas of particularly cold temperatures embryos may require a second year to complete development (Moriyasu and Lanteigne 1998). Particularly for large females, a percentage of the clutch may be comprised of unfertilized eggs that eventually fall off the pleopods. Parasites and fungi cause mortality of embryos. Mortality may be heightened if the development period is 2 years rather than 1 year. Also, it seems plausible that suboptimal temperatures and possibly low dissolved oxygen levels increase the embryonic mortality.

6. Brooding of embryos for multiparous females

In the Gulf of St. Lawrence, the habitat differs between multiparous and primiparous females in that older females mate in intermediate to deep waters (20–140 m) and do not show a clear seasonal movement pattern with depth as the primiparous crabs do (Lovrich et al.

1995). Otherwise, the hypotheses for stage 6 are the same as for stages 5.

7. Hatch timing

Female mound formation may enhance hatching and dispersal of newly hatched larvae by possibly serving as “launch pads” in the congener, Tanner crab (Stevens et al. 1994, 1999). Cues for hatch timing include increased tidal currents associated with the monthly lunar cycle as tidal amplitude, at least in the case of Tanner crab (Stevens et al. 1999), and the presence of senescent phytoplankton in the case of snow crab (Starr et al. 1994). The adaptive significance may be that stronger currents increase larval dispersal, whereas senescent diatoms provide a chemical cue that allows larval hatching to be timed with a post plankton-bloom period when diatoms and copepod nauplii are likely to be present as prey for crab larvae. In the eastern Bering Sea, melting of sea ice is important to generate stratification in early spring (Stabeno et al. 1998) and associated plankton blooms that influence hatch timing. Synchrony of hatching and blooms likely improves larval survival. Colder temperatures may lengthen or delay the hatching period.

8. Zoeal larvae (2 stages)

Zoeae occur in the upper mixed layer over intermediate depth areas. They are abundant from April to June in the Bering Sea (Incze et al. 1987). In Atlantic Canada, after hatching in June in the southern Gulf of St. Lawrence (Moriyasu and Lanteigne 1998) and May and June in Bonne Bay, Newfoundland (Comeau et al. 1999), zoeae remain in the water column until settling during August to October (Lovrich et al. 1995). The durations of both larval stages vary inversely related to temperature (Kon 1970). A longer larval stage associated with lower temperatures means that larvae are vulnerable to plankton predators for a prolonged period of time. However, development of longer spines at cooler incubation temperatures could lessen this effect in snow crab larvae (Webb et al. 2006). Warmer sea surface temperatures may enhance production of copepods (Smith and Vidal 1984) or other prey of snow crab zoeae. In years of low copepod production, there is likely a density-dependent response in zoal ration size. It is hypothesized that crab predation by jellyfish, juvenile pollock *Theragra chalcogramma*, and Pacific salmon *Oncorhynchus* spp. smolts is a function of the abundance of these predatory species. Growth and survival is also likely to be a function of hatch size. Embryos that hatch after a 2-year development period may have lower survival than those that develop in 1 year.

9. Megalops larvae

This stage appears in the water column at the end of July in the southern Gulf of St. Lawrence and during August with settlement in October in the northern Gulf of St. Lawrence and Newfoundland (Lovrich et al. 1995). Most are found in shallow to intermediate depths. Megalopae feed on small copepods and may have lower survival in years when copepods are less abundant. Advection to areas overlying bottoms of suitable temperature and substrate in the zoeal and megalops stages is thought to affect survival through an interplay of geostrophic, tidal and wind-driven currents; this mechanism is currently being investigated in an individual-based model (C. Parada, University of Washington, personal communication). Megalopae settle to the substrate where they metamorphose to juveniles. Successful settlement into mud habitats is thought to be a criterion for good survival (Dionne et al. 2003). Many benthic fishes (Pacific cod is the primary predator in the eastern Bering Sea; Lang et al. 2003) and invertebrates feed on megalopae and recently metamorphosed crabs. It is hypothesized that megalopal survival decreases in years when these predators are more abundant, perhaps creating a “predator pit” from which it is difficult for the snow crab population to recover. Newly settled snow crabs are also cannibalized by larger juveniles (Lovrich and Sainte-Marie 1997), so there may be 2 sources of density-dependent survival rates.

10. Early benthic juveniles (3 instars, age 0+)

Starting in late August this stage is found in waters of 1°C in mud and gravel; in the eastern Bering Sea they occur at depths of 50 to 100 m (Zheng et al. 2001, Orensanz et al. 2004). It is hypothesized that survival decreases with increased abundance of bottom dwelling fish species such as flatfish, Pacific cod, sculpins, and invertebrates—especially octopus. Orensanz et al. (2004) proposed that predation by Pacific cod limits the southern boundary of the distribution of snow crabs. Cannibalism among year classes is likely an important density-dependent survival mechanism, with successful older year classes suppressing young of the year (Lovrich and Sainte-Marie 1997; Sainte-Marie and Lafrance 2002).

11. Later juveniles of ages 1 to 4 years

This stage is found in the same habitat as age-0 crabs. In the eastern Bering Sea, juvenile males and females tend to occur in the inner and middle shelf domains of the northeastern continental shelf (Zheng et al. 2001, Orensanz et al. 2004). They gradually disperse to the

habitat occupied by age 5+ crabs, which is warmer and deeper with temperatures up to 3°C on mud sediments. Body growth may be relevant to survival, because cod predation is highest on small-sized juveniles, age 0 and 1 (Lang et al. 2003). Ultimately, body size affects reproductive potential of the year class—for example, female fecundity is correlated with carapace size (Comeau et al. 1999). Growth rate and molting frequency are likely to be maximal at some temperature optimum and increase asymptotically with prey availability. Intermolt period (measured as degree days) increases linearly with carapace width in Tanner crabs (Paul and Paul 2002). Larger crabs cannibalize smaller ones (Lovrich and Sainte-Marie 1997). The density of predators listed under age-0 juveniles (stage 10) is still relevant to survival rates at this stage. Juveniles bury in soft sediments; insufficient soft sediments could lead to density-dependent mortality. Bitter crab disease associated with a dinoflagellate *Hematodinium* blood parasite (Meyers et al. 1987) infects some crabs in the eastern Bering Sea and northwest Atlantic Ocean. In a mortality study, all naturally infected crabs died (Shields et al. 2005). Although all sizes of crabs are affected, bitter crab disease is most prevalent in immature crabs (Morado et al. 2000, Shields et al. 2005). Bitter crab disease likely kills individuals in proportion to crab density and incidence probably increases with increasing bottom-water temperatures.

12. Adolescent males (ages 5 to 10 years) and prepubescent females (ages 3 to 7 years)

Crabs at this stage generally stay in the middle domain of the eastern Bering Sea (Zheng et al. 2001) except during molting, when they are in shallower water; thus they show seasonal migrations. Size at maturity may increase with growth rate, if maturity is at least partly age dependent. Growth rate and molting frequency likely have a temperature optimum and increase asymptotically with prey availability. Hypothetically, growth rate is density-dependent so that crab density and food availability influence size at maturity through growth rate and molting frequency. As with juveniles of ages 1 to 4 years (stage 11), bitter crab disease is relatively prevalent among adolescent males and prepubescent females, so mortality from these infections impacts mortality during stage 12 as well.

13. Adult (large-claw) males with new shells at maturity molt (sub-legal and legal sizes), ages 5 to 11 years

The distribution of males in this stage is similar to those in stage 12, but the largest males are segregated

from the adult females except during the mating period in winter (primiparous) and spring (multiparous). At that time they move into shallower water to the areas occupied by the females. Food supply is less likely to be limiting to crab growth and reproductive potential in the terminal molt stage, but there is considerable diet overlap between snow crabs and several small-mouthed flatfish species (Tarverdieva 1976, Lang 1992) perhaps leading to competition for prey. So, male snow crab reproductive output could have an inverse relationship with some flatfish species. Mortality during molting may increase with density of Pacific cod that prey on molting large crabs and their limbs (Lang et al. 2003). Mortality may intensify with abundance of predatory amphipods, of which there are two predominant genera in the Bering Sea (Oliver and Slattery 1986) that attack crabs at the site of injury. If the abundance of mature males is high, additional mortality might be due to competition among males for mates. The rate of incidence of bitter crab disease may depend on crab density.

14. Adult (large-claw) males with old shells, up to maximum ages 11 to 17 years (i.e., up to 6 years post-molt to maturity)

In spring, male snow crabs in this stage congregate in the coldest water with multiparous females. One of the major questions for the eastern Bering Sea used to be whether there is a terminal molt for male snow crabs as occurs for females. Although once the subject of much debate, terminal molt is widely accepted for snow crabs (Tamone et al. 2005). Once a terminal molt is attained, the exoskeleton gradually erodes over time and weakened muscle tissue and increased mortality occurs with senescence. Limb loss and amphipod predation are likely to increase with age, likely resulting in increased mortality with age post terminal molt.

15. Adult (large abdomen) females at maturity molt, up to maximum age 10 to 13 years (i.e., up to 6 years post-molt to maturity)

The largest concentrations occur in the coldest waters (< 2°C), especially in the spring. In the eastern Bering Sea, adult females occur predominantly in the outer shelf domain (Zheng et al. 2001). Because mature females are terminally molted, over time they suffer from eroded exoskeletons and weakened muscle tissue. Senescence sets in with associated higher mortality. The rate of mortality may increase with temperatures warmer than 2°C.

Table 1. Events-time table of the life history stages, and summary of hypotheses on formulation of year-class strength of snow crabs. Abbreviations: EBS (eastern Bering Sea), GSL (Gulf of St. Lawrence); SGSL (southern Gulf of St. Lawrence), NGSL (northern Gulf of St. Lawrence), and NF (Newfoundland). Hypotheses are listed regardless of the existence of supporting evidence at this time.

Stage/activity	Location/months Depth/temperature	Hypotheses (Stated as Questions)
1. Ovary development and potential fecundity (prepubescent, pubescent and primiparous females)	<ul style="list-style-type: none"> • Shallowest of depth range for EBS and GSL habitats • Mainly in colder waters <2°C; (late December to late March, February peak; GSL) 	<ul style="list-style-type: none"> • Fecundity is lower for primiparous than for multiparous females due to energy cost of molt? • Pre-molt size of primiparous females is smaller than size of multiparous females and size constrains fecundity? • Temperature (degree-day) is a threshold for complete maturation? Optimum temperatures are required for full oocyte maturation? • Oocyte size and number is a function of temperature, food, and density-dependent effects? • Temperature affects size (smaller when cold) which influences fecundity? • Density-dependent effects on size at maturity that in turn affects fecundity? • Limb-loss in prepubescent stages lowers primiparous fecundity owing to cost in energy budget? • Limb-loss in prepubescent and pubescent stages affects molt size increment?
2. Development of ovary and potential fecundity (multiparous females)	<ul style="list-style-type: none"> • Deeper than pubescent and primiparous females • Mainly <2°C • Right after spawning (May to June) for 1 or 2 years, depends on temperature • EBS: ≤3°C 	<ul style="list-style-type: none"> • Is there a degree-day threshold for complete maturation? • Optimum temperatures are required for full oocyte maturation? • Oocyte size and number depends on temperature, food, and crab density? • Reduced body size at cold temperatures lowers fecundity? • Fecundity declines with senescence? • Leg loss lowers fecundity through energy budget (reduced foraging efficiency)? • Limb-loss at primiparous mating reduces multiparous fecundity owing to reduced foraging efficiency?
3. Mating, egg fertilization and realized fecundity (pubescent and primiparous females)	<ul style="list-style-type: none"> • On molting grounds of pubescent females, shallowest of depth range • December to March with peak in February • Males attracted to females up to 1 month before molt • Mating occurs minutes to hours after females molt; fertilized eggs extruded approximately within 6 hours 	<ul style="list-style-type: none"> • Density and sex ratio affect quantity of sperm stored by females (e.g., males are parsimonious in allocating sperm, females mating later at disadvantage)? • Larger males have larger sperm volumes and mate preferentially with larger females, increasing percent of oocytes fertilized? • Degree of male polygamy is a dome-shaped function of male shell age, perhaps affecting percent fertilization? • Female promiscuity increases with male:female sex ratio and density of males, perhaps increasing percent fertilization from more sperm storage and sperm competition? • Mating does not occur above upper thermal limit?
4. Mating, egg fertilization and realized fecundity (multiparous females)	<ul style="list-style-type: none"> • Right after hatching (May to June) • 1 to 3 months later than primiparous females • Deeper than primiparous females (mainly <2°C) • Mating is facultative if females have sperm in storage from first mating • Fertilized eggs extruded approximately 6 hours after larval hatching 	<ul style="list-style-type: none"> • Density and sex-ratio affect quantity of sperm stored by females (males are parsimonious in allocating sperm, females mating later at disadvantage)? • Larger males mate preferentially with larger females (or vice versa), and larger males have larger sperm volume, perhaps increasing percent fertilization? • Degree of male polygamy is a dome-shaped function of male shell age, perhaps changing percent fertilization? • Female promiscuity increases with male:female sex ratio and density of males, perhaps increasing percent fertilization from more sperm storage and sperm competition? • Mating does not occur above an upper thermal limit?

-continued-

Table 1. Page 2 of 3.

5. Brooding of embryos (primiparous females)	<ul style="list-style-type: none"> • About 15 or 27 months depending on 1 or 2 year cycle (e.g., eggs laid with February peak, hatch May to June, 1 or 2 years later) • Initially shallow, moving to deeper water about 3 months after February, after thermocline formation (GSL) 	<ul style="list-style-type: none"> • Embryo maturation depends on degree-day accumulation (1 or 2 year brooding period)? • Unfertilized eggs remain for several months then fall off; large females lose more eggs than small females? • Loss of embryos due to predators, parasites, fungi? • More embryo loss in two-year brood than one-year? • Temperature change effects on oxygen content and embryo survival?
6. Brooding of embryos (multiparous females)	<ul style="list-style-type: none"> • About 12 or 24 months depending on 1- or 2-year cycle • Depth and temperature distribution as noted in (4), above • No large scale movement occurs 	<ul style="list-style-type: none"> • Embryo maturation depends on degree-day accumulation (1 or 2 year brooding)? • Large females lose more eggs than small females and extrude more unfertilized eggs that remain attached for several months then slough off? • Some loss of embryos due to predators, parasites, fungi? • More embryo loss in two-year brood than one-year? • Temperature changes reduce embryo survival with greater shifts causing more embryo loss?
7. Hatch timing	<ul style="list-style-type: none"> • May to June: coinciding with spring phytoplankton blooms • Depth/temperature as noted in (4) and (6), above 	<ul style="list-style-type: none"> • Mound formation exists and is a prerequisite as larval “launching pads” for hatching? • Tidal currents are cues for hatching with hatching linked to strongest tides? • Higher crab density leads to greater synchrony of hatching? • Greater synchronicity increases larval survival? • Senescent phytoplankton (diatoms) settling through the water column serve as hatching cue? • Colder temperatures lengthen or delay hatching period? • Stratification at ice-edge in spring generates early diatom blooms that trigger hatch timing?
8. Zoea (2 larval stages)	<ul style="list-style-type: none"> • Upper mixed layer • 1 to 1.5 months for each stage, depending on temperature • SGSL: June to July. NGSL: June to August. NF: August? BS: July south of 58°N, other times for other areas? 	<ul style="list-style-type: none"> • Advection to juvenile grounds affects survival through the interplay of geostrophic, tidal, and wind-driven currents? • Survival is a density-dependent function of food? • Low temperature delays development and increases mortality? • Warmer temperatures (up to an optimum) promote production of copepod nauplii as prey? • Predation increases with abundance of juvenile pollock, cod, jellyfish, amphipods, euphausiids? • Growth and survival is a function of hatching size? • Larval survival is lower for 2-year embryo development than 1-year development?
9. Megalops	<ul style="list-style-type: none"> • As early as August (NGSL, NF), late July (SGSL) • Settling at shallow to intermediate depths at temperatures <3°C 	<ul style="list-style-type: none"> • Advection to juvenile grounds affects survival through the interplay of geostrophic, tidal, and wind-driven currents? • Cannibalism within year class causes density-dependent survival? • Decrease in survival with lower zooplankton prey? • Water column predation increases with abundance of juvenile pollock, cod, jellyfish, amphipods, and euphausiids? • High survival depends on settlement on mud substrates with refugia (e.g., small structures) in cold water? • Benthic predation increases with abundance of demersal fish predators?

-continued-

Table 1. Page 3 of 3.

10. Early benthic juveniles (3 instars, age 0+)	<ul style="list-style-type: none"> • Peak abundance in coldest water <1°C • Mud, gravel • Stage begins in late August, lasting up to 1.5 years • No large scale movements • Hiding in rafts of macroalgal debris 	<ul style="list-style-type: none"> • Space and food limitations (e.g., small structure habitat and cold water)? • Survival reduced by predation by groundfish (e.g., eelpouts, cod, yellowfin sole, rock sole and sculpins)? • Survival reduced by predation by invertebrates (e.g., octopus?) • Density-dependent cannibalism among year classes, with larger juveniles feeding on smaller juveniles? • Decrease in survival with increase in temperature?
11. Juvenile ages 1 to 4	<ul style="list-style-type: none"> • The same bottom as noted in (10), above • Coldest (<1°C to 2°C) • EBS: 50 to 100 m • Dispersing with increasing age into other habitats, including mud bottoms in warmer, deeper areas • Seasonal migrations 	<ul style="list-style-type: none"> • EBS: distribution determined by inner front strength? • Optimum temperature for molting frequency and growth increment? • Growth depends on availability of prey? • Survival decreases with cod abundance and overlapping distribution? • Eelpouts and sculpins are predators? • Cannibalism of larger juveniles on smaller juveniles? • Space and food limitations owing to areas with small structure habitat and cold water? • Disease (especially bitter crab) increases mortality, perhaps affected by temperature and/or density?
12. Adolescent males, ages 5 to 10; prepubescent females ages 3 to 7	<ul style="list-style-type: none"> • GSL: highly migratory, more than juvenile • Temperatures <3°C 	<ul style="list-style-type: none"> • Size at maturity increases with growth rate? • Ambient temperature affects molting frequency and growth increment and in turn affects size at maturity? • Smaller size at maturity at higher density? • Skipping annual molt increases with density – delays maturity? • Disease and bitter crab syndrome increases mortality, perhaps affected by temperature and/or density?
13. Adult large claw male, newshell: sublegal + legal. Ages 5 to 11 at maturity molt to ages 11 to 17	<ul style="list-style-type: none"> • Growth (maximum size) positively correlated with temperature up to 4°C • Largest males are segregated from adult females • Males upslope to females as hatching time approaches 	<ul style="list-style-type: none"> • Is the existence of a terminal molt dependent on temperature or crab density? • Competition with flatfish for food? • Predation by cod, skates, large-bodied groundfish during molting? • Predation by amphipods following limb loss and injuries? • Increased mortality after mating from competition among males? • Increased mortality after maturity? • Disease and bitter crab syndrome increases mortality, perhaps affected by temperature and/or density?
14. Adult large claw males, oldshell (sublegal and legal sizes) to ages 11 to 17	<ul style="list-style-type: none"> • Congregate in coldest water with multiparous females (pre-death) 	<ul style="list-style-type: none"> • See (13), above • Senescence affects virility? • Limb loss increases with age?
15. Adult large abdomen females 4 to 7 at maturity molt to ages 10 to 13	<ul style="list-style-type: none"> • Largest concentrations in coldest waters, mainly <2°C 	<ul style="list-style-type: none"> • Mortality increases with temperature increases? • Mortality increases and condition decreases with number of mates? • Senescence affects virility?

DISCUSSION

Many hypotheses about snow crab productivity and survival are associated with the multiple life history stages of this species. Taken collectively, the potential mechanisms of year-class formation are very complex involving many environmental and ecological factors often operating in multiplicative ways over multiple life stages and habitat locations. During any one life stage several factors may combine to influence survival and productivity and hence subsequent year-class success. The influence of even the readily measurable variable—summer ocean temperature—will be difficult to understand because of its role in multiple stages. Temperature is an interesting variable to consider, because of ongoing warming trends in the eastern Bering Sea (Overland and Stabeno 2004). A warmer than usual temperature at one time/place/life-history stage could enhance year-class strength, but the same temperature level could cause decreased productivity at another time/place/stage. For example, as indicated in Table 1, slightly warmer sea-surface temperatures in May and June could increase the supply of copepod prey for zoeae and so enhance survival. However, the same temperature could decrease survival during development of the embryos attached to adult females in deeper, usually colder areas.

A systematic examination of potential temperature effects, stage by stage from Table 1, shows that the role of temperature differs enormously in the processes of the different stages. Temperature affects the development of oocytes (stages 1 and 2) and embryos (stage 5) in similar ways. Oocytes develop internally, whereas embryo development is external because they are attached to the female's abdomen. Embryos are subject to predation by nemertean worms, and the rate of infestation may be accelerated in years with warm temperature anomalies. Development rate is likely to be a dome-shaped function of temperature, with an optimum level $< 3^{\circ}\text{C}$. In years with an extensive pool of cold bottom water in the eastern Bering Sea, crabs with attached embryos could find themselves in temperatures lower than optimum, with consequent inhibition of embryo development. There is evidence in the eastern Bering Sea that an extensive cold pool forms in some years (Azumaya and Ohtani 1995) that inhibits year-class strength formation in the congener species, Tanner crab (Rosenkranz et al. 2001). Alternatively, snow crabs are more cold-adapted than Tanner crabs (Somerton 1981), so the response is likely to be species specific with different thermal optima. At the same time, completion of either oocyte or embryonic development likely requires an accumulation of a

critical number of degree-days. Because of this, 2 years might be required for completion of snow crab embryo development during successive cold years.

In stage 3, one temperature hypothesis is that warm anomalies in late winter or spring (e.g., $> 3^{\circ}\text{C}$) could inhibit mating. For stage 7, temperature likely affects hatch timing but the mechanisms are unclear. A hypothesis suggested during the workshop was that cold temperatures in May and June could lengthen or delay the hatch period and cause a mismatch with spring plankton blooms that, in turn, are more dependent on high nutrients and a stable upper water column than on temperature. For stage 8, zoeal instars occur in the upper mixed layer at warmer temperatures than frequented by adults. Cool years may inhibit development of the small-bodied copepods preyed on by the zoeae and as well delay the molting of zoeal instars. An extended period in the zoeal stage would likely cause increased predation mortality.

The next temperature hypotheses are for stages 10 and 11, the early benthic juveniles. These small crabs are distributed in very cold water $< 2^{\circ}\text{C}$. The conjecture is that there is a dome-shaped survival relationship with temperature, with an intermediate-temperature optimum for somatic growth and molting. Decreased survival is expected to occur in years with lower or higher than optimum temperatures.

Stage 12 crabs (adolescent males and pre-pubescent females) are distributed in slightly warmer water and would likely have a slightly higher temperature optimum for body growth than do the early juveniles, with compounding effects on size and age at maturity. Adult crabs, stage 13, may have a distribution in slightly warmer water, up to 4°C , and a warmer temperature optimum for gonad and somatic tissue development.

Other than temperature, additional relevant factors include (1) densities of predators (the suite of predator species differs across life stages), (2) density-dependent cannibalism among early juvenile instars, (3) size frequencies of both males and females, and sex ratio in relation to reproductive function, (4) egg and embryo parasites and predators, (5) environmental cues for embryo hatching, (6) favorable advection or retention of pelagic larvae, (7) density-dependent availability of prey items for juveniles, and (8) the interaction of food rations and temperature on molting frequency and somatic growth.

The multiplicity of hypotheses and life stages creates a rather tangled web of mechanisms for future investigation. However, we believe that several particular avenues of research are most likely to yield understanding about the variation of year class success. We propose what appears to us as the most promising approaches

for research at sea and in the laboratory, and through computer modeling by life history stage.

For investigation into stages 1 and 2, at-sea summer surveys should collect mature females for histological examination of oocyte and embryo development along with associated ambient bottom temperature at each collection site. The purpose would be to examine the hypothesis that development is inhibited in years of extensive cold pool formation. It would be valuable to compare two or more snow crab populations in conducting this research so as to examine the generality of the relationships over a wide range of conditions. Also, it would be valuable to examine embryo clutches carried by the females to record the extent of nemertean predation in relation to bottom temperature.

Another particularly critical stage seems to be stage 8, the zoeae. A study goal would be to understand their distribution in the summer with respect to associated sea surface temperature and concentrations of diatoms and copepod nauplii. This work should be carried out in a 3-year study for interannual comparisons. Results would bear heavily on the hypotheses concerning larval survival.

At the same time, juvenile (stages 10 and 11) distributions should be investigated with respect to bottom temperature, bottom habitat type, and the presence of predators, such as yellowfin sole *Limanda asper*, flat-head sole *Hippoglossoides elassodon*, Pacific cod, and skates. This research would investigate hypotheses of distributional relationships and predation mortality and should be carried out over a 3-year study. On the same cruises, the summer distribution of adult snow crabs could be examined in relation to maturity stages and

reproductive condition. This survey should include collection of bottom temperature measurements and characterization of bottom habitat type, pursuant to the hypotheses regarding these stages.

Laboratory research on the development of embryos in controlled temperature tanks would reveal the relationship between development and temperature, and would help confirm the at-sea findings in the proposed survey. Laboratory studies of the settlement preferences of megalops larvae would add supportive evidence to the reasons for their observed at-sea distributions and may help explore the possibility of limited critical habitat for settlement.

Length-based analyses of survey and fishery data (e.g., Zheng et al. 1998, 2002, Turnock and Rugulo 2006) can provide estimates of year-class strength useful for retrospective computer-based modeling. Hypotheses for stage 1 and 2 could be investigated by examining relationships between year-class success and the annual extent of the bottom cold pool. Hypotheses for stage 8 could be investigated by examining possible relationships between winds and larval advection. Year-class success should be compared to abundance trends of predators, lagged appropriately to examine mortality effects on juveniles. As species distribution may be more important than abundance, annual changes in the overlap of geographic distributions of juveniles and their predators should be examined from survey data. These and other potentially important recruitment hypotheses can be investigated in the context of a dynamic simulation model that considers potential conflicting and/or synergistic mechanisms that are time sequenced according to the different life stages.

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APPENDIX

Appendix 1. List of Workshop Participants

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