

Cannibalism in Dungeness crab *Cancer magister*: effects of predator-prey size ratio, density, and habitat type

Miriam Fernández*

Pontificia Universidad Católica de Chile, Departamento de Ecología, Casilla 144-D, Santiago, Chile

ABSTRACT: Cannibalism between age classes has been reported for Dungeness crab *Cancer magister* Dana, and hypothesized to cause the cyclic behavior of the fishery. Recently, cannibalism among young-of-the-year (YOY) Dungeness crabs has been documented, and proposed as an alternative hypothesis to explain recruitment failure of later cohorts of megalopae in intertidal shell habitats already occupied by older YOY crabs. Furthermore, cannibalism among juveniles has also recently been reported for other crab species. This study experimentally addressed whether: (1) cannibalism rate by age classes 0+, 1+ and 2+ of Dungeness crabs *Cancer magister* of both sexes on YOY conspecifics is affected by habitat type; (2) cannibalism rate among YOY is affected by conspecific density and prey-predator asymmetry; and (3) YOY mutual interference and prey-predator asymmetry affect consumption rate. Predation rate by older crabs (age classes 1 and 2) on YOY was highest in mud habitat, intermediate in low shell density, and lowest in the high shell density treatment. These results show that shell habitat enhances production of YOY crabs by increasing survival. Despite the fact that shell habitat decreased cannibalism rate of larger conspecifics on YOY, it did not affect cannibalism rate among juveniles. YOY crabs did not consume carapaces of conspecifics, while larger crabs consumed entire prey; this difference in amount of hard parts consumed suggests that although cannibalism may be common among YOY, it may not be detected by stomach analysis. Consumption of megalopae was affected by prey density, and also by the asymmetry between the prey and the predator. As predator density increased, the total consumption of megalopae increased, but proportional mortality per predator decreased. When other instar stages were used as prey, prey-predator asymmetry and prey density were not as important factors as predator density on cannibalism rate. Megalopae were the most vulnerable prey, and under certain circumstances YOY conspecifics may be able to decimate cohorts of settling megalopae. However, megalopae may find refuge from cannibalism when predator-prey size ratio is low, predator density is high, and probably when relative abundance of alternative prey is high (laboratory experiments were conducted using only conspecifics as prey). Cannibalism, or other processes that may have evolved in response to cannibalism, may be important factors regulating crab recruitment in natural populations and limiting crab production in artificial habitats.

KEY WORDS: Dungeness crab · Recruitment · Cannibalism · Artificial habitat

INTRODUCTION

Cannibalism is a common phenomenon in many terrestrial and aquatic taxa (Fox 1975, Polis 1981, Elgar & Crespi 1992), including brachyuran crabs (Klein Breteler 1975, Reise 1985, Kurihara & Okamoto 1987, Tunberg & Creswell 1988, Fernández 1994, Perkins-

Visser et al. 1996, Moksnes et al. 1997). In many taxonomic groups cannibalism is associated with an asymmetry between cannibal and victim; generally, the victim is at a more vulnerable life history stage than the cannibal (Elgar & Crespi 1992). For many species, relative rather than absolute size appears to prevail (DeAngelis et al. 1979, Bry & Gillet 1980, Polis 1981), but there are exceptions to such size generalizations (Ricker 1954, Banerji & Prasad 1975, Forney 1976, Fernández 1994, Moksnes et al. 1997, 1998). The result of

*E-mail: mfernand@genes.bio.puc.cl

the cannibalistic interaction will depend not only on the asymmetry between cannibal and victim, but also on the short-term behavioral response of the predator (cannibal) to prey (conspecific) densities. The relationship between prey consumption per predator and prey density can be density-independent, density-dependent, or inversely density-dependent (Holling 1959, Hassell 1978).

Cannibalism between age classes has been reported for Dungeness crab *Cancer magister* Dana (MacKay 1942, Butler 1954, Gotshall 1977, Stevens et al. 1982), and there is evidence of cannibalism within age class (juveniles; Jacoby 1983, Karpov 1983, Fernández et al. 1993a,b, 1994). Cannibalism between age classes may be responsible for most of the mortality of newly settled crabs in unprotected habitats (mud), and cannibalism among young-of-the-year (YOY) might account for most of the mortality in sheltered habitats (Fernández et al. 1993b). Botsford & Wickham (1978) proposed that density-dependent, between-year-class cannibalism may generate cyclic fluctuations in the abundance of Dungeness crab in the California fishery (see also Higgins et al. 1997). However, there is no empirical evidence of within- or between-age-class, density-dependent cannibalism in Dungeness crab.

Cannibalism has also been suggested as an alternative hypothesis to explain recruitment failure of subsequent cohorts of megalopae in habitats saturated by older YOY crabs (Fernández et al. 1993a). Extremely high densities of settling megalopae (more than 200 m⁻²) were heavily preyed upon in habitats colonized by larger conspecifics (Fernández 1993a); those habitats were occupied by high densities of first and second benthic stages. However, at saturating levels of predator (cannibal) densities, such as those found in artificial shell habitat for Dungeness crab (Armstrong et al. 1992, Dumbauld et al. 1993), predator interactions might affect the response of predators to different prey densities. Mutual interference may adversely affect crab searching efficiency or feeding rate (Mansour & Lipcius 1991, Iribarne et al. 1995), and stabilize predator-prey dynamics by providing partial refuge for prey. Although cannibalism may affect natural populations of Dungeness crab as well as the production of artificial habitats (Armstrong et al. 1991, 1992), the effects of habitat structure, predator-prey size ratio, and conspecific density on cannibalism rate are unknown. The objectives of this study were to examine experimentally whether: (1) cannibalism rate by age classes 0+, 1+ and 2+ of Dungeness crabs *Cancer magister* of both sexes on YOY conspecifics is affected by habitat type; (2) cannibalism rate among YOY is affected by conspecific density and prey-predator asymmetry; and (3) YOY mutual interference and prey-predator asymmetry affect consumption rate.

MATERIAL AND METHODS

Effect of habitat type on cannibalism efficiency. In order to investigate whether cannibalism is affected by predator size, predator sex, and habitat type, laboratory experiments were performed using 3 age classes, male and female crabs as predators, and 3 habitat types. Aquaria (40 l, surface area 0.20 m²) were filled with a 5 cm layer of mud collected in the intertidal zone and estuarine (14 to 16°C temperature; 25 to 27‰ salinity) water. Three habitat types (treatments) were used: mud (MUD), low shell density (LSD), and high shell density (HSD). In the LSD treatment 12 oyster *Crassostrea gigas* shells were deposited over the mud in 3 groups of 4 oysters each (covering 20% of the total area of the tank; see Dumbauld et al. 1993 for comparable treatment *in situ*). In the HSD treatment a continuous layer of shells was deposited over the mud (100% shell cover). In HSD and LSD treatments the shell arrangement was similar, so it can be assumed that the same type of habitat per unit of area covered by shell was offered in the 2 shell treatments.

Three predator age classes (Wainwright 1994) were utilized: 0+ (25 to 29 mm carapace width), 1+ (60 to 70 mm carapace width), and 2+ (90 to 110 mm carapace width); in all cases only 1 predator per tank was used and individuals were starved for 24 h prior to the experiment. The satiation level of the predator was not quantified. The intermolt stage was not determined, thus this factor may account for some of the variability observed in consumption rate (Lipcius & Herrnkind 1982). Hard shell crabs were always used (for prey and predator), and the trials in which the predators molted during the experimental time were not used. The effect of prey (J1: 5 to 8 mm carapace width) vulnerability in relation to hours since molt is not clear (Visser 1997), and was not considered in the experiment since it was not possible to monitor all the prey during the experimental time. Eight 0+ crabs (9 to 18 mm carapace width) were offered as prey. Prey size resembled that found in artificial, intertidal oyster shell assemblages by late summer (Armstrong et al. 1991, 1992). Crabs were collected in intertidal shell habitat (0+ prey and predators) and by trawls in the South Channel area (1+ and 2+ crabs) of Grays Harbor, during spring and summer in 1991 and 1992. Predators and prey were measured (carapace width), and the predator's sex identified. Mean predator size and number of replicates for each treatment are reported in Table 1. No differences in mean predator size were detected among habitat treatments (Table 1). Prey were assigned to instar stages following Dinnel et al. (1993). In each trial the following prey composition was used: 4 J2 Crab (9 to 12 mm), 2 J3 (13 to 15 mm), and 2 J4 (16 to 19 mm). Ten control trials (no predator) were performed, and 100% survival was found.

Table 1. *Cancer magister*. Mean predator size (and standard error) and number of replicates conducted per habitat type for each age-class predator, and the results of the ANOVA conducted to test for no differences in mean predator size among habitats for each age-class predator

Age class	X_{size} (mm)	SD	$N_{replicates}$			ANOVA		
			Mud	LSD	HSD	F	df	p
0+	28.5	0.54	16	11	12	0.13	2,36	0.88
1+	64.6	0.34	31	16	20	0.017	2,64	0.98
2+	97.8	0.73	15	18	14	0.06	2,44	0.94

The number of surviving prey was recorded at the end of the 24 h trials. Cannibalism rate in this experiment indicates the number of YOY crabs consumed per predator per day. A 3-way ANOVA was used to test for differences in the mean number of prey eaten among habitat type, predator sex, and predator age class. The response variable was not transformed because the assumptions of the ANOVA model were met.

In order to assess the type of remains left by 0+, 1+, and 2+ predators when attacking conspecifics, the remains were categorized into 2 types, (1) no remains or pieces \leq half carapace and (2) pieces $\geq \frac{3}{4}$ carapace or whole carapace, and recorded in each trial. The proportion of type (1) remains consumed was estimated for each trial as follows: number of type (1) remains/number of crabs consumed. The data were log-transformed in order to meet the assumptions of the ANOVA model, and a 1-way ANOVA was used to test for differences in the mean proportion of type (1) remains among predator age classes.

Effects of prey-predator asymmetry and prey density on cannibalism rate among YOY Dungeness crab. The consumption rate of YOY Dungeness crabs as a function of smaller YOY density was studied under laboratory conditions. Tanks (20 l, surface area 0.1 m²) were filled to a depth of 5 cm with defaunated (sieved through a 0.5 mm screen) mud collected from the estuary and estuarine water. A continuous layer of shell was deposited over the mud. Crabs were collected in intertidal shell habitat between 1992 and 1993, when the experiments were conducted. Megalopae and second instar crabs were used as prey. Two predator instar stages were utilized for each prey group; for megalopae, J1 and J2 crabs were used as predators. Third and fourth instars were the predators when J2 crabs were the prey. Megalopae to second instar crabs are found in early summer, whereas second to fourth instar crabs are found in intertidal shell habitat between mid and late summer (Armstrong et al. 1991, Dumbauld et al. 1993).

A single predator, starved for 24 h, was used per tank. The satiation level of the predator was not quan-

tified. Hard shell prey and predator were always used, and when predators molted, the trial was not considered in the analysis. The intermolt stage was not determined, and it may account for some of the variability observed in consumption rate (Lipcius & Herrnkind 1982). In the Dungeness crab, cannibalism (attacks) may not take place for 24 h after molting, and the effect of prey (J1) vulnerability in relation to hours since molt is not clear (Visser 1997). The experimental design used here, which does not homogenize the intermolt stages, reflects natural conditions with prey and predators at different intermolt stages interacting in the same habitat. Thus, the results may show the cannibalism rate (and its variability) observed in nature better than the potential for cannibalism that may occur under predetermined scenarios (equal intermolt stages).

For the megalopae experiments, 5 prey densities were used: 1, 2, 3, 5, and 8 megalopae tank⁻¹ (10 to 80 megalopae m⁻²). For J3 to J4 predators, 6 prey (J2) densities were used: 1, 2, 3, 4, 5, and 7 crabs tank⁻¹ (10 to 70 crabs m⁻²). Controls for prey survival (no predator) were run for all prey density treatments; survival was 100% for densities ranging between 1 and 3 megalopae and between 1 and 5 J2. Megalopae survival was 97% for densities higher than 5 individuals tank⁻¹, and 99% for J2 prey in the highest crab density treatment. More than 5 trials were conducted for the control, or for each combination of predator size and prey density. Prey were not replaced as they were consumed since it was not possible to assess when consumption occurred within the shell habitat. At the end of the 48 h trial, surviving crabs were counted. Cannibalism rate in this experiment indicates number of YOY crabs consumed per predator in 48 h. No attempt was made to determine the parameters of a functional response relationship, given the variability in consumption rate and because prey were not replaced. Instead, a 2-way ANOVA was used to test for differences in the mean number of prey eaten and proportional mortality among prey density and between predator size treatments for each prey type. Natural log and square-root transformations were used when the assumptions of the ANOVA model were not met.

Effects of prey-predator asymmetry and mutual interference on cannibalism rate among YOY Dungeness crab. Two laboratory experiments were conducted to evaluate the effect of prey-predator asymmetry and YOY predator density on cannibalism rate. Crabs were collected in intertidal shell habitat between 1992 and 1993, when the experiments were conducted. Tanks (20 l, surface area 0.1 m²) were filled to a depth of 5 cm with defaunated (sieved through a 0.5 mm screen) mud collected from the estuary and estuarine water. Predators were starved for 24 h before the experiment was run. The intermolt stage was not determined but hard

shell prey and predator were always used. The trials in which predators molted were not used in the analysis. The following experiments were conducted:

(1) Variable prey-predator asymmetry, prey density, and predator density. In this experiment the relative size between predator and prey changed, as well as prey and predator densities. Megalopae were used as prey and J1 or J2 as predators. Two prey densities (5 and 8 crabs tank⁻¹) and 3 predator densities (1, 5 and 10 crabs tank⁻¹) were utilized.

(2) Constant prey-predator asymmetry and prey density, and variable prey-predator instar stages and predator density. In this experiment the prey-predator asymmetry (1 instar stage of difference) and prey density were constant (10 crabs tank⁻¹), but the instar composition as well as the predator density varied. The following combinations of prey and predator were used: (1) megalopae and J1; (2) J1 and J2; and (3) J2 and J3. In the low predator density treatment 1 crab tank⁻¹ was always used, whereas the high density treatment varied depending on the instar stage. For J1 and J2, 10 crabs tank⁻¹ (100 crabs m⁻²) were used, and for J3 only 5 crabs tank⁻¹ (50 crabs m⁻²) were utilized. In each experiment the smallest YOY crab was considered the prey and the largest the predator. Prey were not replaced as they were consumed since it was not possible to assess when consumption occurred within the shell habitat. Controls (no predators) were also run. The experiments ran for 48 h, and more than 5 replicates were conducted for each combination of predator and prey densities. Mean prey survival in the control was 97 % for megalopae and 98 % for J2 prey.

Cannibalism rate in this experiment indicates number of YOY crabs consumed per predator in 48 h. A 3-way ANOVA was used to test for differences in the mean number of megalopae eaten, mean number of megalopae eaten per predator, and mean proportional mortality per predator as a function of prey density, predator density, and predator sizes (J1 and J2). A 2-way ANOVA was used to test for differences in the mean number of prey eaten, and mean number of conspecifics eaten per predator for the second experiment. Prior to analysis proportional mortality data were arc-sine transformed to normalize the data and remove heteroscedasticity.

RESULTS

Effect of habitat type on cannibalism efficiency

Predator sex did not influence the mean number of prey eaten ($F_{1,151} = 2.66$, $p > 0.05$). After removing the sex as a factor from the analysis, interaction between habitat type and predator age class was found ($F_{4,144} = 2.7$, $p = 0.03$), precluding direct conclusions about the

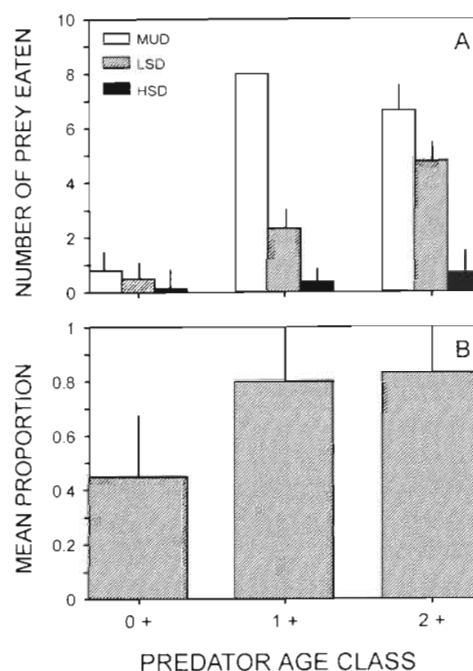


Fig. 1. *Cancer magister*. Effect of habitat complexity on cannibalism rate. (A) Mean number of 0+ (9 to 18 mm carapace width) Dungeness crab eaten by 0+ (21 to 29 mm carapace width), 1+ (60 to 70 mm carapace width), and 2+ (90 to 110 mm carapace width) Dungeness crab in mud, low shell density (LSD), and high shell density (HSD) habitats. Vertical lines indicate 1 standard error; 1+ crabs consumed all the prey in all the trials in the mud habitat. (B) Mean proportion of the consumed 0+ Dungeness crab (9 to 18 mm) for which no remains or only small pieces of carapaces were found when 0+, 1+, and 2+ conspecifics were the predators. Vertical lines indicate 1 standard error. Number of replicates always >10

main effects (Underwood 1981). The habitat type by predator age class interaction effect was due to the dramatic increase in the number of prey eaten in mud habitats for 1+ and 2+ predators, the smooth increase in the mean number of prey eaten as predator age class increased for LSD, and the lack of effect in the mean number of prey eaten in HSD among predator age class (Fig. 1A). In MUD, 1+ and 2+ predators consumed more prey than in any other habitats. Intermediate consumption was found for 1+ and 2+ in LSD. At HSD the consumption of 1+ and 2+ crabs did not differ from 0+ consumption (Fig. 1A).

The mean proportion of remains of type (1) (\leq one-half carapace or no remains) was significantly different among predator age classes (Fig. 1B; $F_{2,67} = 7.19$, $p < 0.01$). 0+ predators left all or most of the carapace of smaller 0+ prey, while 1+ and 2+ left very small pieces of the prey carapace or no remains at all (Fig. 1B). Since continuous observations were not conducted, it is unclear whether the proportion of remains of type (2)

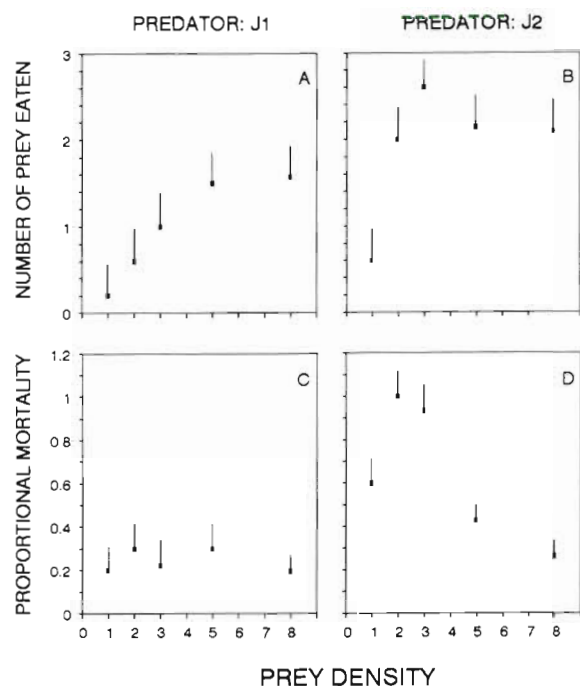


Fig. 2. *Cancer magister*. Effects of prey-predator asymmetry and prey density on cannibalism rate. (A, B) Mean number of megalopae eaten by J1 and J2 conspecifics over 48 h, and (C, D) proportional prey mortality under laboratory conditions at different prey densities. Vertical lines indicate 1 standard error. N always > 5

found when 1+ or 2+ were the predators were remains from crabs consumed by the predators, or by 0+ conspecifics (other prey). However, since no consumption was found in the control, it can be assumed that all prey were consumed by the predator. It is unknown whether cannibalism among YOY occurred only after molting or on hard shell prey. If it occurred immediately after molting, whole carapaces found as remains could be from the molts.

Effects of prey-predator asymmetry and prey density on cannibalism rate among YOY Dungeness crab

The mean number of megalopae consumed by conspecifics was affected by both predator size ($F_{1,51} = 12.6$, $p = 0.00008$) and megalopae density ($F_{4,51} = 6.05$, $p = 0.0005$). The interaction term was not significant ($F_{4,51} = 2.04$, $p = 0.29$). J1 consumed fewer megalopae than J2, and the consumption was higher at densities higher than 3 megalopae tank⁻¹ (30 megalopae m⁻²; Fig. 2A,B). Proportional mortality of megalopae was also affected by predator size ($F_{1,51} = 11.3$, $p = 0.0015$) and megalopae density (Fig. 2C,D; $F_{4,51} = 4.02$, $p = 0.0066$). The interaction term was not significant ($F_{4,51} = 2.01$, $p = 0.11$). Proportional mortality of megalopae

was higher for J2 than for J1 predators. However, there was not a clear pattern for the effect of megalopae density; 2 homogeneous groups were detected (1, 2, 5 and 8 megalopae, and between 2 and 8 megalopae).

The mean number of J2 prey consumed was not significantly different between J3 and J4 predators ($F_{1,65} = 3.4$, $p = 0.07$), and prey density had a marginal effect on the number of J2 consumed ($F_{5,65} = 2.3$, $p = 0.05$); 2 homogeneous groups were detected (between 1 and 5 J2, and between 2 and 7 J2 tank⁻¹; Fig. 3A,B). The interaction term was not significant ($F_{5,65} = 0.14$, $p = 0.47$). Proportional crab mortality was neither significantly different between predator sizes ($F_{1,65} = 2.3$, $p = 0.13$), nor among prey (J2) density treatments (Fig. 3C,D; $F_{5,65} = 0.07$, $p = 0.9$). The interaction term was not significant ($F_{5,65} = 0.4$, $p = 0.84$).

Effects of prey-predator asymmetry and mutual interference on cannibalism rate among YOY Dungeness crab

(1) Variable prey-predator asymmetry, prey density, and predator density. The mean number of megalopae eaten was affected by predator size and predator density, but not by prey density (Fig. 4A,B, Table 2). Con-

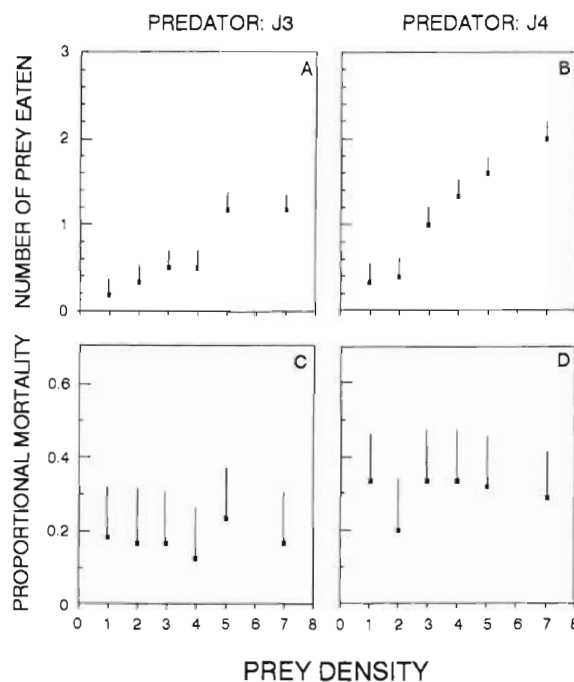


Fig. 3. *Cancer magister*. Effects of prey-predator asymmetry and prey density on cannibalism rate. (A, B) Mean number of second instar (J2) Dungeness crab eaten by J3 and J4 conspecifics in 48 h, and (C, D) proportional prey mortality under laboratory conditions at different prey densities. Vertical lines indicate 1 standard error. N always > 5

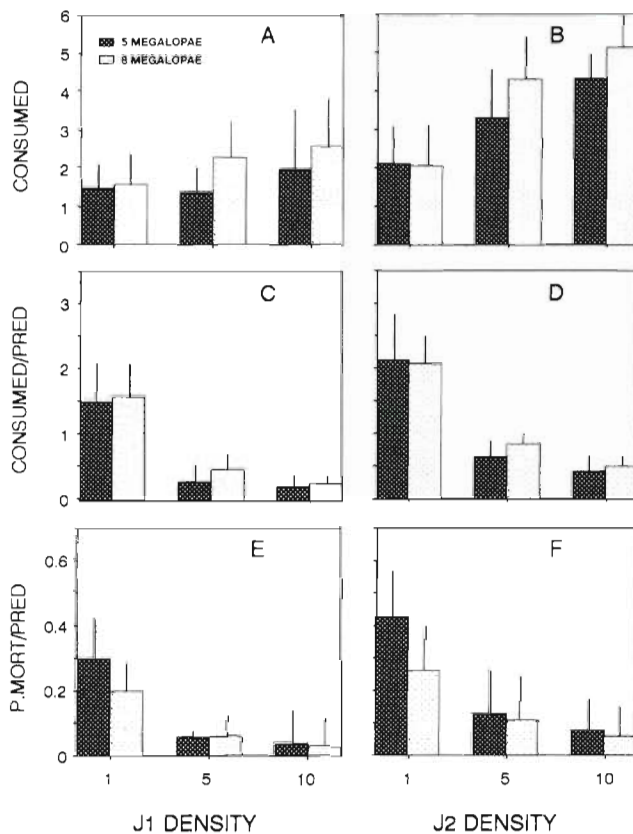


Fig. 4. *Cancer magister*. Effects of prey-predator asymmetry, prey density and predator density on cannibalism rate. Mean number of Dungeness crab megalopae eaten by (A) J1 conspecifics and (B) J2 conspecifics in 48 h; mean number of megalopae eaten standardized per (C) J1 predator and (D) J2 predators, and mean proportional mortality per (E) J1 predator and (F) J2 predators at 2 prey and 3 predator densities (crabs per tank). Prey densities were 5 megalopae (black bars) and 8 megalopae (stippled bars). Vertical lines indicate 1 standard error. N always > 5

sumption increased as the asymmetry between the cannibal and the victim increased, and also as predator density increased. The mean number of megalopae consumed per predator was also affected by predator density and predator size (Fig. 4C,D, Table 2). Consumption per predator was higher for J2 than for J1, and decreased as predator density increased. Prey density did not play any role. In none of the trials were all prey consumed, so complete absence of prey was not a factor. The same factors, predator density and size, had an effect on the mean proportional mortality per predator (Fig. 4G,H, Table 2). Mean proportional mortality per predator was higher for J2 predators, and lower at high predator densities. In all cases the interaction effects were not significant (Table 2).

(2) Constant prey-predator asymmetry and prey density, and variable prey-predator instar stages and

predator density. A significant interaction between prey-predator stages and predator density precluded direct conclusions about the main effects on the mean number of prey consumed ($F_{2,47} = 19.2$, $p < 0.0001$; Underwood 1981). The interaction was due to the increase in the mean number of megalopae eaten by J1 as predator density increased, while for the remaining prey-predator instar combinations there was a decrease in the mean number of prey eaten (Fig. 5A). The mean number of prey eaten per predator was significantly lower at high than at low predator density (Fig. 5B; $F_{1,47} = 97.4$, $p < 0.00001$), and the pattern was consistent for the 3 prey-predator size combinations analyzed (Fig. 5B; $F_{2,47} = 1.99$, $p = 0.148$).

DISCUSSION

Cannibalism seems to be a common behavior among brachyuran crabs, largely overlooked despite the importance it may have on crab population dynamics. Evidence of cannibalism between age classes in crabs has been reported for several decades (e.g. Dungeness crab: Butler 1954, Gotshall 1977, Stevens et al. 1982);

Table 2. *Cancer magister*. Results of the ANOVAs conducted to test for the effect of predator size, predator density and prey density on the response variables: number of megalopae eaten, number of megalopae consumed per predator, and proportional mortality per predator

Response variable	F	df	p
Number of megalopae eaten			
Predator size (A)	32.2	1, 69	<0.00001
Predator density (B)	11.7	2, 69	<0.00001
Prey density (C)	3.4	1, 69	0.066
A × B	3.5	2, 69	0.05
A × C	0.02	1, 69	0.88
B × C	0.93	2, 69	0.4
A × B × C	0.04	2, 69	0.96
Number of megalopae consumed per predator			
Predator size (A)	7.6	1, 69	0.007
Predator density (B)	25.3	2, 69	<0.00001
Prey density (C)	0.06	1, 69	0.53
A × B	0.01	2, 69	0.91
A × C	0.06	1, 69	0.52
B × C	0.03	2, 69	0.81
A × B × C	0.04	2, 69	0.74
Proportional mortality per predator			
Predator size (A)	8.7	1, 69	0.0043
Predator density (B)	27.8	2, 69	<0.00001
Prey density (C)	2.99	1, 69	0.088
A × B	0.07	2, 69	0.93
A × C	1.03	1, 69	0.31
B × C	1.08	2, 69	0.34
A × B × C	0.28	2, 69	0.75

however, assessments of the relative importance of this factor for the population dynamics of crabs are still scarce. Cannibalism among YOY has only recently received attention (Fernández 1994, Perkins-Visser et al. 1996, Moksnes et al. 1997, 1998). The first evidence of cannibalism among juvenile crabs came from occasional observations in communal rearing tanks under laboratory conditions (Klein Breteler 1975, Reise 1985, Tunberg & Creswell 1988). Recent studies done for other purposes have also provided evidence of cannibalism among juvenile crabs (e.g. ontogeny of behavior: Jacoby 1983; recruitment failure: Fernández et al. 1993a; growth: Perkins-Visser et al. 1996).

Moksnes et al. (1997) studied specifically cannibalism among juvenile blue crabs, and reported that cannibalism rate was affected by prey density, predator density, and habitat type. Habitat type definitely affects between-age-classes cannibalism in Dungeness crabs; larger crabs consumed all available prey in mud habitats under laboratory conditions (at relatively low prey density). Similar results were reported from field experiments, where high mortality of low density, tethered crabs in mud habitats was suggested to be due to cannibalism between age classes (Fernández et al. 1993b). Although the potential for cannibalism exists, the real impact of cannibalism between age classes in Dungeness crab is still unknown. Furthermore, in order to assess the importance of cannibalism, experimental work should accompany field data in the light of the differential pattern of ingestion modes between age classes. The percentage of YOY Dungeness crab consumed by 1+ and 2+ conspecifics decreases as predator age increases (Stevens et al. 1982). The percentage is higher for 0+ crabs (24 %) and declines to half of this value for 1+ and 2+ crabs, which consume mostly fish in unsheltered habitats (Stevens et al. 1982). The same pattern of increasing cannibalism until certain predator size, and a switch to other prey afterwards, was reported for the snow crab (Lovrich & Sainte-Marie 1997). However, cannibalism among younger conspecifics may have been underestimated. In the snow crab the whole prey (first instar) is ingested by larger conspecifics (no reports on mode of ingestion by similar size conspecifics; Lovrich & Sainte-Marie 1997). A similar pattern is reported here for the Dungeness crab, and previous studies of stomach content analyses of YOY Dungeness crab have failed to identify carapaces or other hard parts as indicators of cannibalism among YOY (J1 to J5-6 instar crabs; Stevens et al. 1982). These differences could be due to the method of attack, or to when the attack occurs (only soft prey). Thus, the assessment of cannibalism among YOY should not rely on the presence of hard parts. The pattern of consumption poses the problem of identifying the impact of cannibalism. Stomach

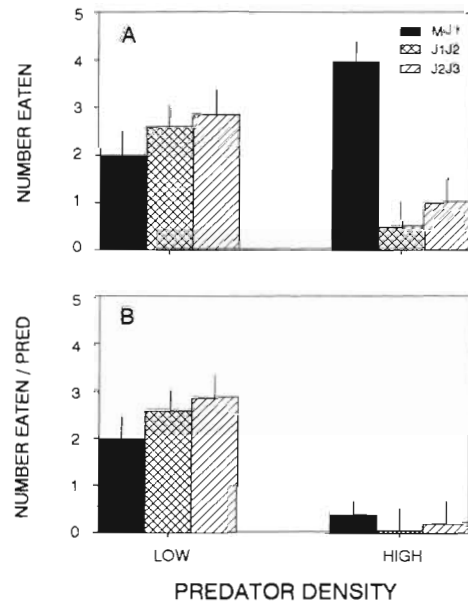


Fig. 5. *Cancer magister*. Effects of prey-predator instar combinations and predator density on cannibalism rate. (A) Mean number of prey eaten by conspecifics in 48 h for each instar stage combination at low and high predator density, and (B) mean number of prey eaten standardized per predator.

Vertical lines indicate 1 standard error. N always > 5

analysis alone may not be enough to assess cannibalism in natural populations, because the pattern of conspecific ingestion depends on the size of the predator (or the asymmetry between YOY prey and the predator).

The outcome of the experiments presented here could have been different if alternative prey had been offered. However, cannibalism among YOY occurs even in the presence of alternative prey, although the preference for alternative prey versus conspecifics varies depending on the prey offered (Visser 1997). It is not clear if the total number of prey (conspecifics) attacked could vary depending on the presence of alternative prey, because consumption is not reported in numbers (Visser 1997).

Cannibalism among YOY Dungeness crabs is not affected by habitat complexity, probably because juvenile crabs share the same habitat type (but see Moksnes et al. 1997 for differences with the blue crab). This pattern of consumption implies a lack of refuge for the prey, and it may have important consequences for the mortality rate of juvenile crabs in complex habitats. In fact, cannibalism among YOY was suggested to be the main source of mortality in artificial shell habitats (Fernández et al. 1993b) and to decimate an extremely large supply of larvae in habitats colonized by larger conspecifics (Fernández et al. 1993a). Although overall survival in shell habitats is higher than in adjacent

open mud flats, shelter availability in cannibalistic species may not be as efficient for juvenile crabs as for other invertebrates. Moksnes et al. (1998) also showed that cannibalistic juveniles cause predation rates similar to or higher than other predators in nursery habitats.

The importance of prey-predator asymmetry and prey density was not consistent across prey stages, and it may be related to prey vulnerability. The probability of having access to soft, vulnerable prey may be very high when megalopae are the prey (in relation to J2 prey). The pattern of vulnerability observed may not depend on the experimental conditions, and rather reflect the conditions in nature. The megalopa is the most vulnerable stage; the time from settlement to metamorphosis into J1 in the Grays Harbor estuary is very short (6 to 12 h; Eggleston & Armstrong 1995). Even in the cases where molting was delayed in the presence of conspecifics, 60% of the megalopae molted during the 96 h experimental time (Fernández et al. 1994). This implies that if megalopae are present, there is always access to vulnerable (soft) prey. This factor could also explain the higher variability in the data observed for J2 prey in comparison to megalopae. Visser (1997) reported little variation in mortality (cannibalism) estimates in comparison with the experiments shown here, using prey (J1) that had molted up to 24 h prior to the experiment. However, no clear changes in proportional mortality of newly molted J1 crabs were detected depending on hours since molt (Visser 1997). Vulnerability could also be used to explain the differences in consumption rate of megalopae and J2 under different prey densities. J1 and J2 predators increased the consumption of megalopae as prey density increased, whereas only a marginal effect on consumption of J2 prey was detected when J3 or J4 were used as predators. Also, in the first case consumption increased as the asymmetry between the prey and the predator increased, which may indicate that prey were available (vulnerable) and consumed until satiation was reached. Instead, in the second case consumption may have occurred based on opportunities to have access to vulnerable prey. Although in both cases predators may respond in the same way to an increase in prey density if prey vulnerability were equal, the conditions of prey vulnerability in nature are not equal. A clear functional response to megalopae density was also found in the blue crab (Moksnes et al. 1997).

Increasing predator densities decreased significantly the consumption rate per predator, irrespective of the asymmetry between the prey and the predator, the instar stages involved in the interaction, and prey density. Prey density was always high in order to avoid prey depletion, and a 37% change in megalopae den-

sity (5 to 8 crabs) did not affect the number of megalopae consumed per predator, or proportional mortality of megalopae per predator. Instead, a dramatic decrease in both variables was observed as predator density increased, for all the combinations of prey and predator stages used. Prey may find a refuge at high predator densities because mutual interference affects the searching and handling efficiency of the predators (Mansour & Lipcius 1991, Iribarne et al. 1995). Predator efficiency may also be related to the vulnerability of the prey. The decrease in mean consumption rate per predator was more dramatic for J1 and J2 prey than for megalopae, despite the asymmetry between the prey and the predator being constant (1 instar stage). For J2 and J3 predators, the number of prey eaten decreased as predator density increased, suggesting that even vulnerable prey may not have been consumed (assuming that prey vulnerability in both predator density treatments was equal).

A decrease in cannibalism rate by doubling the density of conspecifics has been reported for Dungeness (Visser 1997) and blue (Moksnes et al. 1997) crabs. A similar decrease was observed in this study for J1 and J2 Dungeness crabs consuming megalopae. However, the most dramatic change occurred between a single predator and more than 1 predator. No major changes were observed on doubling predator density from 5 to 10 crabs. The effect of mutual interference in the blue and Dungeness crabs had already been reported for clams, where prey vulnerability (molting) did not play any role (Mansour & Lipcius 1991, Iribarne et al. 1995). Although mutual interference clearly affects cannibalism among YOY under laboratory conditions, dispersal, a density-dependent mechanism that occurs irrespective of food availability, may take place *in situ* (Iribarne et al. 1994). Density-dependent dispersal may generate density-dependent cannibalism between age classes, by forcing YOY to emigrate from sheltered habitats to unprotected areas where cannibalism between age classes is higher.

The combined roles of the asymmetry between prey and predator, prey density and predator density are very important factors in regulating recruitment of the Dungeness crab. Annually, in the Grays Harbor estuary the Dungeness crab exhibits multiple cohorts (Dinnel et al. 1993). Furthermore, the pattern of settlement of a single cohort may vary and it should certainly have an effect on the survival of the settling megalopae. Eggleston & Armstrong (1995) reported that although megalopa density showed a pronounced peak, each cohort of megalopae lasted a few days. Moreover, predator density and size may also vary depending on the strength and the time elapsed since the previous settlement. Thus, the outcome of cannibalism could vary, producing different patterns of recruitment even

under similar conditions of annual larval supply (sum of all cohorts). Although the potential for cannibalism continues over time, the major impact of this behavior on crab recruitment may happen in a very short period of time. In fact, within a week a very strong cohort of megalopae was decimated in habitats colonized by high densities of J1 and J2 Dungeness crabs (Fernández et al. 1993a).

The implications of cannibalism among YOY for the habitat enhancement program and for the population dynamics of Dungeness crab are similar. Artificial shell habitats, as well as other complex, natural habitats, increase survival of juvenile Dungeness crab by reducing predation and cannibalism between age classes. As a result, crab production increases during the first 4 mo of intertidal, benthic existence (Fernández et al. 1993b). In spite of the observed pattern of increased juvenile abundance in sheltered habitats, the potential for production in sheltered habitats is limited by YOY behavior. The recruitment to natural populations, or the maximum production of juvenile stages within artificial habitats constructed to enhance the overall population abundance, may be the result of the trade-off between preference for shelters, cannibalism among YOY within sheltered habitats, and dispersal.

Acknowledgements. I thank O. Iribarne and J. Orensanz for suggestions made in the early stages of this study. G. Williams and O. Iribarne provided field assistance. The manuscript was improved by the comments of C. Foote, P. Jumars, J. Skalski, R. McConnaughey, A. Palma, E. Visser, and 3 anonymous reviewers. Prof. D. Armstrong provided great facilities to conduct this research project, interesting hours of discussion, and also helpful comments. I was supported by PEO Peace Foundation, Encyclopaedia Britannica, and a Fulbright Fellowship. This project was also partially supported by the Fundación Antorchas (Argentina, Project A-13342/1 to M.F. - 1995) and the Washington Sea Grant Program (Project No. NA36RG0071-01 to David Armstrong).

LITERATURE CITED

- Armstrong DA, McGraw KA, Dinnel PA, Thom RM, Iribarne OO (1991) Construction dredging impacts on Dungeness crab, *Cancer magister*, in Grays Harbor, Washington and mitigation of losses by development of intertidal shell habitat. FRI-UW-9110, University of Washington, Seattle
- Armstrong DA, Dinnel PA, Iribarne OO, Fernández M (1992) Use of intertidal oyster shell to enhance 0 + Dungeness crab production in Grays Harbor estuary (WA). Proc Int Crab Rehab & Enh Symp Kodiak, Alaska. University of Kodiak, Kodiak, p 125-140
- Banerji SR, Prasad D (1975) Observations on reproduction and survival of *Anabas testudinus* (Bloch) in Bihar region. J Inl Fish Soc India 6:6-17
- Botsford LW, Wickham DE (1978) Behavior of age-specific density-dependent models and the northern California Dungeness crab (*Cancer magister*) fishery. J Fish Res Board Can 35:833-843
- Bry C, Gillet C (1980) Reduction of cannibalism in pike (*Esox lucius*) fry by isolation of full-sib families. Reprod Nutr Dev 20:173-182
- Butler TH (1954) Food of the commercial crab in the Queen Charlotte Island region. Fish Res Bd Can Prog Rep Pac Coast Stn 99:3-5
- DeAngelis DL, Cox D, Coutant C (1979) Cannibalism and size dispersal in young-of-the-year largemouth bass: experiment and model. Ecol Model 8:133-48
- Dinnel P, Armstrong DA, McMillan RO (1993) Evidences for multiple recruitment-cohorts of the Puget Sound Dungeness crab, *Cancer magister*. Mar Biol 115:53-63
- Dumbauld B, Armstrong DA, McDonald TL (1993) Use of intertidal oyster shell as habitat enhancement to mitigate loss of subtidal juvenile Dungeness crab (*Cancer magister*) habitat caused by dredging. Can J Fish Aquat Sci 50:381-390
- Eggleston D, Armstrong D (1995) Pre- and post-settlement determinants of estuarine Dungeness crab recruitment. Ecol Monogr 65(2):193-216
- Elgar M, Crespi B (1992) Ecology and evolution of cannibalism. In: Elgar M, Crespi B (eds) Cannibalism: ecology and evolution among diverse taxa. Oxford Science Publications, Oxford, p 1-12
- Fernández M (1994) Recruitment of Dungeness crab, *Cancer magister* Dana, in artificial, intertidal habitats of the Grays Harbor Estuary. PhD dissertation, University of Washington, Seattle
- Fernández M, Armstrong DA, Iribarne OO (1993a) First cohort of young-of-the-year Dungeness crab, *Cancer magister*, reduces abundance of subsequent cohorts in intertidal shell habitats. Can J Fish Aquat Sci 50:2100-2105
- Fernández M, Iribarne OO, Armstrong DA (1993b) Habitat selection by young-of-the-year Dungeness crab *Cancer magister* Dana and predation risk in intertidal habitats. Mar Ecol Prog Ser 92:171-177
- Fernández M, Iribarne OO, Armstrong DA (1994) Ecdysial rhythms in megalopae and first instar Dungeness crab *Cancer magister* Dana. Mar Biol 118:611-615
- Forney J (1976) Year class formation in the walleye (*Stizostedion vitreum vitreum*) population of Oneida Lake, New York, USA, 1966-1973. J Fish Res Board Can 33:783-92
- Fox LR (1975) Cannibalism in natural populations. Annu Rev Ecol Syst 6:87-106
- Gotshall DW (1977) Stomach contents of northern California Dungeness crab, *Cancer magister*. Calif Fish Game 63:43-51
- Hassell M (1978) The dynamics of arthropod predator-prey systems. Monographs in population biology. Princeton University Press, Princeton, NJ
- Higgins K, Hasting A, Sarvela J, Botsford L (1997) Stochastic dynamics and deterministic skeletons: population behavior of Dungeness crab. Science 276:1431-1435
- Holling CS (1959) The components of predation as revealed by a study of small mammal predation of the European pine sawfly. Can Entomol 91:293-320
- Iribarne OO, Fernández M, Armstrong DA (1994) Does space competition regulate density of juvenile Dungeness crab *Cancer magister* Dana in sheltered habitats. J Exp Mar Biol Ecol 183:259-271
- Iribarne OO, Armstrong DA, Fernández M (1995) Environmental impact of intertidal juvenile Dungeness crab habitat enhancement: effects on bivalves and crab foraging rate. J Exp Mar Biol Ecol 192:173-194
- Jacoby CA (1983) Ontogeny of behavior in the crab instar of Dungeness crab *Cancer magister* Dana 1852. Z Tierpsychol 63:1-16
- Karpov K (1983) Effect of substrata type on survival and growth in high density communal cultures of juvenile

- Dungeness crab, *Cancer magister*. In: Wild P, Tasto RN (eds) Life history, environment and mariculture studies of the Dungeness crab, *Cancer magister*, with emphasis on the central California fishery resource. Calif Dep Fish Game Fish Bull 172:311–318
- Klein Breteler WCM (1975) Laboratory experiments on the influence of environmental factors on the frequency of moulting and the increase in size at moulting of juvenile shore crabs, *Carcinus maenas*. Neth J Sea Res 1: 100–120
- Kurihara Y, Okamoto K (1987) Cannibalism in a grapsid crab, *Hemigrapsus penicillatus*. Mar Ecol Prog Ser 41:123–127
- Lipcius RN, Herrnkind WF (1982) Molt cycle alterations in behavior, feeding and diel rhythms of a decapod crustacean, the spiny lobster *Panulirus argus*. Mar Biol 68: 241–252
- Lovrich G, Sainte-Marie B (1997) Cannibalism in the snow crab *Chionoecetes opilio* (O. Fabricius) (Brachyura: Majidae) and its potential importance to recruitment. J Exp Mar Biol Ecol 211:225–245
- MacKay DCG (1942) The Pacific edible crab, *Cancer magister*. Bull Fish Res Board Can 62:1–32
- Mansour R, Lipcius R (1991) Density-dependent foraging and mutual interference in blue crabs preying upon infaunal clams. Mar Ecol Prog Ser 72:239–246
- Moksnes PO, Lipcius RN, Pihl L, van Montfrans J (1997) Cannibal-prey dynamics in young juveniles and postlarvae of the blue crab. J Exp Mar Biol Ecol 215:157–187
- Moksnes PO, Pihl L, van Montfrans J (1998) Predation on postlarvae and juveniles of the shore crab *Carcinus maenas*: importance of shelter, size and cannibalism. Mar Ecol Prog Ser 166:211–225
- Perkins-Visser E, Wolcott TG, Wolcott DL (1996) Nursery role of seagrass beds: enhanced growth of juvenile blue crabs (*Callinectes sapidus* Rathbun). J Exp Mar Biol Ecol 198:155–173
- Polis GA (1981) The evolution and dynamics of intraspecific predation. Annu Rev Ecol Syst 12:225–251
- Reise K (1985) Tidal flat ecology. Ecological studies, Vol 54. Springer-Verlag, Berlin
- Ricker WF (1954) Stock and recruitment. J Fish Res Board Can 11:559–623
- Stevens B, Armstrong DA, Cusimano R (1982) Feeding habits of the Dungeness crab *Cancer magister* as determined by the index of relative importance. Mar Biol 72:135–45
- Tunberg BG, Creswell RL (1988) Early growth and mortality of the Caribbean king crab *Mithrax spinosissimus* reared in the laboratory. Mar Biol 98:337–343
- Underwood AJ (1981) Techniques of analysis of variance in experimental marine biology and ecology. Oceanogr Mar Biol Annu Rev 19:513–605
- Visser EP (1997) Competition, cannibalism, and prey limitation: factors compromising the effectiveness of shell habitat mitigation for early benthic phase *Cancer magister* in Grays Harbor, WA. PhD dissertation, University of Washington, Seattle
- Wainwright T (1994) Individual growth and population size structure in *Cancer magister*. PhD dissertation. University of Washington, Seattle

Editorial responsibility: Otto Kinne (Editor),
Oldendorf/Luhe, Germany

Submitted: August 25, 1998; Accepted: November 26, 1998
Proofs received from author(s): May 21, 1999