The reproductive ecology and fecundity of *Cancer* crabs

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ABSTRACT

Patterns in *Cancer* reproduction varied within the general themes of life history, behavior, and body size. Patterns existed in the maturation and mating of these crabs, in the processes of extrusion and oviposition of their eggs, and in their size-fecundity relationships. Fecundity and reproductive potential were defined in terms of the number of eggs per brood and the potential number of broods over the life span of an individual. The patterns in egg production and fecundity were correlated with aspects of maturation, adult size and seasonality. Egg production appeared constrained by the number of juvenile and adult instars, crab longevity, body size and the habitat/climatic regime. These constraints may be surmounted at the expense of crab growth or adult size; changes in egg production may result from precocious maturation or from modifications in the energetics of production.

1 INTRODUCTION

Efficient management of commercial crab fisheries requires knowledge of the reproduction and life history of the exploited species. Considering the commercial importance of some *Cancer* crab stocks, it is surprising how little is known about the reproductive biology and reproductive ecology of most species. While the physiology of spermatogenesis, oögenesis and fertilization have been reported for several species of Brachyura, an analysis of fecundity and reproductive ecology of most species is lacking.

Here I review and synthesize the reproductive ecology of the genus *Cancer*. Aspects of maturation, mating and reproductive behavior, egg extrusion, oviposition, fecundity and brood mortality are presented. Factors affecting reproduction, such as seasonality and temperature, are described, and the temporal patterns of egg production are presented. In addition, the reproductive potential is estimated for each species.

2 MATURATION AND MATING

Spermatogenesis, oögenesis and fertilization are integral components of maturation and mating. These processes have received wide attention in the brachyurans (e.g. Adiyodi & Subra-

moniam 1983, Pochon-Masson 1983), including *Cancer* (Langreth 1969, Eurenius 1973). Spermatogenesis and oögenesis are closely tied to circadian rhythms and neurosecretory hormone cycles (e.g. Adiyodi & Subramoniam 1983, Charniaux-Cotton & Payen 1988). Crab reproduction, therefore, has a strong temporal component which may be regulated by seasonal and biochemical cues.

2.1 *Maturation*

Several studies have examined sexual maturation in male and female *Cancer* crabs. A female crab capable of mating may possess unripe gonads. Hence, to determine maturity, the following should be examined: completeness and maturation of gonads, presence of secondary sexual characteristics (including pre-pubertal and pubertal molt characters), minimum and average size at first copulation, molt increment vs. size for female crabs, and the obvious presence of sperm plugs or eggs.

Maturation, as defined by the ability to copulate, in *Cancer* occurs at the pubertal molt. Considerable variation exists in the number of juvenile instars that occur prior to maturation (Table 1). For most species of *Cancer*, 9 to 10 juvenile instars precede maturity which occurs

Table 1. Maturity and reported longevity of various female *Cancer* crabs. Unknown data are indicated by (–); incomplete data, (?); carapace width, CW.

Species	References	Number of juvenile instars	Years to maturity (from megalopa)	Minimum size at maturity (CW in mm)	Maximum number of instars	Maximum age (years)
C. antennarius	Carroll (1982)	10-12	1.5-2	73	16	7
C. anthonyi	Anderson & Ford (1976)	11-13?	2?	89	16?	–
C. borealis	Carpenter (1978)	–	2?	89	–	–
C. gracilis	Orensanz & Gallucci (1988)	9-10	2	54	12	4?
C. irroratus	Krouse (1976)	5-9	2	14	14	7-8
C. magister	Orensanz & Gallucci (1988)	9-10	2	95	13	8?
C. oregonensis	Orensanz & Gallucci (1988)	4-5	0.5	10	11	–
C. pagurus	Bennett (1974)	–	–	91	–	–
C. productus	Orensanz & Gallucci (1988)	9-10	1	70	13	4
C. setosus	Gutierrez & Zuniga (1976)	7-8	2	83	12	5

Table 2. Variation in the minimum and maximum size of ovigerous *Cancer irroratus* with latitude; sites listed from north to south. *Mature non-ovigerous crabs.

Location	References	Minimum size	Maximum size	Sample size (N)
Northumberland Strait	Scaratt & Lowe (1972)	60	99	53*
Bay of Fundy	Campbell & Eagle (1983)	41	100	50
Northern Main	Krouse (1972)	55	99	6635
Rhode Island	Reilly & Saila (1978)	14	82	31
Mid-Atlantic Bight	Haefner (1976)	21	100	130*
Chesapeake Bay	Shotton (1973)	28	106	32

approximately two years after settlement of the larval megalopa. These species attain maturity at a minimum size of about 90 mm carapace width (CW) (e.g. *C. anthonyi, C. borealis, C. magister* and *C. pagurus*). The notable exception is *C. gracilis* which attains but 54 mm CW after a similar number of juvenile instars over two years (Table 1). *Cancer oregonensis* has the fewest juvenile instars; it achieves maturity after 4 to 5 juvenile instars within approximately 6 months of settlement (Orensanz & Gallucci 1988). *Cancer productus* retains the average number of juvenile instars, but has a short maturation period of approximately one year (Orensanz & Gallucci 1988).

The minimum size at maturity is partially dependent upon the number of juvenile instars (based on the minimum number of juvenile instars, $R = 0.773$, $P < 0.05$, $N = 8$; Table 1). The number of adult instars may also be dependent upon the number of juvenile instars. However, the number of juvenile instars of *C. irroratus* may increase with latitude (Table 2). Northern populations of *C. irroratus* attain sexual maturity at a relatively large size after 13 to 14 juvenile instars (Krouse 1976), while populations off Rhode Island attain maturity after 5 to 9 juvenile instars (Reilly & Saila 1978).

Individual crabs mature at different rates and sizes. Hence, the size at which 50% of the population matures is often used to indicate the 'typical' size at which crabs are considered adults (Wenner et al. 1974, Campbell & Eagle 1983, LeFoll 1986). While this estimate may be indicative of maturity for a local population, considerable variation is reported between populations. For example, *C. irroratus*, matures at a larger adult size in the boreal waters of the Bay of Fundy and Nova Scotia (Campbell & Eagle 1983) than it does off Rhode Island and in waters around the Chesapeake Bay (Table 2) (Haefner 1976, Reilly & Saila 1978). Similarly, *C. pagurus* matures at a larger size in the northern waters of England than it does off southern Brittany (Brown & Bennett 1980, LeFoll 1986). Further, the contribution of smaller crabs to the overall production of eggs may be small (Gutierrez & Zuniga 1976), but if small mature crabs are abundant they may account for substantial egg production (Hankin et al. 1985).

2.2 *Mating*

The two most important factors in the mating of crabs are the maturity of the individuals and their stages in the molt cycle (Hartnoll 1969). In addition, behavioral aspects that affect the locating of mates and the probability of successful matings are important features of recently described mating systems.

Chemical cues are used by some *Cancer* species to attract mates. Prior to ecdysis and mating, female *C. antennarius* and *C. anthonyi* secrete a mating pheromone into the surrounding water that attracts male crabs at distances of up to 30 cm (Kittredge et al. 1971). Male crabs are both attracted to and placated by the pheromone (Kittredge et al. 1971). Upon contact with the pheromone, a male crab approaches and gently clambers over the female, positioning himself dorsally over her. Although an attraction to female crabs was noted in *C. pagurus* (Edwards 1966), a mating pheromone has not been detected in the urine or surrounding seawater of 'precopula' females (Hartnoll & Smith 1979). Work with *C. pagurus* is inconclusive; pheromones may not necessarily be released over the entire course of 'precopula.' Rather, they may be secreted over a much shorter time and have a short period of biological activity, as in *Portunus sanguinolentus* (Christofferson 1970).

The male and female crab remain in the mating embrace for some time. The precopulatory embrace or 'precopula' lasts from 3 to 21 days in *C. pagurus* (Edwards 1966), at least 8 days in *C. magister* (Snow & Nielsen 1966), and at least 13 days in *C. borealis* (Elner et al. 1985). The male and female are positioned sternum to sternum (Snow & Nielsen 1966), or sternum to carapace (Edwards 1966); or they switch between these positions (Williamson 1904, Elner et al. 1985). When ecdysis is imminent, the female signals her impending molt to the male, via increased antennal and chelar activity (Snow & Nielsen 1966). The male crab assists ecdysis of the female crab by helping to push off her exuvium (Edwards 1966, Snow & Nielsen 1966). Upon ecdysis, the male carefully positions the female sternum to sternum and copulation takes place.

Copulation was first described for *Cancer pagurus* (Williamson 1904). Additional observations have been provided by Pearson (1908), Butler (1960), Edwards (1966), Snow & Nielsen (1966), Hartnoll (1969), Shotton (1973) and Elner et al. (1985). Copulation occurs immediately or shortly after the female crab molts and lasts longer than 2 hours (Edwards 1966, Snow & Nielsen 1966, Elner et al. 1985). Successful mating only occurs when the female crab is immediately post-molt (Edwards 1966, Hartnoll 1969, Elner et al. 1985).

Spermatophores transferred at copulation break open during intercourse and release spermatozoa into the oviducts (Williamson 1904, Shotton 1973). The released spermatozoa travel up the oviducts into the internal spermathecae. Sperm plugs seal the oviducts after copulation. Sperm plugs may function to keep spermatozoa in the spermathecae, to lubricate the oviduct, and/or to stop forced mating by dominant male crabs (Williamson 1904, Edwards 1966, Hartnoll 1969, Elner et al. 1985). Sperm plugs in *C. pagurus* are thought to arise from male secretions (Hartnoll 1969), although Williamson (1904) suggests that they may originate from the glands lining the spermathecae of the female.

Some male *Cancer* crabs are polygynous. In laboratory studies, a single male *C. pagurus* mated with 10 female crabs (Edwards 1966). Large male *C. pagurus* force smaller male crabs off and away from 'precopula' females. Female crabs do not appear to select larger males and, in the absence of large males, successfully mate with smaller males (Edwards 1966). Males of *C. magister* also mate with more than one female in the laboratory (Butler 1960). The presence of mating marks on the carapace of trapped male crabs is used to indicate their mating history (Cleaver 1949, Butler 1960).

After copulation, the male and female crab remain in a postcopulatory embrace. The embrace lasts from 1 to 12 days or until the new carapace of the female is sufficiently hardened for her protection (Edwards 1966). Males removed from females during the postcopulatory embrace return to embrace the females (Edwards 1966, Elner et al. 1985). The use of chemical cues has not been investigated during this period. After mating and the postcopuolatory embrace, the

males of many species molt (Edwards 1966, Hartnoll 1969). In extreme cases, the male molts several months after the female (Haefner & Van Engel 1975).

2.2.1 *Mating seasonality*

Molting and mating of mature *Cancer* crabs exhibit distinct seasonal patterns (Fig. 1). The majority of the species molt and mate from late winter (February-March) to mid autumn (October-November), with a mating peak in summer (Fig. 1). Little if any mating occurs in late autumn and early winter. Many females approach oviposition or were ovigerous at that time (Fig. 2). Exceptions to the seasonal pattern are those crabs that breed year-round (*C. antennarius* and *C. anthonyi*), those with a relatively long and irregular brooding season (*C. irroratus* and *C. productus*), and those found in the southern hemisphere, where the austral summer is from December to February (*C. setosus*).

Variations within a species in the seasonal patterns of molting and mating are numerous and occur between distinct stocks or latitudes (see Conan 1985). For example, *C. pagurus* molts during summer off northwest England, during autumn off Scotland (Broekhuysen 1936), year round off southwest England (Bennett 1974), and during spring and autumn off Brittany (Drach 1949). Similarly, *C. irroratus* molts during summer and autumn in the northern portion of its range, and during winter and spring in the southern portion of its range (Scaratt & Lowe 1972, Haefner & Van Engel 1975, Krouse 1980). These patterns may be related to seasonal changes in temperature, photoperiod or primary productivity (Conan 1985, see also 4.2).

2.2.2 *Mating systems*

Distinct mating systems have recently been proposed for three species of *Cancer* crabs (Oren-

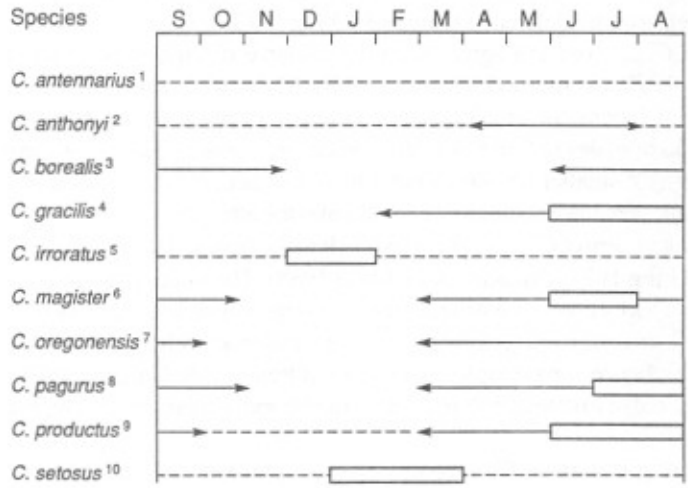

Figure 1. Molting and mating seasons for females of various species of *Cancer* crabs; (box) peak (5% of female population) in the number of molting females, (solid line) moderate levels (5%) of molting and mating, (dashed line) low levels (1%) of molting and mating. Note in some cases the proportion of molting or mating females in a population has been determined subjectively on the basis of descriptions in references. References: [1] Carroll (1982), Carroll & Winn (1988); [2] Winn (1985), Carroll & Winn (1987); [3] Haefner (1977), Carpenter (1978); [4, 7, 9] Knudsen (1964); [5] Krouse (1972, 1976), Terretta (1973), Reilly & Saila (1978); [6] MacKay (1942), Cleaver (1949), Butler (1961); [8] Bennett (1974), Brown & Bennett (1980); [10] Gutierrez & Zuniga (1976).

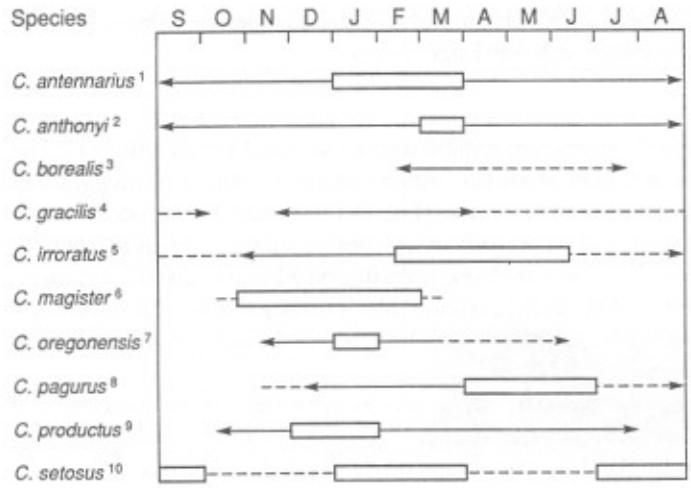

Figure 2. Ovigerous or brooding seasons of various species of *Cancer* crabs; (box) peak in the number of ovigerous females, (solid line) many (5%) ovigerous females in population, (dashed line) few (1%) ovigerous females in population. Note in some cases the proportion of ovigerous females in a population has been determined subjectively on the basis of descriptions in references. See Table 1 for references unless noted: [2] Reilly (1987); [4, 6, 7, 9] Orensanz & Gallucci (1988).

sanz & Gallucci 1988). These mating systems are based on the polygynous behavior of male crabs, the behavioral dynamics of the species and the structure of the populations. Directed by sexual selection, these mating systems may be driven by 'the ability of a portion of the population to control access of others to potential mates' (Emlen & Oring 1977).

The mating behavior of *C. oregonensis* agrees with the resource defense hypothesis of polygyny (Emlen & Oring 1977, Orensanz & Gallucci 1988). Males of *C. oregonensis* indirectly control access to small 'harems' of female crabs by dominating critical resources, in this case, small refuges. The ratio of males to females in the population is low, as large males are outnumbered by their 'harem' of smaller females (Orensanz & Gallucci 1988). In effect, the male crabs defend or dominate separate refuges to which females are attracted.

The structure of the mating system of *C. gracilis* corresponds to the female defense hypothesis of polygyny (Emlen & Oring 1977, Orensanz & Gallucci 1988). The males of *C. gracilis* directly control access to females by contests with other males and by an increased activity over that of females. Females of *C. gracilis* form large aggregates, and males actively staying within the aggregate increase their chance for multiple copulations (Orensanz & Gallucci 1988). Aggregating females are assured of a mate and increase their likelihood of mating with a highly competitive, dominant male.

The structure of the mating system of *C. magister* closely approximates the explosive breeding assemblage of the male dominance hypothesis of polygyny (Emlen & Oring 1977, Orensanz & Gallucci 1988). Males and females of *C. magister* converge during a short but highly synchronized mating period (Butler 1961, Diamond & Hankin 1985). A male-dominated sex ratio ensures that females find mates, but the highly synchronous mating period drives the sex ratio of mating crabs towards unity. Consequently, searching behavior to find a mate increases in importance. Sequestering of females or the dominating of subordinates appears less important during this synchronized mating period (Orensanz & Gallucci 1988).

3 EXTRUSION AND OVIPOSITION

3.1 *Extrusion*

Fertilization is internal in *Cancer* and presumably occurs in the oviduct. Contractions of the surrounding muscles squeeze ova out of the ovary, through the oviduct and out onto the pleopods (Binford 1913). Spermathecal secretions lubricate the oviduct for the passage of eggs during extrusion (Anilkumar & Adiyodi 1977). The eggs then become attached to setae on the pleopods.

Oviposition does not occur immediately after copulation. In *Cancer antennarius*, oviposition occurs approximately 11 weeks after mating (Carroll 1982). Extrusion in *C. magister* occurs 3 months after mating; and in *C. pagurus*, extrusion occurs more than 4 months after mating (Figs. 1 and 2). Viable sperm remain in the spermathecae for over six months (Shields pers. observ.) and indirect evidence suggests that sperm may remain viable for over one to two years (Pearson 1908, Knudsen 1964, Ebert et al. 1983, Hankin et al. 1985, Orensanz & Gallucci 1988).

3.2 *Egg attachment*

The process of egg attachment to the setae of the pleopods among the Decapoda has been much debated. In shrimps and lobsters, an attachment cement is secreted at oviposition by glands in the pleopods (see Fisher & Clark 1983). Secretions from the pleopod have not been observed in crabs (Cheung 1966). Glandular openings, however, have been observed on the exopods of the pleopods of *C. anthonyi* (Okazaki 1988). Further work may elucidate the role of the exopods in egg attachment.

The outer egg coat of the crab egg has been shown to effect the attachment of eggs to the maternal pleopods (Goudeau & Lachaise 1980, Goudeau & Lachaise 1983). The attachment of eggs occurs when the outer coat contacts the seta of an endopod; the external face of the outermost vitelline membrane sticks to the seta, elongates and hardens to form a funiculus, stalk, or connectant (Goudeau & Lachaise 1983). Curiously, eggs do not adhere readily to each other, rather, the strong adhesion of eggs occurs only to the setae of the endopod of the pleopod. Perhaps an epoxy-type 'resin' is secreted onto the setae prior to or during extrusion. The 'resin' could interact with its counterpart on the surface of the chorion to form a strong bond. Alternatively, aeration by the maternal pleopods, which ensures that eggs come into contact with the setae, could rupture the chorion, and the perivitelline cement first observed by Williamson (1904) then effects the attachment of eggs. In any case, the attachment of eggs to the setae remains unclear for *Cancer* crabs as well as for most brachyurans.

3.3 *Oviposition*

3.3.1 *Ovipositional behavior*

A female *Cancer* crab precedes oviposition by selecting a suitable substrate for extrusion. She typically burrows into sand or a 'soft' bottom substrate. There, she extrudes eggs into the incubatory chamber formed by her abdomen and the surrounding substrate. A soft substrate was required for the proper retention of eggs of *C. anthonyi, C. irroratus, C. magister,* and *C. pagurus* (Krouse 1980, Howard 1982, Ebert et al. 1983, Shields pers. obs.).

Changes in behavior occur during oviposition and brooding. Ovipositing crabs are quiescent during and immediately after extrusion. Female *C. pagurus* remain quiescent throughout the ovigerous period; they do not actively enter traps (Brown & Bennet 1980) nor do they feed (Howard 1982). However, ovigerous females of *C. antennarius* and *C. anthonyi* are not quiescent and actively enter commercial traps (Shields pers. obs.). Further, ovigerous females of *C. magister* enter traps in their early breeding period and later become less abundant in traps (Hankin et al. 1985).

3.3.2 *Reproductive migrations*

The patterns of migration in relation to reproduction for *Cancer* crabs were recently reviewed (Orensanz & Gallucci 1988). The females of *C. magister, C. pagurus* and *C. productus* migrate several kilometers to offshore breeding grounds. A distance of 230 miles was recorded for one female *C. pagurus* (Edwards 1979). In addition, the early zoeal larvae of these species may often be found several kilometers offshore (Nichols et al. 1982). *Cancer setosus* migrates shorter distances to deeper waters (Gutierrez & Zuniga 1976).

Migrations are not necessarily to offshore locations. The females of *C. borealis, C. irroratus* and *C. pagurus* appear to migrate inshore and offshore; their migrations appear related to habitat (i.e. substrate type for suitable oviposition) (Edwards 1979, Krouse 1980), or thermal preferences (Jeffries 1966, Haefner & Van Engel 1975). Some crabs do not migrate and remain in the same general area, for example, *C. antennarius* and *C. anthonyi* (Carroll 1982, Winn 1985). Further, the migratory patterns of male crabs may differ from conspecific females (Orensanz & Gallucci 1988).

4 EMBRYOGENESIS

4.1 *Brooding time and temperature*

The effect of temperature on crustacean egg development has received much attention (e.g. Perkins 1972, Wear 1974). Low temperatures decrease and high temperatures increase the rate of embryogenesis. Wide variations in development times are notable between species of *Cancer* and these variations may be, in part, the result of climatic conditions. In general, those species inhabiting cold waters ($< 10°C$) have much longer embryogenic periods than did those inhabiting warmer waters ($> 10°C$) (Table 3).

Four studies have elucidated the effect of temperature on the embryos of *Cancer* crabs. Mayer (1973) and Wild (1983b) found that temperatures above 13°C hasten embryogenesis *in vitro* and cause significant mortality to the embryos of *C. magister* (see 5.4.1). Lower temperatures increase egg survival and decrease the rate of embryogenesis. Shirley et al. (1987) found that temperatures at or above 10°C hasten embryogenesis *in vivo* but do not cause significant mortality to the embryos of *C. magister*. Embryogeneis of *C. magister* took 160 d at 5°C, 60 d at 10°C, and 42 d at 15°C. Development ceases at 1°C (Shirley et al. 1987). The embryos of *C. anthonyi*, a warmer water species, follow a similar pattern, but at higher temperatures (Shields & Kuris 1988). Embryogenesis of *C. anthonyi* takes approximately 55 d at 10°C, 42 d at 15°C, and 27 d at 20°C. Embryos exposed to 4°C for 10 days cease development, but resume normal development upon being returned to 15°C (Shields & Kuris 1988).

Diapause, wherein embryogenesis slows or stops, was observed in two species of *Cancer* (Table 3). The embryos of *C. pagurus* undergo a uniform period of diapause that remains

Table 3. Egg development time, number of broods per year, range in size of ovigerous females, and reported range in fecundity per brood in various *Cancer* crabs. Unknown data are indicated (?), and embryonic diapause. D: Ambient seawater temperature during the brood period is for the location/area where the study occurred (Knudsen 1964, Rathbun 1930, Carroll 1982, Wild et al. 1983, Le Foll 1986, Shields pers. observ.).

Species	References	Embryogenic development (in days)	Female size (mm CW)	Reported range in fecundity per brood	Range in temperature while brooding
C. antennarius	Carroll (1982), Shields et al. (unpubl. data)	50- 60	116-143	$= 1.0 \times 10^6$	10-16
C. anthonyi	Shields et al. (submitted)	40- 45	90-153	$0.7\text{-}3.3 \times 10^6$	10-20
C. borealis	Haefner (1977), Carpenter (1978)	?	105-139	$0.3\text{-}1.6 \times 10^6$	8-14
C. gracilis	Knudsen (1964), Orensanz & Gallucci (1988)	?	54-100	?	7-11
C. irroratus	Krouse (1976), Haefner (1976), Reilly & Saila (1978), Campbell & Eagle (1983)	176-235 D	14-106	$4.4\text{-}567.7 \times 10^3$	8-21
C. magister	Orensanz & Gallucci (1988), Wild (1983a, b, c), Hankin et al. (1985)	90-120	110-171	$0.5\text{-}1.5 \times 10^6$	9-14
C. oregonensis	Knudsen (1964), Orensanz & Gallucci (1988)	103-118	10- 43	$1.0\text{-}3.3 \times 10^4$	7-11
G. pagurus	Edwards (1979), Brown & Bennett (1980), Le Foll (1986)	235-265 D	115-205	$0.5\text{-}3.0 \times 10^6$	7-18
C. productus	Toole (1985)	= 120	70-129	?	7-14
C. setosus	Gutierrez & Zuniga (1976)	?	83-151	$0.6\text{-}1.7 \times 10^6$	–

unaffected by changes in water temperature (Wear 1974). However, the embryos of *C. irroratus* have a variable period of diapause that is affected by changes in water temperature (Haefner 1976, Reilly & Saila 1978). The variable timing of diapause in the embryos of *C. irroratus* may synchronize hatching of larvae over a one to two month summer season (see 4.2).

The effect of temperature on embryogenesis was noted in field studies of *C. irroratus* and *C. magister*. Embryos of *C. irroratus* oviposited early in the reproductive season (late fall-early winter) hatch at a similar time as those oviposited later in the season when water temperature is increasing (Haefner 1976). Embryos of C. magister hatch after 90 days in central California (Point Lobos-Point Arena) vs 120 days in the colder climes of Washington and further north (MacKay 1942, Butler 1960, Wild 1983b).

4.2 *Eclosion*

Hatching in species of *Cancer* occurs when the embryo reaches the prezoea stage (Pearson 1908, Wear 1974). Prezoeae of *C. anthonyi* appear to imbibe water and enlarge in size before hatching (Shields pers. observ., cf. Davis 1965). Hatching of *Cancer anthonyi* prezoeae typically occurs at night or in relative darkness.

During the process of eclosion, female *Cancer anthonyi* actively aid the hatching process (Shields et al. in press). Females stand upon their walking legs and aerate the clutch vigorously by agitating the pleopods. In addition, the branchiae appear to direct water currents anteriorly through the brood, facilitating zoeal eclosion and escape from the egg mass. After eclosion, female crabs either immediately strip the hatched remnants and detritus from their pleopods (*C. antennarius, C. anthonyi,* Kuris & Wickham 1987; Shields pers. obs.; *C. pagurus,* Williamson 1904) or lose the adhering detritus at their next molt (*C. magister*, Kuris & Wickham 1987). Since female *C. magister* may oviposit a second brood prior to molting (Ebert et al. 1983), they may strip their pleopods of detritus before extrusion.

Hatching of *Cancer* larvae may be synchronized with seasonal primary productivity. Hatching typically occurs in the spring for *C. anthonyi* and *C. antennarius*. Along the southern California coast primary production is at its highest at this time (Mullin 1986). The larvae of *C. borealis, C. irroratus* and *C. pagurus* also hatch when nutrient levels are high, i.e. in the summer months (from comparison with Harvey 1955, Dunbar 1979).

5 FECUNDITY

5.1 *Brood size*

Brood size of *Cancer* crabs shows a conservative relationship with body size between species (Table 3). For example, the brood size reported for the smallest *C. magister* (450 000 eggs at 110 mm CW) is equivalent to that of the largest ovigerous *C. irroratus* (440 000 eggs at 100 mm CW). In addition, temperature may indirectly affect brood size by directly affecting the size at which crabs mature (e.g. *C. irroratus, C. pagurus*; see 2.1).

In general, the smaller *Cancer* species (*C. irroratus* and *C. oregonensis*) produce relatively fewer eggs at a given size than do the larger species. There is, however, one notable exception. For its size, *C. anthonyi* produces relatively and absolutely more eggs per brood than any other *Cancer* crab, including both of the larger species, *C. magister* and *C. pagurus* (Table 3). Given the strong size-fecundity relationship found in brachyuran families (Hines 1982, Hartnoll 1985), it is surprising that *C. magister* and *C. pagurus* carry fewer eggs than the smaller *C. anthonyi*. Differences in water temperature cannot explain the differences in the fecundities between these species, because *C. antennarius* and *C. productus* – two species that are sympatric with *C. anthonyi* (Nations 1975) – do not have an increased brood size in relation to their species size (Table 3).

5.2 *Size-fecundity relationships*

Reproductive output per brood in brachyurans is strongly correlated with body size (carapace width) and weight within a species (Hines 1982, Hartnoll 1985). The body size–clutch size (fecundity) relationship was investigated in six species of *Cancer*. Fecundity was linearly or logarithmically correlated with body size, or not correlated with body size (Table 4).

Table 4. Size-fecundity relationships for different species of *Cancer*. Key to symbols: [a]Fecundity estimated from total number of eggs per brood. [b]Fecundity estimated from total number of eggs per second pleopod. [c]Carapace length used to calculate values. [d]Relationship calculated from mean carapace length and mean fecundity. NR: Not reported. [e]Fecundity estimated from internal ova and external eggs. $^{+}0.05 < P < 0.10$, $^{*}P < 0.05$, $^{**}P < 0.01$.

Species	References	Slope	Intercept	r	N
Linear					
C. anthonyi	Shields et al. (in press), Shields (unpubl. data)	5551[b]	-371040	0.559*	220
Logarithmic					
C. anthonyi	Shields et al. (in press), Shields (unpubl. data)	2.308[b]	0.646	0.554**	220
C. irroratus	Reilly & Saila (1978)	3.010[a]	-0.335	0.986**	33
C. irroratus	Campbell & Eagle (1983)	2.553[a]	0.583	0.857**	50
C. magister	Hankin et al. (1985)	NR	NR	≈0.245*	85
C. pagurus	Le Foll (1986)	4.174[ac]	-2.417	0.720**	29
C. pagurus	Edwards (1979)	3.633[a]	-1.854	0.708**	16
No significant logarithmic relationship					
C. anthonyi	Shields et al. (in press), Shields (unpubl. data)	1.020[a]	4.267	0.449	12
C. borealis	Shields et al. (in press), Shields (unpubl. data)	0.977[ac]	3.869	0.273	14
C. magister	Hankin et al. (1985)	NR	NR	NR	35
C. setosus	Gutierrez & Zuniga (1976)	1.449[ad]	3.101	0.719+	6

Size-fecundity data for *Cancer* are highly variable. Thus, logarithmic tranformations of fecundity ($\log \text{Fecundity} = b \log CW \pm \log a$) are used to reduce heteroscedasticity, stabilize the variance, and provide a better fit to regression models. The regression coefficients (slopes) of those relationships that fit logarithmic regression models vary from 2.308 to 4.174 (Table 4).

The lack of relationship between body size and fecundity for *C. borealis*, *C. magister*, and *C. setosus* may have several causes (Table 4). (1) Large female crabs (155 mm CW) may be senescent and produce fewer eggs than smaller, more virile females (Gutierrez & Zuniga 1976, Hankin et al. 1985, Orensanz & Gallucci 1988). (2) Large female crabs do not molt annually (Pearson 1908, Ebert et al. 1983, Hankin et al. 1985), hence they may possess less stored sperm, and thus fertilize fewer eggs than smaller crabs (Pearson 1908). (3) The narrow range in size of adult females, coupled with high variation in fecundity, may reduce the ability to detect a significant correlation (see below).

The senescence hypothesis states that large adult female crabs are senescent because of their decreased molting probability, the decline in their number of eggs per brood, and their low annual survival rates. The data supporting the senescence hypothesis have potentially con-

founding variables. First, the proposed mortality rate (hence, senescence) of older females of *C. magister* is based on the collection of crabs in shallow, inshore waters during spring (Diamond & Hankin 1985). At that time, younger, smaller females migrate inshore, molt and mate. Since older females did not molt annually (Hankin et al. 1985), their molting and mating pattern differs from that of younger crabs. Such older females may remain offshore. Hence, their mortality rate, based on inshore trapping in the spring (Hankin et al. 1985), may be exaggerated. Second, adults of *C. gracilis* and *C. productus* which are thought to have died of senescence (Orensanz & Gallucci 1988) may have died from disease, changes in temperature, or from the severity of winter storms (El Niño in 1983). The range in sizes of these dying or dead crabs and the fact that most crab mortality occurred in a single year (1983) argues against senescence as a physiological process in these crabs. Further, with lab-held *C. anthonyi*, second or third broods in an instar are significantly smaller than the first brood in an instar even if the crab were to molt again (Shields et al. in press). Factors producing such effects may include reduction in the quality of sperm stored from copulation at the previous molt. Hence, such broods cannot be used as evidence for senescent processes. Third, egg predation in broods of *C. magister* by a nemertean, *Carcinonemertes errans*, was sufficiently intense at that time (1983) to reduce the fecundity of the large, late instar females, further reducing the number of eggs present in their broods (Kuris & Wickham 1987) (see also 5.4.2).

Sampling procedures may also account for the lack of a statistically significant relationship between body size and fecundity in some of these species. For *C. borealis*, the lack of relationship between size and fecundity may be due to the narrow range of the female sizes examined, the variation inherent in fecundity, and the small sample size (size range = 100.5-119.7, mean fecundity = 763 793 ± 132112 eggs per brood, N = 14; from Carpenter 1978). For *C. anthonyi*, log crab size (CW) was positively correlated with log fecundity per pleopod ($R = 0.554$) when the sample size was large. Yet, total fecundity from 12 crabs revealed no significant relationship with body size ($R = 0.449$; Shields et al. in press). The partial correlation of log crab size with log total fecundity was, however, significant when log fecundity per pleopod was held constant (Partial correlation – $R = 0.635, P < 0.05, N = 12$; Shields et al. in press).

5.3 *Broods per instar and seasonality*

As with fecundity, the number of broods per instar may be size-dependent in *Cancer* crabs. Recent adult instars (i.e. A1, A2) appear to molt annually (*C. magister*) or semi-annually (*C. oregonensis*) (Hankin et al. 1985, Orensanz & Gallucci 1988). These young adults generally produce one brood per instar which corresponds to one brood per reproductive season. Older adult crabs (e.g. *C. magister* 155 mm CW; *C. pagurus* 170 mm CW) which do not molt annually (Pearson 1908, Hankin et al. 1985) produce more than one brood per instar (Table 5) (Hankin et al. 1985, Orensanz & Gallucci 1988), and infrequently produce more than one brood per reproductive season (Knudsen 1964, Orensanz & Gallucci 1988).

Generally, one brood per instar typifies annual reproduction for most species of *Cancer* (Table 5). However, two species, *C. antennarius* and *C. anthonyi*, regularly oviposit two or more broods per instar (Shields et al. in press, Shields pers. observ.). Since both species have short embryogenic periods (Table 3), it is apparent that they produce more than one brood per reproductive season. The mating and reproductive seasons of *C. setosus* suggest that it, too, may regularly produce more than one brood per instar (Gutierrez & Zuniga 1976).

The breeding season of most species of *Cancer* appears to be winter (Fig. 2). Of the ten species examined, all bore eggs between January and March. For at least seven of these species,

Table 5. Broods per instar (potential number of broods per instar in late instars), maximum number of adult instars, mean fecundity per brood (in millions of eggs, mean size in parentheses), and the reproductive potential of individual female *Cancer* crabs. Unknown data is indicated by (–), incomplete data by (?). Note that the potential number of broods per instar is not equivalent to the number of broods per reproductive season which in most cases is one brood per year. Reproductive potential calculated by: Estimated number of adult instars × mean fecundity at mean size × number of broods per instar (when capable of producing more than one brood per year).

Species	Broods per instar	Maximum number of adult instars	Mean fecundity at mean size	Individual reproductive potential (millions of eggs)
C. antennarius	1-2	5	1.0 (120)	5.0-10.0
C. anthonyi	3-4	2-4	2.6 (130)	15.6-41.6
C. borealis	1 (?)	–	0.8 (120)	–
C. gracilis	1 (2)	2	– (65)	–
C. irroratus	1	1-6?	0.3 (83)	0.3-1.8
C. magister	1 (2)	3-4	1.0 (131)	3.0-4.0
C. oregonensis	1 (2)	6	0.02 (21)	0.1-0.2
C. pagurus	1 (3)	3-4	1.2 (153)	3.6-4.8
C. productus	1 (2)	3	– (107)	–
C. setosus	1 (?)	2-3?	1.0 (105)	2.0-3.0

the period between January and March represents a peak in their reproductive season. The females of three species (*Cancer anthonyi*, *C. antennarius*, and *C. setosus*) oviposit year round, with peak periods in the winter. *Cancer setosus* had two peaks in reproduction (Gutierrez & Zuniga 1976). One peak occurs in January through March, which corresponds with the peak breeding season of crabs in the northern hemisphere; the other occurs in late June through September, the austral winter season. Ovigerous *C. irroratus*, *C. pagurus* and *C. productus* are found throughout much of the year but there is a distinctive peak in reproduction in the winter or spring.

Most species of *Cancer* do not have a well defined reproductive season (Fig. 2). In contrast, *C. magister* has a synchronized reproductive season. Virtually all of the females present in a population of *C. magister* mate and lay eggs within a month or two of each other (Wild 1983a, b, Orensanz & Gallucci 1988). Northern populations (e.g. Washington) of *C. magister* bred later in the season compared to southern populations (e.g. central California) and in northern stocks synchrony is reduced (MacKay 1942). Oviposition in *C. magister* occurs in October-November in central and northern California, but it occurs progressively later at more northern latitudes (MacKay 1942, Cleaver 1949, Butler 1961, Wild 1983a, b). Similar observations were made with *C. irroratus* in relation to water temperature (Terretta 1973).

5.4 *Brood mortality*

Brood mortality may affect fecundity and natality of crabs. Physical, chemical and biological factors may cause brood mortality in *Cancer*. *Cancer* crabs brood their eggs on pleopods in an open clutch; hence, the distal protions of the clutch may be exposed to a variety of potentially harmful agents.

5.4.1 *Physical factors*

Mechanical damage may be incurred on the periphery of the clutch of *C. anthonyi* (Shields

1987, Shields et al. in press). As ovigerous crabs forage, the outermost eggs of their clutches contact the substrate. This may weaken or abrade the egg coats. Egg mortality due to mechanical damage is estimated to be 4.0-6.0% of the embryos of the margins of the clutch (Shields 1987, Shields et al. in press). Negligible mortality due to abrasion occurs in the medial portion of the clutch.

Water temperature may also contribute to egg mortality and under extreme conditions may lead to massive mortality *in vitro* and *in vivo*. Wild (1983b) found that the embryos of *C. magister* experienced higher mortality at 17°C than did those held at lower temperatures. Hatching success was inversely correlated with temperature. Curiously, mortality was notable at the ambient temperature (13°C). Mayer (1973) observed that embryos of *C. magister* experienced massive mortalities at 15° and 20°C after only 3-6 days. Shirley et al. (1987) found negligible mortality *in vivo* at temperatures between 5° and 15°C, but substantial mortality at 1°C. *Cancer anthonyi* had a wider range of thermal tolerance; embryos survived for over 10 days at 4° and 20°C (Shields & Kuris 1988). *Cancer* crabs appear to have a thermal limit in their distribution of 4° to 23°C (MacKay 1943). Since crab embryos are sensitive to warm temperatures, the thermal limit could directly affect egg and larval survival in the transition zones.

5.4.2 *Chemical factors*

Pollutants have been cited as causal agents in egg mortality and in the decline of certain crab stocks (Wild 1983c). The role of pollution in the collapse and non-recovery of the *Cancer magister* fishery off central California has received little attention. An increase in pollutants (chlorine) temporally matched the decline in the fishery (Horne et al. 1983). Several pesticides affected the ability of embryos to hatch *in vitro* (Buchanan et al. 1970, Caldwell 1977). Concentrations of pesticides required to kill embryos were higher than those killing larvae.

Other organic pollutants affect *Cancer* egg production and fecundity. Ovarian necrosis in *C. magister* results from an increase in organic solutes leached from timber at log transfer facilities (O'Clair & Freese 1988). Ovigerous crabs found in contact with the bark deposits have fewer eggs, reduced survivorship, and inhibited feeding responses when compared with crabs from sites adjacent to log transfer facilities and crabs from control sites. Similarly, crabs exposed to oiled sediments produce fewer eggs and less hardy larvae than do unexposed crabs (Karinen et al. 1985).

The effects of several metals in embryo survivorship, hatching success, and prezoeal survivorship have been documented for *Cancer anthonyi* (Macdonald et al. 1988). Metal toxicity levels for *C. anthonyi* embryos are similar to those causing toxicities in zoeae of *C. magister* (Glickstein 1978, Martin et al. 1981). Various metals, particularly iron and copper, delay hatching of *C. anthonyi* embryos at concentrations 100-times lower than those causing mortalities. Further, manganese and iron are selectively adsorbed to the vitelline membrane of embryos of *C. pagurus* following extrusion (Martin 1976). Apparently, embryo mortality is delayed due to the added protection of the vitelline membrane, which reduces the rate of metal absorption. Since crab embryos imbibe water at or near hatching (Davis 1965), hatching success may have declined due to an increased exposure to the various metals (Macdonald et al. 1988).

5.4.3 *Biological factors*

Several biological agents cause egg mortality in *Cancer* crabs. Bacteria, fungi, nemertean worms, and amphipods have all been observed parasitizing or eating crab eggs and embryos. Bacteria may cause substantial mortality in the broods of *C. magister* (Fisher 1976, Fisher & Wickham 1976). In controlled experiments, bacterial filaments and egg mortality increase in

the presence of nutrients and in the absence of antibiotics (Fisher 1976). These results, however, may have been confounded by the presence of the egg predator *Carcinonemertes errans* (Wickham 1979b). In an *in vitro* analysis, bacteria do not contribute significantly to egg mortality of *Cancer anthonyi* (Shields & Kuris 1988). In the same analysis, the fungus *Lagenidium callinectes* leads to significant mortality only at high temperatures and high zoospore densities. The nemertean worm, *Carcinonemertes epialti*, contributes most to the egg mortality of *Cancer anthonyi* (Shields & Kuris 1988, Shields et al. in press).

Nemertean worms have been found at high densities on several different species in several crab populations (Wickham 1986, Kuris & Wickham 1987, Shields & Kuris 1987). Brood mortality is high in these crab populations and reaches levels where virtually all of the eggs in a local population are eaten (Wickham 1986, Shields & Kuris 1987). These worms have been implicated in the non-recovery of the central California stock of *Cancer magister* (Wickham 1979a, 1986, Kuris & Wickham 1987). Their role in the collapse and non-recovery of this crab stock remains in contention (see Kuris & Wickham 1987).

The impact of brood mortality on certain populations of *C. magister* has led to the suggestion that the causal factors may contribute, in part, to the cycling of crab populations (Wickham 1979a; but see Hankin 1985, Jamieson 1986). While the roles of these factors and agents are difficult to determine in nature, their study remains important to our understanding of the biology and environmental sensitivity of these commerically important crabs.

6 REPRODUCTIVE POTENTIAL AND REPRODUCTIVE PATTERNS

6.1 *Reproductive potential*

Reproductive potential has been previously quantified in terms of fecundity, size at maturity, fishing mortality, proportion of females in each size class, and growth of individuals in a population (Campbell & Robinson 1983). Populations chosen for examination in this manner typically reproduce but once per year. A developing model may provide a comprehensive analysis of the impact of these variables on reproductive potential (Hartnoll & Gould 1988). Information on size at maturity, growth, proportions in size classes, and fishing mortality are lacking for most of the species of *Cancer* examined.

Here, I quantify reproductive potential in terms of the individual crab. Reproductive potential is the total number of eggs produced throughout the *maximum* adult life span (lifetime reproductive success) of an individual of the species (Shields et al. in press). The maximum adult life span was chosen for four reasons: late instar females may contribute most to the overall egg production of their cohort; hence, they may contribute most to the fitness of the species; estimates of mortality rates are unknown or unreported for most species; and confounding correlations between fecundity and mortality rate are eliminated. Estimates of the reproductive potential of an individual crab are based on (1) the mean fecundity at the mean size, (2) the minimum and maximum number of mature instars, (3) the minimum and maximum number of broods per instar, and (4) in relation to (3), the number of broods oviposited per year (see below and Table 5). This estimate represents a crude but effective means of examining the influence of life history constraints on the reproductive potential of *Cancer* crabs.

For example, the reproductive potential, R_p, of *Cancer magister* is derived by:

$$R_p = Fec_{A1} + Fec_{A2} + Fec_{A3''} + \mathrm{Fec}_{A3''}$$

Table 6. Patterns in the reproduction of *Cancer* crabs. See text for further explanation.

Pattern	Mature size	Number of juvenile instars	Number of adult instars	Broods per instar	Relative reproductive potential	Examples
General	Small-large	9-11	2-4	1 (2)	Moderate	*C. pagurus* *C. gracilis* *C. magister*
Precocious maturation	Small	4-5	4-6	1 (2)	Low	*C. irroratus* *C. oregonensis*
Maximal production	Moderate	9-11	3-5	2+	High	*C. antennarius* *C. anthonyi*

where, R_p = mean number of eggs per brood at mean size × number of broods per instar (per year) × maximum number of adult instars. Thus, for *C. magister:* R_p = 1.0 million × 4 = 4.0 million eggs per crab, or where Fec_{A1} is the fecundity of the first adult instar; and $Fec_{A3'}$ and $Fec_{A3''}$ represent the fecundity of the first and second brood of the third adult instar. This estimate is similar to that proposed by MacKay (1942) – 3 to 5 million eggs per crab – and may represent an upper limit.

The reproductive potential of *Cancer anthonyi* is greater than that of any other known *Cancer* species (Table 5). The ability of *C. anthonyi* to bear multiple broods per instar, coupled with its high size-specific fecundity yields this enormous reproductive potential. The effect of longevity or the maximum number of adult instars is observed with *C. irroratus,* which has up to 6 adult instars (varying in size from 28-100 mm CW). A large number of adult instars, coupled with the positive size-fecundity relationship, produces for *C. irroratus* a reproductive potential approaching that of *C. magister*, or in the case of *C. antennarius*, exceeding that of *C. magister*.

6.2 *Patterns in reproduction*

Cancer crabs appear to have three distinct patterns in egg production (Table 6). The general pattern of egg production was typified by those species having 9 to 11 juvenile instars and 2 to 4 adult instars (Table 6). There is usually one brood per instar and per season. These species mature at either small or large sizes. Egg production may be scaled with size such that the size-fecundity relationship is relatively similar between species. Production of a single brood per instar by such species may optimize the use of available food resources.

Abbreviating parts of the life history may lead to a precocious maturation pattern of egg production. Such species have small adult sizes, maximize their reproductive effort by maturing after a few juvenile instars, and increase the number of adult instars (Table 6). The increased number of adult instars, coupled with the potential of producing more than one brood per season (Knudsen 1964, Orensanz & Gallucci 1988) renders a high reproductive potential over the life span of the species. Species characterized by the precocious maturation pattern have a reproductive potential that approaches that of those species with a general pattern of egg production. An advantage of precocious maturation may be an increase in fitness relatively early in the life history of the species.

The maximal production pattern derives from a modification in the energetics of egg production. This pattern conserves the life history constraints of the general pattern (i.e. number of juvenile and adult instars – Table 5), but production energetics are substantially increased (see

below). Species with the maximal production pattern produce more than one brood per instar, have a relatively short embryogenic period, and have extremely high fecundity. Egg production appears to be optimized at the expense of growth as multiple broods within an instar effectively preclude intervening molts. Species having this pattern are of moderate size (90-150 mm CW). Interestingly, species with a maximal egg production are not quiescent when ovigerous. They forage, acquire nutrient resources, and undergo ovarian growth for further egg production while bearing eggs.

7 CONCLUSIONS

Species of *Cancer* crab show variations in their reproductive ecology at intraspecific and interspecific levels. Interspecific variations may be controlled by many factors, including climatic regime, habitat, and biological constraints. The variations in reproductive ecology tend to follow latitudinal or temperature gradients. Temperature influences maturation, molting and mating, synchronized oviposition (*C. magister*), and the duration of embryogenesis (brooding). Lastly, features of the embryonic and larval stages of these crabs lend themselves to studies of environmental sensitivity. An increase in pollution in the habitats used by *Cancer* warrants the use of life history stages as bioassays to monitor the healthiness of crab stocks.

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