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HANDLING EFFECTS, BAIT EFFICIENCY, AND POT BEHAVIOR

A

THESIS

Presented to the Faculty

of the University of Alaska Fairbanks

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By

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Juneau, Alaska

May 1996

THE RED KING CRAB FISHERY:

HANDLING EFFECTS, BAIT EFFICIENCY, AND POT BEHAVIOR

By

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RECOMMENDED:

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ABSTRACT

Red king crabs (*Paralithodes camtschaticus*) are caught by pots in a male-only fishery in Alaska. The objectives of this research were: 1) to examine impacts of the commercial fishery on discarded female and sublegal male crabs; 2) to examine bait efficiency; 3) to document crab behavior to pots; and 4) to develop a model describing catch versus soak time.

I estimated from observer data that 64.6% of crabs in the Bering Sea fishery were females and sublegal males; I simulated commercial crab handling procedures in the laboratory to test effects on discarded crabs. Although body damage increased significantly with increased handling, there were no significant effects on righting time, feeding rate, weight gain, carapace length increment, or survival.

I examined the efficiency of five potential baits (squid, herring, mussel, king crab muscle, and king crab ovary) by observing chemoreception and feeding behavior of the crabs. Chemosensory threshold varied between 10^{-4} to 10^{-6} $g.L^{-1}$, and feeding threshold ranged from 10^{-2} to 10^{-3} $g.L^{-1}$. Crabs were most sensitive to the extract of conspecific muscle, while herring was most effective in arousing feeding behavior. Little difference existed between males and females in chemoreception and feeding behavior.

Behavioral responses of the crabs to crab pots were observed by time-lapse video. Crabs approached the pot from downstream, and 78.3% of crabs searched less than 90° before leaving or entering the pot. The entry success rate was 8.1%. Only large males could begin escape from the bottom panel. Crabs had difficulties in accessing the pot and in escaping from inside the pot. The standard pot appeared inefficient in catching legal males, while it retained many non-legal crabs.

I constructed a general model to describe the relationship between catch and soak time for trap fisheries. The model is expressed as $C_t = ab + a(t - b)\ e^{-ct}$, where C_t is the catch per trap haul at soak time t, and a, b, and c are parameters to be estimated. This model is suitable for both short and long soak times.

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This dissertation is for my wife Lina Chen and our daughter Meng Zhou. They have given me not only emotional support but also direct help with experiments.

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Chapter 1

Effects of Handling on Discarded Red King Crabs

ABSTRACT

A large number of female and sublegal-sized male crabs are caught in the red king crab fishery and must be discarded to comply with the Alaskan regulations. Before being returned to the sea, they suffer aerial exposure, crushing, and deck and water impacts. This study examined the effects of handling on female and sublegal male crabs. On average 64.6% of king crab in the catch were females and sublegal males. The deck impact distance was approximately 60 cm, and the water impact distance was approximately 2 m if crabs were returned from the rail of vessel, or averaged 71 cm if returned from the chute. Maximum aerial exposure duration averages 2.33 min. I simulated handling procedure in the laboratory with 5 treatments: handled once, handled twice, handled three times, modified handling (no deck impact and returned to the sea water via a ramp), and controls. Crabs were categorized in 3 groups: ovigerous females, juvenile females, and sublegal males. After receiving handling treatments, crabs were maintained for 4 months while damage, righting response, feeding rates, weight change,

carapace length increment, and mortality were monitored. Body damage increased significantly with increased handling. One crab died within 24 h of the first handling treatment. However, there were no significant differences in righting responses, feeding rates, weight gain, carapace length increment, or long-term mortality among the five treatments. Normal handling of red king crabs during commercial crabbing activities may not have detrimental effects on the discards.

INTRODUCTION

The Alaska red king crab, *Paralithodes camtschaticus* (Tilesius, 1815), fishery collapsed in the early 1980s. Since then the stock has remained at low abundance and shows little sign of recovery (Otto 1990). Several hypotheses have been proposed to explain this decline, including lethal and sublethal effects of handling during harvest (Thomson 1990; Kruse 1993).

Red king crabs are harvested by crab pots in Alaska, and only males ≥ 121 to 178 mm CW, depending on the statistical area, can be taken (Alaska Department of Fish and Game, 1994-95). In comparison to other fishing gear (e.g., trawl), pots have many advantages; however, a large number of females and sublegal-sized males are incidentally caught. A survey using pots in Kodiak, Alaska reported that 75% of crabs caught were female, and 26% of males were sublegal size (Blau 1988). The male : female ratio in a 1991

Bristol Bay survey was 47:53. In the 1992 survey, the male : female ratio was high (70:30), and while 62% of males were > 165 mm CW (Byersdorfer and Watson 1992), up to 57% of the crabs caught had to be discarded.

Before they are released, discarded crabs are exposed to aerial desiccation and temperature differences between the air and sea water. They may also get crushed, and damaged when dropped on the deck or overboard. The amount of physical trauma received from handling is unknown, and it may have delayed sublethal effects on long-term survival.

The Alaska Department of Fish and Game conducted experimental fishing with pots in 1991 and reported that 2% of crabs were injured and 0.1% died immediately after handling (Byersdorfer and Watson 1992). There was no report on the incidence of handling-induced injury or mortality during commercial fishing. The immediate mortality (47.3%) of king crabs captured by commercial sole trawls was high (Stevens 1990).

Investigation of Dungeness crabs demonstrated that increased handling resulted in 100% mortality after crabs were handled (as they would be by the fishery) four times (unpublished data, T. Shirley). The mortality was not immediate but occurred over a four month period following the handling. Also, the number of missing limbs and percentage of the population missing limbs increased as the Dungeness crab fishery progressed (Shirley and Shirley, 1988). Red king crabs are vulnerable to autotomy (Edwards 1972, Kurata

1963, Niwa and Kurata 1964). Because red king crabs are larger and heavier than Dungeness crabs, and may have fewer adaptations to aerial exposure and impacts because of their subtidal life style, the effects of handling may be more deleterious.

My research hypothesis is that handling has lethal and sublethal effects on discarded crabs. First I measured the crab vessel dimensions related to potential impacts that discarded crabs would suffer. I estimated the aerial exposure duration from field observations, and estimated the number of crabs discarded and the immediate injury and death rate by analyzing data from the king crab observer program. Second, I simulated handling in the laboratory and examined the effects of handling on: 1) body damage which includes limb damage and autotomy; 2) vigor and activity; 3) feeding rate; 4) growth rate; 5) carapace increment after molt; 6) long term survival. Also, I examined the effects of repeated handling on these indices, and whether handling impacts can be ameliorated by alteration of handling techniques.

MATERIALS AND METHODS

Field data collection

Field data were collected during the 1994 Bering Sea fishery. Crab vessels (N = 63) were measured prior to the opening of the fishery. The distance from the rail to the deck, and the distance from rail to the water

surface, chute-water height, sorting table dimensions, and tote dimensions were measured.

The aerial exposure time aboard one commercial crab vessel was measured for each pot with a stop watch. The minimum aerial exposure time was from when the pot entered air until the first crab was returned to the sea; the maximum aerial exposure time was logged when the last crab was released. The total number and number of legal crabs were counted for each pot. Water temperature and air temperature were recorded at 8:00 AM and 2:00 PM (N = 20). Occasionally, crabs fell onto the deck, so the number of crabs falling to the deck was recorded for each pot.

The Mandatory Shellfish Observer Program provided the data collected during the red king crab fishery. Four years of data from 1990 to 1993 were used to estimate the impact of commercial crabbing on discarded crabs. The observers deployed on the catcher/ processor vessels randomly selected approximately 5 pots per one hundred pulled, counted all of the crab according to the pertinent categories, species, and sex. If less than 100 crabs in any category were in the pot, the lengths of all crabs were measured. The minimum legal size was 6.5 inches or 165 mm carapace width (CW) including spines in the Bristol Bay district (Alaska Department of Fish and Game 1994-95). The relationship of CW = -14.11 + 1.27 * CL (carapace length) for southeastern Bering Sea male red king crabs was applied (Rickey and Sheridan

1961) to obtain the legal size of 141 mm in CL, and the CL distribution in the catch was compared to this legal size. All crabs were examined for damage and death.

Laboratory experiments

Sublegal male and female red king crabs were collected in Auke Bay and Barlow Cove, southeastern Alaska, with pots, handled gently, and maintained in sea water during transport. In the laboratory, crabs were kept in tanks with flowing seawater pumped from a depth of 30 m, and each crab occupied approximately 43.5 L water with a flow speed of 17.5 $mL.s^{-1}$. Crabs were fed a mixed diet of fish, squid and mussels *ad libitum*. All crabs were acclimated to laboratory conditions for at least two weeks prior to experimentation. Water temperature ranged from 5.4 to 9.4 °C and salinity was 32 ppt during the experimental period.

Each crab had a numbered cinch tag on its right, third walking leg. No autotomy resulted from capture or holding. Crabs with missing leg(s) were not used. The experiment had 5 treatments and 27 crabs per treatment: 9 ovigerous females, 9 juvenile females, and 9 sublegal males. Because my objective was to examine the effects of handling on discarded crabs, no legal male crabs were used. There were similar-sized crabs in each treatment, and the placement of crabs into each treatment was determined by a randomized

block design. Their carapace lengths ranged from 70.3 to 125.0 mm with a mean of 99.8 mm (±14.1 SD). Wet weight of all crabs was weighed with a electronic balance to nearest 0.1 g. A crab was placed in a tote with a cotton towel on the bottom, and another cotton towel covered the crab. The crab weight was obtained by subtracting the weight of the tote, towels, and water from the total weight. The wet weight ranged from 258.0 to 1481.0 g with a mean weight of 804.9 g (±312.5 SD). The handling procedures for the 5 treatments were as follows.

Treatment 1: handled once. Twenty-seven crabs were placed in a simulated commercial pot (approximately 1/2 the size of a commercial pot, 92*92*45 cm, but of similar box shape). The pot was placed at a height of 60 cm and subsequently tilted at a 45° angle. The door of the pot was opened and crabs were dumped into an empty tank. Crabs tangled in the pot-mesh were shaken to cause them to fall and none were pulled out by hand. Crabs were then dropped from a 3-m height into seawater onto their dorsal surface.

Treatment 2: handled twice. All crabs in this treatment received Treatment 1, then 3 days after the first handling, crabs were handled in the same way, except they were dropped onto their ventral surface.

Treatment 3: handled three times. All crabs in this treatment received Treatment 2, and one more handling 3 days after the second handling.

Treatment 4: modified handling. Crabs were placed in a pot and dumped from 20 cm into a tank filled with sea water of 40 cm depth. Then crabs slid on their ventral surface into sea water from a 45° tilted ramp of 3 m height.

Treatment 5: control. This group received no handling or aerial exposure except during measurements.

During these four treatments, water temperature varied between 7.8 and 8.6 °C and air temperatures varied between 7.6 and 15.3 °C. Aerial exposure time for the last crab returned to the water varied between 10~14 min in Treatment 1, 2 and 3.

All crabs were returned to holding tanks for examination. Crabs used for consumption measurements and molting crabs were isolated. Crabs had low feeding rates or stopped feeding during molting, so the data 10 days before and after molting were excluded from analysis due to significantly lower feeding rates. Most male crabs molted, few juvenile females did, and no ovigerous females molted during the experiment. Weight changes, growth rate, and mortality were analyzed for molted males, unmolted juvenile females, and unmolted ovigerous females.

Body injury and limb autotomy were recorded immediately after each experimental treatment. One day after treatment, the righting time each crab required to turn over when placed on its back under water on the bottom of

the tank was recorded. Righting time is an indicator of integrated muscle coordination and sensory perception. Righting time was measured weekly until week 12. Consumption rates were measured by placing weighed, cut squid into each crab container and weighing the remainder 24 hr later. Before it was weighed, the food was blotted dry with paper towels. Measurements were made of control food soaked for 24 hr in a tank without crabs to determine wet weight changes due to immersion, and consumption was corrected accordingly. Feeding rates were measured twice a week for a subset of 9 crabs in each treatment until week 13. Four months after experimental treatments, wet weights and CL were recorded for all crabs.

Several statistical methods were used to analyze different experiment indexes according to the data characteristics. All data were diagnosed by graphic methods before and after statistical tests. Data transformation was applied if statistical assumptions were violated. Statistical power was calculated for some experimental indexes.

RESULTS

Impact of commercial fishery

During fishing, pots were normally dumped onto a sorting table or into a tote. After sorting the females and sublegal males were slid down from the sorting table to a chute below the deck surface with overflow water from the

tank, and then dropped to the sea or thrown over the rail. This procedure was considered as normal handling in commercial crabbing.

The distance from the lower edge of the pot door to the table was less than 30 cm. A typical tote was 81 (wide) * 142 (long) * 53 (high) cm. The distance from the lower edge of the pot door to the bottom of the tote was about 60 cm. The mean height of a sorting table was 61 cm and the chute was approximately 25 cm lower than the deck surface (Table 1.1). Crabs usually slid down to the chute on a ramp at approximately 45°.

Water impact distances were measured when boats were fully or partially loaded with pots and their holding tanks were partially filled with water. The water impact distance varied with the size of vessels (Figure 1.1). The larger vessels generally had a greater water impact height. If crabs are returned to the sea from the chute, the mean drop distance was <1 m, but if crabs were thrown from the rail, that distance might exceed 2 m (Table 1.1).

The number of crabs in the pot affects the aerial exposure duration (Figure 1.2). The first crab could be overboard within 2 min (mean 1.3 ± 0.23 SD, n = 97) , and the last one within 4 min (mean 2.3 ± 0.47 SD, n = 134). During the 1994 fishing season, the air temperature in Bristol Bay varied from 0.5 °C to 6.6 °C with a mean of 3.0 °C (± 2.13 SD, N = 20), while the water

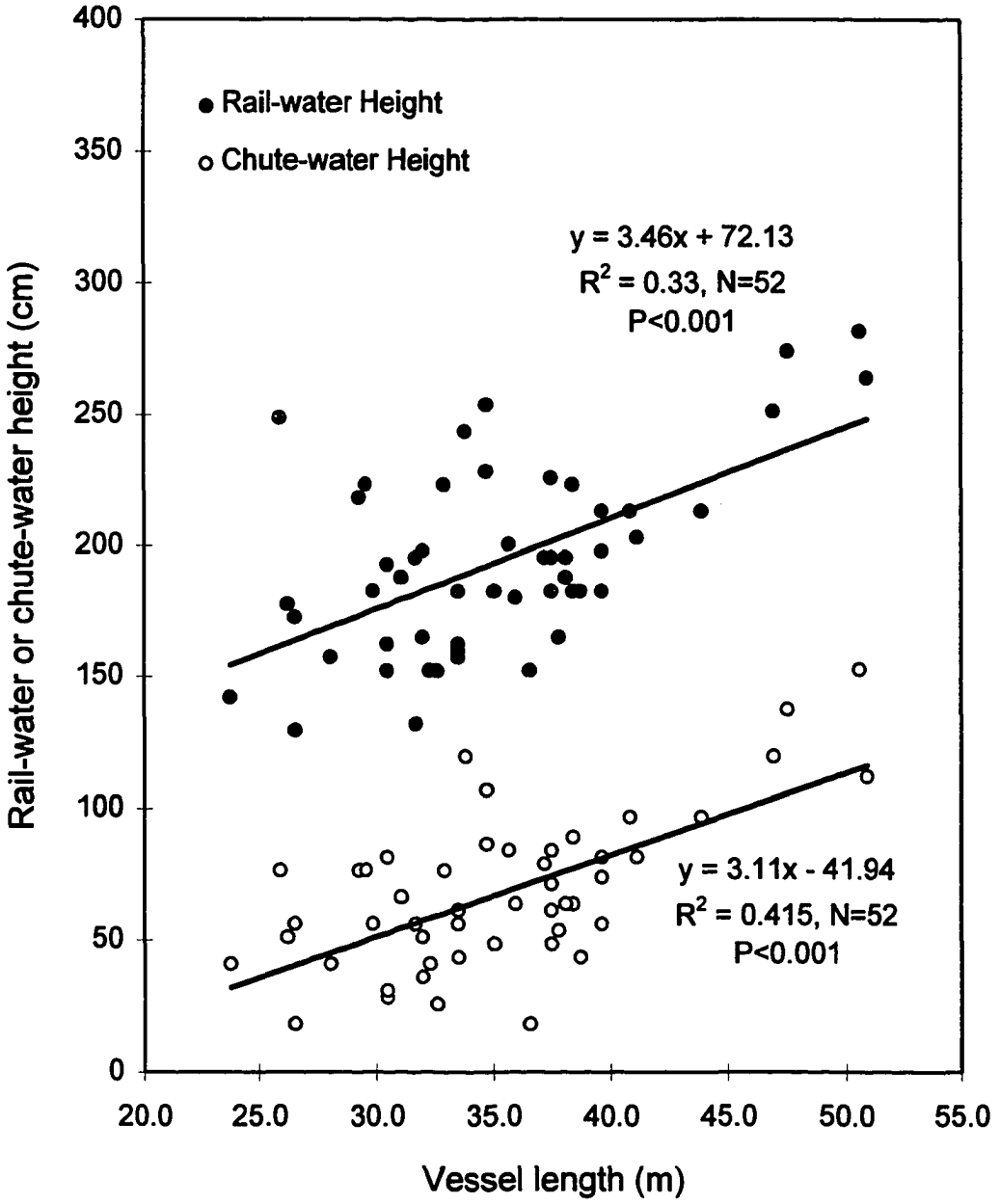

Figure 1.1. Rail-water height and chute-water height versus vessel length for commercial crab vessels.

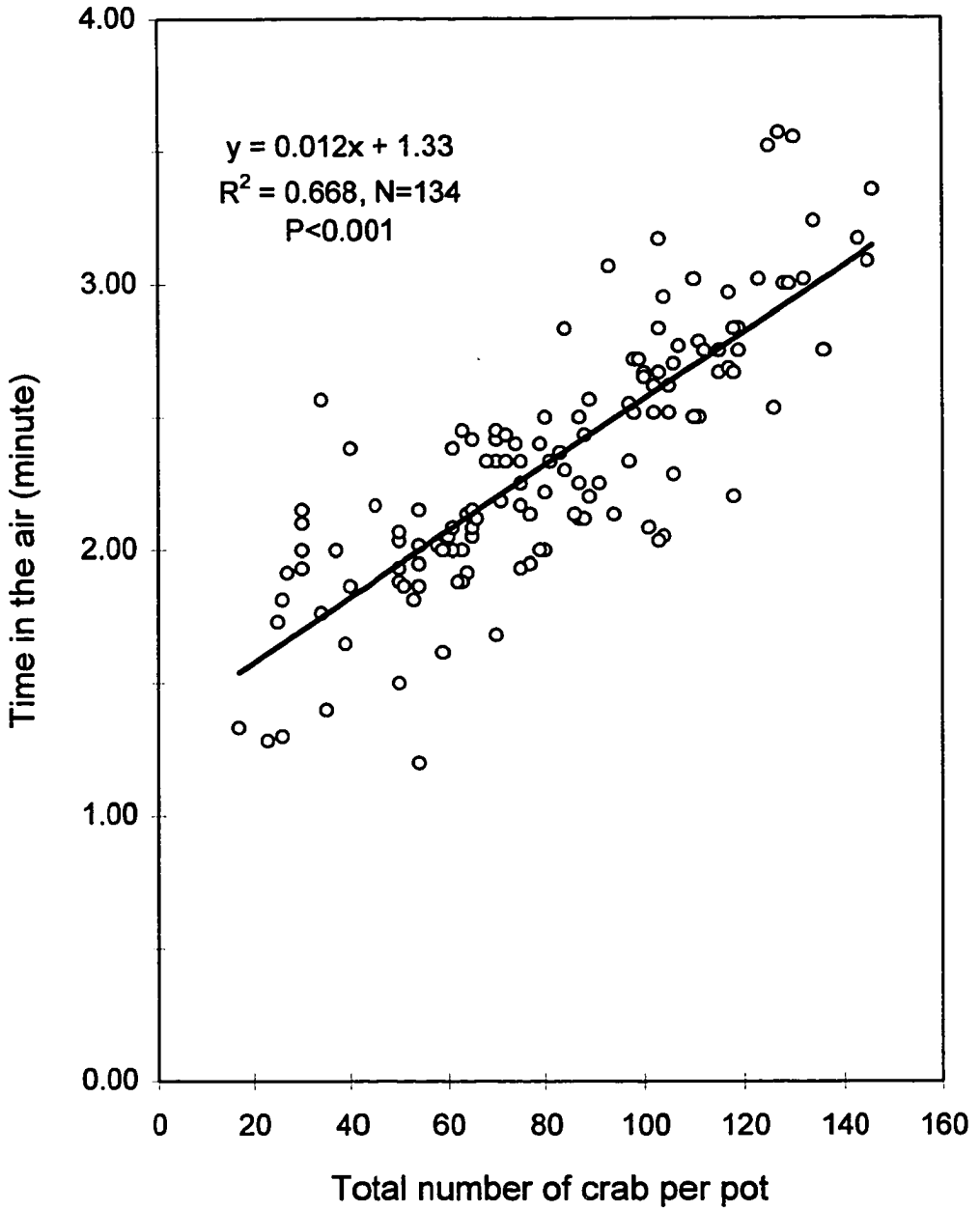

Figure 1.2. Maximum aerial exposure duration versus the total number of crabs in a pot in commercial fishery.

Table 1.1: Measurements (cm) of deck and water impact distances.

	Rail-Deck (n = 63)	Table-Chute (n = 10)	Chute-Water (n = 60)	Rail-Water (n = 61)
Minimum	76	73	18	130
Maximum	147	96	153	282
Mean	104	86	71	198
SD	14.50	7.42	31.4	37.37

temperature was more stable, from 3.5 to 4.4 °C with a mean of 4.0 °C (± 0.30 SD, N = 6).

Some crabs suffered abnormal handling. When the pot door was opened quickly, crabs hanging on the door might be tossed high into the air. An average of 1.41 ± 1.32 SD (N = 108) crabs dropped to the deck rather than into the sorting table. These crabs suffered longer aerial exposure, and might be kicked, smashed, or thrown back to the water from the rail.

Red king crabs as small as 65 mm in CL were retained in crab pots, but few crabs less than 85 mm CL were retained. Crabs smaller than this 141 mm CL must be released (Figure 1.3).

A significant number of female and sublegal-sized male crabs were caught in each pot (Figure 1.4). I calculated that an average of 64.6% (±

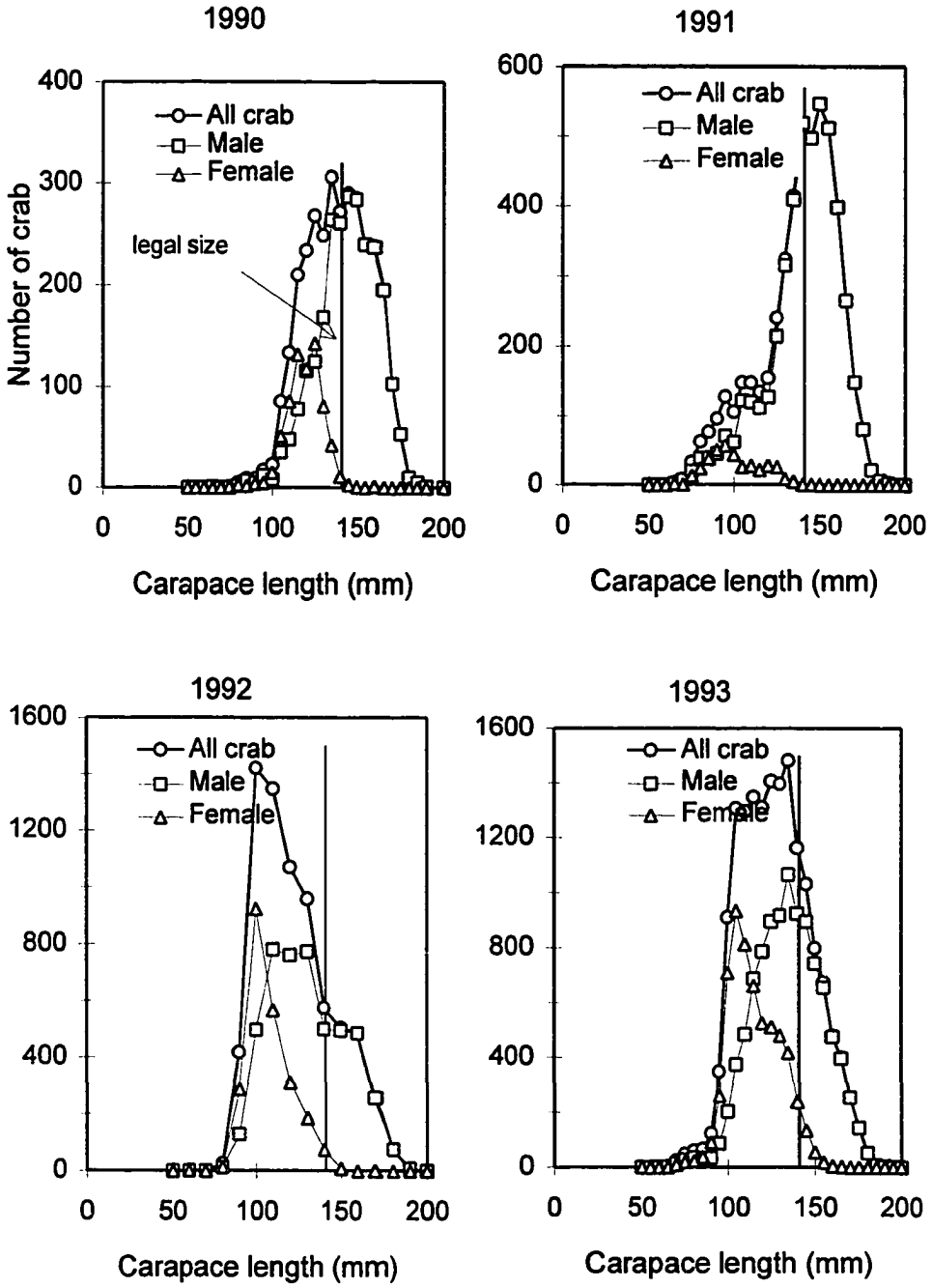

Figure 1.3. Carapace length distribution of red king crab in Bristol Bay fishery in four years.

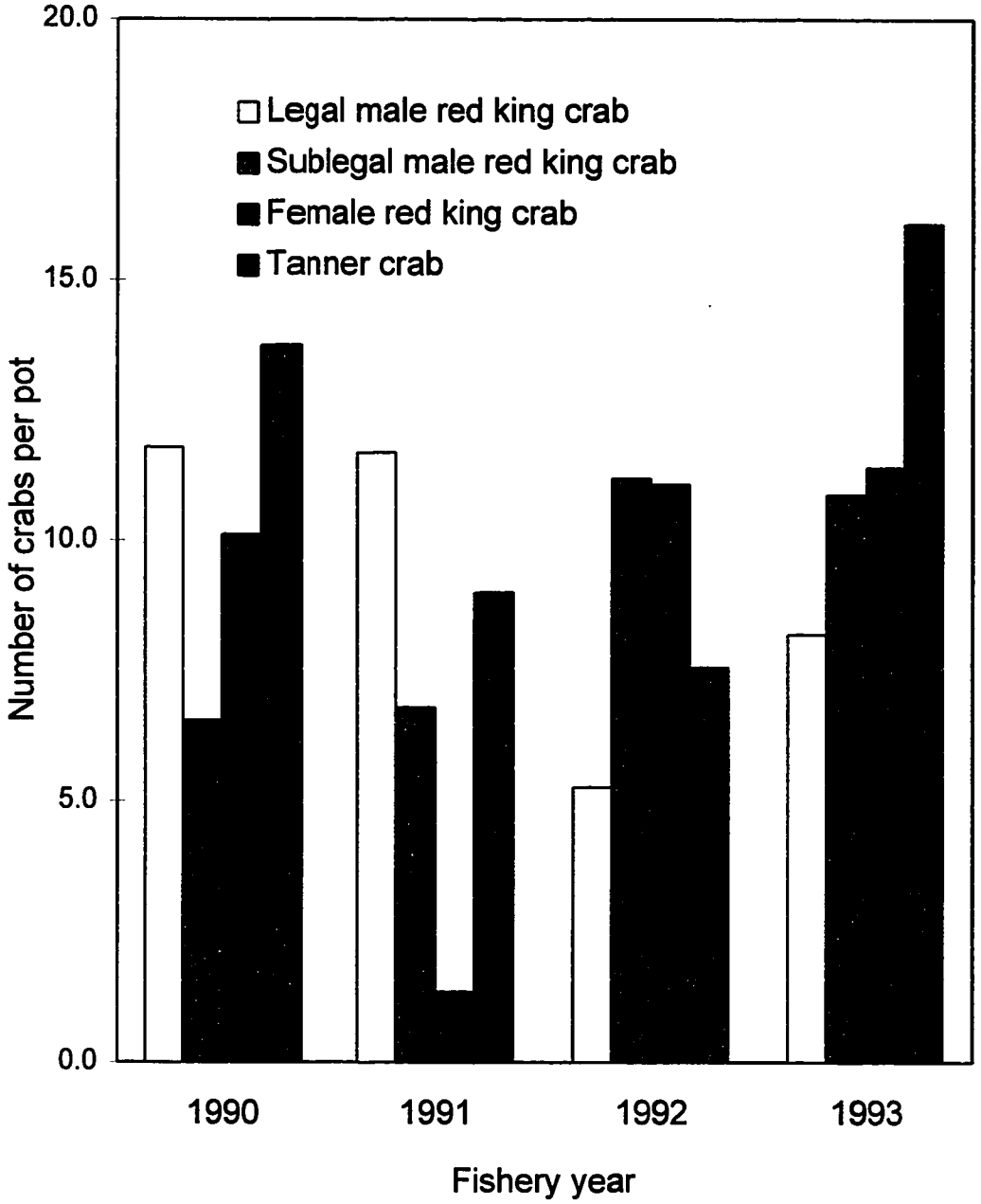

Figure 1.4. Average number per pot of legal male, sublegal male, and female red king crab, and Tanner crab in Bristol red king crab fishery.

18.60 SD for 4 yr) of the red king crabs would be discarded. If the Tanner crab, *Chionoecetes bairdi*, (another commercially important species) was also considered, an average of 75.3% (± 12.2 SD for 4 yr) of the catch had to be returned to the sea. The fishery also caught a small number of other economically important crab species such as snow crab (*Chionoecetes opilio*), Korean hair crab (*Erimacrus isenbeckii*), blue king crab (*Paralithodes platypus*), and golden king crab (*Lithodes aequispinus*). These crabs were also discarded.

The instantaneous injury rate and death rate were low in the red king crab fishery. I calculated that 0.2%±0.002 (mean ± SD, n = 3 yr) of the crab were freshly injured, and the instantaneous death rate was 0.02% ± 0.0002 (mean ± SD, n = 3 yr) in Bristol Bay's 1991, 1992, and 1993 fisheries.

Laboratory experiments

Handling damage increased with repeated handling (Figure 1.5), and spines were the most vulnerable. A significant difference in damage among the Treatments 1~4 occurred for all damage types combined ($\chi^2 = 50.6$, df = 3, $p < 0.001$) and for spine damage alone ($\chi^2 = 37.84$, df = 3, $p < 0.001$). A one-tailed Fisher's exact test was conducted to test the damage in Treatment 1~3 as compared to either Treatment 4 or Treatment 5. For rostrum damage, Treatment 1 and 2 were not significantly different from the control (1-tailed

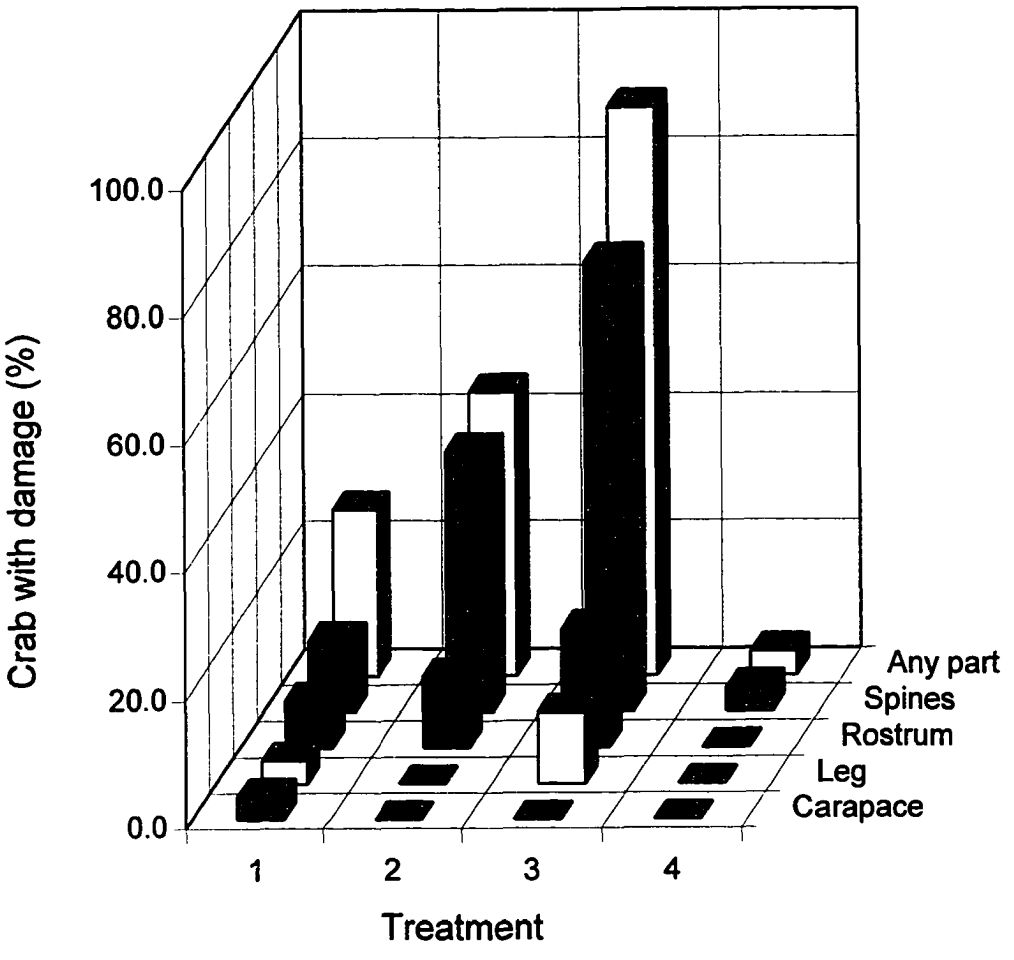

Figure 1.5. percent of crabs with damage after handling in the laboratory. Treatment code: 1 = handled once, 2 = handled twice, 3 = handled three times, 4 = modified handling.

Fisher's exact test, $p = 0.246$ and $p = 0.118$ respectively), while Treatment 3 was ($p = 0.026$). There was no significant difference among treatments for leg ($p > 0.10$) or carapace damage ($p = 0.50$). Eighty-nine percent of crabs handled three times were damaged vs. 26% of the crabs handled once. Only 4% of crabs in the modified handling treatment without deck impact were damaged.

During the righting experiment, 67% of crabs righted themselves within 2 s, and 89% within 3 s, with a maximum of 7.8 s. Data transformation was performed to achieve normality (Table 1.2). Righting time did not differ significantly among the treatments (ANOVA, $df = 515$, $p > 0.10$). However, the righting time was affected by both days after handling and crab groups (ANOVA, $N = 518$, $p < 0.001$). Further tests with Scheffe's method indicated that only males differed from both ovigerous females and juvenile females ($df = 515$, $p = 0.020$ for male vs. ovigerous female, and $p < 0.001$ for male vs. juvenile female), while the righting time between ovigerous females and juvenile females did not differ ($p = 0.056$). A linear regression with a dummy variable z was fitted to the data:

$$\text{Log}_{10}(\text{Righting time}) = 0.224 + 0.003 * \text{Day} - 0.093 * Z$$

where $Z = 1$ when females, and $Z = 0$ when male ($N = 518$, $r = 0.364$, $p < 0.001$, Figure 1.6). During the three months after handling, males required

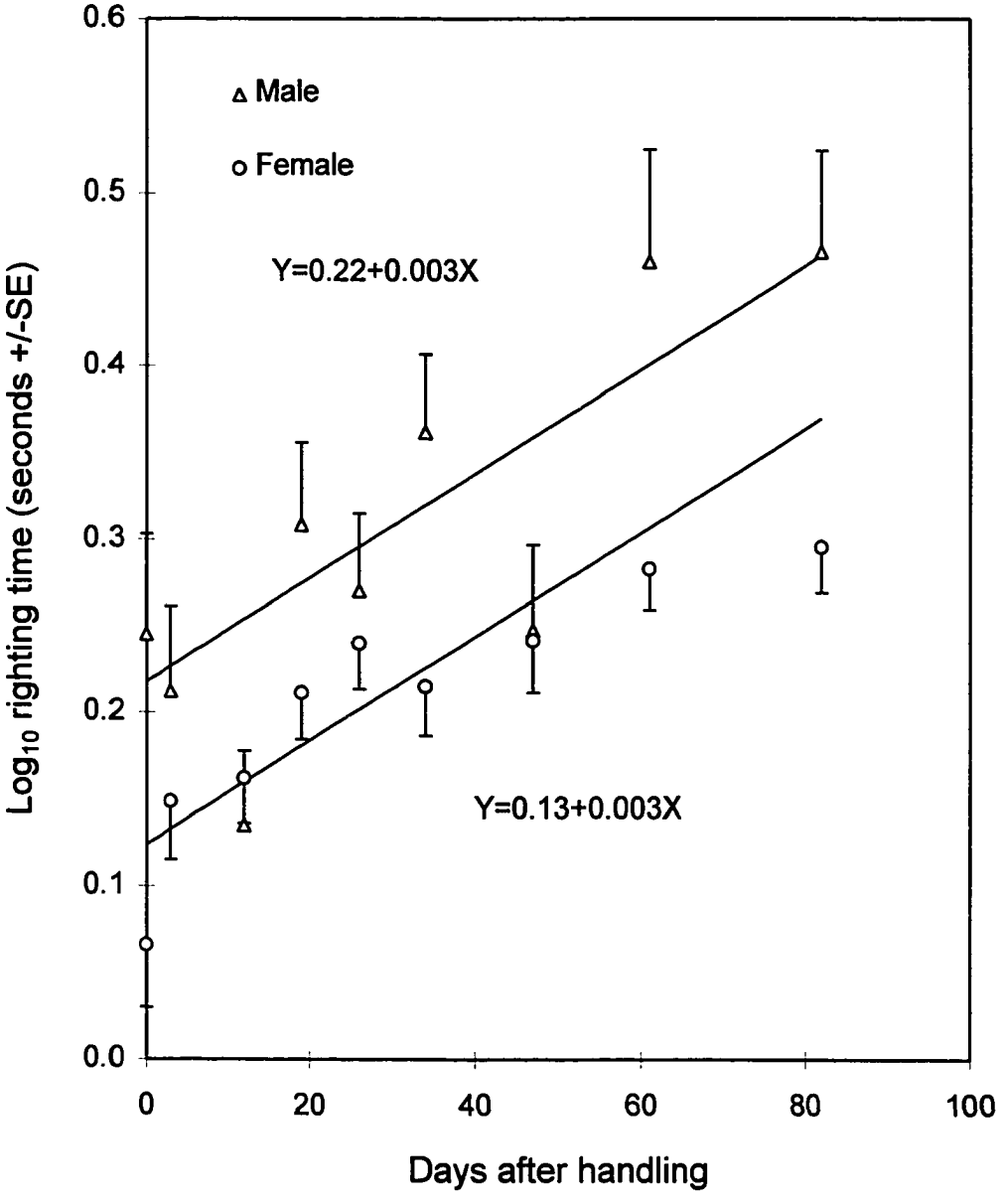

Figure 1.6. Log_{10} righting time of male and female king crabs versus time after handling.

Table 1.2. Mean righting time (seconds) for four crabs. Treatment code: 1 = handled once, 2 = handled twice, 3 = handled three times, 4 = modified handling, 5 = control. Crab groups: OF = ovigerous female, JF = juvenile female, SM = sublegal male.

		Days after handling								
Treat	Group	0	3	12	19	26	34	47	61	82
1	JF	1.34	1.27	1.61	2.77	1.75	1.47	1.71	1.73	2.34
1	OF	2.46	1.03	1.24	1.40	1.90	1.92	1.75	2.25	1.62
1	SM	1.58	1.21	1.47	1.95	1.55	3.32	1.42	1.89	1.90
2	JF	1.19	1.61	1.54	1.72	1.57	2.02	1.90	1.92	2.52
2	OF	2.24	1.86	1.53	1.25	1.80	1.61	1.45	2.53	1.62
2	SM	3.31	2.00	1.05	1.80	2.52	2.24	2.54	3.09	3.11
3	JF	1.10	1.82	1.64	1.71	2.13	1.95	2.76	2.31	1.80
3	OF	1.36	1.47	1.95	1.34	2.37	1.58	1.94	1.58	2.86
3	SM	2.31	2.05	1.22	1.84	2.21	2.48	1.29	3.04	4.48
4	JF	1.20	1.52	1.45	2.07	1.70	1.89	2.27	1.89	2.97
4	OF	1.33	1.26	2.21	3.16	1.22	2.24	1.23	1.08	3.97
4	SM	1.26	1.41	1.30	2.00	2.42	3.02	1.82	2.41	2.59
5	JF	1.02	1.60	1.39	1.72	1.92	1.51	1.41	1.69	1.70
5	OF	0.79	1.70	2.19	2.41	1.58	1.64	1.14	2.57	2.70
5	SM	2.93	1.55	1.34	1.97	2.36	2.82	1.49	4.10	4.67

0.3 to 0.6 s longer to turn over than females, and the average righting time increased from 1.7 to 3.0 s for males and from 1.4 to 2.4 s for females.

Feeding rates did not differ significantly among the treatments, after feeding rates were standardized to g of food consumed per kg of crab wet weight per 24 h (ANOVA, N = 751, df = 4, $p > 0.10$, Figure 1.7, Table 1.3). No significant difference in average feeding rate occurred among the treatments over time (Regression analysis, N = 751, $p = 0.494$, Figure 1.8). There was also no significant difference between the crab groups when feeding rates of each single day were analyzed by two-way ANOVA ($p > 0.05$). However, a significant difference existed between crab groups with a regression method (N = 751, df = 4, $p = 0.001$), and males had significantly lower feeding rate than females (Scheffe's test, df = 743, $p = 0.002$ between males and ovigerous females, and $p < 0.001$ between males and juvenile females), but no difference existed between ovigerous females and juvenile females. Average feeding rates were 51.3 g.kg crab^{-1}.d^{-1} (± 12.9 SD) for ovigerous females, 54.4 g.kg crab^{-1}.d^{-1} (± 17.4 SD) for juvenile females, and 46.4 g.kg crab^{-1}.d^{-1} (± 13.5 SD) for sublegal males.

Stepwise regression was performed to analyze the effects of treatment, crab group, and original weight on final weight using the following model:

W_2 = Constant + Treatment + Group + W_1 + Treatment * Group + Treatment * W1 + group * W1 + Treatment * Group * W1,

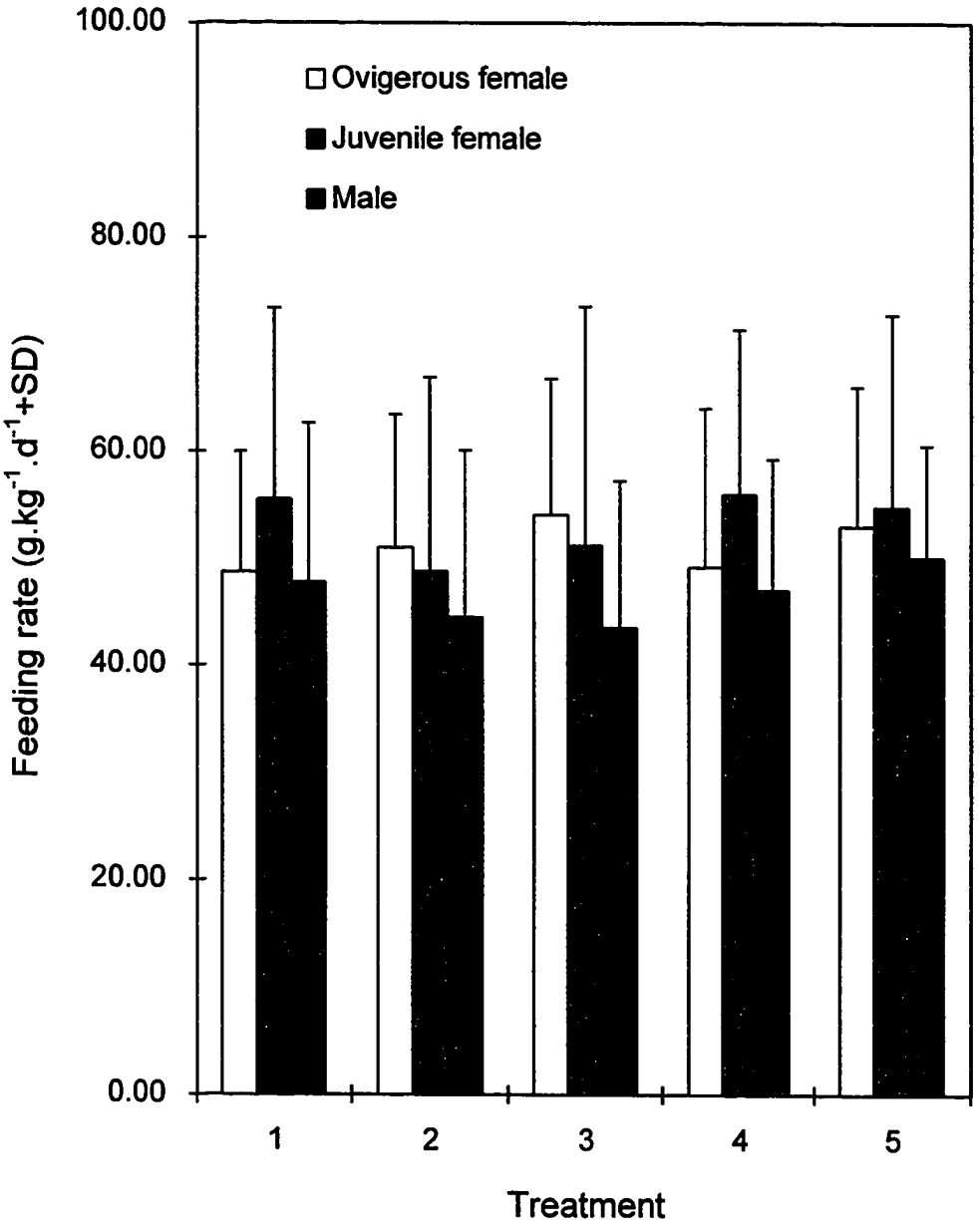

Figure 1.7. Average feeding rate of red king crab. Treatment codes: 1 = handled once, 2 = handled twice, 3 = handled three times, 4 = modified handling, 5 = control. No significant difference existed between treatments. Error bars are one standard deviation of the mean.

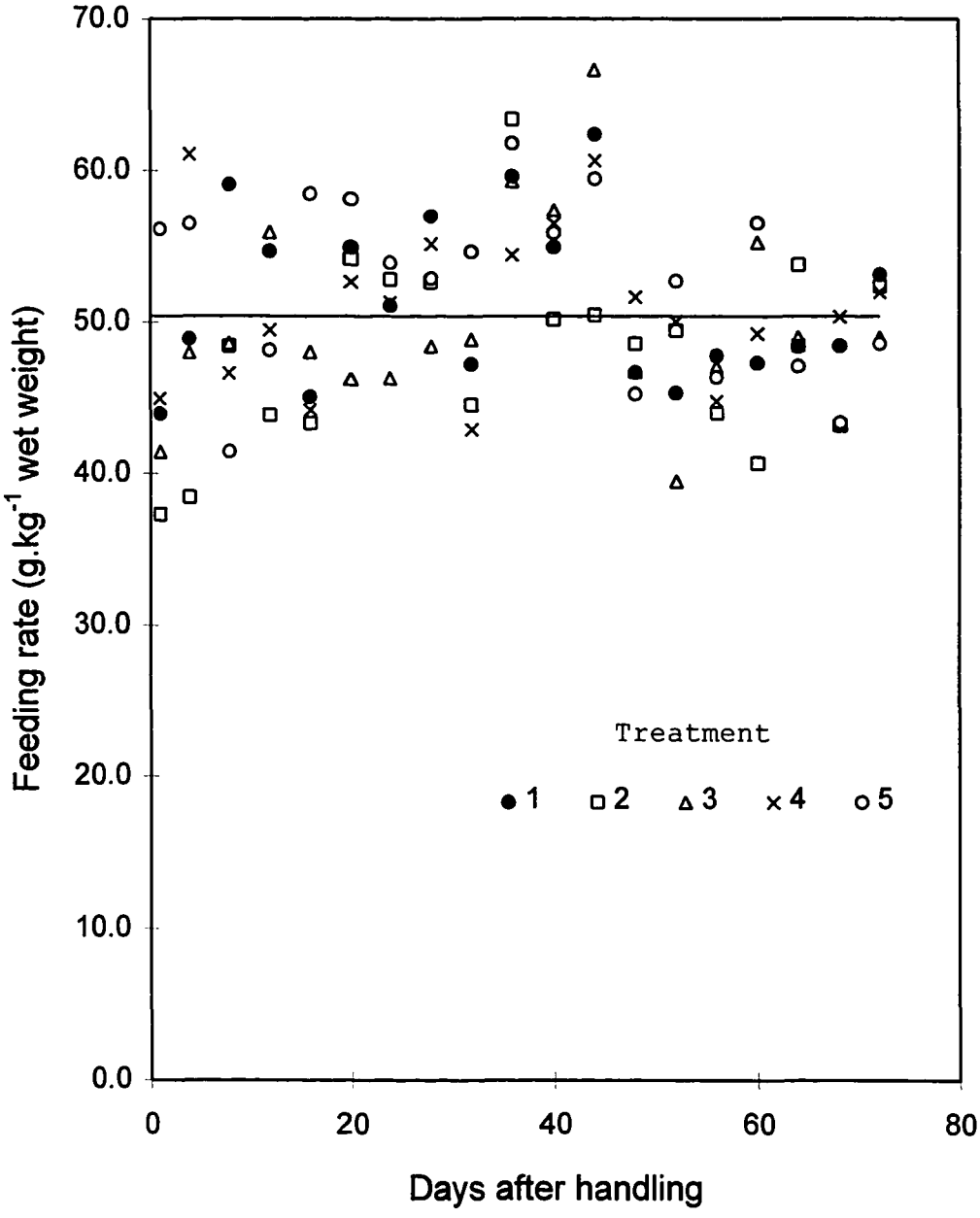

Figure 1.8. Feeding rate of red king crab over time after handling. Treatment code: 1 = handled once, 2 = handled twice, 3 = handled three times, 4 = modified handling, 5 = control. No significant difference existed between treatments and over time.

Table 1.3. Mean feeding rate ($g.kg^{-1}.d^{-1}$). Treatment code: 1 = handled once, 2 = handled twice, 3 = handled three times, 4 = modified handling, 5 = control. Crab groups: OF = ovigerous female, JF = juvenile female, SM = sublegal male.

Treat	Crabs	Mean	N	SD
1	OF	48.70	55	11.27
	JF	55.54	52	17.83
	SM	47.74	46	14.85
2	OF	51.01	57	12.40
	JF	48.77	38	18.13
	SM	44.48	50	15.65
3	OF	54.10	57	12.68
	JF	51.20	55	22.35
	SM	43.51	52	13.78
4	OF	49.19	48	14.82
	JF	56.03	57	15.37
	SM	47.04	46	12.30
5	OF	53.03	57	12.98
	JF	54.81	57	17.98
	SM	50.07	29	10.50

where W_1 = weight at the beginning, W_2 = weight at the end of the experiment. Only group and W_1 were significant factors ($N = 101$, $p < 0.001$ for both group and W_1). Neither significant difference between treatments, nor interaction between any factors was found in the model ($N = 101$, $p > 0.10$). Since most male king crabs molted during the 4 mo experiment, the growth data were further analyzed separately by sex.

The relationship between W_2 and W_1 was significantly different between ovigerous females and juvenile females (ANCOVA, $N = 74$, $p = 0.005$, Figure 1.9). Two linear regression equations were fitted, ovigerous females: $W_2 = 1.05W_1 + 26.8$ ($N = 34$, $R^2 = 0.9889$, $p < 0.001$); and, juvenile females: $W_2 = 1.05W_1 - 6.2$ ($N = 39$, $R^2 = 0.9965$, $p < 0.001$). Ovigerous females gained more weight than juvenile females did in 4 mo.

During 4 mo and after one molt, the wet weight of males increased from an average of 785.6 g (± 284.5 SD, N = 20) to 1093.4 g (± 347.7 SD, N = 20) in the manner of $W_2 = 1.21W_1 + 141.4$ ($N = 20$, $R^2 = 0.9833$, $p < 0.001$, Figure 1.9). For females, the growth rate, expressed by $(W_2 - W_1)/W_1$ in $g.kg^{-1}$, did not differ among treatments (ANOVA, $N = 72$, $df = 4$, $p > 0.10$), but differed significantly between ovigerous and juvenile (ANOVA, $N = 72$, $df = 1$, $p = 0.004$), and W_1 had interaction with these two groups of females (ANOVA, $N = 72$, $df = 1$, $p = 0.036$). Ovigerous females had a higher growth rate than juvenile females (Table 1.4, Figure 1.10). However, the growth rate

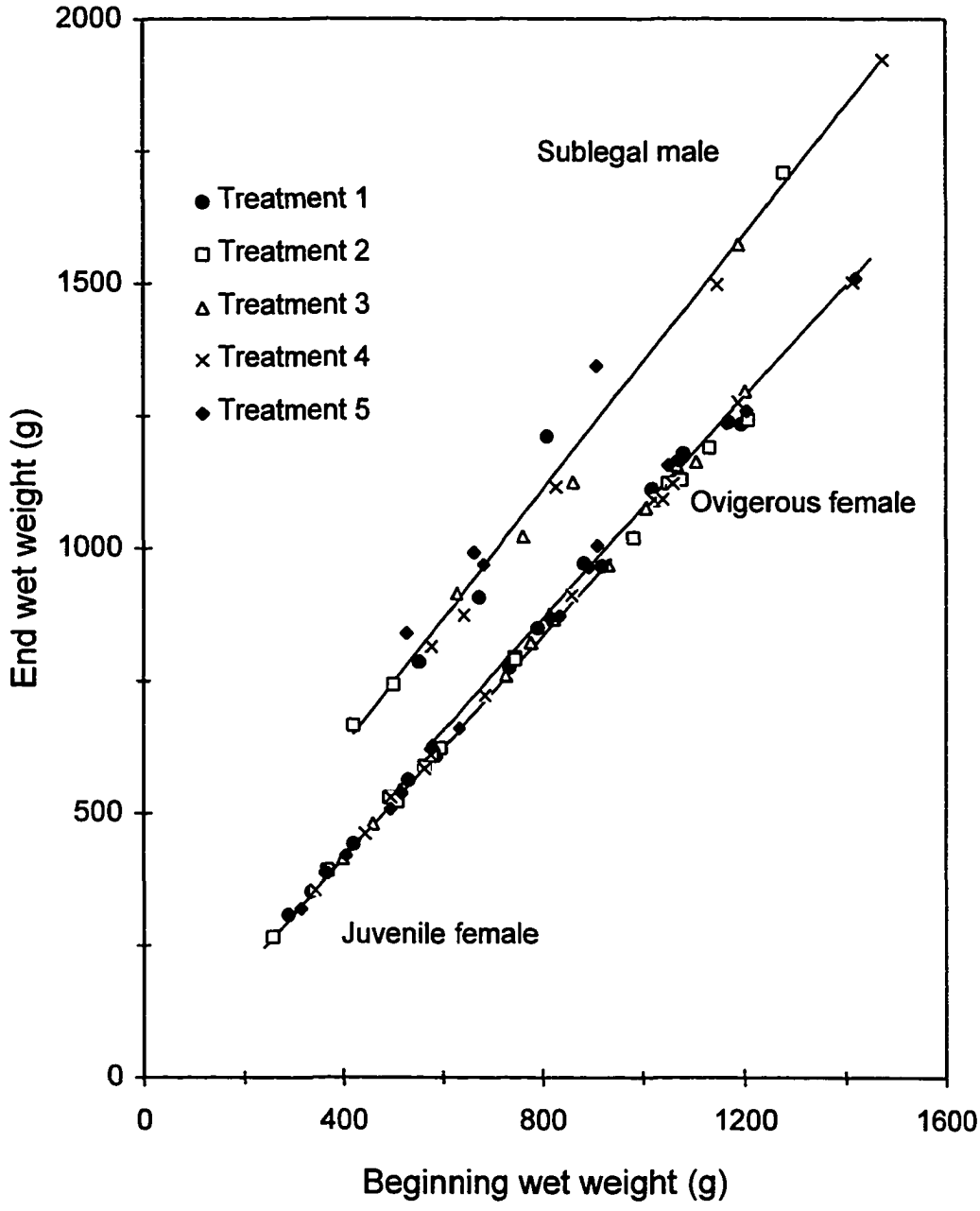

Figure 1.9. Relationship between wet weight at the beginning and at the end of the four month experiments for three groups of crabs. No Significant difference existed between treatments.

Molted males did not have different growth rates among treatments (ANOVA, N = 20, df = 4, p = 0.051). The largest difference in growth rates occurred between Treatment 4 (Modified handling) and Treatment 5 (Control) where crabs in Treatment 5 had a mean growth rate of 111.6 $g.kg^{-1}$ greater than crabs in Treatment 4, but the difference was not significant (Scheffe's test, df = 14, p = 0.115). Growth rate decreased with crab weight in the manner of: growth rate = 577.5 - 0.21 * W1 (N = 20, R^2 = 0.445, p = 0.001, Figure 1.10).

Carapace length after molt (CL_2) was only related to carapace length before molt (CL_1) (ANCOVA, N = 28, df = 1, p < 0.001) and was not affected by treatments (ANCOVA, N = 28, df = 4, p = 0.122). The relationship was: $CL_2 = 10.5 + 1.004 * CL_1$ (N = 28, R^2 = 0.959, p < 0.001, Figure 1.11). The mean growth data were summarized by crab groups (Table 1.4).

Table 1.4: Summaries of growth during the four month experiment.

	Growth rate ($g.kg^{-1}$ wet weight)			CL increase (mm)
	Ovigerous female(n=35)	Juvenile female(n=37)	Molted male (n=20)	Molted male (n=28)
Mean	66.6	50.4	412.3	10.9
SD	19.4	14.5	89.6	2.4

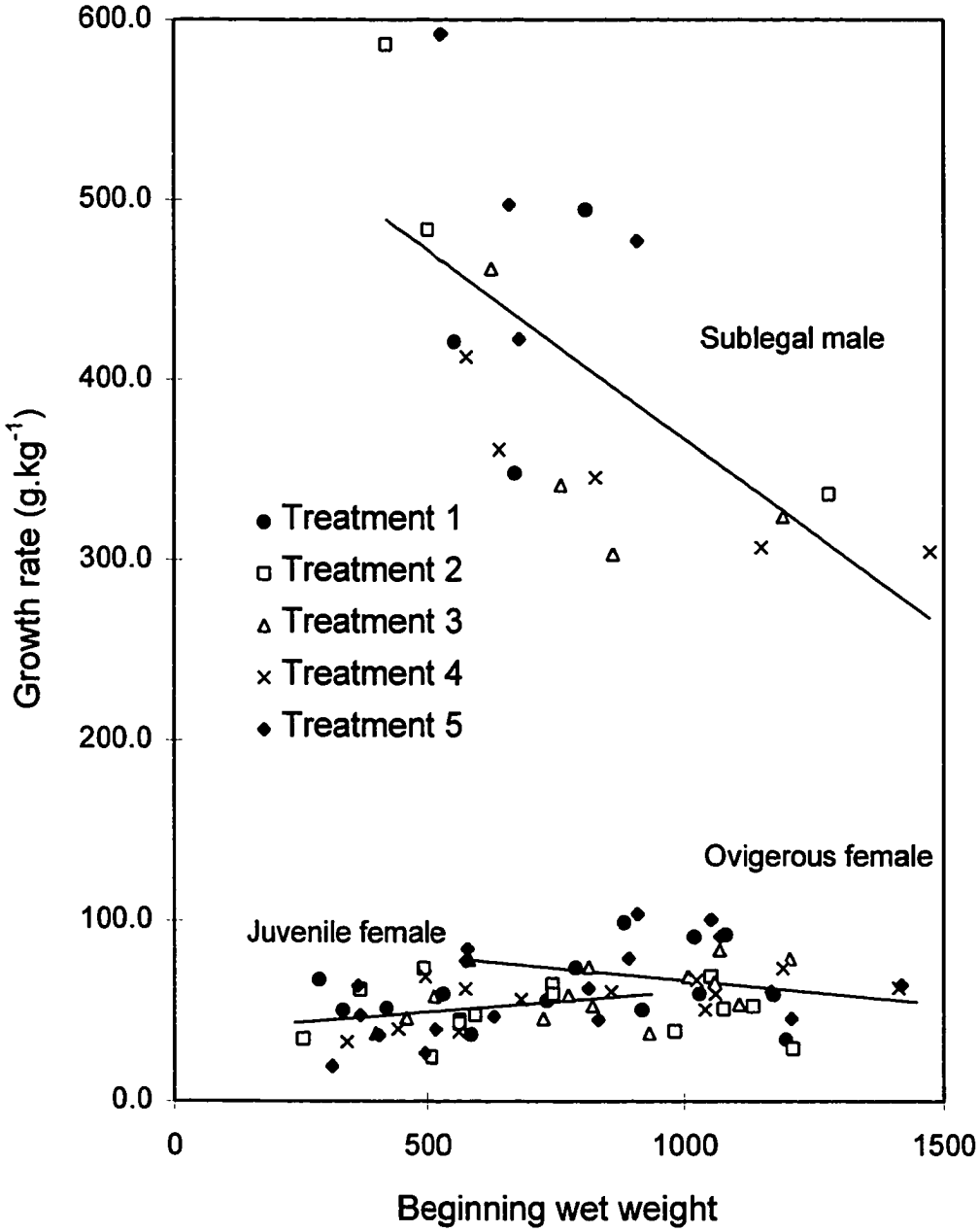

Figure 1.10. Growth rates (wet weight gain/wet weight at the beginning of the experiment) during the four months experiment. No significant difference existed between treatments.

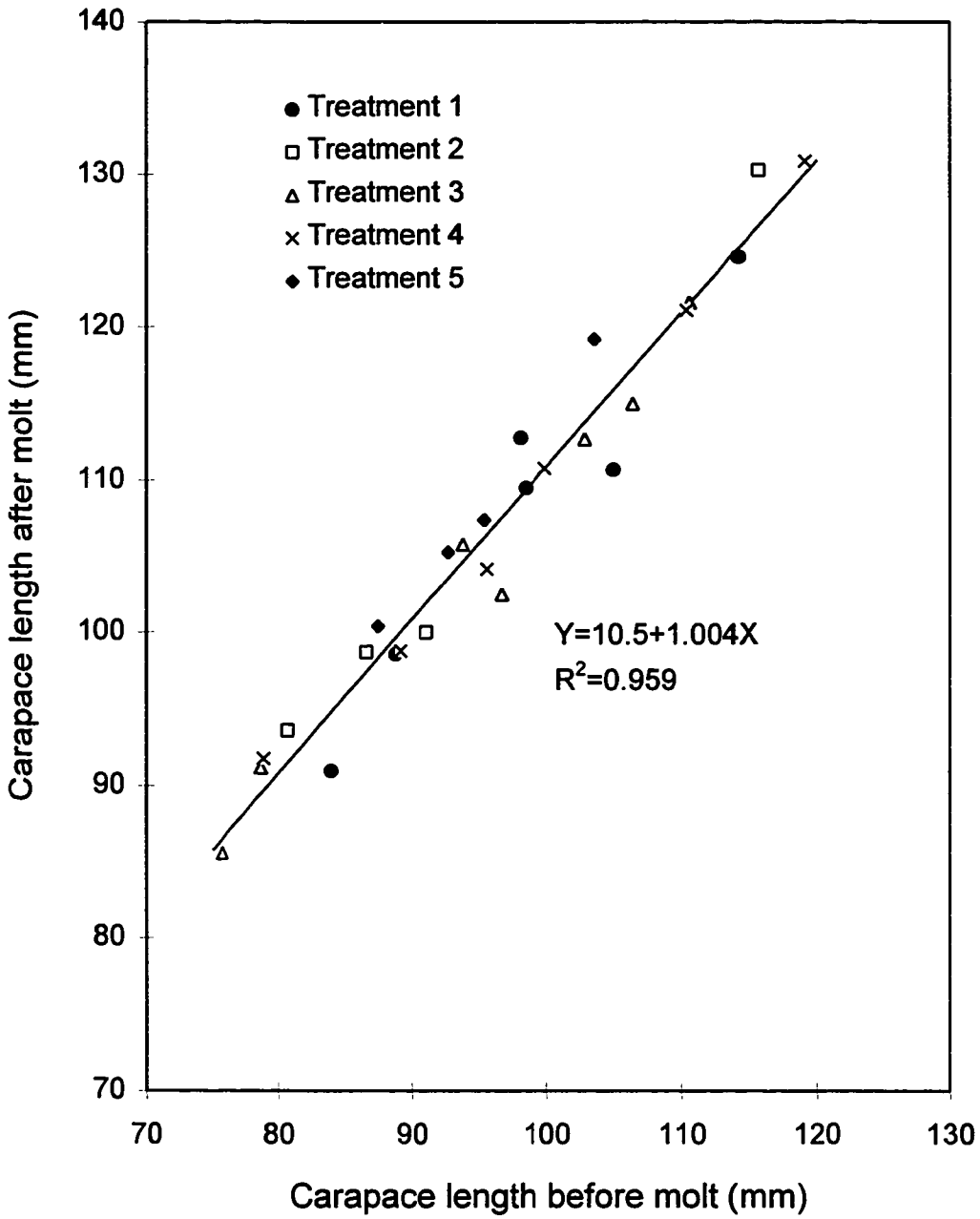

Figure 1.11. Carapace length increment of molted male red king crabs. The treatment codes are the same as in Figure 1.7. No significant difference existed between treatments.

was not related to carapace length for both juvenile females and ovigerous females.

Mortality was relatively low in all treatments (Table 1.5). A total of 18 of the 135 crabs used in the experiment died over the 4 mo study; 6 of the mortalities were due to experimental error (such as crabs crawling out of the tank, water flow accidentally stopping, and a crab injured by a falling tank divider). There were 2 mortalities (7.4%) of unknown causes in each treatment, except in Treatment 2 which had 4 (14.8%). In Treatment 1, one crab died within 24 hr of the handling treatment and was considered to be an acute mortality. All other unknown mortalities were considered delayed mortalities. There were no significant differences in mortality among the five treatments (G-test, df = 4, p = 0.695), even when the mortality in Treatment 2 (14.8%) was compared to mortalities in other treatments (one-tail Fisher's exact test, p = 0.335).

Table 1.5. Mortality during the four month experiment. The number in parentheses were mortalities due to experimental error. Treatment code: 1 = handled once, 2 = handled twice, 3 = handled three times, 4 = modified handling.

Treat. 1	Treat. 2	Treat. 3	Treat. 4	Control
2 (+2)	4 (+1)	2	2 (+2)	2 (+1)

Statistical power (1 - β) was calculated for experimental indexes (Cohen 1988). First, the effect size index (f) was obtained by

$$f = \sqrt{\frac{(k-1)F}{kn}},$$

where k is the number of treatments, n is the replicates per treatment, and F is the usual ratio of the treatment mean square (MS_t) to the error mean square (Ms_e) from ANOVA output (Search-Bernal 1994). Then a computer program (Rothstein et al. 1990) was used to obtain the statistical power. When α was set at 0.05, and the two-tailed power test was adopted, the (1 - β) value was 0.72 for feeding rate, 0.75 for male growth rate.

DISCUSSION

Although injury rate and immediate mortality are low in the red king crab fishery, the numbers of discards were high. In 1990, 3,120,326 legal males were landed in the Bristol Bay red king crab fishery, and in 1991, 2,630,446 were landed (Westward Region Shellfish Staff, 1992). By applying the average discard rate (64.6%), discards were 6.6 million crabs in 1990 and 4.8 million crab in 1991. The results from my laboratory study indicated that there were no significant differences in activity (measured in righting time), feeding rate, weight gain, carapace increase, and mortality among the five handling treatments. Although body damage significantly increased with

handling, the damage was limited to the spines and rostrum, and did not affect the crab's survival in the laboratory.

Male king crab had a longer righting time and a lower feeding rate than females. I explain this difference as a result of the molting activity of males, even though I excluded the data measured 10 days before and after the time of ecdysis. Between September 15 and January 15, 29 males molted, while only 3 juvenile females molted and no ovigerous females molted. The larger size of male crabs might also contribute to the longer righting time. However, the slight differences (< 1 s) in righting time between male and female crabs, although statistically significant, may have little biological significance.

The average carapace length increase (10.9 mm) after one molt for male crabs is comparable to other studies. In a tagging study, males with CL from 104 mm to 179 mm gained 8 mm to 28 mm in one year (Bright et al. 1960). In another tagging study, the average growth per molt was 12.5 mm for males with CL of 65~138 mm (Powell et al. 1983). In my study, growth rate decreased with crab size as reported for fish (Ricker 1975).

My results contrast with many other studies in crustacean fisheries. In these simulated handling experiments, after handling and aerial exposure, crabs and lobsters had increased injury, reduced vigor, decreased growth, and increased mortality (Brown and Caputi 1983, 1985; Davis et al. 1978; Kennelly et al. 1990; Simonson and Hochberg 1986).

Besides the probable difference in tolerance of stress between red king crab and the other species studied, the conservative handling techniques in my laboratory experiment might have contributed to this contrast. In other handling experiments, the animals were treated more traumatically. For example, in a mortality study of declawed stone crabs (*Menippe mercenaria*), 47% of the declawed crabs died from the trauma of double amputation and 28% from single amputation (Davis 1978). Declawing caused high mortality; however, it should be noted that the stone crab has large chelae that constitute 51% of the total weight of an intact crab. Amputating two chelae left a crab less than half its original weight. Also a significant amount of body fluid was lost due to declawing. In another declawing study of stone crabs (Simonson and Hochberg 1986), the animals were exposed to the air for 2~6 hr and then the chelae were amputated. Mortality increased to 100% for crabs that suffered aerial exposure for 6 h and then were declawed. However, if these crabs were wetted with seawater once every hour during the exposure before being declawed, the mortality decreased to 23%. The long aerial exposure plus declawing (which was more than 25% body weight for one claw) was fatal to the crabs.

Removing one cheliped from the blue crab (*Callinectes sapidus*) did not alter the molt increment, percent wet weight increase, or molting frequency. Multiple limb loss significantly reduced the molt increment and the

percentage weight increase in the first molt after amputation, but did not affect the duration of the intermolt. By the second molt following amputation, molt increments for crabs missing four limbs did not differ significantly from those of intact animals (Smith 1990).

Kennelly et al. (1990) found that 60~70% of spanner crabs (*Ranina ranina*) with one or more dactyls removed died within 50 days, while 100% of crabs with whole limbs removed died after 8 days. The high vulnerability to death is probably related to reluctance of spanner crabs to autotomize limbs.

In a laboratory experiment of the effects of aerial exposure on the rock lobster *Panulirus cygnus*, an expected time for 50% mortality within two weeks decreased from 233 to 99 min with increasing temperature, and a time of 387 min for lobsters exposed to air under shade (Brown and Caputi 1983). However, no mortality was evident when the exposure time was less than 40 min, even under direct sunlight at the highest temperature regime of the experiment (31~35 °C). In another study of rock lobsters exposed to air, all 8 lobsters exposed to air for 60 min at 34~35 °C died before their second molt after the exposure; however, no difference in mortality was observed for crabs exposed for 0, 15, and 30-min at 34~35 °C. There was also no difference in mortality for the rock lobsters exposed to air for 0, 15, 30, 60, and 120 min when the air temperature was lower (20~21 °C). The observed effect was that

increasing aerial exposure duration decreased growth increment (Brown and Caputi 1985).

Aerial exposure experiments on red king crab and Tanner crab demonstrated that exposure to cold air reduced vigor, feeding rates (Tanner crab), and growth (red king crab) (Carls and O'Clair 1990). Exposure also caused limb autotomy in Tanner crabs, and mortality in both species in severe situations. However, the exposures were severe, and in contrast, mortality measured 128 days after exposure for king crab did not increase significantly unless temperatures were below -4.6 °h (the unit is the product of temperature and duration of exposure) exposure, and for Tanner crab until -3 °h. Vigor did not significantly decrease until -4.6 °h for king crab and -2.2 °h for Tanner crab. Tanner crab did not feed significantly less until -2.7 °h. King crab emersed at temperatures greater than freezing had no trend in growth with exposure. Tanner crab weights did not correlate with exposure. Exposure of ovigerous crabs generally did not affect eggs or mortality of subsequently released zoeae unless the female died.

In an aerial exposure study of Dungeness crab (*Cancer magister*), after exposure for 5, 15, 30, and 60 minutes, hard-shell crabs did not have a significant difference in recovery rate among exposure periods. Although soft-shell crabs had a significantly lower recovery rate than hard-shell crabs,

tests for differences among exposure periods for softshell crabs could not be made due to the small sample size (Kruse et al. 1994).

More direct support for results like those found during my study came from two recent studies of the effects of handling and discarding on the mortality of Tanner crabs (MachIntosh et al. 1996). In the first study with three treatments, one group of crabs was dropped once into sea water from a height of 2.5 m, one group was dropped four times at two day intervals, and one group was not handled. In the second study with four treatments, three groups received physical injury to the merus/carpus joint, coxa, or carapace, respectively, while the fourth was an unhandled control. There was no significant differences in mortality between the control and any treatment group in either experiment after 60 days.

These results suggest that commercial crustacean species have the capacity to endure stresses of certain magnitudes without detrimental effect. My laboratory simulation was comparable to typical handling procedures in the commercial fishery. Deck impacts, aerial exposure, and water impact should have minimal effects on discarded female and sublegal red king crabs, IF these crabs are handled in the normal manner which I have described.

In contrast to the normally handled crab, some crabs experience abnormal handling. In most commercial crabbing situations, these crabs will remain aerially exposed for a long time before being returned to the sea. The

size of the sorting table comparing to the width of the pot door will affect the number of crab receiving abnormal handling. Also, the fishermen's skill and concern are important factors. It is assumed that crabs receiving abnormal handling will suffer more, and the impact will be more severe. Further study should estimate the size of this subpopulation and quantify the impact to these crabs. It is also essential to educate fishermen to take greater care with female and sublegal male crabs.

My results do not imply that handling has deleterious impacts on red king crabs. But, does discarding contribute to the decline of the red king crab? During pot retrieval, hundreds of sea birds are waiting for the discarded bycatch and used bait; whether birds cause damage to the crabs in unknown. More importantly, are there any predators that feed on these returned crabs when they descend from the water surface to the benthos? Predators have been reported to be particularly voracious on crabs (Kennelly et al. 1990) and lobsters (Brown and Caputi 1983) while these benthic species were sinking in the water column. Also, what effect does disorientation have on feeding and responses to benthic predators once the crabs have reached the bottom? Many of these potential indirect effects on crab survival warrant investigation.

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Chapter 2

Chemoreception and Feeding Response of Red King Crabs to Potential Bait Extracts

ABSTRACT

Laboratory experiments were conducted to study the chemosensation and feeding behavior of red king crab (*Paralithodes camtschaticus*). Five extracts of squid, herring, mussel, king crab muscle, and king crab ovary were used as test solutions. Change in antennular flicking rate was employed as an index of detecting chemicals. Chemosensory threshold varied between 10^{-4} to 10^{-6} $g.L^{-1}$ for the five extracts. Crabs were most sensitive to conspecific muscle, but least to mussel. Movement of maxillipeds, probing of chelipeds, movement of walking legs, and body elevation indicated the onset of feeding behavior. Among these indicators, movement of maxillipeds was most sensitive. Feeding thresholds ranged from 10^{-2} for ovary to 10^{-3} $g.L^{-1}$ for herring extract. Herring was the most effective natural bait for red king crabs, while little difference may exist between sexes and life stages for chemosensation and feeding sensitivity.

INTRODUCTION

The type, quality, and quantity of the bait are key factors affecting the catch in trap fisheries (Miller 1990). The following generalizations have been concluded from studies: fresh bait is more effective than stale bait; marine fish and invertebrates are more attractive than terrestrial animals as bait; cut bait is more efficient than live prey; the best artificial bait is no better as an attractant than a good natural bait; and single compounds are not as attractive as mixtures (Heatwole et al. 1988; Mackie and Grant 1980; McLeese 1970; Miller 1990; Zimmer-Faust and Case 1982, 1983). Also, artificial baits have been developed (Hunter et al. 1990; Mackie and Grant 1980; McLeese 1970). In the experiment with spanner crab *Ranina ranina*, Skinner and Hill (1987) found that females responded more rapidly than males to a food stimulus, and suggested that females might be more catchable in baited nets than were males. Male hermit crab (*Ragurus geninus*) was attracted by "female water" from a chamber containing females (Imafuku 1986). Despite the many studies on other decapods, however, there have been no bait efficiency studies on red king crabs, *Paralithodes camtschaticus*, one of the most important commercial species in Alaska.

Decapod foraging behavior depends on chemosensation (Rittschof 1992). Studies have been conducted for some decapod species to inspect their chemosensory behavior and feeding behavior, and to find their threshold to

different chemicals (McLeese 1970; Pearson and Olla 1977; Pearson et al. 1979; Rittschof and Buswell 1989; Zimmer-Faust and Case 1983), however, no chemosensory study on king crabs has been published.

The present work investigated the chemosensory behavior and feeding behavior of red king crabs, and compared the efficiency of potential baits. Since antennules functioned as distance chemoreceptors for decapods (Hazlett 1971), antennular flicking pattern was used as an indicator of chemoreception. Chemoreceptors on maxillipeds and leg tips were essential in feeding behavior (Derby and Atema 1982), the movements of maxillipeds, chelipeds, walking legs, and body were employed as indicators of feeding behavior.

MATERIALS AND METHODS

The experimental crabs

Red king crabs were captured by pots near Juneau, southeastern Alaska, and transported to the laboratory immediately. Crabs were kept in rectangular aquaria supplied with flowing sea water. Frozen salmon and squid were provided as food twice a week. The aquaria were covered with green fiber glass boards which provided a dim light condition in the tank. Crabs were deprived of food for at least 24 h before being transferred to the testing apparatus.

Crabs were divided into four categories: Juvenile females (JF), ovigerous females (OF), small males [SM, ≤ 110 mm in carapace length (CL)], and large males (LM, > 110 mm in CL). The mean carapace length (in mm) and standard deviation for these four categories were: 89.0 ± 7.4, 115.6 ± 4.8, 100.3 ± 6.4, and 120.5 ± 6.8. Only crabs without carapace or appendage damage and without any sign of molting were used.

Test apparatus

Four rectangular test aquaria were constructed with identical dimensions of 31*22*17 cm with a volume of 11.6 L each. The aquarium was opaque but covered with a transparent plexiglass board to permit observations (Figure 2.1). Filtered sea water passed through a PVC pipe then split into four Tygon tubes (1.2 cm diameter), each of which had a valve and a flow meter to enable monitoring and fine adjustments of water flow. The Tygon tubing carried the water into a glass funnel which connected to plexiglass tubing (3.8 cm diameter * 23 cm length). The tubing had 18 small holes (0.3 cm diameter) in its center at one side. When the tubing was placed in the tank, these holes were positioned between 6~13 cm from the tank bottom. The mouth parts, antennules, and antenna of a tested crab faced toward these holes. Sea water flowed through the plexiglass tubing and entered the aquaria through these holes. The water flow rate was adjusted to 37 $mL.s^{-1}$. After

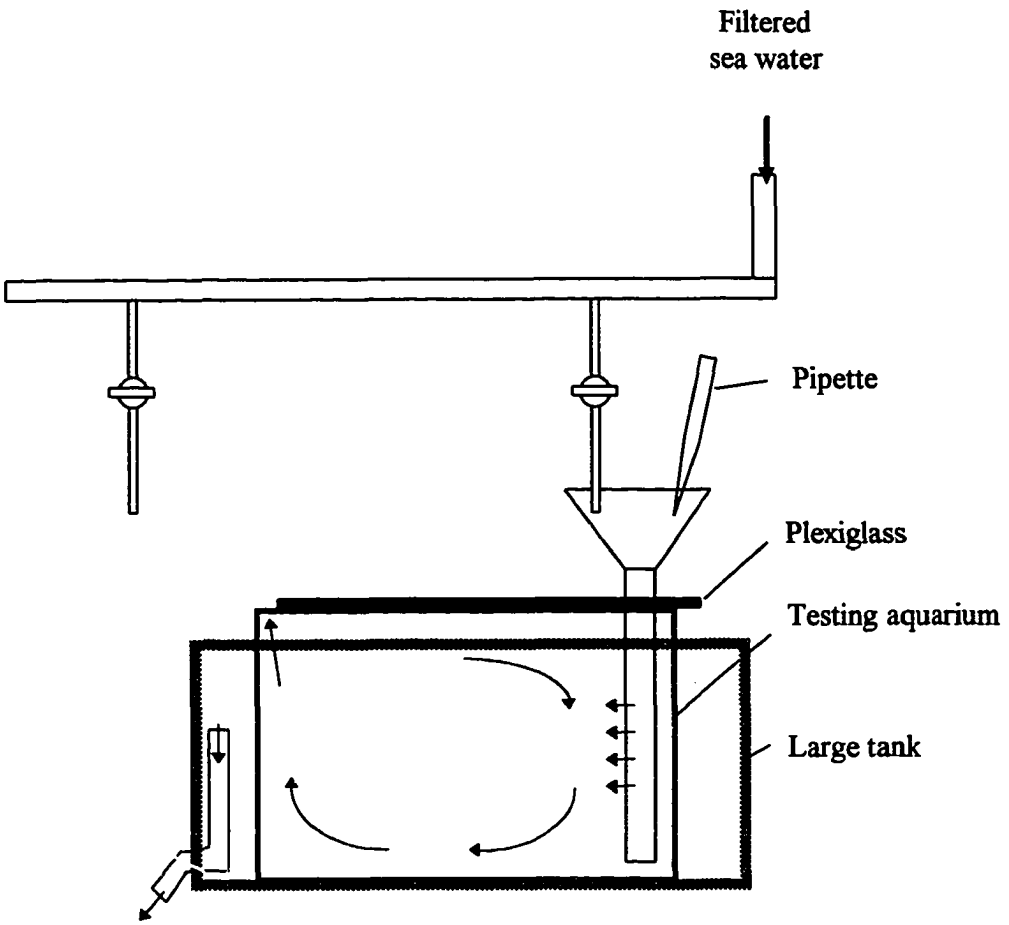

Figure 2.1. A schematic diagram of the experimental apparatus.

circulating in a testing aquarium, the water flowed out from the top rear of the aquarium. A large housing tank received and drained the water (Figure 2.1). Water temperature varied between 4.5~6.0 °C, and the salinity was 32‰ during the experiment from March to May, 1994.

The experimental solutions were injected into the glass funnel from a pipette and mixed with the sea water before entered the testing aquarium. For each trial, a 5 mL solution was delivered in 3 s into the inflow water.

To observe the water circulation and to estimate the dilution factor, a dye was introduced into the tank in the same manner as experimental solution, i.e., 5 mL of food dye was delivered in 3 s with a pipette into the glass funnel. During the dye study, the aquarium contained a crab to account for the water volume a crab would displace. Samples were collected in six locations within the aquarium at a depth of approximately 12 cm from the bottom (center of the inflow holes): right front, right rear, central front, central rear, left front, and left rear. Only the samples from the central front of the aquaria were used to examine the dilution, because this was where a crab "head" would be located during testing. Water was sampled at 5 s intervals and the samples were tested with a Beckman DU-64 Spectrophotometer with filtered sea water as a blank. All four aquaria were measured three times. The peak concentration at the central front of the aquaria was attained 5 s after the dye was added. The dilution factor was

$1.4*10^{-3}$ ($\pm$ $0.46*10^{-3}$ SD), and this factor was used for adjustment of test solutions.

Test solutions

Mollusca, crustacean, and fish are important foods for red king crab in nature (Jewett and Feder 1982). In this study, Pacific herring (*Clupea harengus*), opal squid (*Loligo opalescens*), and bay mussel (*Mytilus trossulus*) were selected as potential baits because of red king crab food preference in natural habits and their availability for commercial purposes. In addition, extracts from female red king crab muscle and ovary were tested to examine for avoidance response to conspecific chemicals or attraction to male crabs. Five extract types were used in the experiment.

Fifteen grams of soft tissue from each of the five bait types were collected, ground in a glass mortar for 10 min, mixed with sea water filtered through a 0.4 μm membrane, blended with a magnetic stirrer for 15 min, and centrifuged at 12,000 g for 15 min. These preparations were performed under low temperature (4 °C). The solid remains were weighed and oven dried at 65 °C for 64 h. The dry weights were converted to wet weights according to previously established standard linear equations that described the relationship between wet and dry weights for the five bait types. These linear equations were expressed as Wet weight = a * Dry weight. The constant a

varied from 3.61 for herring to 4.98 for king crab muscle. The amount of substance in the liquid phase after centrifugation was obtained by subtracting the remaining wet weight from 15 g for each specimen. Each supernatant was diluted with filtered sea water to make an initial extract solution at a concentration of 5 $g.L^{-1}$. This solution was decanted, divided into small aliquots, and stored at -70 °C. Before each trial, an aliquot was thawed and diluted with filtered sea water to make a stimulant at a series of concentrations from 10^{-15} to 10^{1} $g.L^{-1}$. The test solutions were kept in a water bath at the ambient sea-water temperature and shaken immediately before use. Sea water filtered through a 0.4 μm membrane was used as control.

Response indexes and threshold determinations

In preliminary trials feeding behavior was observed to include an increase in antennular and buccal appendage flicking, cheliped grabbing, leg movement, body elevation, and active searching. A significant increase in antennular flicking rate (increased flicking rate, IFR) was used as an index of detection of the testing solution. With no stimulus, red king crabs spontaneously flicked their antennules, and the flicking rate ranged from 6 to 29 per 30 s (N = 96) in laboratory tanks. No difference was detected among different crab groups (ANOVA, $p = 0.135$, $df = 3$, $N = 112$, Table 2.1). The change of flicking rate between the first 30 s and the following 30 s ranged

from 0 to ±9 with a mean of -0.07 (± 3.46 SD, N = 96). The 95% tolerance interval was: mean ± 1.98*SD = 6.7. A crab was considered to have detected a test solution if either side antennular IFR ≥ 7 in 30 s. By this determination, when a crab demonstrated a IFR ≥ 7 in 30 s, the probability of change in spontaneous flicking rather than detection of solution was 5%. Chemosensory threshold was defined as the solution concentration at which 50% of the crabs responded (IFR ≥ 7 in 30 s). This concentration was also called the median effective dose--ED_{50}.

Table 2.1. Increase in spontaneous antennular flicking rate (IFR) between the first and second 30 s. OF = ovigerous female, JF = juvenile female, LM = large male, SM = small male.

	OF	JF	LM	SM
No. crabs	32	26	24	30
Mean	0.28	-0.2	0.42	-0.5
SD	2.54	4.11	3.83	3.51

Test solutions were introduced only when the crab was resting. The appearance of waving maxillipeds, probing and grasping of chelipeds, leg movement, and body elevation were considered as indexes of the onset of feeding behavior. These responses corresponded to the behavior when food

was provided to the crab. The feeding threshold was defined as the solution concentration at which 50% of the crabs displayed any of the above behaviors.

Test procedures

Preliminary observations indicated that the feeding behavior of red king crabs was not disturbed by the presence of an observer. No detectable change was observed when crabs were fed with the tank cover open or closed. Foraging and feeding behavior could hardly be interrupted even when the crab was pulled away with tongs. Therefore, the responses to the test solutions were observed directly through the transparent plexiglass on the top of the aquaria. A single crab was transferred from the holding tank to an experimental aquarium 30 min prior to testing. Observations were made 1 min before stimulant introduction. Then 5 mL of filtered sea water or test solution was added into the inflow water in 3 s (3.2 ± 0.8 SD, $n = 8$), and antennular flicking counting began 10 s (9.7 ± 1.3 SD, $n = 10$) after the introduction. The counting was made separately for each side of antennule, and continued for 30 s for each antennule. All other positive feeding responses in this period were also recorded.

To avoid crab adaptation to chemicals, the test started with the controls (sea water), then solutions were introduced from the lowest concentration (10^{-15} g.L^{-1}) to the highest concentration (10^{1} g.L^{-1}). Twenty min were

allowed to eliminate the test solution in the water before the next solution gradient was offered. A new extract type was introduced no earlier than 3 h after the previous type was terminated. Each crab received all five types of extracts, but the same individual was never tested twice with identical solutions.

The experiment involved four crab groups, five extract solutions, and four test aquaria. To avoid the effects of aquaria and the test order of solutions, orthogonal experimental tables were used to arrange each trial order. A total of 40 crabs, 10 each of juvenile females, ovigerous females, small males, and large males, were tested.

RESULTS

Behavioral responses to test solutions

When resting in the experimental aquaria, red king crabs usually did not move their legs and chelipeds. The two antennules regularly flicked, and frequently shifted their orientation. Both antennules could flick synchronously or individually, and they commonly oriented toward the same direction. The flicking intensity changed in frequency rather than in magnitude. Antennae frequently moved rapidly in all directions. The beating of maxilla scales and exopodites of the second and the third maxillipeds could

be seen infrequently. Occasionally, grooming of antennules occurred, where the third maxilliped stretched upward to wipe the lowering antennules.

When low concentration solutions were introduced into the aquaria, an increase in the antennular flicking rate was the first response indicating detection of chemicals. This increase might occur in both left and right antennules, or only on one side. Also, maxillipedal exopodites and maxilla scales might increase beating, depending on the concentration of the solutions. While the behavioral change in antennae lacked a clear trend, antennular grooming rate appeared to decrease when a crab was sensing the odor. For convenience, the behaviors above were considered as chemosensation.

At high concentrations of stimulants, crabs displayed food searching and feeding related behavior, in addition to heightened chemosensory behavior mentioned above. Legs probed, chelipeds extended and grasped, and the body of the crab might be elevated if the legs moved enough. The second maxillipeds extended and contracted as if bringing food to the mouth. The third maxillipeds moved up and down, and their dactyls might touch the mouth. These behaviors were similar to foraging and feeding when food was presented to the crabs, and were defined as feeding behavior to distinguish from the chemosensory behaviors.

Relationship between antennular flicking rate at solution concentrations

The antennular flicking rate for a resting red king crab in the testing aquarium ranged from 13 to 53 flicks.min^{-1} (N = 56 individuals). The increase of flicking rate (IFR, the flicking rate of the previous minute subtracted from the flicking rate of the second minute) ranged from -11 to 12 min^{-1} with a mean of -0.55 flicks.min^{-1} (± 5.1 SD, N = 56). This spontaneous IFR increased when the control solution (filtered sea water) was introduced into the aquarium (ANOVA, $p = 0.015$, N = 112, df = 1). A mean of 2.2 IFR (± 6.6 SD, N = 56) was recorded for sea water test.

For most extract types except king crab muscle extract, the relationship between the IFR and the solution concentration could be viewed in two distinct phases: concentration below $1.4*10^{-8}$, and above $1.4*10^{-8}$ g.L^{-1} (Figure 2.2). The mean IFR fluctuated between 2 and 4 min^{-1} at concentrations from $1.4*10^{-18}$ to $1.4*10^{-8}$ g.L^{-1}. At these low concentrations, no significant difference was detected between extract types and sea water (ANOVA, $p = 0.228$, df = 2, N = 535), and among extract types (i.e., squid, herring, mussel, and crab ovary; ANCOVA, $p = 0.622$, df = 3, N = 673). Also, solution concentration did not significantly affect the flicking rate within this range ($p = 0.068$). However, the IFR at concentrations below $1.4*10^{-8}$ g.L^{-1} was also significantly higher than the spontaneous IFR (Scheffe's test, $p < 0.0001$).

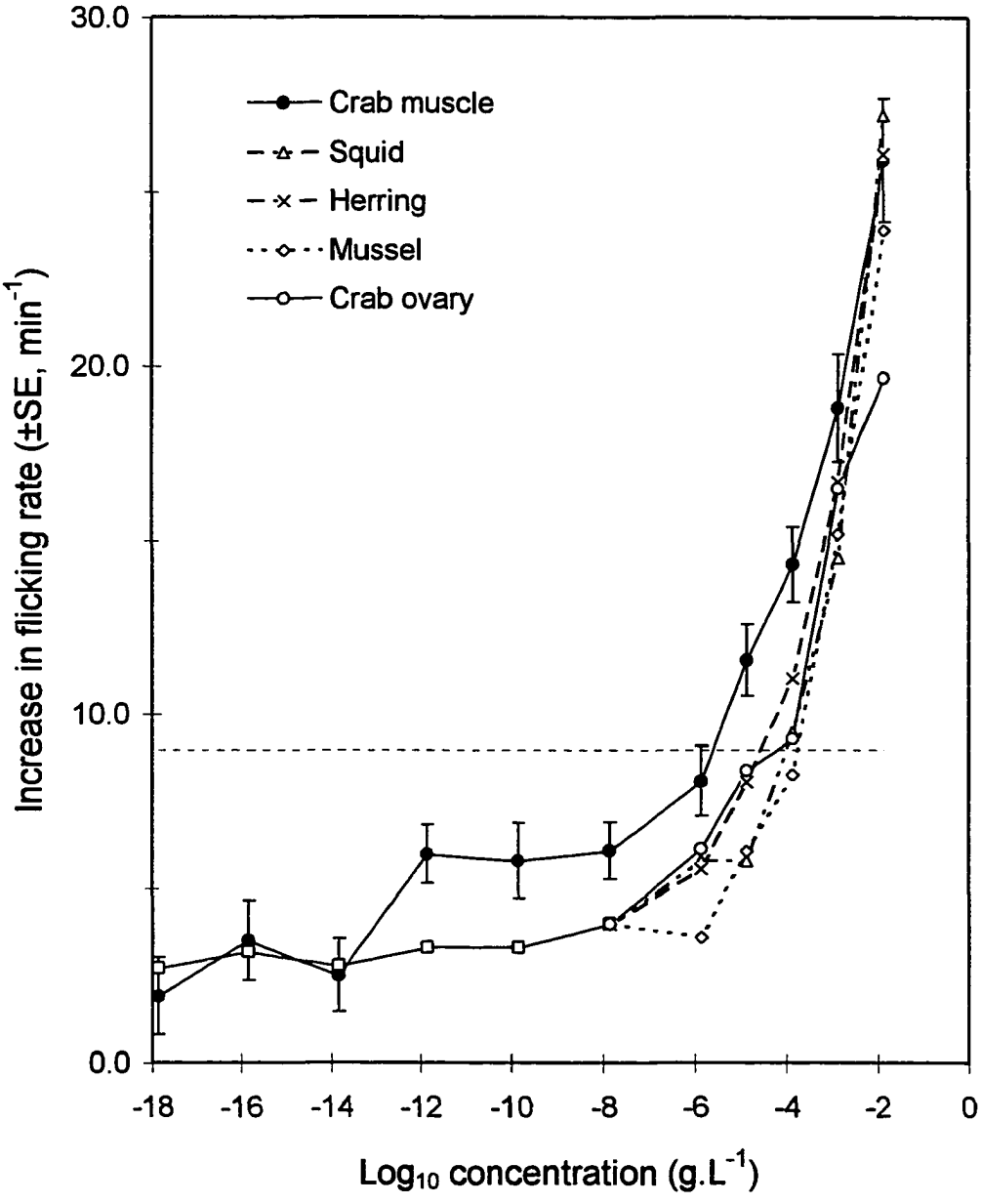

Figure 2.2. Increase in antennular flicking rate (IFR) and $\log_{10}$ concentration of five extracts. The dashed line indicates the IFR = 9 min^{-1} which is the mean + 95% tolerance interval of spontaneous flicking rate.

Crabs appeared to be more sensitive to the extract made from king crab muscle. The IFR for crab extract was similar to that for sea water and other extracts when the concentration was equal or below $1.4*10^{-14}$ $g.L^{-1}$ (Scheffe's test, $p = 0.123$, $N = 477$). Nevertheless, the IFR was significantly higher than other extracts and sea water when the concentration was between $1.4*10^{-12}$ and $1.4*10^{-8}$ $g.L^{-1}$ (Scheffe's test, $p = 0.001$, $N = 535$, Figure 2.2).

At solution concentrations above $1.4*10^{-8}$ $g.L^{-1}$, IFR increased rapidly with concentration. Both crab groups and extract types significantly affected the IFR ($p = 0.037$ for crab group and $p = 0.013$ for extract types, ANCOVA after exponential data transformation, $N = 761$, $df = 3$). Further analysis showed that, for extract types, crab muscle extract was more effective than other extracts ($p < 0.0001$), and herring was more effective than mussel ($p = 0.023$, Bonferroni adjustment). The difference between crab groups only existed in mussel extract, where juvenile females displayed a higher IFR than OF and SM ($p = 0.046$).

Chemoreception thresholds

A crab was considered to have detected the solution if the antennular flicking rate of either the left or right side increased 7 or more in 30 s. The responding rate, the percentage of crabs that detected the solution, was then calculated. Loglinear analysis was applied to examine the effects of extract

type, crab groups, and solution concentration on the responding rate. The original model involved all of the second-order interactions among the five extract types, four crab groups, and six solution concentrations ($1.4*10^{-8}$ to $1.4*10^{-2}$ $g.L^{-1}$). The final model obtained by the backward elimination method contained only the extract type and concentration (if concentration was removed, $p < 0.0001$, $df = 5$; if extract type was removed, $p = 0.0007$, $df = 4$). This result indicated that crab groups did not significantly affect the responding rate. So responding rates were combined for all four crab groups for further analysis.

A logistic model was used to simulate the relationship between responding rate and solution concentration for the five extract types. The responding rate to sea water was 16%. The model was expressed as

$$R = \frac{1}{1+e^{-(a+bC)}} + 0.16,$$

where R is responding rate (%), C is solution concentration, and a and b are parameters. The chemoreception threshold concentration at which 50% of the crabs detected the solution was then calculated (Table 2.2, Figure 2.3).

Crabs were most sensitive to the extract from king crab muscle. The estimated threshold of -5.83 logarithmic unit ($1.4*10^{-6}$ $g.L^{-1}$) was greater than that for all other bait extracts. Among the three potential baits (squid, herring, and mussel), herring was the most effective stimulant, while mussel

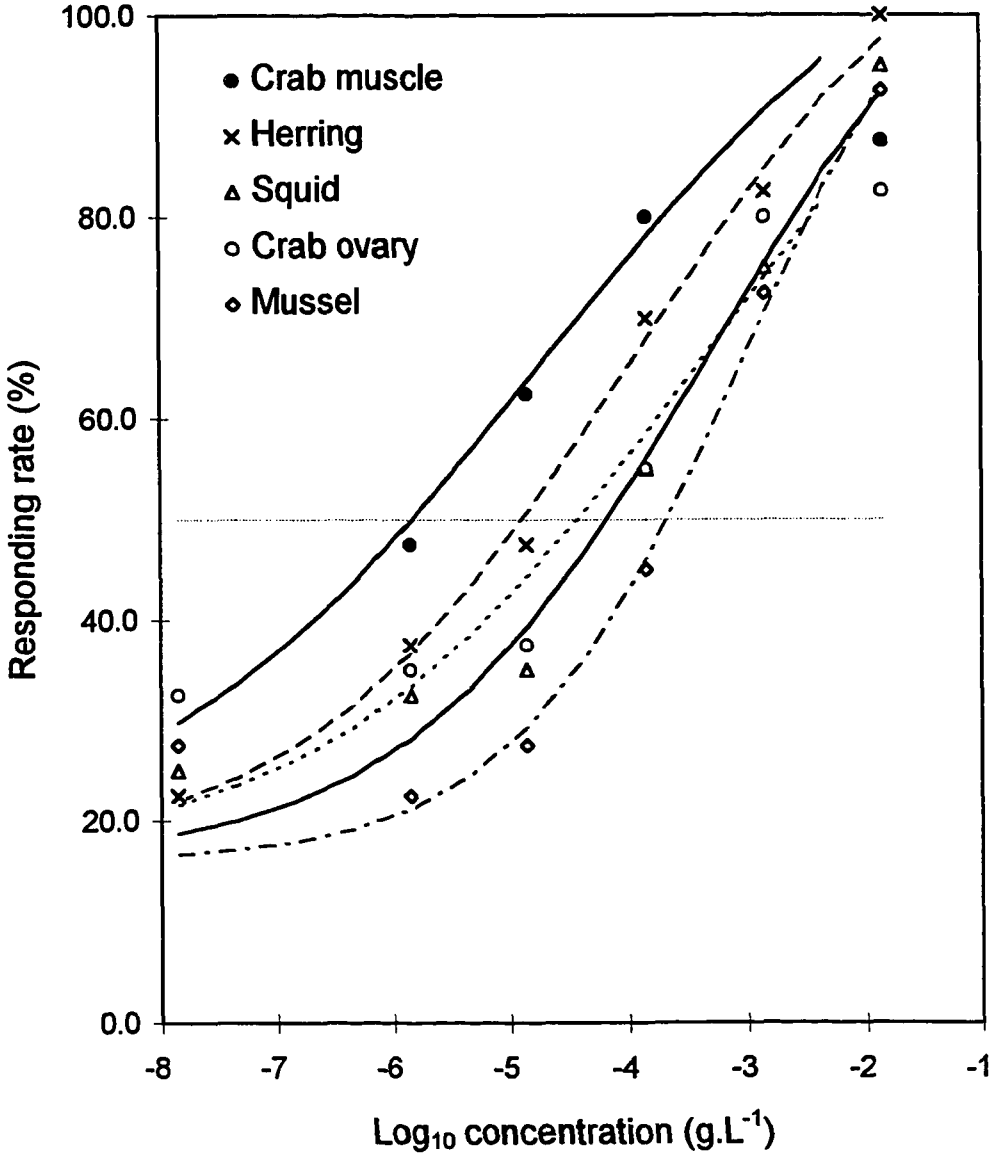

Figure 2.3. The relationship between the percentage of crabs detecting the five extracts and the solution concentration. The dash line indicates a 50% responding rate.

was the least. An interesting phenomenon was revealed when crabs were tested with extracts of crab muscle and ovary, where responding rates were suppressed at concentration greater than $1.4*10^{-3}$ $g.L^{-1}$ (Figure 2.3).

Table 2.2. Logistic model for responding rate and the estimate of chemoreception threshold for detecting five type of extracts. The model is expressed as $R = \frac{1}{1+e^{-(a+bC)}} + 0.16$. The threshold is $\log_{10}$ concentration at which 50% of the crabs detected the testing solutions.

	a	*b*	R^2	Threshold
Squid	2.63	0.79	0.978	-4.17
Herring	2.81	0.71	0.992	-4.89
Mussel	3.12	1.03	0.969	-3.67
Crab muscle	2.73	0.58	0.985	-5.83
Crab Ovary	2.13	0.63	0.866	-4.42

Indexes for feeding behavior and feeding thresholds

When exposed to a high solution concentration or fed, crabs displayed a variety of behaviors associated with feeding. Movement of the second and third maxillipeds, probing and grasping of chelae, moving and walking movement of legs, and body elevation were readily observed, so these four activities were recorded and used as feeding indicators. Since the four

feeding activities only occurred at high solution concentrations, e.g., from $1.4*10^{-4}$ to $1.4*10^{-2}$, only these three concentrations were used for further analysis.

A loglinear model was used to examine the effects of extract type, feeding index, crab group, and solution concentration on responding rate. All four factors were found to significantly interact with response ($p < 0.0001$ if any one of these factors was removed from the model).

To inspect the sensitivity of the four feeding indexes, the logit model was used (Norusis 1993):

$$\ln\left(\frac{R}{1-R}\right) = a + b \times C,$$

where R is the responding rate, C is the concentration, and a and b are parameters. Data were combined by crab groups and extract types. The four indexes had a parallel slope b (parallelism Chi-square test, $p = 0.266$, $df = 7$), and it was estimated to be 1.52. The intercept a was 4.17, 3.30, 2.98, and 2.14 for movement of maxillipeds, probing by chelae, leg movement, and body elevation, respectively (Goodness-of-fit chi-square test, $p = 0.402$, $df = 7$, Figure 2.4). These indexes significantly differed from each other, except probing by chelae and leg movement (Relative median potency comparison, Norusis, 1993). The threshold concentration at which 50% of the crabs exhibited feeding behavior was estimated from these equations. Obviously,

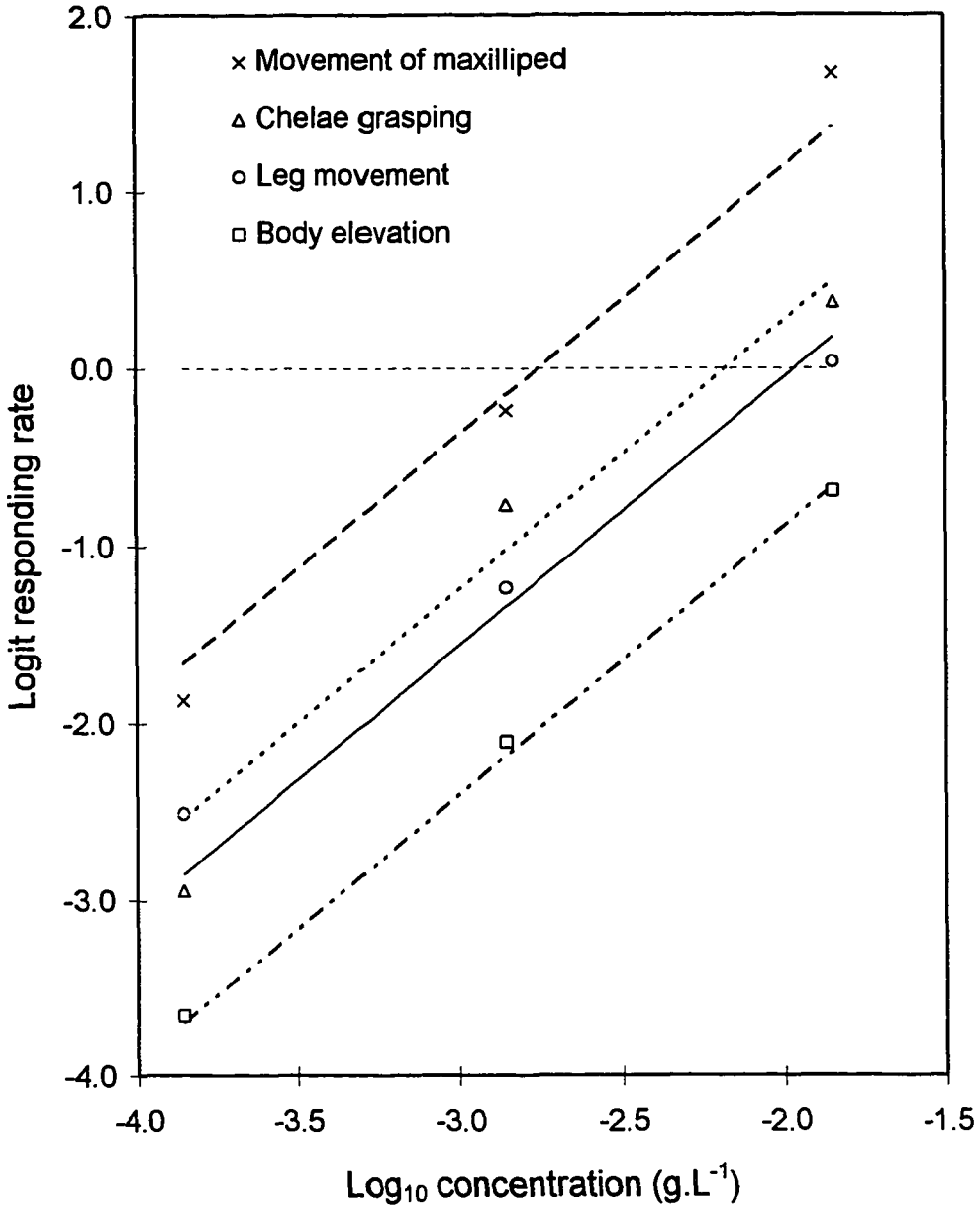

Figure 2.4. Responding rate after logit transformation with regard to four feeding behavior indexes and solution concentration. The dashed line indicates a 50% responding rate.

movement of maxillipeds was the most sensitive index for feeding response, and body elevation was the least sensitive, while probing of chelae and leg movement were in between (Table 2.3).

A similar logit model was applied to test the feeding sensitivity of the four crab groups. Only movement of maxillipeds was adopted as the feeding behavior here, since it was the most sensitive behavior. Also, only three extract types were used, i.e., herring, squid, and mussel. The four crab groups had a parallel slope b = 1.96 (parallelism Chi- square test, p = 0.516, df = 7). The intercept a was 4.3, 6.3, 5.6, and 5.4 for JF, OF, SM, and LM, respectively (Figure 2.5). Comparison of relative potency indicated that juvenile females had a significantly higher feeding threshold than others, and large males also had a significantly higher threshold than ovigerous females (Table 2.3).

The logit model was also employed to explore the feeding sensitivity on the five types of extracts. Again, movement of maxillipeds was used as a feeding index, and the four crab groups were combined. The parameter b = 1.52 for all extracts, and a equaled to 3.98, 4.61, 4.01, 3.14, and 2.93 for squid, herring, mussel, crab, and ovary, respectively (Parallelism Chi-square test, p = 0.263, df = 4; Goodness-of-fit Chi-square test, p = 0.148, df = 9). According to the comparison of relative potency, the five extracts could be divided into two distinct groups: herring, mussel, and squid as one group, and

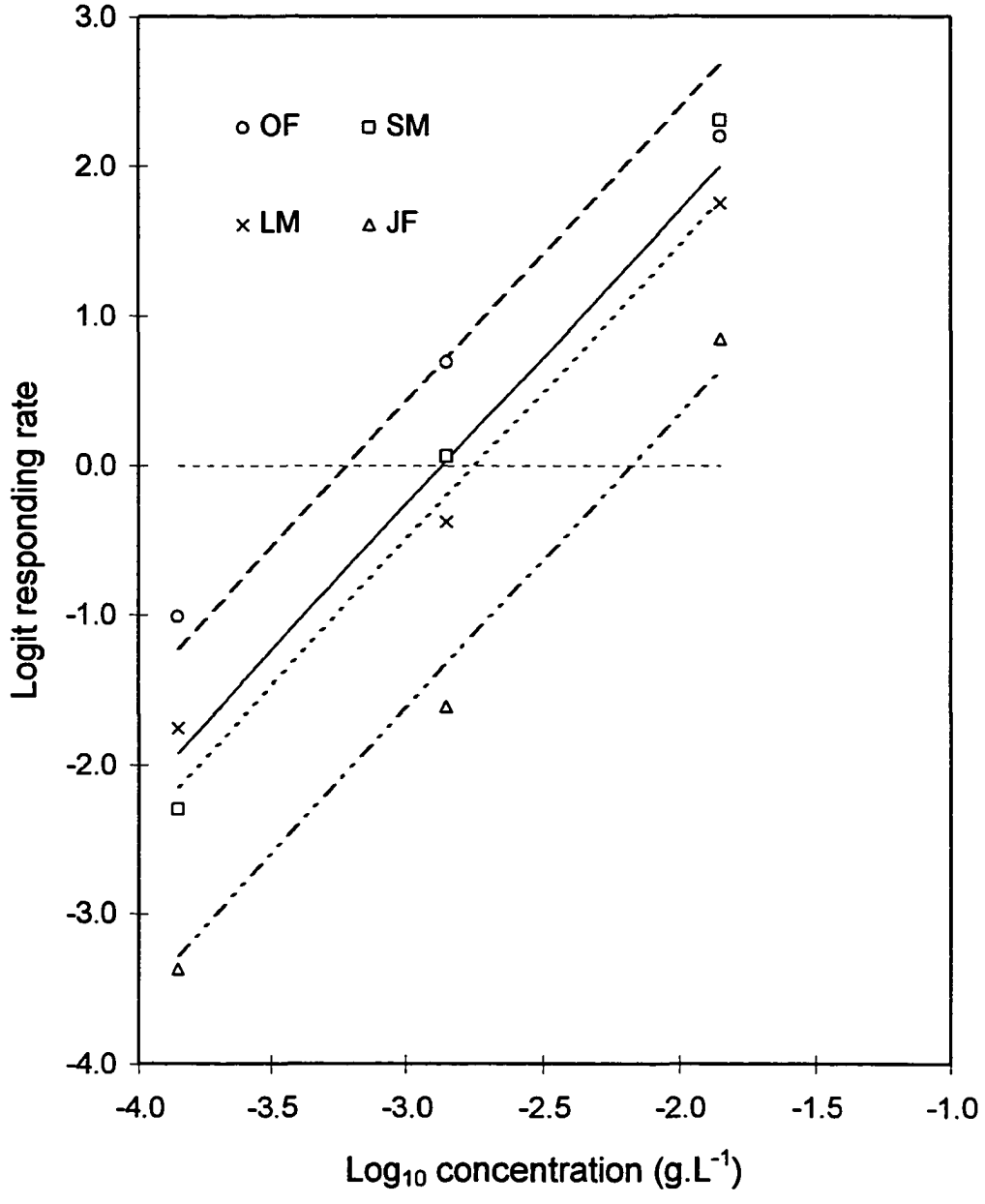

Figure 2.5. The relationship between responding rate for movement of maxillipeds after logit transformation and solution concentration for four crab groups. The dashed line indicates a 50% responding rate.

crab muscle and ovary as another group. The two groups of extracts significantly differed from each other, but not within the group, although crabs were most sensitive to herring extract, and least sensitive to extract made from king crab ovary (Figure 2.6, Table 2.3).

Table 2.3. Threshold concentrations for feeding behaviors. The four feeding behaviors were movement of maxillipeds, probing of chelae, legs movement, and body elevation. The four crab groups were JF = juvenile female, OF = ovigerous female, SM = small male, and LM = large male. Threshold was the $\log_{10}$ solution concentration at which 50% of the crabs responded.

Behavior	Maxillip.	Chelae	Legs	Body
Threshold	-2.75	-2.18	-1.97	-1.41
±95% CI	0.16	0.16	0.13	0.20

Crabs	JF	OF	SM	LM
Threshold[a]	-2.17	-3.21	-2.87	-2.75
±95% CI	0.28	0.28	0.25	0.28

Bait	Squid	Herring	Mussel	Crab muscle	Crab Ovary
Threshold	-2.62	-3.03	-2.64	-2.06	-1.92
±95% CI	0.41	0.41	0.40	0.42	0.42

[a] Feeding behavior was movement of maxillipeds.

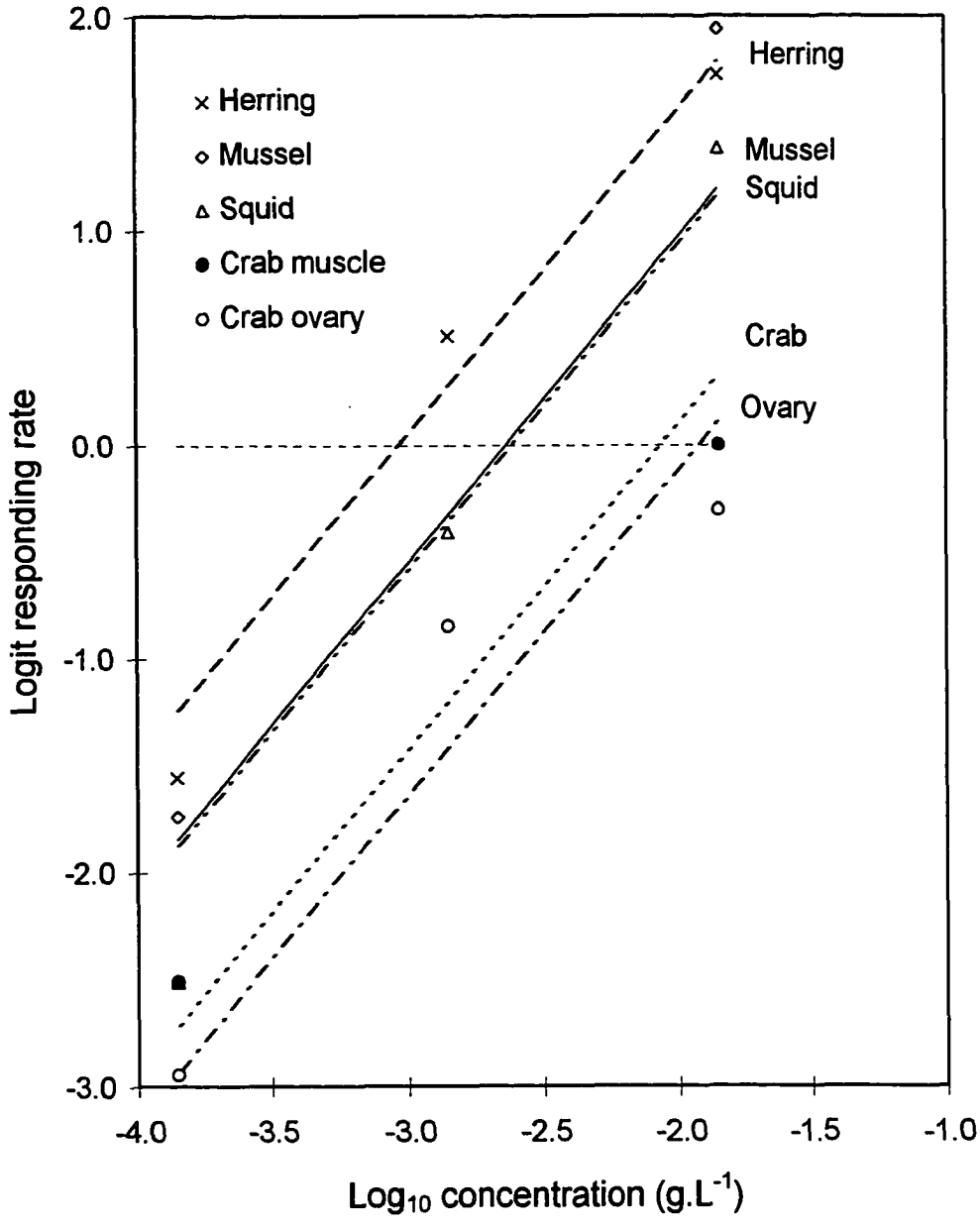

Figure 2.6. The relationship between responding rate for movement of maxillipeds after logit transformation and solution concentration for the five extracts. The dashed line indicates a 50% responding rate.

Responses to king crab ovary extract by crabs of different sexes and sizes

The results failed to reject the null hypothesis that crabs of different sex-size categories (JF, OF, SM, LM) had the same IFR when tested with king crab ovary extract with the same concentration (ANCOVA after data transformation, $p = 0.127$, $N = 197$, $df = 3$). Additionally, no difference was found between crab categories for the chemoreception responding rate (percentage of crabs with IFR≥7 in 30 s). However, the responding rate for feeding behavior was different among crab categories. At concentrations of $1.4*10^{-3}$ and $1.4*10^{-2}$ $g.L^{-1}$, ovigerous females had a significantly higher responding rate for waving behavior of maxillipeds than JF, SM, and LM (G-test, $p = 0.034$, $df = 3$). At $1.4*10^{-2}$ $g.L^{-1}$, 80% of OF demonstrated waving of maxillipeds while only 30% of JF, SM, and LM did.

DISCUSSION

Criteria for chemosensation and threshold determination

The antennules, the pereiopod dactyls, and the mouthparts have been considered as the primary chemosensory organs of decapods (Ache 1982). While mouthparts and dactyls are considered analogous to vertebrate tongues, antennules are believed to be analogous to vertebrate noses (Carr and Derby 1986; Rittschof 1992), and have been shown to function as distance chemoreceptors (Hazlett 1971). Since it is readily noticeable, antennular

flicking has been used widely as a behavioral indicator for chemosensory studies (Daniel and Derby 1991; Pearson and Olla 1977; Pearson et al. 1979, 1981; Rebach et al. 1990; Zimmer-Faust and Case 1983). However, the optimum behavioral criterion to determine whether a crab or a lobster has detected chemicals has not been clearly determined. Researchers chose different criteria in their studies. While the criterion was not clearly identified in some papers, Pearson and Olla (1977) defined a sharp increase in the antennule flicking rate accompanied by abrupt onset of continuous and vigorous gill bailing as the criterion of detection. In two other studies, Pearson et al. (1979, 1981) defined detection as being when there was an abrupt change in the orientation of the antennules within 30 s after solution introduction and if the ratio of the antennular flicking rate between after and before solution introduction was 1.5 or higher. This criterion value was determined from a 95% tolerance interval of spontaneous flicking ratio when no solution was added. Rebach et al. (1990) considered that detection occurred when the flicking ratio between after and before introduction of the solution was proportional to the concentration and greater than 1.

Although it is difficult to tell whether a crab senses the odor when the test solution is near the threshold concentration, the criterion determined by the toleration interval appears to be more acceptable. If one asserts that detection occurs when the flicking ratio (before and after solution

introduction) is proportional to the concentration and greater than 1, the risk of error seems too high. For example, at concentration 10^{-13} $g.L^{-1}$, the mean antennular flicking rate for *Cancer irroratus* before solution introduction was 71.1 (± 17.3 SD, N = 15), and it increased to 74.4 (± 19.4 SD, N = 15) (Bebach et al. 1990). Assuming the flicking rate had a normal distribution, we can estimate that 43.0% of crabs had an initial flicking rate greater than 74.4, while 43.3% of crabs had a flicking rate lower than 71.1 after solution introduction.

I chose the change of antennular flicking rate determined by tolerance interval of spontaneous flicking as the criterion in this study. However, for red king crabs, the flicking rate difference before and after solution introduction appeared to be more sensitive than the change of its ratio. This difference (flicking rate after injection of stimulus minus the flicking rate before injection of the stimulus) was also used as a behavioral index in a chemosensory study in lobster (Daniel and Derby 1991).

As different criteria have been applied to determine the detection of chemicals, different criteria have been chosen to determine the chemosensory threshold. For example, the concentration at which 50% of crabs detected the stimulus has been defined as the threshold for blue crabs (*Callinectes sapidus*) and Dungeness crabs (*Cancer magister*) (Pearson and Olla 1977, Pearson et al. 1979). The lowest tested concentration to which the proportion of responding animals was significantly greater ($p < 0.05$) than the proportion responding to

filtered sea water, was defined as the threshold for spiny lobster, *Panulirus interruptus* (Zimmer-Faust and Case 1983). Daniel and Derby (1991) defined threshold as the concentration necessary to elicit a 10% response for the *Panulirus argus*. Rebach et al. (1990) determined the chemosensory threshold for rock crab (*Cancer irroratus*) by directly comparing the change in antennular flicking rate before and after solution injection. They defined the detection threshold as the lowest concentration when the flicking rate after solution injection exhibited a statistically significant increase.

In addition to experimental error, variation in sensitivity to external stimulus commonly exists between individuals. To ascertain a threshold for a group of animals, the median lethal or effective dose, LD_{50} or ED_{50} should be the appropriate criterion. Therefore, the concentration at which 50% of the crabs responded was chosen as the threshold in this experiment. This criterion is similar to that used for blue crab and Dungeness crab (Pearson and Olla 1977; Pearson et al. 1979), where the resulting chemosensory thresholds have been widely accepted (Ache 1983; Daniel and Derby 1991; Rebach et al. 1990; Zimmer-Faust and Case 1983). However, the application of a straight line regression or a quadratic regression (Daniel and Derby 1991) between responding rate and solution concentration is inappropriate. With a wide range of solution concentrations, the relationship between the responding rate and concentration should be an "S" shape rather than a straight line (Derby et al. 1984; Handrich and Atema 1987). Use of different regression models may

result in distinctive threshold concentrations. For example, the threshold concentration for Dungeness crab appeared to be higher than 10^{-7} g.L^{-1} (Pearson et al. 1979, Figure 2) or between $10^{-4.6}$ and $10^{-5.6}$ g.L^{-1} (Pearson et al. 1979, Table I) while it was calculated to be $4.8*10^{-10}$ g.L^{-1} by linear regression.

Red king crab chemosensory threshold and efficiency of extracts

Because great differences exist in experimental methods, stimulant types, and criteria used, it is difficult to compare chemosensory threshold between species. Using the criterion described in this study, red king crabs have a higher threshold than many decapod species in other studies. I tried to use another method to determine the chemosensory threshold--a method based on a direct examination of the increase of flicking rate after solution injection. Because a crab increased its antennular flicking rate after detecting chemicals, and the IFR was greater with increasing concentration, a reasonably high mean IFR from a group of crabs can be employed as an indicator of threshold. This reasonably high IFR can be determined by the 95% tolerance interval of spontaneous antennular flicking rate. From observations on 28 crabs, I obtained an mean IFR of spontaneous flicking as -0.57 min^{-1} (± 4.4 SD). The 95% tolerance interval was -0.57 ± 9.0 flicks.min^{-1}. The solution concentration at which the mean IFR ≥ 9 min^{-1} was then defined as the

chemosensory threshold for this category of crabs. A model of $IFR = a + be^{dC}$ was fit to each extract type. In this model, a, b, and d are parameters while C is the concentration. Threshold concentrations at which IFR = 9 were calculated from the models and compared with thresholds obtained through the median effective dose (ED_{50}) method (Table 2.4).

Table 2.4. Red king crab chemosensory threshold determined by two methods for five extracts. The ED_{50} method defined the threshold as when 50% crabs responded, while the direct IFR method defined the threshold as a mean IFR = 9 min^{-1}.

Method	Squid	Herring	Mussel	Crab muscle	Crab ovary
ED_{50}	-4.17	-4.89	-3.64	-5.83	-4.42
Direct IFR	-3.93	-4.43	-3.87	-5.86	-4.51
Difference	-0.24	-0.46	+0.24	-0.03	+0.09

The thresholds determined by the two methods differed by less than 0.5 logarithmic unit. In comparison to studies on other decapod species, these two methods of determining threshold tend to be more conservative. If detection is defined as when IFR is significantly higher than IFR for sea water, red king crab chemosensory thresholds will be much lower than determined by

the previous two methods. For example, the threshold concentration should be less than 10^{-12} g.L^{-1} for extract of crab muscle.

Indexes for feeding behavior

Feeding behavior involved movement of maxillipeds, grasping by chelipeds, probing by legs, and locomotion (Derby and Atema 1982). Many decapods share similar feeding behavior (Derby and Atema; Fine-Levy et al. 1989; McLeese 1970; Pearson and Olla 1977; Pearson et al. 1979; Zimmer-Faust and Case 1983). Since feeding behavior can be scored dichotomously, i.e., occurring or not occurring, feeding activity is more readily judged. However, the activity varied with stimulant concentration. For spiny lobster, *Panulirus interruptus*, the threshold for leg probing was 10^{-6} g.L^{-1}, while the threshold for locomotion was 10^{-4} g.L^{-1} (Zimmer-Faust and Case 1983). The feeding responses (defined as feeding motions of the mouthparts and a sweeping motion of the first pair of walking legs) of the American lobster (*Homarus americanus*) occurred at a lower concentration than walking responses did (McLeese 1970). Pearson et al. (1979) defined feeding behavior to begin when a Dungeness crab probed the substratum with its chelae and/or exhibited a rapid and coordinated movement in which the dactyls and chelae moved to bring an object forward and up to its mouth. These previous studies did not examine the sensitivity of different behaviors associated with feeding. In red king crab, the onset of maxilliped movements, probing by chelipeds and

walking legs, and body elevation required different concentrations. I inspected these behaviors and found that the maxilliped movements were the most sensitive indicator related to feeding, and the body elevation was the least sensitive index, while probing and grasping by chelipeds and movement of walking legs occurred at similar stimulant concentrations.

The methods used for behavioral measurements in this study and others did not consider the quality of behavior. Movement can be described by the movement analysis method (Bartenief and Lewis 1980; Dell 1970). If the observation of crab feeding behavior employs the movement analysis method (quality of flow, weight, time, and space), finer changes in behavior may be detected. Future studies on feeding behavior should consider using the movement analysis method.

Efficiencies of different extracts and biological significance

Red king crabs had the most sensitive chemosensation to the extract made from muscle of their conspecifics. The chemosensory threshold to crab muscle extract was one or more orders of magnitude lower than to other extracts. The antennular flicking rate to crab extract at concentration as low as 10^{-12} $g.L^{-1}$ was significantly higher than responses to sea water. Red king crabs might sense the chemical from conspecific muscle as an alerting signal rather than potential food. Crayfish (*Orconetes virilis*) can detect chemicals released from disturbed conspecifics and displayed alerting behavior (Hazlett

1990). Although red king crabs were very sensitive to conspecific muscle extracts, the threshold for feeding behavior was significantly higher than that for herring, squid, and mussel. This phenomenon may support the hypothesis that king crabs regard chemicals from conspecific muscle as an alerting signal rather than as food. Avoidance responses to dead conspecifics are common in marine decapods. Traps containing both bait and freshly crushed spider crabs significantly reduced the catch of spider crabs (Richards and Cobb 1987). Rock lobster catches were greatly reduced by including dead rock lobster with the bait normally used in the traps (Hancock 1974). Spiny lobsters (*Panulirus interruptus*) avoided entering traps baited with dead lobsters, excised lobster thorax and abdominal muscle (Zimmer-Faust et al. 1985). In a field experiment, pots baited with dead red king crab did not attract live king crab to the pots (High and Worlund 1979).

Some results may conflict. In our laboratory, when king crabs were fed with newly killed conspecifics, initially many crabs avoided it, but after a while might feed on the crab meat. Cannibalism occurred commonly during molting (Brodersen et al. 1989). McLeese (1970) showed that freshly prepared extracts of lobster muscle (*Homarus americanus*) caused more feeding and walking responses by live lobsters of the same species than other compounds at high concentration (110 ppm). Since crabs demonstrated both positive and negative responses to extract of conspecifics, I assume that muscle of conspecifics may contain both chemicals functioning as alerting signals and as

food. The characteristic response, either positive or negative, depends on quality and quantity of these chemicals, and the crabs adaptation to these chemicals

Among the three potential baits, herring, squid, and mussel, red king crabs had the lowest chemosensory threshold and lowest feeding threshold to herring extract. For most marine crustaceans, excitatory extracts are an assemblage of common metabolites of low molecular weight, including amino acids, quaternary ammonium compounds, nucleosides and nucleotides, and organic acids (Carr and Derby 1986). Amino acids and amines have been considered the major feeding attractants (Daniel and Bayer 1989; Zimmer-Faust and Case 1982). Extract from herring must be composed of more excitatory chemicals than squid and mussel. Herring is traditionally used as the bait in king crab fishery, although it was less effective than squid for Dungeness crab (Cancer magister) (Breen et al. 1985). This study verifies herring to be a strong attractant for king crab, albeit it provides a lower growth rate than mussels and shrimp for juvenile king crabs (Brodersen 1992).

Variance in chemosensation and feeding behavior by sex and size

Juvenile female, ovigerous female, small male, and large male king crabs had similar chemosensory thresholds. However, the four crab groups had differences in their feeding thresholds. Ovigerous females had the lowest feeding threshold while juvenile females had the highest. I ascribe these

results to crab molting activity. Juvenile females experienced peak molting during the experimental period (March to early May) in our laboratory, while most ovigerous females molted during May and June. The physiological condition long before and after molt may affect their appetite. Rock lobsters (*Jasus lalandii*), which have an annual molt cycle, did not feed for 44 d pre- and 34 d postmolt (Zoutendyk 1988). Red king crabs decreased or stopped feeding for at least one week pre- and postmolt (personal observation, unpublished data).

Extract made from king crab ovary did not excite male crab chemosensory or feeding responses more effectively than that of females. Ovigerous females had a lower feeding threshold to ovary extract than the other crab groups. This difference was basically the same as to other extracts. The attempt to change catchability of the different sexes by using any of these tested baits appears to be unsuccessful.

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Chapter 3

Behavioral Responses of Red King Crab to Crab Pots

ABSTRACT

High bycatch of female and sublegal male king crabs in the fishery are of concern to fishermen and management agencies. The efficiency of gear currently used in the fishery needs to be improved. This study examined behavioral responses of red king crabs to pots under laboratory conditions with time-lapse video. Crabs approached the pot from downstream, 82% of searches were confined to within 135° of the downstream direction, and 78.3% of crabs searched less than 90° before leaving or entering. The probability of entry success increased with the number of approaches. Crabs which failed to enter made an average of 2.6 approaches compared to 3.9 approaches for crabs which entered. The entry success rate was 8.1%. No significant differences in approach, search, and entry were found between ovigerous females, juvenile females, legal-sized males, and sublegal-sized males. Legal males had a significantly lower escape attempt rate and the ensuing escape rate, i.e., 1.9% $h^{-1}.crab^{-1}$ escape attempt rate and 12.5% escape rate in two days for legal males, vs. 8.2% $h^{-1}.crab^{-1}$ escape attempt rate and

54.2% escape rate for the other three crab groups. Crabs depend on chemical cues during foraging, approaching, and searching. The current king crab pot is not efficient because crabs have difficulties in accessing the entrances and non-legal crabs have difficulties in escaping.

INTRODUCTION

The red king crab, *Paralithodes camtschaticus*, fishery was once the most economically important fishery in Alaska. A peak landing of 84,000 t of red king crab occurred in 1980, valued at $168.7 million (United States Department of Commerce 1981). Unfortunately, this fishery has declined since the early 1980s, and shows no definite sign of recovery (Otto 1990). The crab pot is the only legal gear permitted in Alaska to harvest king crabs. The pots catch a large number of female and sublegal-sized crabs. Zhou and Shirley (1996) estimated that in the Bering Sea fishery on average 64.6% of the red king crab in the catch were females and sublegal crabs. These crabs must be returned to the sea to comply with state regulations. This high discard rate and handling frequency in the fishery has frustrated both fishermen and the management agencies, and has been suspected to negatively affect the fishery (Kruse 1992). Although Zhou and Shirley (1995) did not find severe impacts of handling on discarded crabs, the effect of potential

predation on discarded crabs during their descent to the bottom and the effect of disorientation after the crabs settle on the bottom in a new location are unknown. Reducing the bycatch of female and sublegal male crabs is one strategy to limit the potential risk to the discarded crabs, to improve fishing efficiency, and to protect the crab fishery. However, few studies address king crab fishing methods, its behavior with regard to fishing gear, and the effectiveness of pots on different sizes and sexes of crabs.

The responses of other crab species and lobsters to traps have received more attention. Observations have been made on the behavior of some crab species around the fishing pots (Miller 1978, 1979a; Smith and Sumpton 1989; Sumpton et al. 1995; Vienneau et al. 1993). Many variables affect catch rates, sex ratio, and size composition. It is possible to improve the sex ratio and size ratio in the catch as well as catch efficiency by designing better fishing gear and methods (Miller 1990).

The primary objectives of this study were to observe red king crab behavior near and inside pots, and to examine pot efficiency with regard to entry and escape. Experiments were carried out in a laboratory tank, and the behavior was observed by means of a close-circuit video system and time-lapse video recorder. The behavior was quantified from recorded video tapes. These efforts provide a first step for further study on limiting bycatch of

female and sublegal male crabs while increasing the catchability of legal males.

MATERIALS AND METHODS

Crabs

Male and female red king crabs were collected by king crab pots near Juneau, Alaska. These crabs were handled gently in a manner to reduce thermal and salinity shock, and immediately transported to the laboratory and kept in tanks supplied with flowing seawater from an intake at a depth of 30 m in Auke Bay, Alaska. Crabs were categorized into four groups: ovigerous female (OF), female without eggs (juvenile female, JF), legal-sized male (LM, ≥ 178 mm CW), and sublegal-sized male (SM, < 178 mm CW). Carapace length (CL) and width (CW) were measured for all crabs, and crabs were marked on the merus of the second to the fourth walking legs with an aluminum tag to allow ease video identification. Crabs were fed fish and squid twice a week, but were deprived of food two days before each experiment. Only undamaged crabs with no missing legs and obvious injury were used. Before each trial, crabs were checked for signs of ecdysis. Crabs with any indication of molting were not used. Crab sizes ranged from 64.9 mm to 181.9 mm CL (115.3 mm ± 22.4 SD) (Figure 3.1).

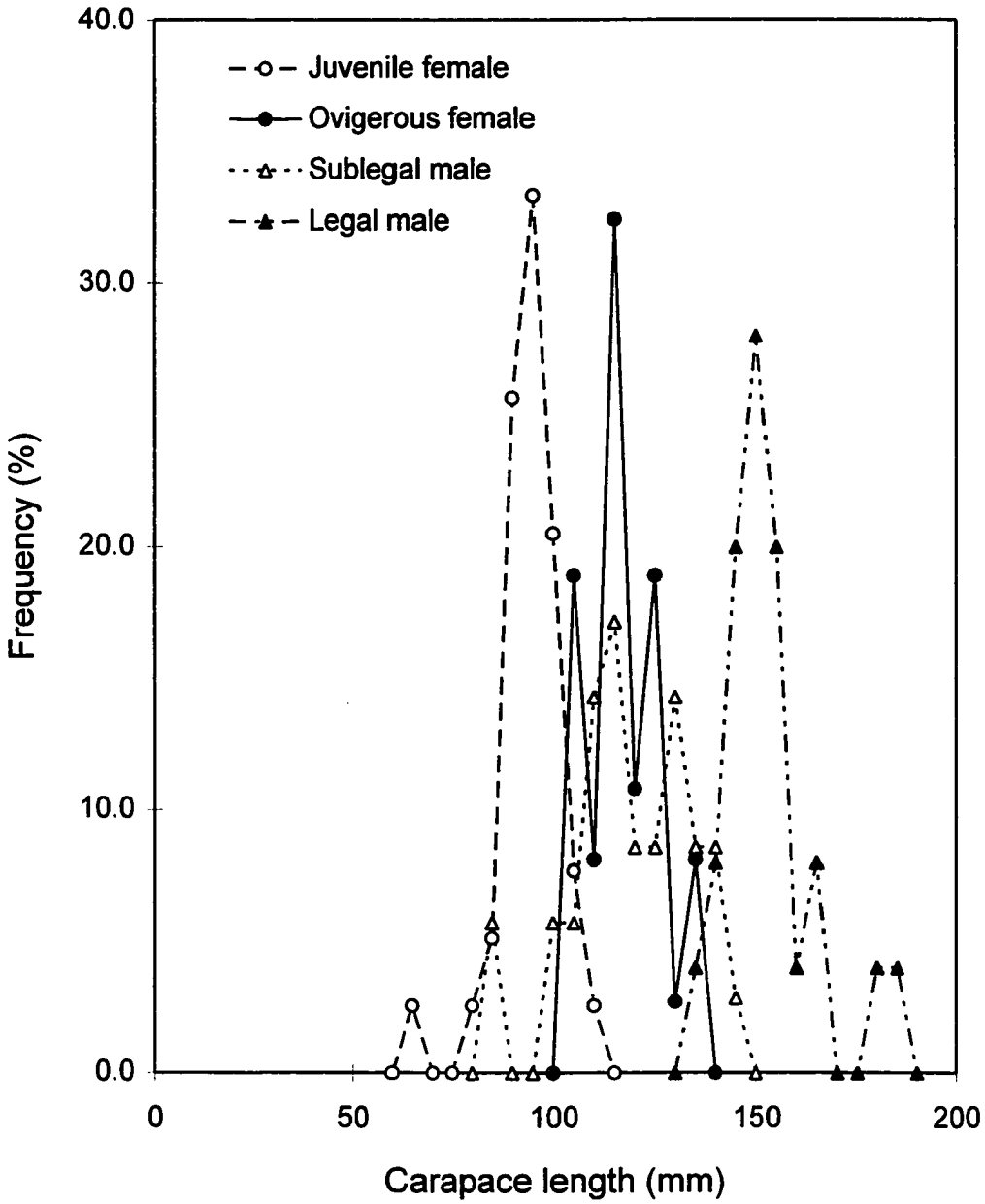

Figure 3.1. Carapace length distribution for crabs used in the experiment.

The king crab pot and bait

King crab pots have a variety of shapes (pyramidal, conical, round, and box-shaped) and dimensions. Standard commercial king crab pots are box-shaped. Pot dimensions may range from 150 to 240 cm (5~8 ft) square and from 67 to 99 cm (26~39 in) high. Pots have two tunnels on opposite sides of the pot. The entrance frames vary from 89 by 19 cm (35 by 7.5 in) to 102 by 20 cm (40 by 8 in). Several mesh sizes between 8.9 and 20 cm (3.5 and 8.0 in) are used on various pots (unpublished data; High and Worlund 1979). Frozen herring in porous plastic jars of approximately 2-liter volumes is typically used as bait in the commercial king crab fishery.

Since the experimental tank was only 5 meters in diameter, a simulated king crab pot with dimensions reduced from the standard king crab pot to 100*100*60 cm was used in this study (Figure 3.2). The two entrance openings were 90*20 cm. Tar treated knotted nylon mesh of 15 cm (6 in) stretch mesh was used for the web. Five hundred grams of frozen salmon cut in approximately 2 cm^3 cubes was placed in a 1-liter cylindrical perforated jar (9 cm diameter by 20 cm high) and hung in the pot as bait.

Experimental tank

One round covered outdoor tank with a diameter of 5 m and a height of 1.6 m was equipped with one inflow pipe and one standpipe for outflow. The

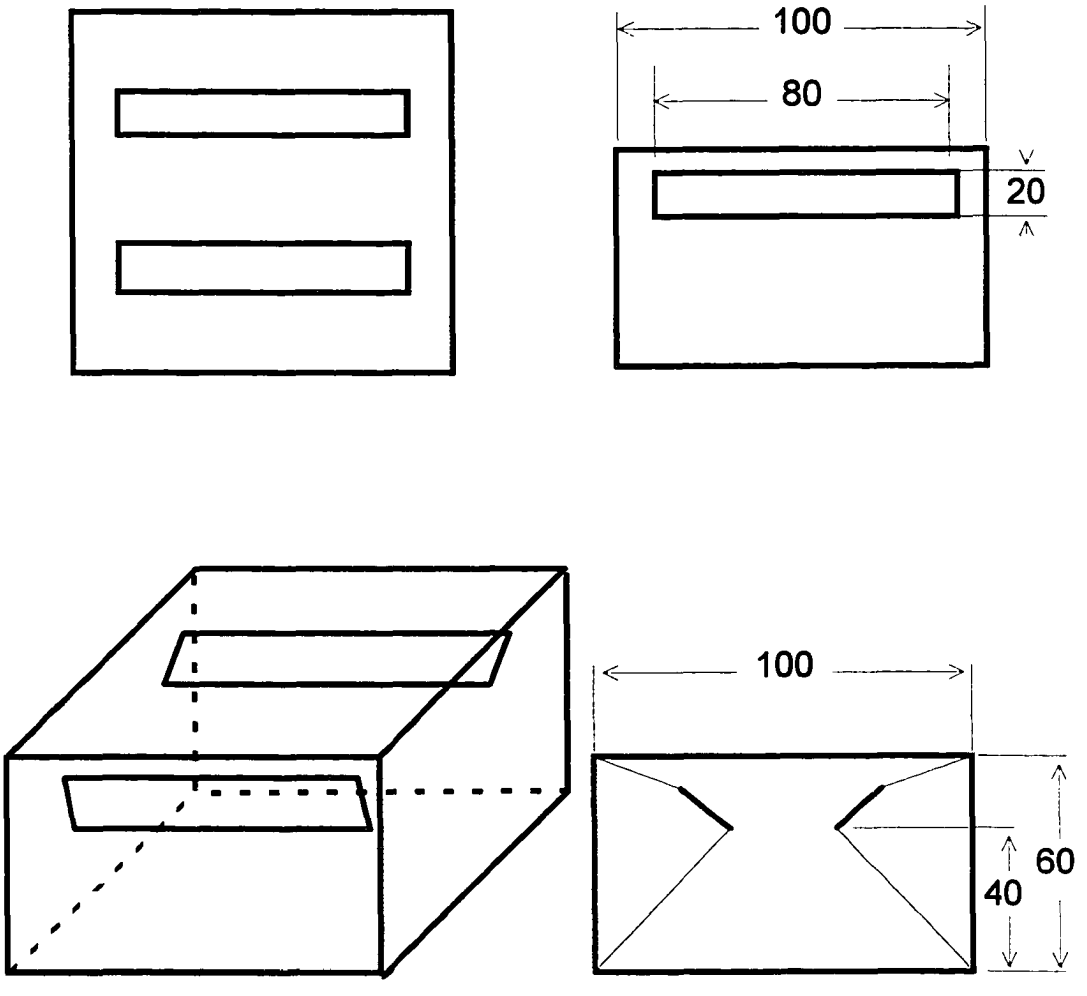

Figure 3.2. Dimensions of simulated king crab pot (cm) used in the present study.

simulated pot was deposited at the middle between the center and the wall of the tank (the center of the pot was approximate 1.25 m from either the center or the wall of the tank). The two entrances of the pot were parallel to the current direction (Figure 3.3). Filtered sea water pumped from a depth of 30 m at ambient temperature and salinity flowed into the experimental tank and filled it to a depth of 0.7 m. The inflow pipe paralleled the tank wall at a 20-cm height above the bottom of the tank and 20 cm from the tank wall. Water flow was 17.75 ± 0.26 L min^{-1} (mean ± SD, n = 7), and circulated in a clockwise gyre in the tank. The current velocity was measured at the surface and at a depth of 20 cm from the bottom. At the center of tank the speed was nearly zero, and it linearly increased from the tank center toward the tank wall. The current speed and the distance from the center of the tank had a linear relationship:

(1) at the surface, $V = 0.96D$ ($r = 0.991$, $n = 4$), and

(2) at the 20-cm depth, $V = 1.19D$ ($r = 0.982$, $n = 4$),

where V = velocity ($m.min^{-1}$) of the current, D = distance (m) from tank center. Because the inflow pipe opening was located at 20 cm from the bottom, the current speed at this layer was higher than on the surface. At a distance of 1 m from the tank center, the current speed was 0.96 $m.min^{-1}$ on the surface, but 1.19 $m.min^{-1}$ at a depth of 20 cm off the bottom. Water temperature ranged from 4.4 to 7.6 °C, and salinity was 30 ppt during the

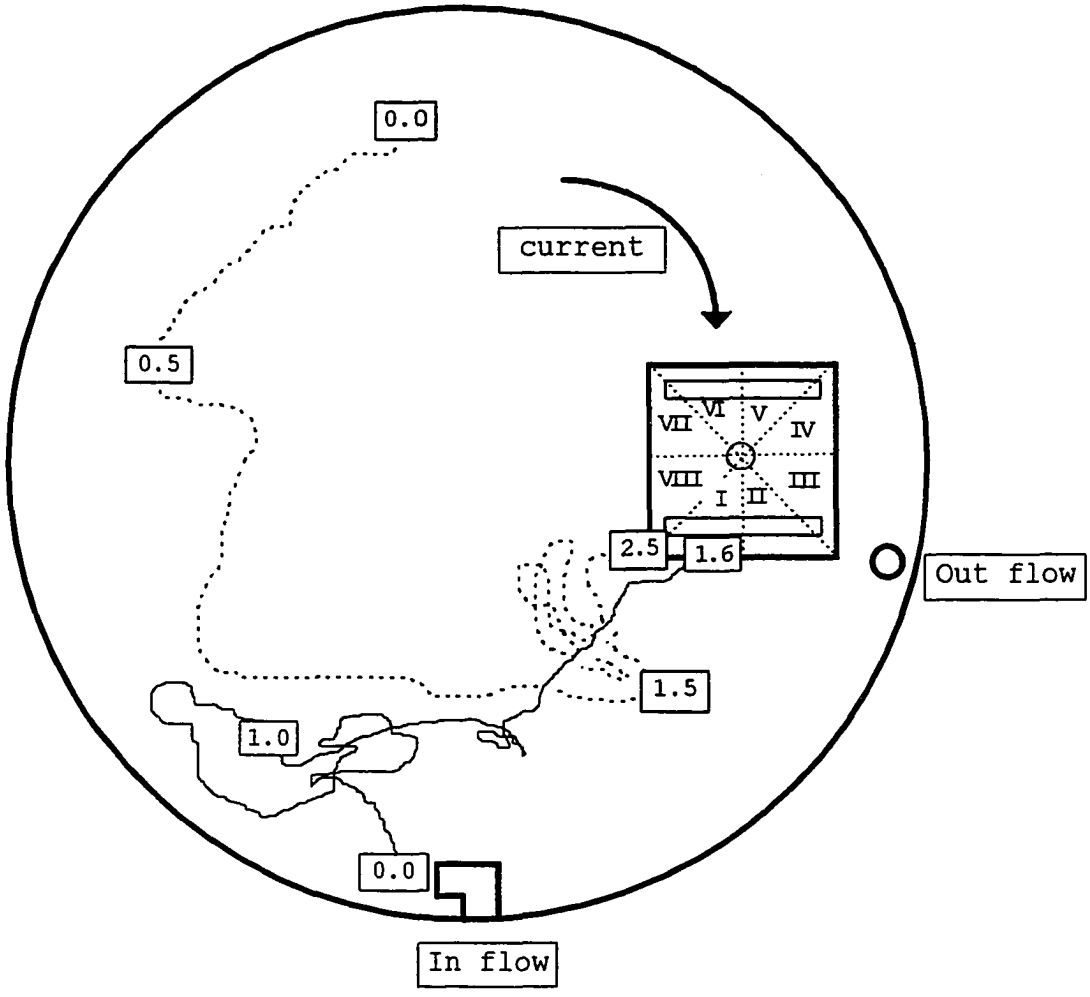

Figure 3.3. Example of the foraging tracks of two red king crabs in the experimental tank. The time is shown in minutes starting from 0.0. The pot was divided into 8 sectors relative to the direction of current.

experimental period.

To inspect the bait plume dispersion pattern, 236 ml Rit liquid dye (black) was released at the center of the pot 20 cm off the bottom. The resulting dye dispersion was monitored with a video recorder. Dye dispersed in all directions and reached the pot edges in 30 sec, but from this point it only dispersed downstream and to the center of the tank, not upstream and to the wall of the tank. The plume occupied about 47% of the total area of the tank in 5 minutes. A high density of the color concentrated downstream and at the center of the tank, while the plume was diluted near the tank wall. The plume could hardly be seen after 1 hour.

Observation system

The tank was illuminated by artificial white light. Four 33 w, fluorescent lights were hung over four sectors of the tank. The lights were hung 3.0 m above the water surface. Another standard light of 100 w was hung at the center of the tank 4 m high from the water surface. Illuminance was 8 to 11 lux on the water surface. Two low-light video cameras (Cohu solid state camera, Model 4815-5000, and FOCUS Vision 4, Model FS-412), one suspended 4 m above water level over the tank's center and one suspended 3 m over the crab pot. The former camera provided a view of the whole tank, and the latter camera provided a close up view of the pot and the crabs inside

and near the pot. These two video cameras were connected to two TV-monitors in an observation room. Crab behaviors were recorded continuously via a time-lapse recorder (GYYR TLC 1800) and by real time observation.

Experimental protocol

Two experiments were carried out from late October to December 1994: an entering experiment and an escape experiment.

(1) Entering experiment

Eight crabs, two each of OF (ovigerous female), JF (juvenile female), LM (legal male), and SM (sublegal male) were tested in each trial. After being deprived of food for two days, 8 crabs were transferred into the experimental tank. After 20 h of acclimatization to the tank, one simulated king crab pot was placed at approximately 0.7 m from the center and from the wall of the tank with the funnels orientated parallel to the current direction (Figure 3.3). Then 500 g of frozen salmon fillet in a porous bait jar was lowered into the center of the pot 25 cm from the bottom.

The behaviors of all the crabs were observed and recorded for two hours. Nineteen trials were conducted. After each trial, water in the experimental tank was replaced before the next group of crabs were placed in the tank. Individual crabs were used only once. A total of 152 crabs was tested.

Some activities related to the pot were defined as follows:

Forage: A crab moved about in the open area on the tank bottom without contacting the tank wall.

Approach: A crab moved toward the pot and contacted the pot with its anterior end or lateral front. While touching the pot, chelipeds, legs, or body moved actively in a mode of searching for food. The crab behavior exhibited fully-developed efforts: moved in focused directions, hurried gaits, strong weight, and bound flow (Dell 1991). This definition excluded some behavior such as when a crab contacted the pot while moving backward or laterally without probing the pot mesh. Also it excluded a crab whose front was touching but stayed quietly rather than moving actively.

Leave: After approaching, a crab departed (no physical contact with the pot) from the pot for at least one body dimension (including the appendages) from the nearest site of the pot, and for at least one minute. If the crab returned and touched the pot again from a distance less than one body dimension and within one minute, the behavior was not scored as leaving but as a continuous approach.

Entry: A crab entered the pot and released its hold on the entrance.

Escape: A crab inside the pot crawled out the pot through the entrance and broke contact with the entrance.

(2) Escape experiment

Sixteen crabs, 4 each of OF, JF, LM, and SM, were transferred into the simulated pot without bait, and the pot was placed approximately 0.7 m from the center and the wall of the tank as in the entering experiment. The behaviors were continuously monitored for 48 h. A total of 4 trials and 64 crabs were used for escape observations.

Escape attempt was defined as a crab having at least 6 out of 8 walking legs (3 pairs of thoraxic appendages and one pair of chelipeds) in contact with the side panel(s) or top panel of the pot. In this position a crab was hanging on the side panel(s) or top panel rather than in the normal position when the crab stayed on the bottom panel. Escape occurred when a crab exited completely through the entrances or through the mesh.

Data analysis

All data were graphically diagnosed before and after statistical analysis. Especially, the outliers, collinearity, independence, normality, and homogeneity of variances were examined. Parametric statistical methods were first chosen if assumptions of normality, independence, and homogeneity were valid. Data transformation was applied when necessary. If parametric methods were not appropriate, non-parametric methods then were used.

RESULTS

Forage and approach

Crabs usually did not forage straight toward the pot and approach it directly. The foraging tracks were more likely to be meandering near the pot (Figure 3.3). Crabs moved back and forth downstream and appeared to follow the strongest chemical cue. The positive response to the bait odor was low, and not all the crabs which initiated foraging approached the pot. Only 51.3% (78/152) of the crabs in the experiment approached the pot. No significant difference in the number of crabs that approached between the four crab groups was detected (ANOVA, N = 78, DF = 3, F = 2.132, P = 0.104, Table 3.1).

The approach direction toward the pot was not random. Most crabs approached the pot toward sector I and its nearest sectors, sector II and VIII (Figure 3.3). This approach pattern was the same for the four crab groups (Friedman two-way ANOVA statistic = 6.338, p = 0.096, DF = 3, case = 8 sectors). The number of approaches was significantly different among the eight sectors (Friedman test, statistic = 23.958, p = 0.001, DF = 3, case = 4 crab groups). The multiple comparison method for the Friedman test (Conover, 1980) was used to compare the number of approaches in each sector. The number of approaches in sector I, the downstream direction, was significantly higher than any other sector (Figure 3.4). The number of

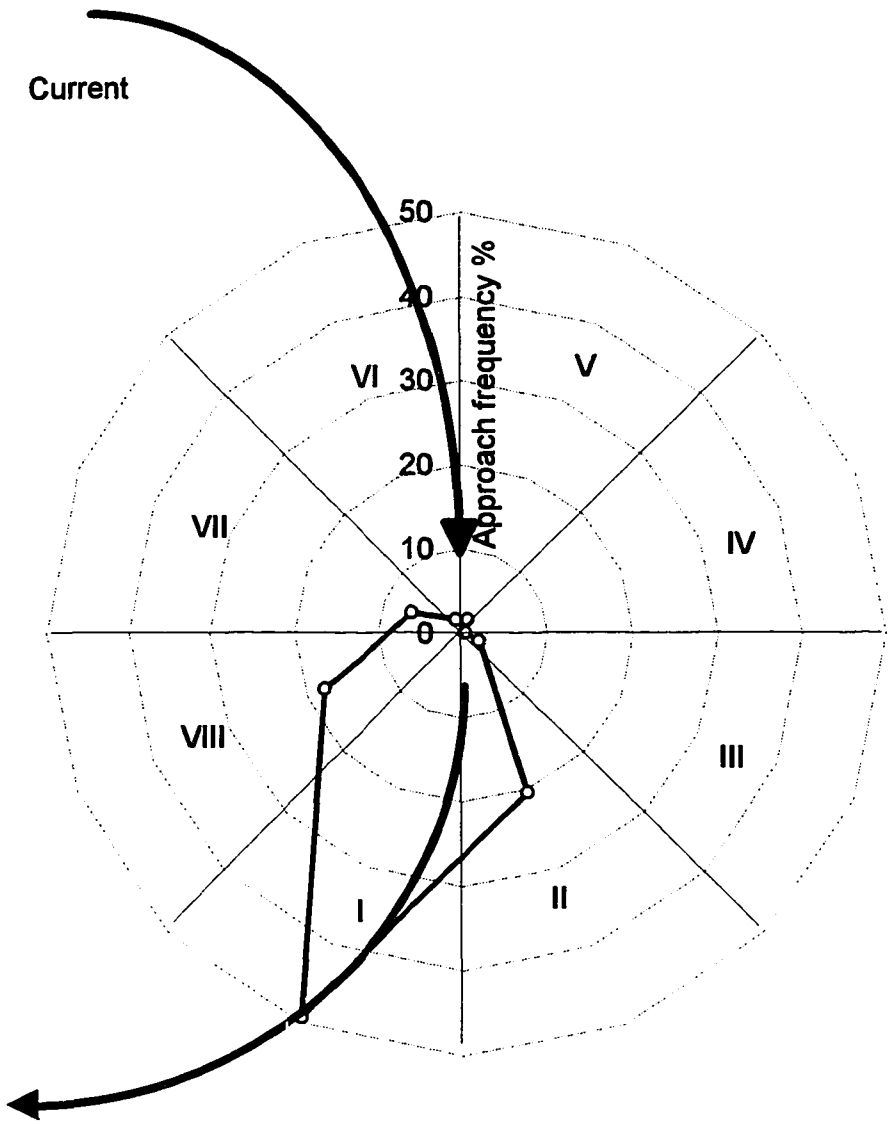

Figure 3.4. Approach frequency in each direction toward the experimental pot for all crabs combined.

approaches in sectors II and VIII were also significantly higher than any other sector except sector I.

Table 3.1

Summary of red king crab responses to crab pots.

Crab Groups	No. of crabs approached	No. of Approaches	No. of Entry	No. of Escape	Entry rate	Entry Success rate
OF	22	84	5	1	.23	.06
JF	20	58	4		.20	.07
LM	21	44	5(+1)	(1)	.24	.11
SM	15	35	4		.27	.11
Sum(±SD)	78	221	18(+1)	1(+1)	.23(±.03)	.08(±.03)

Groups: OF = ovigerous female, JF = juvenile female, LM = legal male, and SM = sublegal male. One legal male escaped and re-entered again. Entry rate = Number of crabs entered/Number of crabs approached. Entry success rate = Number of crabs entered/Number of approaches. No significant differences were found in number of approaches, entry rate, and entry success rate between the four crab groups.

Individual crabs might make more than one approach when they failed to enter the pot. The number of approaches per crab varied from 0 to 11. For

crabs failing to enter the pot, more than 40% only made one approach and never returned again in the two-hour experimental period, while a few crabs approached more than 10 times. No difference in the number of approaches per crab was found among the four crab groups (ANCOVA, $p = 0.942$, $N = 78$, $DF = 3$). As the numbers of approaches per crab increased, the number of crabs making that number of approaches decreased exponentially (Figure 3.5). The mean number of approaches was 2.6 ($\pm$ 2.1 SD, $n = 60$).

For crabs which eventually entered the pot, most (27.8%) entered on the first approach, while some failed nine times before successfully entering (Figure 3.5). The frequency distribution of the numbers of crabs versus the number of approaches per crab was significantly different between crabs that entered and crabs that did not entered. The curve for crabs which entered had a flatter slope (-0.73) than did the curve for crabs which did not enter (-1.26) (ANCOVA, $p = 0.011$, $df = 1$, $N = 21$). Crabs which entered approached more times than crabs which did not enter. The mean number of approaches to successfully enter was 3.9 ($\pm$ 2.63 SD, $n = 18$), which was greater than that of crabs which did not enter (2.6 $\pm$ 2.13 SD).

Entrance searches

When crabs approached the pot, they displayed a variety of behaviors with regard to the mesh, bait odor, and other crabs. Poking through the mesh

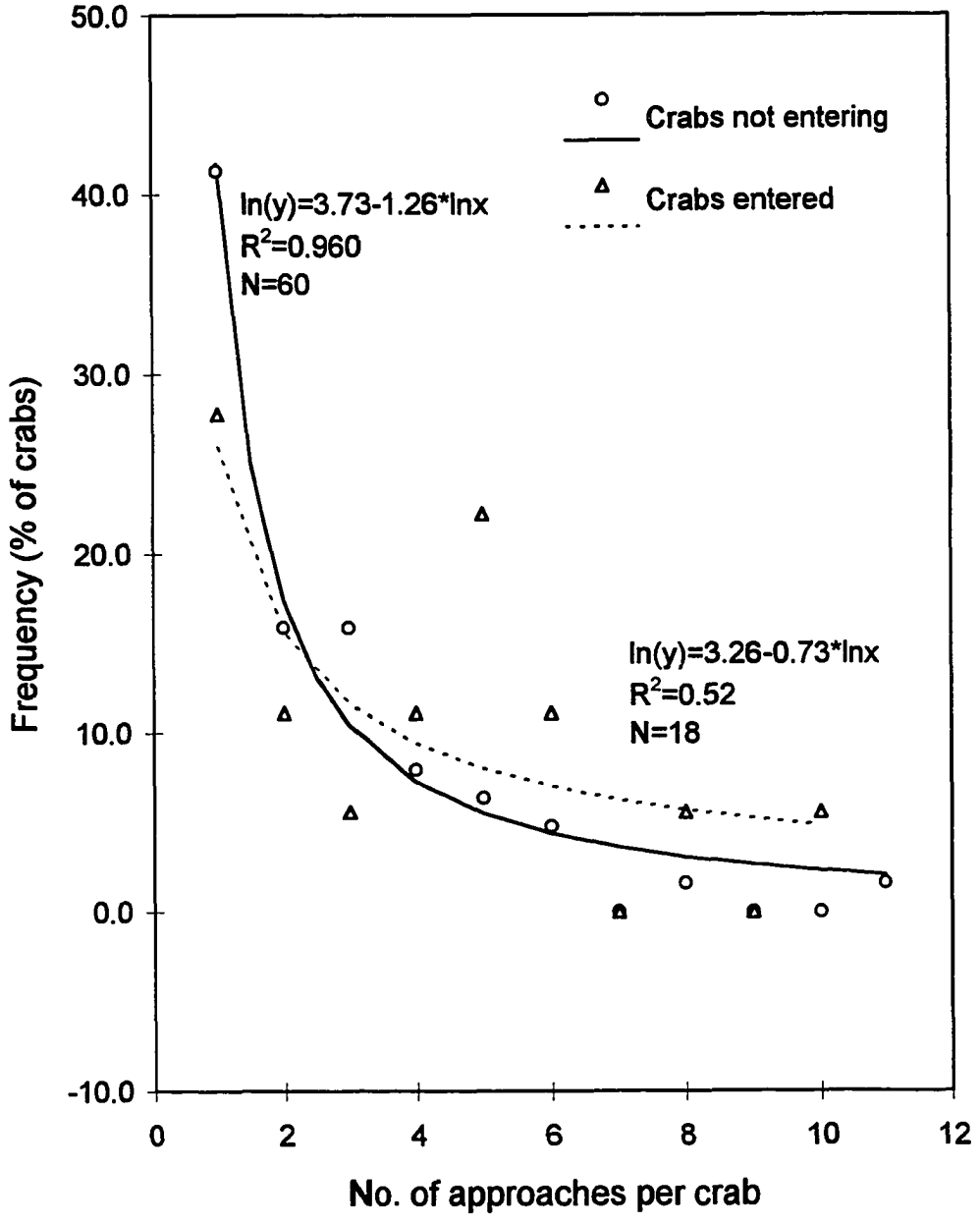

Figure 3.5. Frequency distribution of number of approaches per crab for crabs which failed to enter the pot and crabs which eventually entered the pot.

was the most common behavior, in which one or two chelipeds were extended into the pot through the mesh, the anterior part of the body touched the mesh, and the chelae gripped and waved while the walking legs forced backward on the floor. After an interval of ineffective efforts, the crab withdrew its chelipeds and inserted them into another part of the mesh. This behavior was typically observed on the downstream side, and it lasted from minutes to > 30 min. Grasping was another common behavior, where one or two chelae gripped the material of the pot, either the mesh or the rebar, and the crab occasionally raised its chelae to its mouth even though the chelae were empty. Crabs also pushed the mesh with their chelae. Accompanying these behaviors, crabs actively fumbled with their chelipeds along the mesh back and forth within a small range while their abdomens touched the floor. During this kind of search, some crabs might climb onto the tunnels, side panels, and even on the top panel.

Most crabs only searched on the downstream side. Eighty-two percent of searches occurred in sector I, II, and VIII (Figure 3.6). No crab searched in sector IV. This searching pattern was the same for the four crab groups (Friedman test statistics = 0.938, $p = 0.816$, DF = 3, 8 sectors), but significantly different between the sectors (Friedman test statistics = 26.854, $p < 0.001$, df = 7, 4 crab groups).

The center of mass for searching was determined by circular statistical

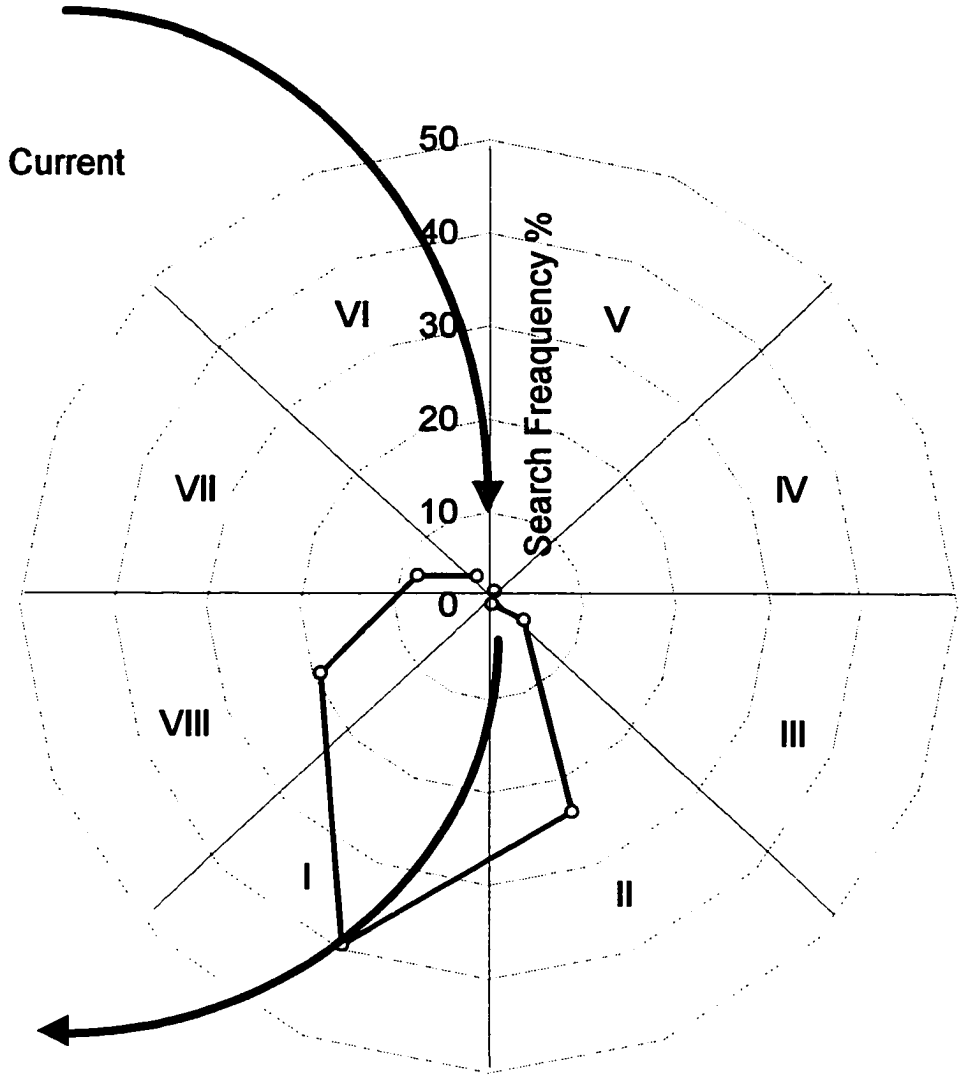

Figure 3.6. Search frequency in each sector.

methods (Batschelet 1981). The directions at the middle of each sector were assigned as (n-1)*45°, i.e., for 0, 45, 90, ...315° for sector I, II, III, ... VIII respectively. Each search was fixed in location by a unit vector. The mean vector *m* was defined as:

$$m = \frac{1}{n}(e_1 + e_2 + \cdots + e_n), \quad r = |m|,$$

where *n* is the total number of searches, *e* is a unit vector of each search, and *r* is the length of the mean vector. When using a rectangular coordinate system with *X* and *Y* axes and origin *O*, and ϕ_i being one of the *n* observed angles and e_i the corresponding unit vector, we will have the center of mass $\bar{x}$ and $\bar{y}$ at the angle of $\bar{\phi}$:

$$\bar{x} = \frac{1}{n}(\cos\phi_1 + \cos\phi_2 + \cdots + \cos\phi_n), \qquad \bar{y} = \frac{1}{n}(\sin\phi_1 + \sin\phi_2 + \cdots + \sin\phi_n).$$

$$\bar{\phi} = \begin{cases} \arctan(\bar{y}/\bar{x}) \text{ if } \bar{x}>0 \\ 180^\circ + \arctan(\bar{y}/\bar{x}) \text{ if } \bar{x}<0 \end{cases}$$

The mean vector of all crabs was $r = 0.659$, and the mean angle $\bar{\phi} = 18.48°$. This means that the searching activity was concentrated downstream with a slight tendency towards sector II. The mean angular deviation was $s = [2(1-r)]^{1/2} = 47.29°$. Two thirds of the searches were within the range $\bar{\phi} \pm s = 18.48° \pm 47.29°$.

An average of 39.8% of the crabs searched within 45° (one sector), and

78.3% of the crabs searched within 90° (2 sectors) before leaving or entering the pot. No crab searched one complete circle around the pot (360° or 8 sectors) (Figure 3.7). For crabs which failed to enter the pot, each crab searched a mean angle of 88.8° (± 11.8°) before leaving (Table 3.2). No significant difference was detected between the four crab groups for the angle searched before leaving (Kruskal-Wallis on-way ANOVA, statistics = 4.89, p = 0.602, DF = 3, N = 203). Similar results were found for crabs entering the pot (Kruskal-Wallis on-way ANOVA, statistics = 1.86, p = 0.602, DF = 3, N = 18).

Crabs that entered the pot searched a significantly greater angle than crabs that did not enter (G-test statistics = 14.652, df = 5, p = 0.012). An average of 66.7% of crabs that entered searched within 90° (2 sectors) before entering. Individual crabs searched an average 112.5° (± 10.49 SD) before entering.

The duration of the entrance search before leaving or entering varied from less than one minute to more than one hour. Logarithmic transformation was performed to achieve better normal distribution of search duration. The null hypothesis of no difference between crab groups could not be rejected both for crabs that did not entered and crabs that entered (ANOVA, for crabs not entered p = 0.556, DF = 3, N = 203; for crabs entered, p = 0.853, DF = 3, N = 17). However, crabs which entered spent a significantly longer time

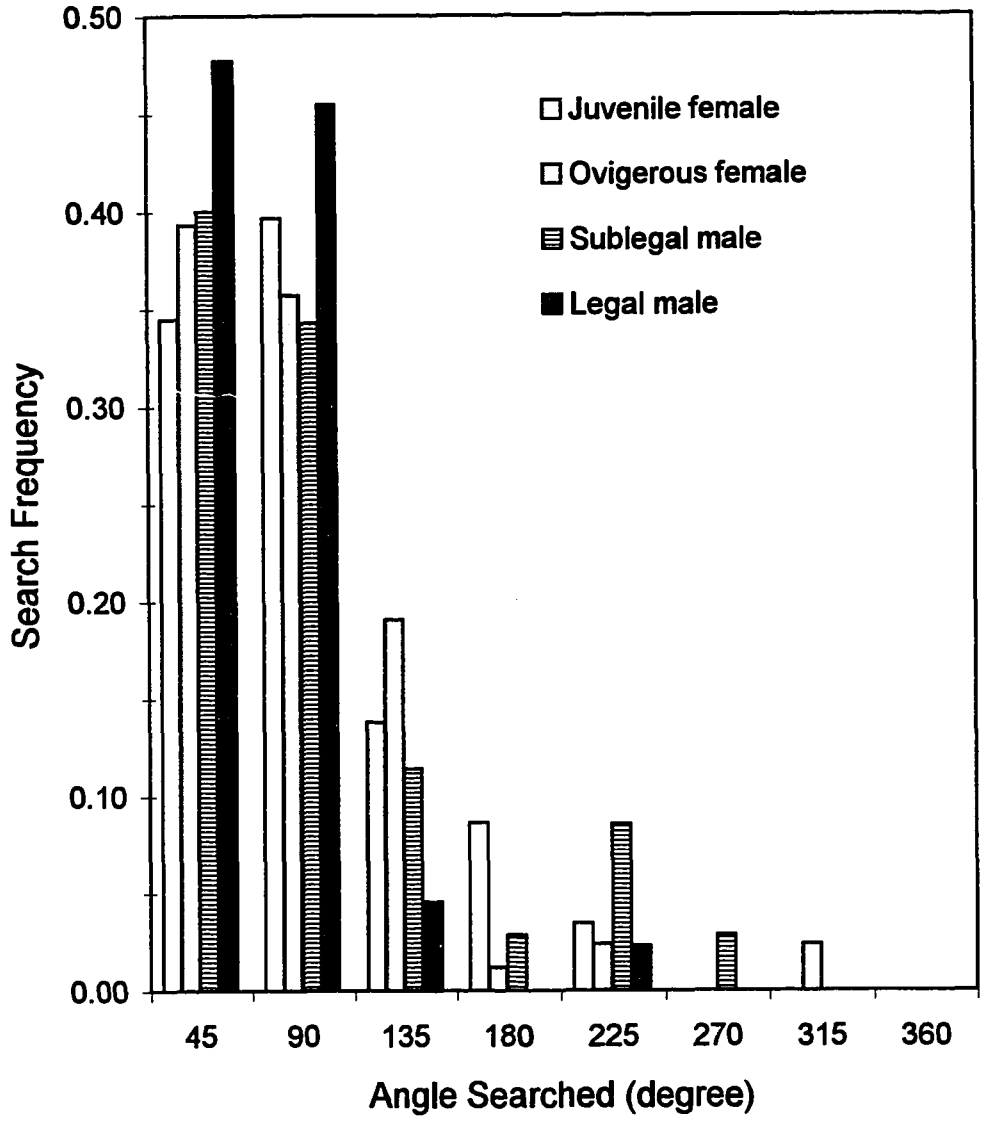

Figure 3.7. Angle searched around the pot circumference during one search.

searching than crabs which did not enter (ANOVA, df = 1, F = 6.237, p = 0.013, N = 211, Table 3.2).

Table 3.2

Some characteristics of search and entry for red king crabs near an experimental crab pot.

	Crabs not entered, N=203	Crabs entered N=18
Search duration[a] (min±SD)	4.2±6.6	9.6±15.0
Angle searched (degree)	88.8±11.8	112.5±10.5
Entry duration[b] (min±SD)		0.83±0.87

[a] Search duration was from when the crab touched the pot to when the crab either entered the pot or left the pot.

[b] Entry duration was from when a leg was inserted into the entrance to when the crab entered completely into the pot.

Search duration and angle searched were significantly different between crabs which did not enter and crabs which entered.

Entry

After searching around the pot, a crab might locate the entrances into the pot. Crabs entered the pot by front entering or lateral entering. For a big crab, the chelipeds and walking legs could touch the bottom panel of the pot

before the other legs detached from the entrance, so the crab stepped into the pot. However, a small crab had to fall into the pot because its legs were not long enough to reach between the entrance and the bottom panel.

Crabs had a low entry success rate (No. entry/No. approaches) (Figure 3.8). There was no significant difference among the four crab groups (Kruskal-Wallis statistic = 0.699, p = 0.873, DF = 3, N = 52). The overall entry success rate proportionally was 0.081 (18/221) for all crabs. The entry rate (No. of crabs entered/No. of crabs approached) varied from 0.20 for juvenile females to 0.27 for sublegal males (Figure 3.8), with a mean of 0.23 (±0.03 SD) for all crabs. In one trial, one legal male which entered exited but re-entered the pot again after searching on the tunnel.

The entry rate and the number of approaches per crab had a linear relationship, if the two extreme points at high approach number were excluded due to the few crabs which approached (Figure 3.9).

Forty-seven percent of crabs which entered approached from sector I and II, while 72.2% (13/18) of crabs which entered the pot entered from the downstream entrance (located in sector I and II). The upstream entrance had a similar pattern: a few more crabs entered (27.8%, or 5/18) than crabs approaching (21.1%) from sector V and VI. Crabs which approached from sector VII and VIII might enter not only through the downstream entrance, but also via the upstream entrance (Figure 3.10). The crabs which entered

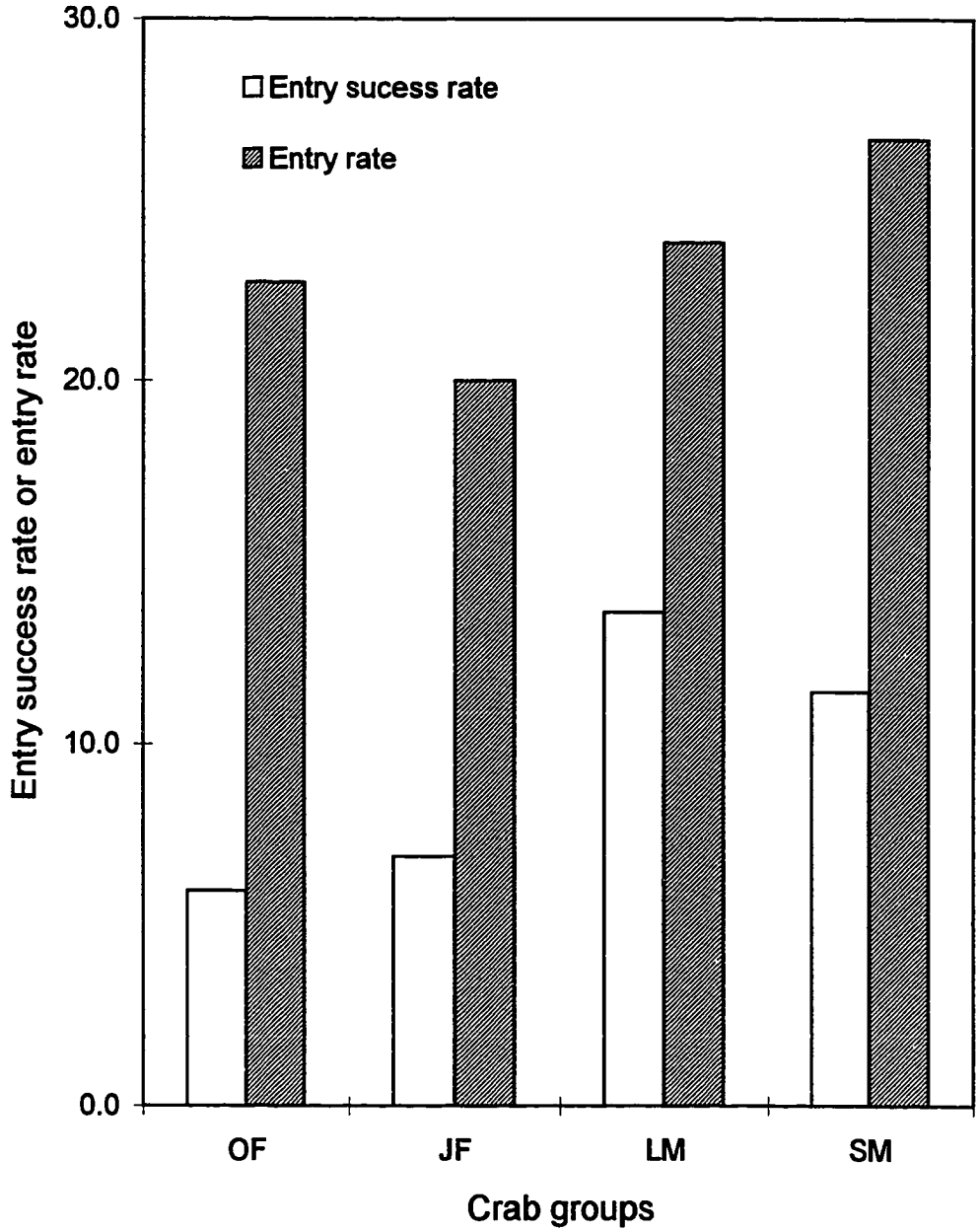

Figure 3.8. Entry success rate (=No. of entry/No. of approaches) and entry rate (=No. of crabs entered/No. of crabs approached) in two hours.

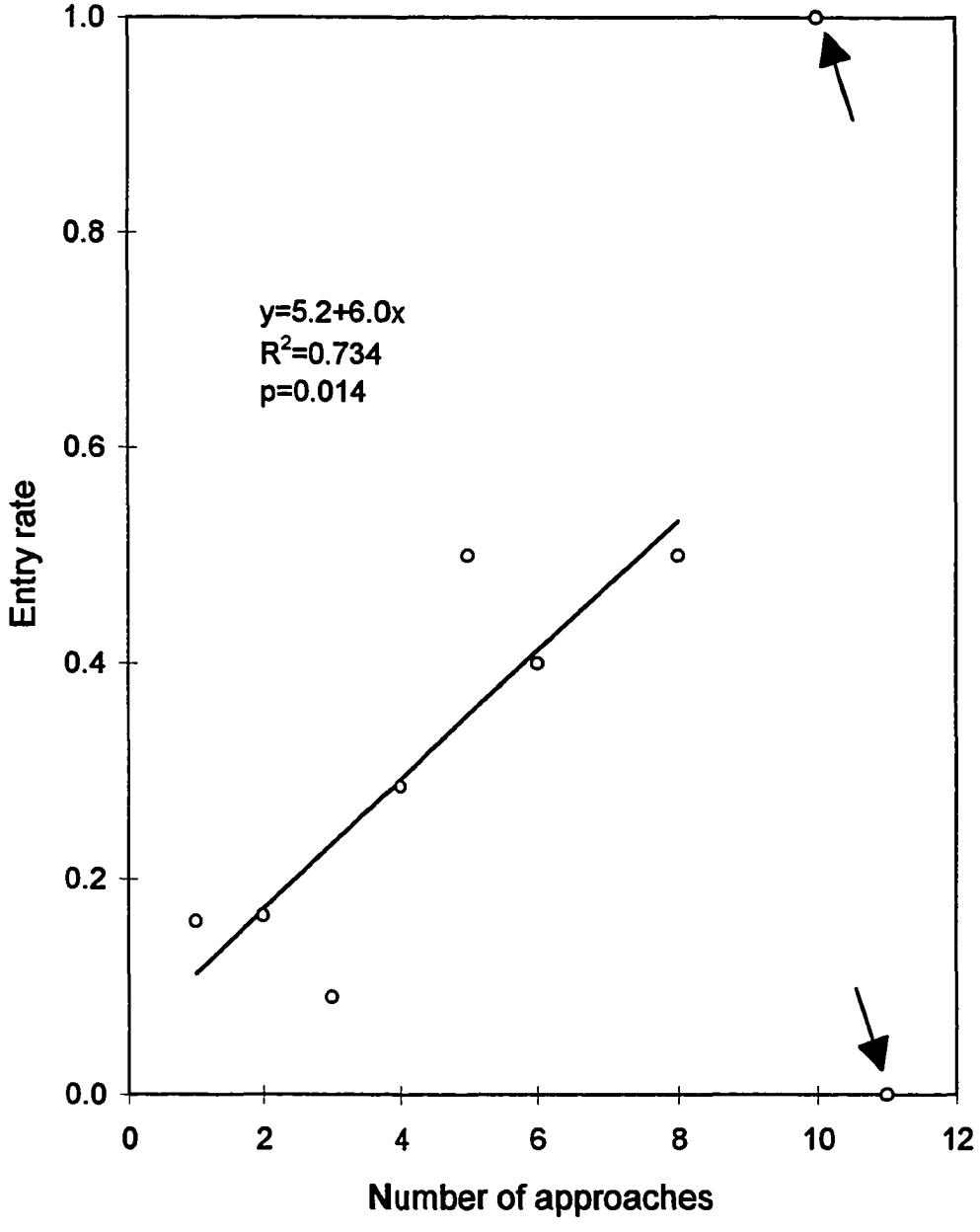

Figure 3.9. Relationship between the number of approaches and entry rate (No. of crabs entered/No. crabs approached). The two points for entry rate=0 and 1 were treated as outliers due to the low number of crabs approaching.

from upstream behaved differently from the crabs which entered through the downstream entrance. On the tunnel of the downstream entrance, crabs appeared to move up and down, and from left to right quite a bit before entering, apparently following the bait odor. Their movement efforts were in hurried, direct, bound, and strong gaits. Some crabs left after moving around for a period, while some found the entrance and entered. In contrast, when crabs approached from upstream, they usually either left shortly after touching the pot, or crawled directly up the tunnel and entered the pot. It seemed that these entries were not by exploring the odor but by wandering. Compared to crabs which entered from downstream, they exhibited their behavior in sustained time, unfocused direction, free flow, and light weight. Similar behavior was observed at least once in the downstream entrance in an escape experiment where a legal male reentered the pot without bait.

Entry duration (from the time when the first leg was inserted into the entrance to the time when the crab was completely inside the pot) ranged from 0.22 to 3.02 min with an average of less than 1 min (Table 3.2). Although legal males required a longer time than females to enter the pot, the null hypothesis of no difference for the four crab groups could not be rejected (ANOVA, $F = 3.253$, $p = 0.06$, $DF = 3$, $N = 18$, statistical power = 0.733 at $\alpha = 0.05$, or 0.85 at $\alpha = 0.10$).

Crabs assumed different body positions while entering the entrance.

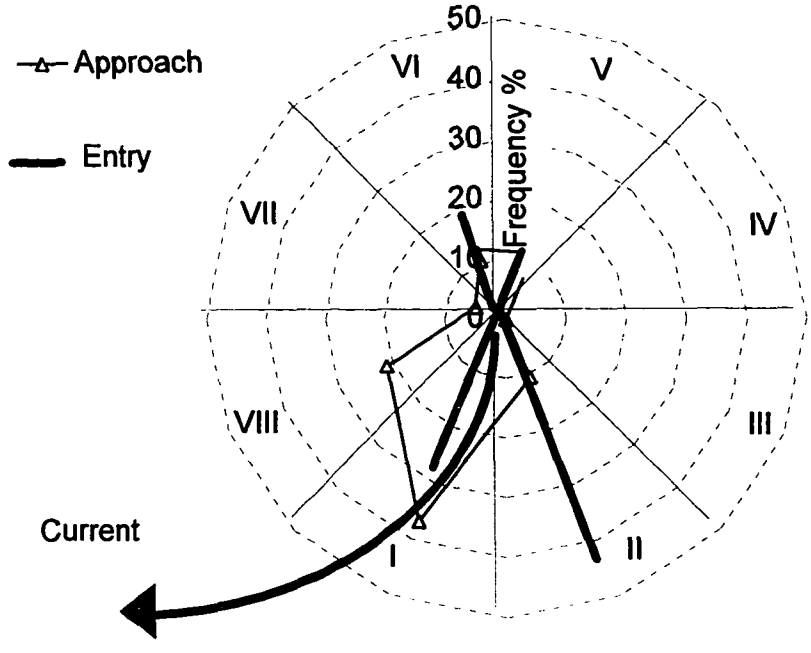

Figure 3.10. Approach frequency and entry frequency for crabs which entered the pot with regard to current direction.

Most crabs (52.9%) entered anterior end first, 29.4% with their right legs entering first, 11.8% with their left legs entering first, and 5.9% with the right anterior-lateral side directed forward. These frequencies of entering position were statistically significant (G-test, $p = 0.006$, $DF = 3$, $N = 18$). However a conclusion could not be made on whether crabs preferred entering with their right legs first or with their left legs first (Fisher's exact test, $p = 0.398$), due to the low statistical power (power = 0.23 when $\alpha = 0.05$).

Escape attempts

Crabs were inactive after being placed in the pot. While moving, they moved slowly within a small range, or might crawl on other crabs. When a few crabs remained inside the pot after the others had escaped, they appeared to spend more time in the upstream direction. Occasionally, crabs climbed the side panels, upper and lower tunnel panels, or even hung onto the top panel.

Escape attempt rate [EAR, No. of attempts/(No. of crab in the pot*h)], was calculated over an interval of 6 h. The EAR differed among crab groups and time (ANCOVA, $p = 0.001$, $DF = 3$, $N = 108$ for crab groups, and $p < 0.001$, $df = 5$ for time). However, significant differences existed only between legal males and others, but not within OF, JF, and SM (ANCOVA, $p = 0.509$, $df = 2$). The EAR increased and then decreased for OF, JF, and SM (Figure

3.11) with a mean of 8.2% $h^{-1}.crab^{-1}$ (± 0.046 SD). Legal males had a lower and more constant EAR (mean 1.9% ± 0.007 SD).

For crabs which failed to escape, the escape attempt duration (EAD, duration when a crab was associated with a panel other than the bottom) did not differ by crab groups (ANCOVA, p = 0.143, DF = 3, N = 85), but changed with time (ANCOVA, p = 0.027, N = 85). The EAD increased slightly with time (t in hour) a crab was in the pot, [log(EAD) = -1.157 + 0.007t, R = 0.18, N = 85]. The EAD ranged from 1.2 min to 106.8 min, with a mean of 10.3 minutes (± 14.9 SD).

Crabs had a preference in escape attempt location. More crabs (73 out of 109, or 70.0%) crawled on the panel close to the tank wall (panel B) than on the panel closer to the center of the tank (panel A) (Friedman's test, p = 0.046, df = 1, N = 109). This preference was similar for all crab groups (G-test, p = 0.526, DF = 3). Only large males could reach the entrance from the bottom panel (Table 3.3). Interestingly, four crabs which already had crawled out the entrance went inside the pot again.

Escape

Most crabs began escape from side panel. When crawling on one side panel and reaching the corner between a tunnel and the side panel, the crab extended one or more walking legs or a cheliped across to the tunnel. After

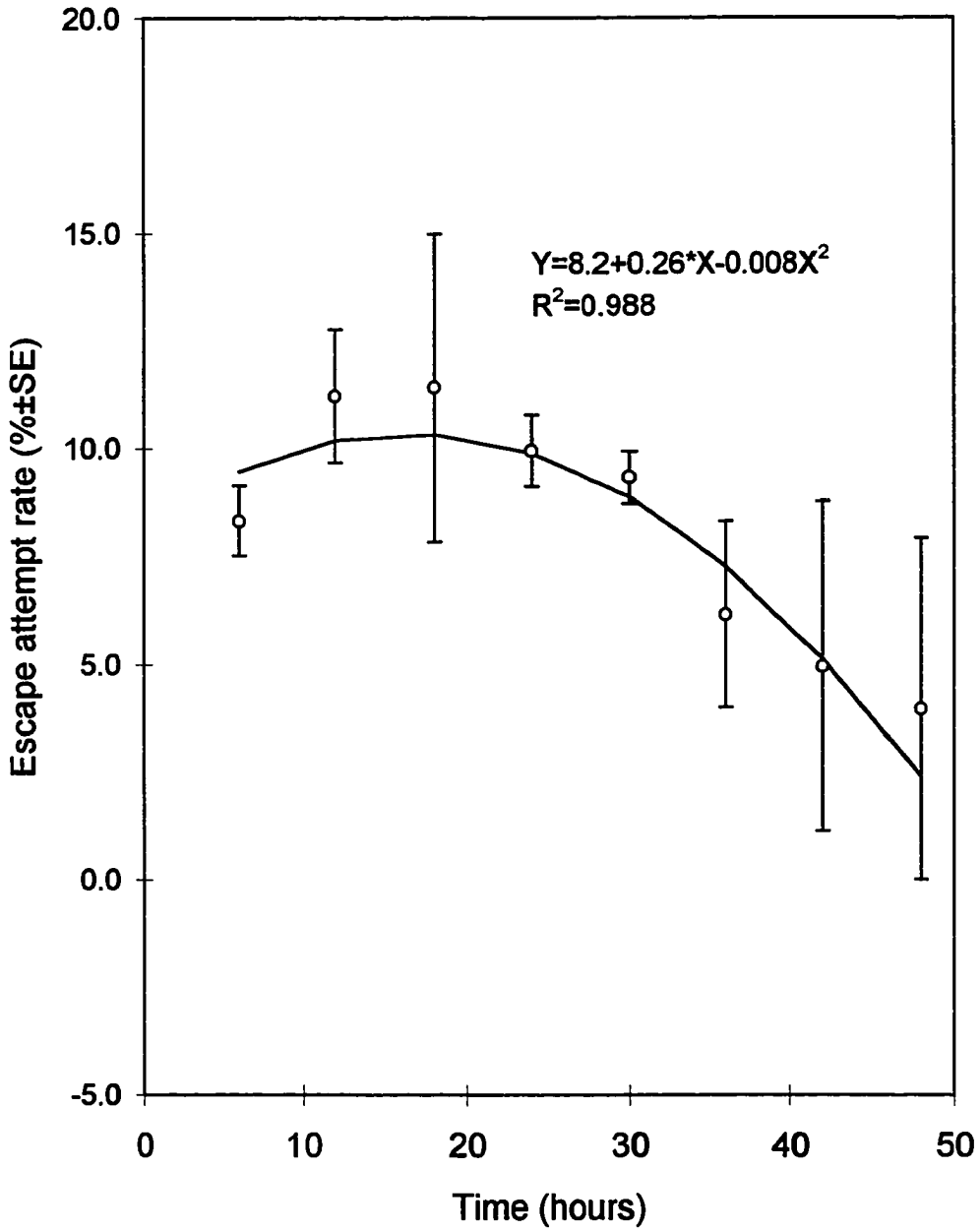

Figure 3.11. Escape attempt rate (No. escape attempts.crab^{-1}.h^{-1}) over time for red king crabs in an experimental pot , excluding legal males.

Table 3.3

Escape attempt duration (EAD, mean±SD) and the escape attempt location (EAL, expressed as the number of attempts) for crabs which failed to escape.

		Ovigerous Female	Juvenile female	Legal male	Sublegal male	Sum (%)
EAD (min)		12.5±14.3	8.2±6.2	5.2±5.3	11.6±20.0	10.3±14.9
EAL	A	10	13	3	10	36(31.0)
	B	22	16	7	28	73(62.9)
	Top	2			1	3(2.6)
	Bottom			3	1	4(3.4)

A = panel closest to the center of the tank; B = panel closest to tank wall; Top = top panel; Bottom = bottom panel. No significant differences were found in EAD and EAL between the four crab groups.

landing on the entrance, the leg(s) contracted and pulled the body over to the entrance with the assistance of the other side legs pushing on the side panel. As soon as legs of both sides of a crab were on the tunnel, the crab just readily walked out of the pot. Only large crabs could start escape from the bottom panel. A crab underneath the tunnel grasped the mesh of the lower tunnel with chelae. Chelipeds and the first walking legs groped up toward the entrance while the third walking legs stepped backward and extended to raise the body. When the first walking legs and the chelipeds reached the entrance opening,

the crab climbed up and exited.

The escape rate (No. crabs escaped/initial No. crabs) in two days experiment ranged from 12.5% (2/16) for legal males to 56.3% (9/16) for females. OF, JF, and SM had significantly higher escape rates than legal males (G-test, $p = 0.022$, $DF = 3$), but no difference was found within these three crab groups (G-test, $p = 0.920$, $df = 2$) (Figure 3.12). The mean escape rate for these three groups was 54.2% ($\pm$ 0.298 SD, $N = 12$). Most crabs escaped by starting from the side panels (Table 3.4), which is difficult in standard pots because of a wider gap between the side panel and the entrance. If escapes from the side panels were excluded, only male crabs escaped and the mean escape rate in two days was only 4.7%.

All crabs but one escaped only from the entrances. A juvenile female escaped through a mesh opening near the bottom panel. This crab measured 90.1 mm in CL and 95.5 mm in CW, and the mesh size was 152.4 mm. It required 18 min for the crab to squeeze through the mesh.

Legal males had the lowest escape success rate (ESR, No. crabs escaped/No. escape attempts) (Figure 3.12). However, I could not reject the null hypothesis of no differences between the crab groups (G-test, $p = 0.527$, $DF = 3$). The lower escape rate of legal males was mainly due to the low EAR rather than the ESR.

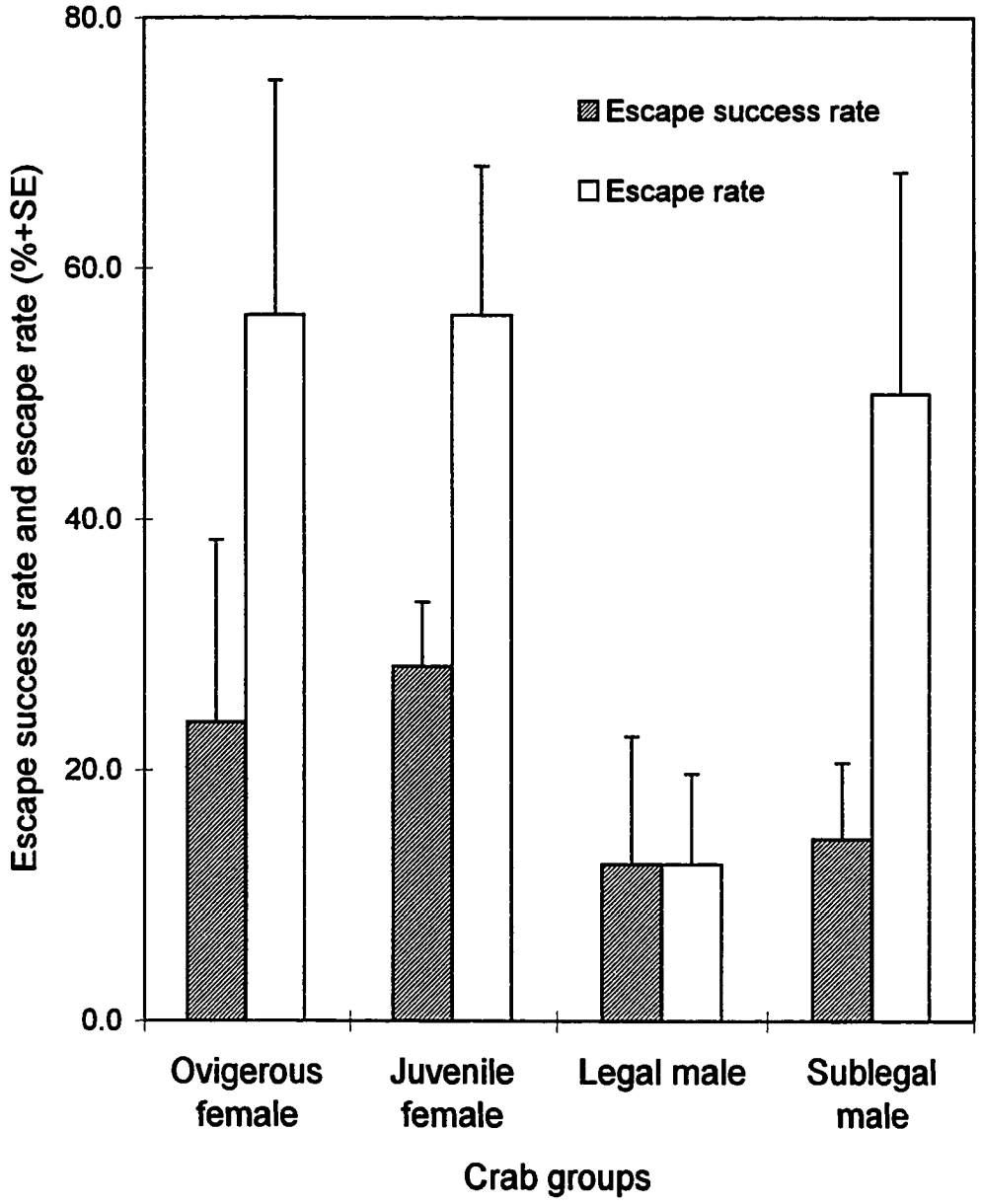

Figure 3.12. Escape rate (No. of crabs escaped/initial No. of crabs) in two days, and escape success rate (No. of crabs escaped /No. of escape attempts).

Table 3.4

Escape behavior

		Ovigerous Females	Juvenile Females	Legal Males	Sublegal Males	Sum (%)
Start from	Panel A		3		5	8(28.6)
	Panel B	9	6		2	17(60.7)
	Bottom P.			2		2(7.1)
	Top panel				1	1(3.6)
Escape entrance	Down stream	2	6		3	11(39.3)
	Up stream	7	3	2	5	17(60.7)
Escape position	Right	4	8	1	6	19(67.9)
	Left	3	2	1	2	8(28.6)
	Front	1				1(3.6)
EAD (min)		7.2±7.8	6.6±4.8	3.6±2.4	6.6±3.6	6.6±5.4
ED (min)		1.1±0.8	1.49±0.9	1.0±0.8	1.8±1.8	1.4±1.2

Panel A = panel closest to the center of the tank; Panel B = panel closest to the wall of the tank; Escape position = the first side of the body entering the entrance; EAD = escape attempt duration (mean±SD); ED = escape duration, from the time when the first leg inserted the entrance to when the crab was completely out of the entrance (mean±SD). No significant differences were found in escape behavior between the four crab groups.

The cumulative escape rate for all crab groups indicated an exponential function of time (Figure 3.13). At the end of 48 hours, the escape rate reached 43.75%.

Because the simulated pot had a narrower gap between the side panel and the entrances than a standard commercial pot, it was easy for crabs to crawl from the side panels to the entrances. Most crabs (89.3%) initiated their escape from the side panels. As in the escape attempt, more crabs preferred to escape from the panel close to the tank wall than from the panel close to the center of the tank (60.7% versus 28.6%). However, the null hypothesis of no differences in preference of side panel could not be rejected ($\chi^2 = 3.24$, $p > 0.05$, $df = 1$, statistic power = 0.73 at $\alpha = 0.05$). More crabs escaped by their right side than by their left side ($\chi^2 = 4.48$, $p < 0.05$, $df = 1$). No differences in the escape attempt duration (ANOVA, $p = 0.815$, $DF = 3$, $N = 28$) and escape duration (ANOVA, $p = 0.677$, $DF = 3$, $N = 28$) were found between the four crab groups (Table 3.4).

DISCUSSION

The dependence of forage, approach, and search on chemotaxis

Decapods possess a well-developed chemical sense. The chemoreceptors in crustaceans take the form of hairlike setae (sensilla) on the external cuticle. The distribution of chemosensory sensilla occur at multiple

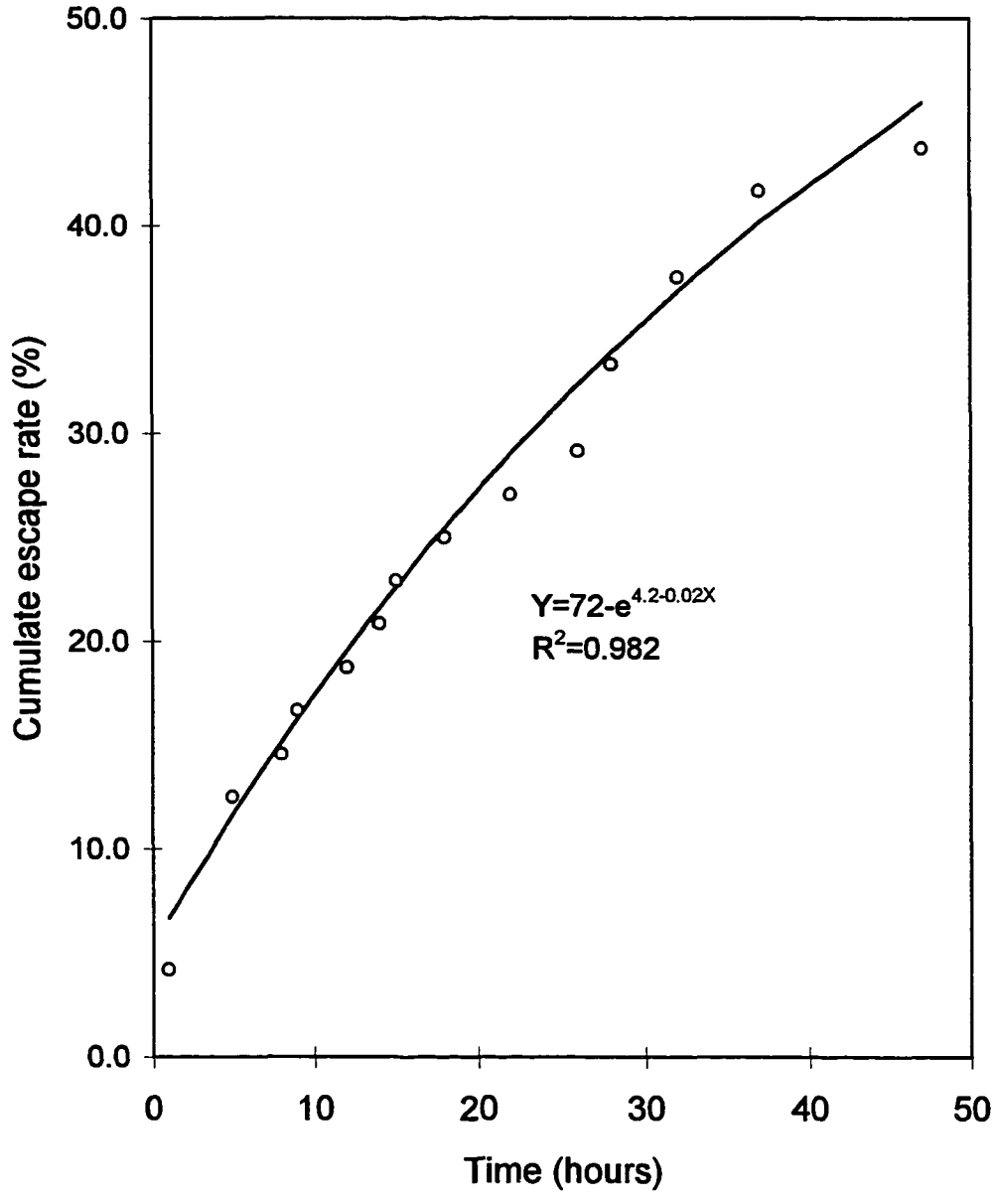

Figure 3.13. Cumulative escape rate (No. of crabs escaped/total crabs used) for all crabs combined in two days.

loci on the body and appendages, but the entire cuticle is not chemosensitive. The first antennules, the pereiopod dactyls, and mouthparts are the primary chemosensory organs of decapods (Ache 1982). The function of the antennules has been studied more thoroughly than that of the other chemosensory systems. While the lateral antennular flagella appear to be involved in initiating search and in determining the direction of odor sources (Devine and Atema 1982; McLeese 1973, 1974), the walking legs are used primary for local food searching and recognition (Derby and Atema 1982).

Like many other crustaceans, red king crabs are directed to potential food resources by chemotaxis, i.e., by tracking chemical cues. This behavior is an orientation reaction in which bilateral balance is the essence of the reaction (Fraenkel and Gunn 1961). In an ideal chemotaxis, the animals align themselves in the direction of the stimulus and move straight towards it. The chemical stimulus must be continuously received to sustain the behavioral response. McLeese (1973) reported that orientation of lobsters resulted chiefly from differential stimulation of bilateral chemoreceptors, with the animal turning or moving toward the side of maximum stimulation. In an experiment on attraction of predatory blue crabs (*Callinectes sapidus*) to odor released by clam prey, Zimmer-Faust et al. (1995) found that both rheostaxis and chemotaxis were necessary for successful orientation. Perception of chemical cues caused crabs to move in the upstream direction, but feedback

from attractant distributions directly regulated movement in the plume. Blue crabs frequently approached the lateral edges of plumes as they walked upstream towards an attractant source. When crabs did reach the edge, they nearly always turned directly back to the plume (Zimmer-Faust et al. 1995). Orientation mechanisms used by crabs differ from those employed by flying insects. Crabs rely more heavily on spatial aspects of chemical stimulus distributions because their fluid dynamic environment creates a more stable plume structure thus permitting chemotaxis (Weissburg and Zimmer-Faust 1994; Zimmer-Faust 1995).

Moore et al. (1991) showed that the chemotactic orientation of lobster (*Homarus americanus*) occurred in three different phases. Initially (far from the source), the odor cue switched the lobster into a different state: sampling the local area to determining an initial source direction. During this initial phase, lobsters accelerated and began to walk more directly toward the source. At an intermediate stage, both the walking speed and headings toward the source were constant. During the last stage when the animals were close to the source, they switched from a distance orientation mediated by the antennules to a local food search mediated by the walking legs. Red king crabs reacted similarly, and their foraging tracks appeared to meander when crabs moved close to the pot. This phenomenon may be due to odor plume characteristics. Since the bait was hung 25 cm off the bottom, the odor may

not reach the floor near the pot, and the strongest odor close to the bottom is assumed to be some distance downstream from the pot. Observations on the behavior of snow crab (*Chionoecetes opilio*) revealed that when the current was weak, crabs approached the trap and concentrated under or close to the trap. As the current intensity increased, the crabs moved away from the trap. This appearance was identified as an "attraction tunnel" (Vienneau et al. 1993). Miller (1980) observed that dye releases revealed a horizontal angle of dispersion of 30°, and he assumed that the vertical angle of dispersion was also 30°. He expressed the relation between the height of the bait above the crabs (Y) and distance downstream (X) before the bait odor reached the crab as: $X = Y\cot\theta$ (here $\theta = 15°$). Some king crabs foraged downstream but did not approach the pot. This result may be explained by the bait plume being too high near the pot, and the crabs lost the odor while following it. Also, turbulence within the water flow causes a fluctuating odor signal (Moore and Atema 1991). Perception of chemical cues biases locomotion upcurrent, and feedback from the odorant stimulus distributions regulates subsequent stopping and turning while crabs approach the bait (Weissburg and Zimmer-Faust 1994). When following a chemical cue, crabs need to detect a difference in concentration between the strongest stimulus and background. The sensitivity of receptors in detecting the threshold of "just noticeable

difference" (Zimmer-Faust 1991) must be important to ensure a more direct forage track.

The nervous system of decapods is simple compared to vertebrates and chemotaxis is less flexible behavior (Fraenkel and Gunn 1961). Because of the requirement of symmetry in chemotaxis, it is understandable that a majority of crabs only searched a narrow range around the pot. When crabs searched around the pot, the necessity of continuous perception of chemical cues limited the searching activity within the range of the odor plume. Miller (1980) observed that when the trap was set so the entrance was not downstream of the bait, *Cancer irroratus* at the side of the trap very closely tracked meanders of the current carrying the bait and dye plume, often moving only a few centimeters to the left or right of the dye. In this study, 78.3% of the crabs searched within 90° of the downstream entrance, similar to sand crab (*Portunus pelagicus*), where approximately 70% of the crabs searched less than 90° around cylindrical pots (Smith and Sumpton 1989). Because crabs are so dependent on bait odor, and the current in the field only flows in one direction during a certain period, these factors are important in the design of traps. If chemotaxis is the only mechanism leading crabs to search for the entrance, no difference in search angle should occur whether the pot is rectangular or round.

In many studies, there are low entry success rates because the entrances are oriented in a direction other than parallel to the current. For example, the entry success rate for *Cancer productus* was only 0.07 when the entrances were perpendicular to the current, but it increased to 0.65 when the entrances were parallel to current (Miller 1979a). The orientation of entrances with regard to current had a similar effect on the entry success rate of red king crabs (Zhou and Shirley, unpublished data).

While most crabs entered from the downstream side, a few crabs entered from the upstream side. Behavior of crabs that entered from upstream indicated that they wandered into the pot rather than being led into the pot by bait odor.

From this study as well as other studies on decapod responses to baited traps, one conclusion that can be reached is that the response of crabs and lobsters to baited traps is simple and inflexible: they are restricted to following the chemical cues. Foraging track, approach direction, and search angle are all dependent upon the essential factor--bait odor.

Escape attempt and escape behavior

Crabs placed in the pot appeared inactive, as reflected by the low escape attempt rates. However, when crabs entered the pot themselves while searching for the bait, they were more active, and continuously moved about.

Consequently, these crabs achieved a higher escape rate (Zhou and Shirley, unpublished data). Tracing the odor within a pot with bait must have played a role in stimulating crab activity. Crabs may be shocked by handling when being placed in the pot and have low activity. The initial state of activity may affect the subsequent behavior within a limited period. If this is also true in the field, the escape rate from experiments in which crabs were placed in pots may be conservative when extrapolating to a fishery or from lost pots (High and Worlund 1979; Stevens et al. 1993).

While inside the pot, crabs tended to stay on the upstream side of the pot, and had a preference in crawling on the side panel where the current speed was higher and in escaping from the upstream entrance. This behavior has been observed in the field (Stevens et al. 1993). Red king crab larvae were positively rheotatic (Shirley and Shirley 1988). Rheotaxis may function continuously with ontogeny. Both rheotactic and chemical information are necessary for successful orientation (Weissburg and Zimmer-Faust 1994, Zimmer-Faust et al. 1995).

The average escape rate of 54.2% in two days for females and sublegal males was very similar to that of 51.7% in a field study (High and Worlund 1979). Also, the exponential patterns of escape rate over time were very close between the two studies, although the size of pots may affect the escape rate.

Larger traps may have a different threshold for generating an escape attempt (Munro 1974).

More crabs escaped by exiting the pot going to their right than to their left (67.9% vs. 28.6%). This dominance may be ascribed to the asymmetric structure of the cheliped. Red king crabs have a larger and longer right cheliped than left one (Zhou and Shirley, unpublished data). The right cheliped must be more powerful and predominantly used in attack and defense. Significantly higher rates of injury and loss for the right cheliped in red king crabs and blue king crabs (*Paralithodes platypus*) may have been for the same reason (Niva and Kurata 1968; Ivanov 1994). However, this preference for the right side was not observed in the field where 12 escapes were observed (Stevens 1993).

Sex and size variability

No significant difference in behavioral responses to pots existed among the four crab groups, except that legal males had a significantly lower escape attempt rate and the ensuing escape rate than did females and sublegal males. This low escape attempt of males may be ascribed to their molting activity. However, the early symptoms of molting were difficult to detect until two or three days before molting. In decapod fisheries, catchability slowly decreases as ecdysis approaches, then drops to near zero for several days before and

after ecdysis (Miller 1990). In a previous study, male red king crabs molted earlier in the winter than females. During the molting season male crabs had a lower feeding rate than females even when the data that were taken between ten days before and ten days after a crab molted were excluded (Zhou and Shirley 1996).

Pot efficiency

The entry success rate of 8.1% was low. In an experiment using cylindrical pots, sand crabs had an entry success rate of 27.5%, although the definition of approach was slightly different than in my study (Smith and Sumpton 1989). Nevertheless, the low entry success rate in king crabs is close to that reported for the lobster (*Homarus americanus*). In a long term observation (2 months) on lobster response to baited traps, only 11% of the approaches resulted in entry (Karnofsky and Price 1989). *Cancer irroratus* and *Hyas araneus* had 20.3% and 12.1% entry success rates to a top entry pot, respectively (Miller 1978).

The entry success rate of this study is assumed to be an ideal one for the pot, since the pot entrances were parallel to the current, so that the bait odor passed close to or through the downstream entrance. The entry success rate is significantly affected by the orientation of entrances to the current (Miller 1980, 1990; Karnofsky and Price 1989, Vienneau et al. 1993).

However, pot orientation is difficult to control in the fishery, so the entry success rate may be even lower in the field.

Most red king crabs only made one approach in two hours. The mean approach number of 2.6 is comparable to other crabs (Miller 1978; Smith and Sumpton 1989). For *Cancer irroratus* and *Hyas araneus*, individuals that gained entry approached a pot the same number of times on average as the crabs that did not gain entry (Miller 1978). However, in my study, red king crabs which entered a pot made significantly more approaches than crabs that did not enter. This positive correlation between the number of approaches and entry success rate is similar to lobster *Homarus americanus* (Karnofsky and Price 1989). The mean number of approaches to achieve success of 3.9 for red king crabs was comparable to spanner crabs entering a cylindrical trap (mean = 3.6), but higher than their entering a box-shaped trap (mean = 2.6) and lower than their entering a top entrance trap (mean = 9.0) (Sumpton et al. 1995).

Crabs gave up attempts to enter after a few false approaches; this shows a waning in responsiveness. This waning may be ascribed to the degradation of bait quality and quantity, the nervous exhaustion between the sensory cells and the effectors, or the adaptation of the sensory nervous system to the stimulus. Because of the waning, easy entry should be considered in new designs of red king crab pots. This is important in the fishery. In the field,

because crabs are not confined to a limited area around the pot and can stray out of the bait odor plume, and other potential food may be available, crabs may leave after fewer unsuccessful approaches than in the laboratory.

Red king crabs which entered pots spent a longer time and searched a wider angle than king crabs which did not enter pots. This result suggests that entry rates should increase if crabs are motivated to search a wider range. By reducing the mesh size so that crabs cannot thrust their chelipeds through the mesh, it may be possible to stimulate crabs to continue moving.

Obviously, the simulated commerical crab pot used in this experiment was inefficient in both allowing crabs entry and allowing females and sublegal males to escape. Only large male crabs could reach the entrances from the bottom panel when escaping. Therefore, king crab pots in current use are designed to confine crabs, especially females and sublegal males that are too big to exit through the mesh. These pots should be replaced with more efficient designs.

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Chapter 4

A General Model Expressing the Relationship Between Catch and Soak Time for Trap Fisheries

ABSTRACT

Catch per trap haul changes with soak time, and should be standardized when utilized to estimate abundance or develop a fishing strategy. Several models have been used to describe catch per trap haul over soak time in trap fisheries. These models have limitations on fishing duration, or have difficulties in parameter estimation. In this chapter I establish a general model without limitations on soak time. The model is expressed as $C_t = ab + a(t - b)e^{-ct}$; C_t is the catch per trap haul at soak time t; a, b, and c are parameters to be estimated. When sufficient data are used, the term ab denotes an asymptotic catch after an infinite soak time, and a and c depend on local animal density, entry rate, and escape probability. These parameters can be readily estimated by many popular computer programs. This general model provides a fit as good as or better than other models to data with short soak times, and is the only suitable model for long soak times.

INTRODUCTION

Catch per unit effort (CPUE) in trap fisheries can be defined as the number or weight of individuals of the target species caught per trap haul, irrespective of the time that the traps have been set (Bennett 1974). Catch per trap unit effort usually does not increase steadily with trap soak time (Bennett and Brown 1979; Kennelly 1989; Miller 1990). When soak time is standardized, CPUE can be converted to an index of abundance (Miller and Hunte 1987; Robertson 1989). A proper model revealing the relationship between catch per trap haul and soak time is essential to standardize the effect of soak time. Several models have been established to describe this relationship (Austin 1977; Bennett and Brown 1979; Munro 1974; Smith and Jamieson 1989; Somerton and Merritt 1986). In a different application, the models have been used to develop fishing strategy (Austin 1977; Miller 1983, 1990). To achieve the economic optimum in a fishery, fishermen should consider the optimum soak time for traps and consequently the optimum investment in fishing gear.

The existing models can be classified into three categories regarding catch versus soak time: a monotonic increase in catch, an maximum asymptotic catch, and a parabolic shape to the catch curve. These models work well for short soak times, but fail when traps are set for a relatively long time. Also, some models do not readily allow parameter estimation with common

computer programs.

The purpose of this paper is to establish a general model to demonstrate the relationship between catch per trap haul and soak time without a time restriction. Also my goal requires that the model be simple enough for easy estimation of parameters by popular computer programs. The nonlinear regression methods in statistical software of SPSS (Norusis 1993) and SYSTAT (Wilkinson 1990) are used for parameter estimation.

DESCRIPTION OF THE MODEL

Before establishing the model for a trap fishery, I made the following assumptions:

1. The bait is the major attractant of animals into the trap;

2. Escape from the trap is possible. The design of the trap may permit the escape of sublegal animals, e.g., by furnishing escape vents. Some trap designs permit escape slowly by chance, e.g., the standard king crab pots (High and Worland 1979). Since many shellfish fisheries are regulated by a size and sex limitation, escape should always occur at least for sublegal-sized animals. Even for entry-only traps which are equipped with inward opening triggers, legal and sublegal animals may escape gradually (Breen 1987; Muir et al. 1984).

The assumptions should result in the following pattern of catch over soak time. The number of entering animals rapidly increases shortly after the trap is deployed. Because of the effect of trap saturation, decline of local animal density, and decrease of bait quality and quantity, entry rate slows and the catch reaches a maximum. The escape rate increases then exceeds the entry rate, so the total number of animals in the trap decreases gradually. As entry may continuously occur and the escape is more difficult than entry, the decline in the number of animals in the trap should be a slow process and may require a long period. Finally the catch approaches an asymptote and remains at this level after an extended soak time. This asymptotic catch may result from two conditions: Some individuals can never escape because of their size and the selective design of the trap; some animals may stray into the trap after the bait is completely consumed, or enter the trap as shelter. Under the later situation, the entry and escape hold a dynamic balance, so the number of animals in the trap will fluctuate around a mean.

This pattern of catch per trap haul (C_t) over trap soak time (t) is shown in Figure 4.1. The shape of the curve is similar to Ricker's recruitment curves (Ricker 1975). Since the catch is zero at $t = 0$, and the catch approaches an asymptote after a long soak time, by adding a constant term $a*b$ and force $a*b = 0$ at $t = 0$, I obtained the following model which can closely simulate the pattern in Figure 4.1:

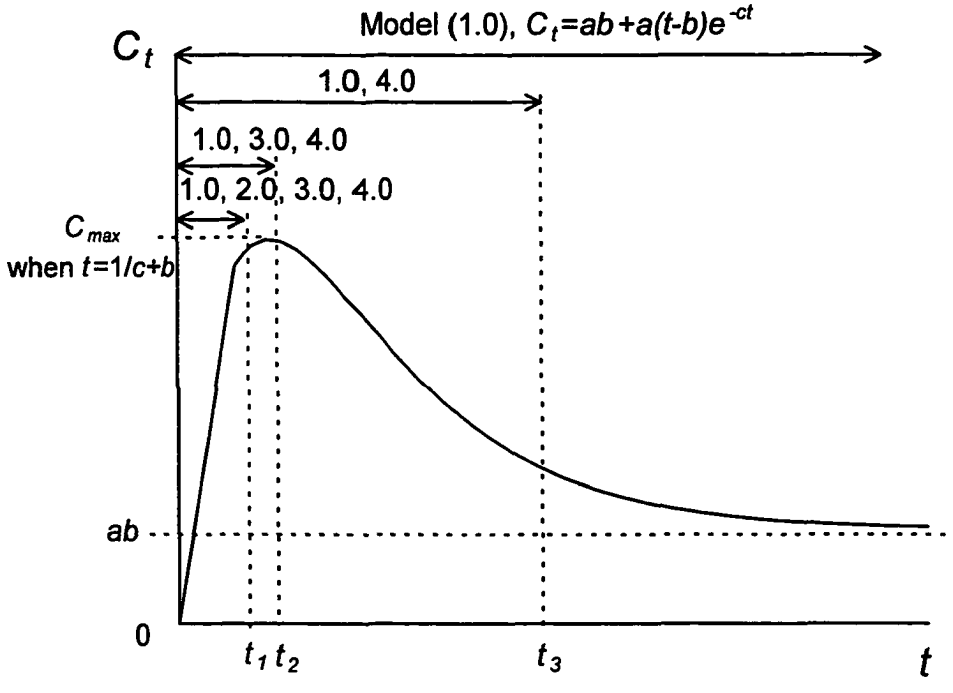

Figure 4.1. The general pattern of the relationship between catch per trap haul C_t and soak time t. Appropriate range and the time limitation on different models (numbers 1.0~4.0) are shown. Model (1.0), $C_t=ab+a(t-b)e^{-ct}$; Model (2.0), $C_t=at^{(1-b)}$; Model (3.0), $C_t=C_\infty(1-e^{-rt})$; Model (4.0), $C_t=aC_\infty(e^{-at}-e^{-bt})/(b-a)$. C_{max} and ab are characteristics of Model (1.0).

$$C_t = ab + a(t - b)e^{-ct} \qquad (1.0)$$

where C_t is the catch at time t, and a, b, and c are parameters to be estimated. When sufficient data are used, the term $a*b$ denotes the asymptotic catch after an infinite soak time, while b forces the catch to zero at time $t = 0$. Parameters a and c depend on local animal density and trap entry rate, while c largely reflects the probability of escape. The time when a trap reaches its maximal catch can be obtained by

$$C_t' = a(1 - ct + bc)e^{-ct} = 0,$$

to have $t_{max} = 1/c + b$. So the maximal catch C_{max} is

$$C_{max} = ab + ac^{-1}e^{-(1 + cb)}.$$

The trap's size selectivity, and animals' behavior will affect the asymptotic catch, the value of ab. If the trap allows all animals to escape, and none will enter it without bait, then the trap will be empty after a long soak time, i.e., $b = 0$, and the model simplifies to

$$C_t = ate^{-ct} \qquad (1.1)$$

The advantages of Model (1.0) and Model (1.1) are significant: it is a general model for trap fisheries without a soak time limitation, and it can be readily estimated by many common computer programs such as statistical or spread sheet software.

APPLICATIONS OF THE MODEL AND COMPARISON WITH OTHER MODELS

Three types of models have been used to describe the relationship between catch and soak time. The simplest one incorporates a power function (Austin 1977; Cleaver 1949; Miller 1983):

$$C_t = at^{(1-b)} \qquad (2.0)$$

or

$$C_t/t = at^{-b} \qquad (2.1)$$

Since it predicts a constantly increasing catch with soak time, this model can only be appropriate for a short duration (Figure 4.1, $t < t_1$).

The maximum asymptotic catch model is applied most widely in the literature (Bennett and Brown 1979; Fogarty and Borden 1980; Miller 1983; Munro 1974; Robertson 1989; Sinoda and Kobayasi 1969; Skud 1979):

$$C_t = C_\infty(1 - e^{-rt}) \qquad (3.0)$$

The parameter C_∞ has been interpreted as a maximum catch after an infinitely long soak time, and r is a constant controlling the rate at which C_t approaches C_∞. Miller (1983) modified this equation to

$$C_t = C_\infty(1-e^{-r\sqrt{t}}) \qquad (3.1)$$

and found a better fit than Model (3.0) for some data sets. These two equations have a similar pattern except that Model (3.1) approaches the asymptote more slowly than (3.0). To distinguish from the model described in

this paper, Models (3.0) and (3.1) are called maximum asymptotic models. The maximum asymptotic models can be used for unbaited traps, entry-only traps, or normal traps before the catch starts to decline (Figure 4.1, $t < t_2$).

Model (2.0), and Model (3.0) are compared to the general model (Model 1.0) by fitting them to several fisheries data sets. The general model appears to be as good as or better than the other two for short soak times (Figure 4.2, Table 4.1). However, if the catch is continuously increasing, which is the typical results with a short soak time, the parameters in Model (1.0) have multiple solutions. For example, in data set A (Figure 4.2), two sets of parameter estimates, a = 48.88, b = -3.56, c = 0.141, and a = 61.21, b = -5.31, c = 0.114, have the same R^2 = 1.000. Also, since there are only four data points, the parameters have large correlation coefficients (>0.99).

The third type of model includes a term for escape so they have a parabolic shape. Somerton and Merritt (1986) developed the following model for king crab traps fished for Tanner crab:

$$C_t = \frac{aC_\infty}{b-a}(e^{-at} - e^{-bt}) \qquad (4.0)$$

The parameter C_∞ and a have the same meaning as in equation (3.0), while b denotes the probability of escape. Since parameters in this model cannot be estimated directly by many computer programs, the equation was

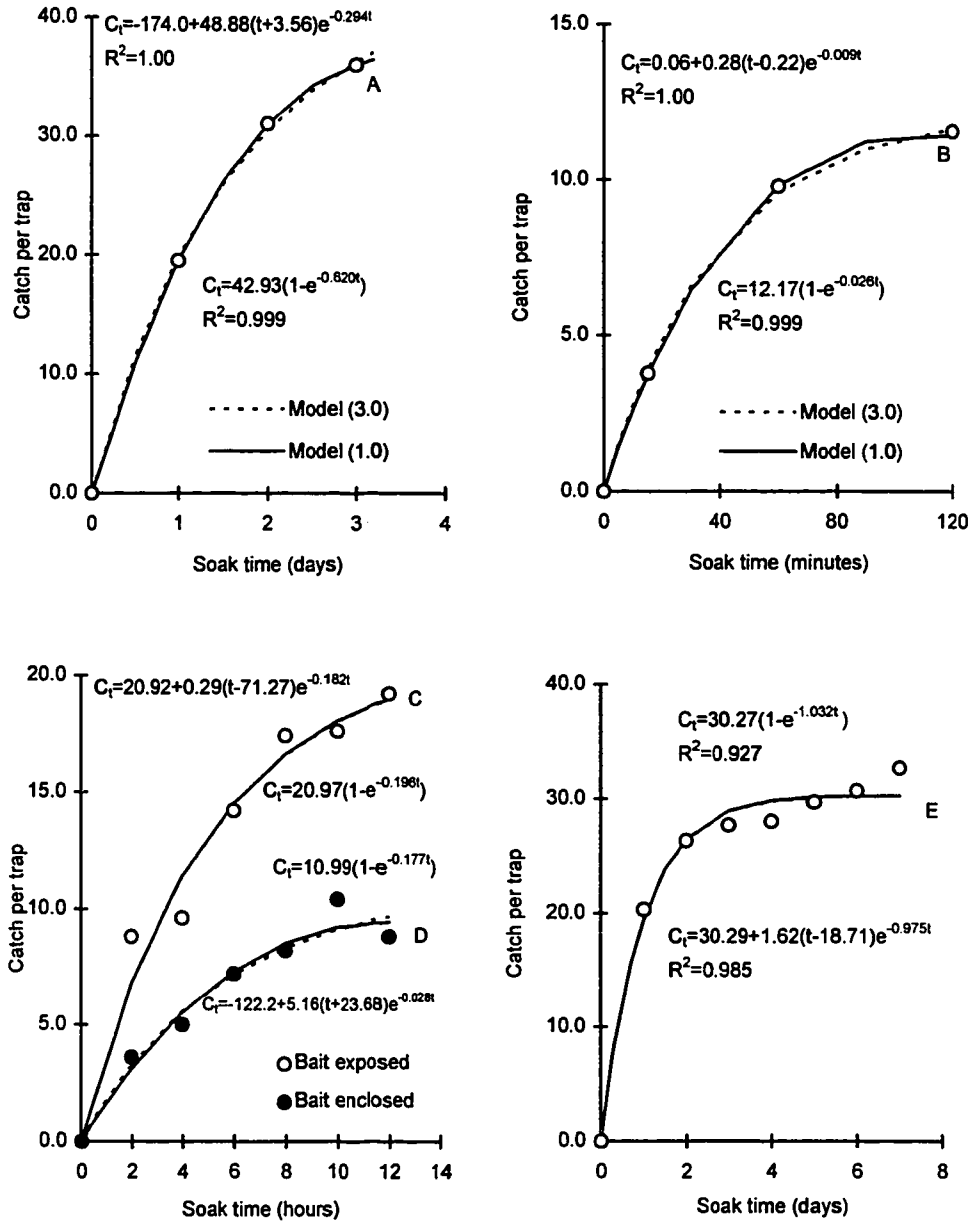

Figure 4.2. Comparison between Model (1.0) and Model (3.0) when fit to data with relatively short soak times, or for entry-only traps. A. *Chionoecetes japonicus* (Sinoda and Kobayasi 1969); B. *Ranina ranina* (Kennelly 1989); C & D. *Cancer productus* (Miller 1979); E. *Chionoecetes bairdi*), entry-only pots, (Somerton and Merritt 1986).

Table 4.1. Parameter estimates of Model (1.0) for the data sets with continuously increasing catch (Figure 4.2), and the comparison of R^2 values for the three models. Para = Parameters, Est = Estimate, SE = Bootstrap estimates of standard error, CI = confidence intervals of the estimates.

				95% CI		R^2 for Models[a]		
Data	Para	Est	SE	Lower	Upper	(1.0)	(2.0)	(3.0)
	a	48.88	4.64	39.59	58.16			
A	b	-3.56	.64	-4.85	-2.27	1.000	.996	.999
	c	.141	.010	.121	.161			
	a	.29	.03	.23	.36			
C	b	71.27	14.09	43.08	99.46	.970	.979	.970
	c	.182	.059	.064	.300			
	a	5.16	3.07	-.98	11.30			
D	b	-23.68	21.01	-65.72	18.35	.968	.952	.962
	c	.028	.019	-.010	.066			
	a	1.62	.19	1.24	1.99			
E	b	18.71	4.11	10.49	26.93	.986	.990	.927
	c	.975	.166	.64	1.31			

[b](1.0) $C_t = ab + a(t - b)e^{-ct}$. (2.0) $C_t = at^{(1-b)}$. (3.0) $C_t = C_\infty(1 - e^{-rt})$.

changed to the number of crabs at time t as a ratio with the number at time 1:

$$\frac{C_1}{C_t} = \frac{e^{-a} - e^{-b}}{e^{-at} - e^{-bt}}, \text{ or } R_t = \frac{A - B}{A^t - B^t} \qquad (4.1)$$

Somerton and Merritt computed the catch ratio R_t from C_1/C_t for each trap, and obtained a relationship between R_t and soak time by nonlinear regression. However, the estimated A resulted in a negative value, and it was an error, since $A = e^{-a} \geq 0$. I was unable to compare the Model (4.0) and (4.1) with Model (1.0).

Smith and Jamieson (1989) constructed a model that involved escape, bait age, and agonistic interactions by considering the net daily change in the number of crabs in a trap as a function of entry and exit rates:

$$dC_t/dt = VR_1R_2 - XC_t \qquad (4.2)$$

Since R_1 and R_2 were nonlinear functions representing the effects of bait and interactions, this equation could not be readily integrated. In addition, as it required considerable effort, the final model which contained 18~24 parameters was not presented. This model also is not compared with Model (1.0) for the parabolic catch.

Model (1.0) provides a reasonable fit for many data sets with parabolic shape (Figure 4.3, Table 4.2). Besides, the parameters a, b, and c are identifiable for typical parabolic catch.

With an extended long soak time, only Model (1.0) can reveal the

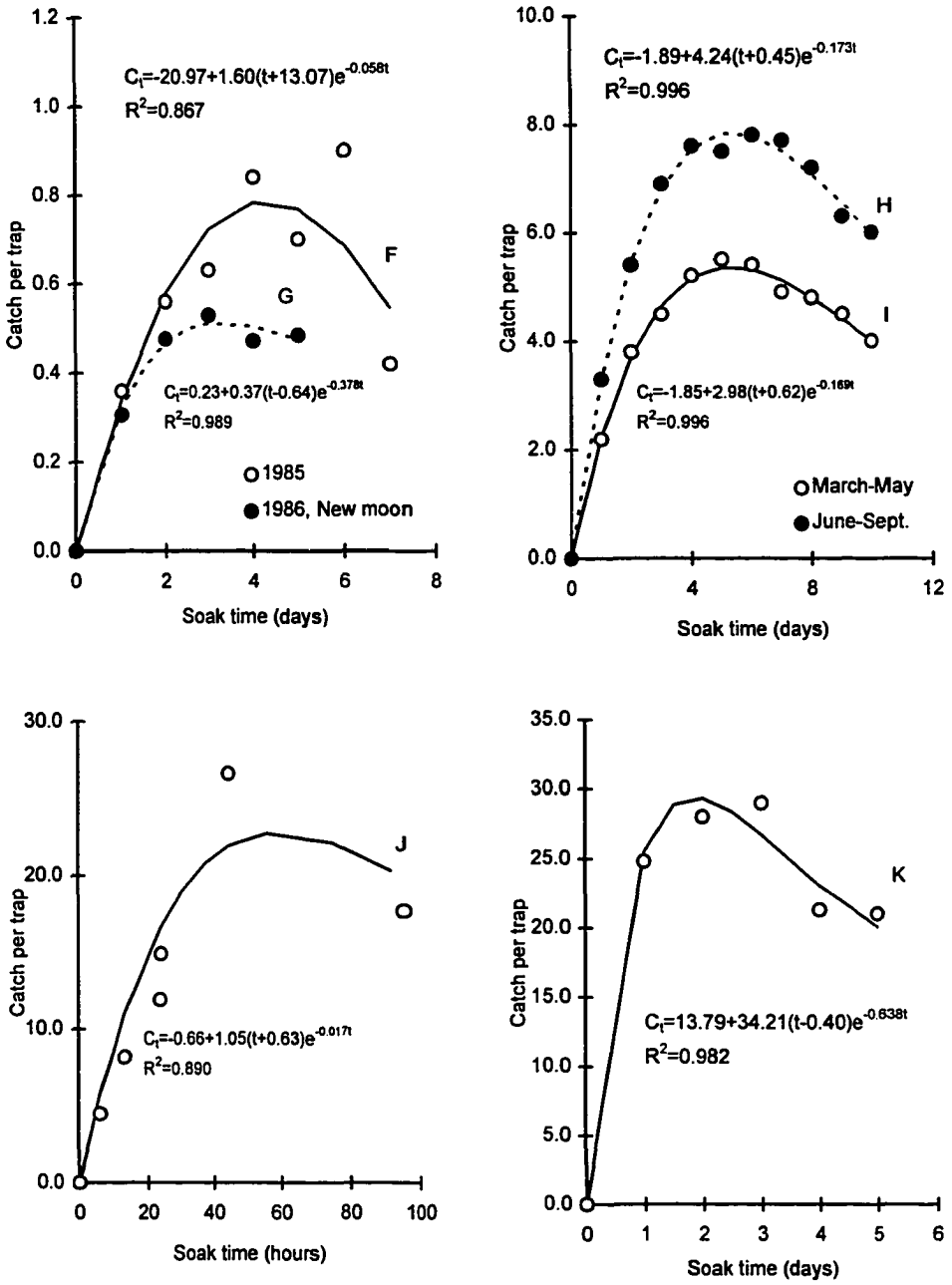

Figure 4.3. Fitting Model (1.0) to parabolic catch over relatively long soak times. F. & G. *Homarus americanus* (Auster 1985, 1986); H & I. *Homarus americanus* (Skud 1979); J. *Lithodes aequispinus* (Sloan and Robinson 1985); *Lutjanus vivanus* (Munro 1974).

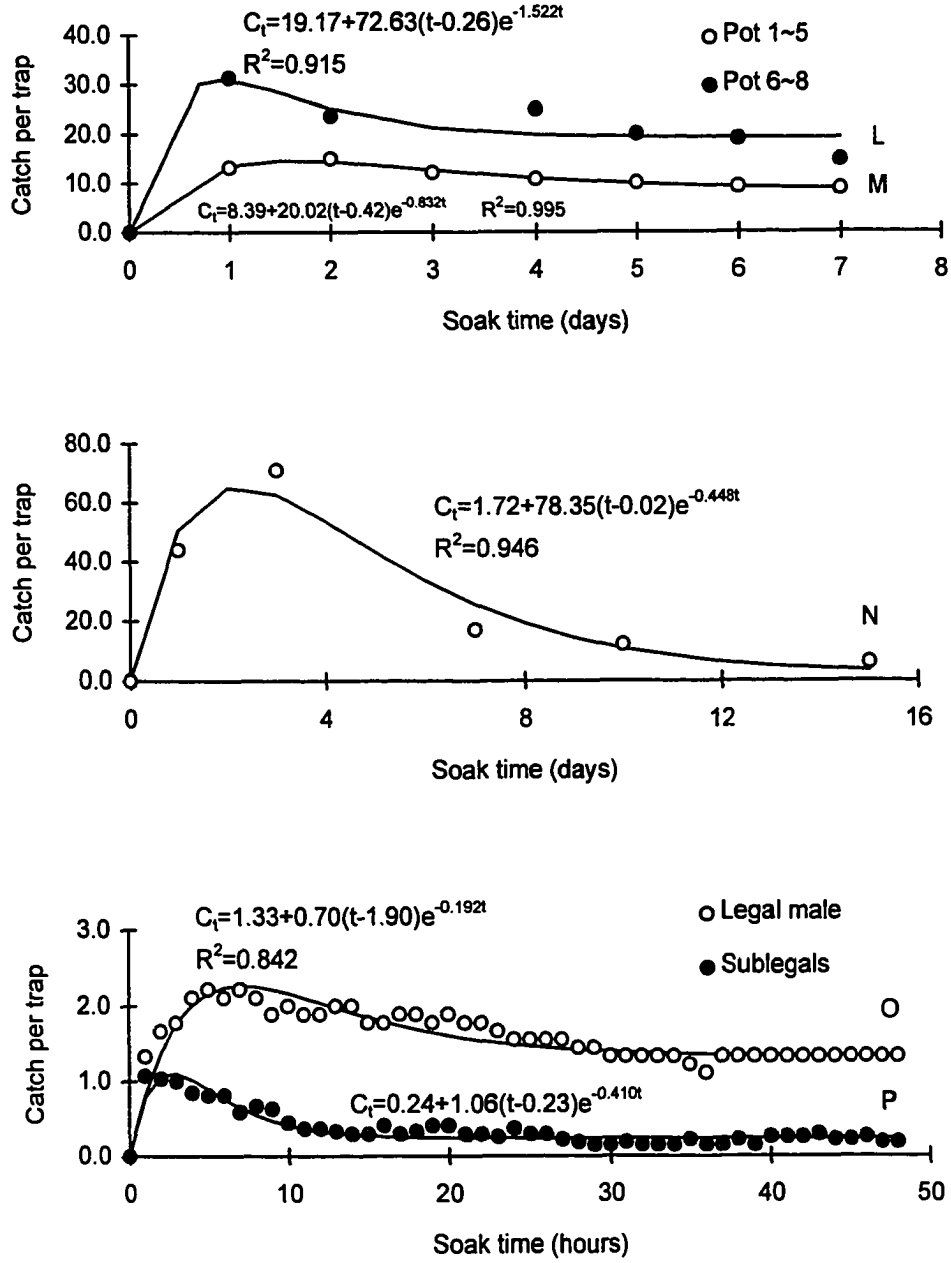

Figure 4.4. Application of Model (1.0) to asymptotic catch with extended long soak times with regard to the time when the catch decline occurs. L. & M. *Chionoecetes bairdi* (Somerton and Merritt 1986); N. *Paralithodes camtschaticus* (High and Worlund 1979); O & P. *Paralithodes camtshcaticus* (Zhou and Shirley, unpublished data).

Table 4.2. Parameter estimates of Model (1.0) for the data sets with parabolic catch (Figure 4.3). The abbreviations are the same as in the Table 4.1.

				95% CI		
Data	Para	Est	SE	Lower	Upper	R^2
	a	1.60	1.09	-.574	3.78	
F	b	-13.07	12.77	-38.61	12.48	.867
	c	.058	.010	.037	.078	
	a	.37	.30	-.23	.96	
G	b	.64	2.55	-4.46	5.74	.989
	c	.378	.706	-1.034	1.971	
	a	4.24	.39	3.46	5.02	
H	b	-.45	.65	-1.75	.86	.996
	c	.173	.018	.138	.209	
	a	2.98	.29	2.40	3.57	
I	b	-.62	.77	-2.15	.91	.996
	c	.169	.023	.122	.216	
	a	1.05	.39	.27	1.82	
J	b	-.63	2.79	-6.22	4.96	.890
	c	.017	.018	-.019	.05	
	a	34.21	32.52	-30.86	99.28	
K	b	.40	.83	-1.26	2.07	.982
	c	.638	.307	.024	1.252	

relationship between catch per trap haul and time (Figure 4.4, Table 4.3). Also, parameters *a*, *b*, and *c* are identifiable. When catch approaches the asymptote, the term *ab* denotes an asymptotic catch. The model can be used by separating crabs into more than one category, such as legal-sized and sublegal-sized ones. This breakdown may allow one to examine the efficiency of trap design. For example, when a trap was exposed to both legal-sized and sublegal-sized red king crabs, significantly more legal crabs were retained than sublegal ones (Figure 4.4, data sets O and P). Unlike in the fishery, data set O and P were successively obtained in the laboratory from the same pots. Since the catch in the same pot was autocorrelated, a systematic error existed between the fitted model and the observed catch, as shown by the residuals (Figure 4.5).

DISCUSSION

Studies on the relationship between soak time and catch per unit effort have occurred for at least five decades, initially in relation to finfish catch by nets and longlines (Miller 1990). Among the several models accepted for trap fisheries, the power function of catch over soak time (Model 2) has limited application because with it catch increases monotonically over time, although it provides good fit within a short period (Figure 4.1, from $t = 0$ to $t = t_1$).

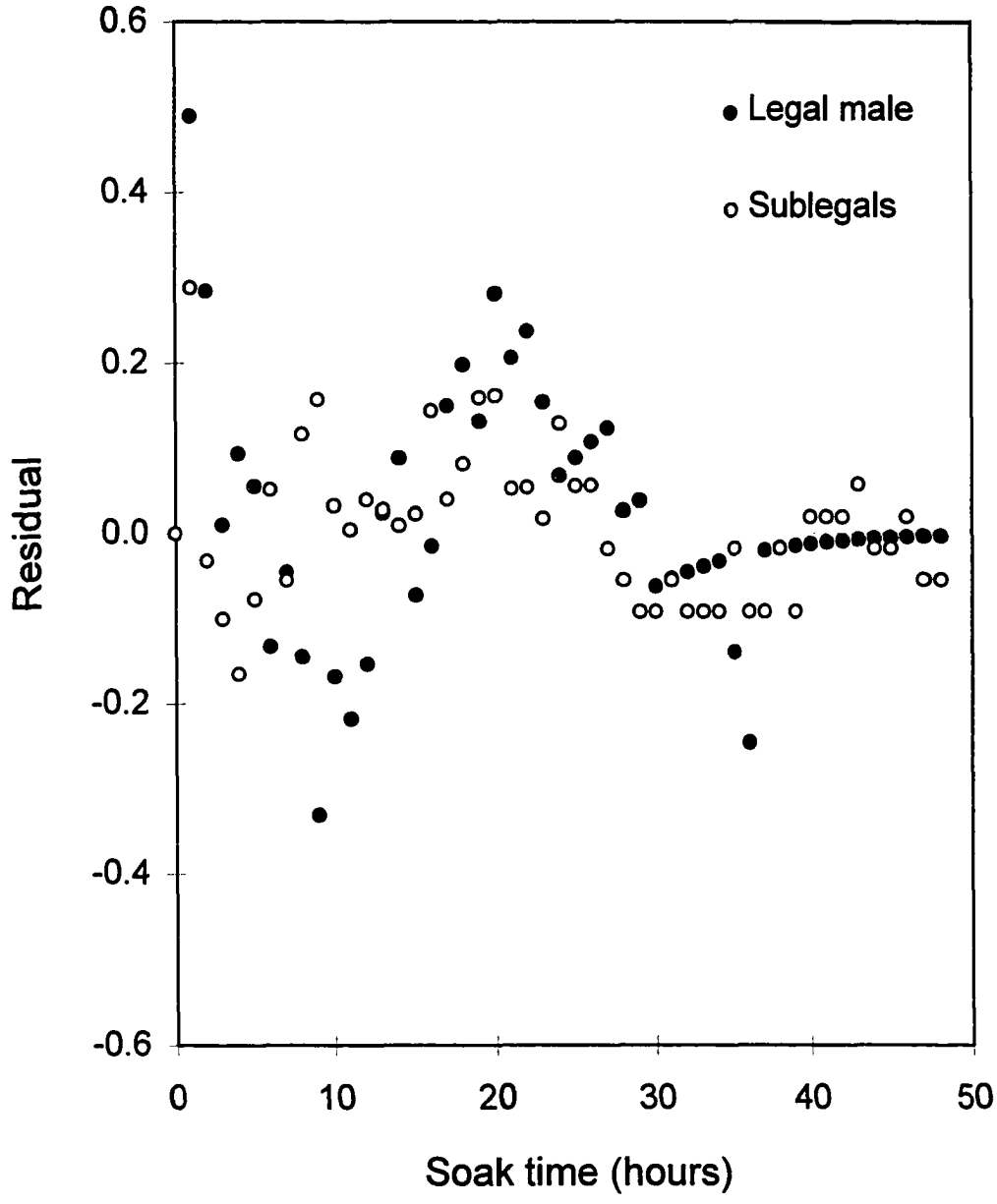

Figure 4.5. Soak time and residuals for Model (1.0) fitted to data sets of O and P in Figure 4.4.

Table 4.3. Parameter estimates of Model (1.0) for the data sets with an asymptotic catch (Figure 4.4). The abbreviations are the same as in the Table 4.1.

				95% CI		
Data	Para	Est	SE	Lower	Upper	R^2
	a	72.63	59.60	-46.47	192.04	
L	b	.26	.12	.02	.51	.915
	c	1.522	.816	-.108	3.156	
	a	20.02	3.58	12.85	27.20	
M	b	.42	.08	.27	.57	.995
	c	.832	.089	.654	1.011	
	a	.70	.09	.52	.88	
O	b	1.90	.22	1.45	2.34	.842
	c	.192	.023	.147	.237	
	a	1.06	.25	.56	1.56	
P	b	.23	.05	.12	.33	.850
	c	.410	.060	.291	.529	

The maximum asymptotic model of $C_t = C_\infty(1 - e^{-rt})$ has been considered as a "typical" catch for trap fisheries (Miller 1983). This model is actually borrowed from the studies on gillnets and longlines fisheries (Gulland 1955; Beverton and Holt 1957). However, trap fishing differs from gillnets and longlines. Fish can hardly escape after they become entangled in a gillnet or on hooks of a longline. In addition, longlines have a fixed number of hooks. Theoretically, a maximum catch of C_∞ can be reached after an infinitely long soak in gillnet and longline fisheries. For trap fisheries, escape is possible, and is required by management policy for sublegals. In fact, the asymptotic catch pattern should not be considered common in trap fisheries. From a review of the literature I found that many asymptotic catches resulted from a relatively short soak time, or the trap was lifted just when the catch began to decline. For entry-only traps, unbaited traps, and continuously baited traps in some experiments, catch per trap haul may approach an asymptote. However, since a given trap design does not have a constant saturation level, C_∞ in a trap fishery is not a constant, as in the longline fishery, even for identical traps (Miller 1979, 1990). Despite the differences between the trap fishery and the gillnet or longline fisheries, Model (3.0) is widely used, and provides a reasonable fit as long as the escape rate does not exceed the entry rate (Figure 4.1, when $t < t_2$). It is sufficient for commercial fishery data, as fishermen usually end the soak before a significant decrease of their catch occurs.

The parabolic type of models were derived from Model (3.0) by adding an escape term (Somerton and Merritt 1986; Smith and Jamieson 1989). Theoretically they are more reasonable than Model (2.0) and (3.0) for trap fisheries, and can be applied to a fairly long soak time (Figure 4.1, $t < t_3$). The main shortcoming exists in the complexity of parameter estimation. Also, these models assume the probability of escape (or retention) is a constant. Yet, probability of escape may differ over time. I have observed that crabs appeared more active and moved more frequently when bait was fresh. Consequently, they had more chances to locate the entrances and gained a higher probability of escape (Zhou and Shirley, unpublished data). For species that have agonistic interactions, the escape probability may increase when the trap holds more individuals. Furthermore, in Model (4.0), the number of crabs in the trap decreases to zero after a long soak time. This may not be true for traps which can selectively retain legal crabs, and for traps used as shelter by crabs.

The application of these models depends on when the catch stops increasing, and when it begins to decline. Many variables have been identified which affect this temporal pattern. Trap size, bait quality and quantity, local animal density, entry rate and escape rate are among the most important ones (Miller 1979, 1990). In some trap fisheries, catch rates decreased significantly after a few hours soak (Hughes et al. 1970; Kennelly 1989), while in other

studies the catch did not decline for several days (Fogarty and Borden 1980; Miller 1990).

Model (1.0) predicts a parabolic curve with an asymptotic catch after an infinite soak time. This asymptotic catch could be the maximum asymptotic as in Model (3.0), an asymptote less than the maximum catch, or a zero. Hypothetically, only this model can be used in all situations without conditions being placed on soak time. As an example of its application for long soak times, this model may describe the number of crabs inside lost traps. Breen (1987) simulated lost traps by baiting the traps and leaving them on the sea floor for one year. Divers examined the traps at intervals and tagged all the crabs caught. The number of Dungeness crabs held in traps increased with time and peaked within approximately two months. Then the number decreased gradually and remained at one to three crabs on average for each trap for several months. The curve has a similar shape as in Figure 4.1. However, the number of crabs increased after 200 days to more than three crabs per trap. This increase cannot be simulated by the general model (1.0).

Because traps are soaked typically for a few days in trap fisheries, only a few data points are available for the curve fitting. It is not uncommon that there are large positive or negative values for the correlation coefficients between estimated parameters. Models which have even only two to three parameters may be overparameterzed. Although this does not necessarily

mean that the model is inappropriate, it may indicate that the model is not parsimonious. A model with fewer parameters may fit the observed data just as well. For example, for the asymptotic catch, Model (3.0) with two parameters fits the data as closely as Model (1.0) with three parameters. Notwithstanding these considerations, one intention of this paper is to demonstrate the flexibility of the general model for a variety of data types. For a specific data set with a short soak time, models with two parameters (e.g., Model 2.0 and Model 3.0) may work well.

If the data demonstrate a continually increasing catch, Model (1.0) results in multiple solutions, i.e., the parameters a, b, and c are not identifiable. When there are multiple solutions with a same R^2 value, any set of the parameters can be used in the model to express the relationship between the catch and soak time. However, the values of these parameters have no biological meaning, and the model can be used to standardize the catch only within the soak time which has been employed for fitting the curve. Similarly, for parabolic catch, the term $a*b$ cannot be extrapolated beyond the soak time as an asymptotic catch. The value ab denotes an asymptotic catch only when sufficient data are available which exhibit a tendency of asymptote after a long soak time.

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APPENDICES

Appendix 1.1. Measurement of commercial crab vessels.

Vessel	Length (m)	Rail-water Height (cm)	Rail-deck Height (cm)	Chute-water Height (cm)
Sea Venture	32.0	198	122	51
Early Dawn	32.9	224	122	77
Aleutian Spray	29.9	183	102	56
Northwest Mariner	32.3	152	86	41
Pacific Mist	26.5	130	86	18
Aleutian Mariner	36.0	180	91	64
Pacific Wind	37.5	196	109	61
Arctic Mariner	35.7	201	91	84
Isaf Jord	50.6	282	104	153
Penguin	50.3		91	
North Sea	38.4	183	94	64
Rosie	29.3	218	117	77
Spirit of the North	47.5	274	112	138
Arctic wind	37.5	226	117	84
Eldan	23.8	142	76	41
Arctic Dawn	29.6	224	122	77
Polar Sea	31.7	196	114	56
Northern Cascade	33.5	163	81	56
Starlite	37.2	196	91	79
Arctic Lady	41.1	203	97	82
American Eagle	36.6	152	109	18
Starward	37.5	183	109	49
Glizzly	37.5	183	86	72
North Pacific	31.1	188	97	66
Bering Sea	34.7	229	117	87
Pacesetter	39.6	213	114	74
Alaska Sea	33.5	157	89	44
Platonida	39.6	198	91	82
Shellfish	28.0	157	91	41
Midnight Sun	26.2	178	102	51
Ocean Ballad	34.7	254	122	107
Island Mist	38.1	188	99	64
Oceanfury	37.8	165	86	54

Appendix 1.1. (page 2)

Vessel	Length (m)	Rail-water Height (cm)	Rail-deck Height (cm)	Chute-water Height (cm)
American Way	32.0	165	104	36
Beauty Bay	38.7	183	114	44
Misty Blue	32.6	152	102	26
Kodiak Queen	43.9	213	91	97
Nuda Island	30.5	193	86	82
Karlafaye	50.9	264	127	112
FraucesM	31.7	132	107	
Aleutian Rover	30.5	163	109	28
Silver Dolphin	38.4	224	109	89
Rebel	26.5	173	91	56
Time Bandit	35.1	183	109	49
Sasitna	25.9	249	147	77
Kustatan	30.5	152	97	31
Viking Queen	33.5	183	97	61
American Viking	38.1	196	107	64
Alaska Sea	33.5	160	91	44
Husky	40.8	213	91	97
Centaurus	45.7		140	
Consulation	39.6	183	102	56
American Star	46.9	251	107	120
Valiant	33.8	244	99	120

Appendix 1.2. Aerial exposure duration (min) in commercial fishery. Total crabs = total number of crabs in the pot; Min. duration = exposure duration for the first crab returned to the sea; Max. duration = exposure duration for the last crab returned to the sea; crabs dropped = number of crabs dropped on the deck rather than on the sorting table.

Total crabs	Legal crabs	Min. duration	Max. duration	Crabs dropped
54	14	0.92	1.87	1
66	26	0.92	2.12	1
77	7	0.93	1.95	0
101	21	0.95	2.08	1
63	13	0.95	2.00	3
110	50	0.98	2.50	2
25	5	0.98	1.73	
79	19	1.00	2.00	2
103	33	1.00	2.03	3
51	11	1.00	1.87	
59	25	1.02	2.00	0
75	15	1.03	1.93	0
91	21	1.05	2.25	1
118	28	1.07	2.20	1
75	15	1.07	2.17	2
89	29	1.08	2.20	1
86	26	1.10	2.13	0
62	12	1.10	1.88	2
89	39	1.12	2.57	1
88	18	1.12	2.12	2
26	6	1.12	1.82	
87	17	1.13	2.12	0
61	11	1.13	2.00	2
63	13	1.17	1.88	0
60	10	1.17	2.05	4
80	10	1.18	2.22	1
94	14	1.18	2.13	1
70	10	1.18	1.68	4
34	4	1.18	1.77	
65	15	1.20	2.08	0

Appendix 1.2. (page 2)

Total crabs	Legal crabs	Min. duration	Max. duration	Crabs dropped
106	16	1.20	2.70	2
105	45	1.20	2.62	2
119	19	1.22	2.83	1
77	17	1.22	2.13	2
61	11	1.22	2.38	
118	18	1.23	2.67	2
71	11	1.23	2.18	3
119	49	1.25	2.75	1
65	15	1.25	2.15	1
105	25	1.25	2.52	1
111	41	1.25	2.50	1
97	17	1.25	2.33	2
115	45	1.25	2.75	3
105		1.25		
83	13	1.27	2.37	3
126	36	1.28	2.53	0
117	27	1.28	2.68	3
65	15	1.28	2.42	4
84	14	1.30	2.30	4
70	16	1.30	2.42	
65	15	1.30	2.05	
115	15	1.33	2.67	0
100	20	1.33	2.65	0
100	30	1.33	2.67	1
106	26	1.33	2.28	1
79	19	1.33	2.40	2
118	38	1.33	2.67	2
80	10	1.33	2.00	2
72	12	1.33	2.33	6
81	11	1.35	2.33	0
132	52	1.35	3.02	0
64	14	1.40	2.13	1
127	57	1.40	3.57	2
102	32	1.42	2.62	1
103	43	1.42	2.83	2

Appendix 1.2. (page 3)

Total crabs	Legal crabs	Min. duration	Max. duration	Crabs dropped
143	43	1.42	3.17	5
30	10	1.42	2.15	
87	27	1.45	2.50	1
104	34	1.45	2.95	2
84	24	1.48	2.83	1
97	27	1.48	2.55	1
103	33	1.50	2.67	0
134	54	1.50	3.23	1
128	48	1.50	3.00	1
129	39	1.50	3.00	1
110	30	1.50	3.02	2
107	37	1.50	2.77	2
75	15	1.50	2.25	2
30	5	1.50	2.10	
63	13	1.50	2.45	
72	22	1.50	2.43	
87	17	1.53	2.50	1
146	46	1.53	3.35	1
136	36	1.53	2.75	2
98	18	1.53	2.72	
99	19	1.55	2.72	0
80	10	1.55	2.50	6
102	32	1.58	2.52	0
112	42	1.58	2.75	1
50	8	1.65	2.03	
125	55	1.67	3.52	0
111	51	1.73	2.78	1
145	65	1.83	3.08	0
93	23	1.83	3.07	1
123	43	1.83	3.02	1
130	40	1.87	3.55	2
34	4	1.95	2.57	0
187	77			0
45	15	1.40	2.17	3
97	37			0

Appendix 1.2. (page 4)

Total crabs	Legal crabs	Min. duration	Max. duration	Crabs dropped
109	39			0
126	46			0
124	34			0
90	30			0
132	32			0
86	16			0
88	28			0
95	25			0
35	5		1.40	1
149	49			1
105	25			1
108	28			1
103	23		3.17	2
74	24		2.40	2
117	47		2.97	2
110	50			2
113	33			2
118	28		2.83	3
125	35			3
114	34			4
54	4		1.20	
58	8		2.02	
50	7		1.50	
30	5		2.00	
50	5		1.93	
104	4		2.05	
54	4		2.02	
50	6		1.88	
30	10		1.93	
40	7		1.87	
50	9		1.93	
40	13		2.38	
70	17		2.45	
70	14		2.33	
50	9		2.07	

Appendix 1.2. (page 5)

Total crabs	Legal crabs	Min. duration	Max. duration	Crabs dropped
88	18		2.43	
98	28		2.52	
54	14		1.95	
129	29			
68	8		2.33	
27	7		1.92	
39	9		1.65	
17	5		1.33	
27	7			
42	12			
23	3		1.28	
29	9			
53	13		1.82	
64	14		1.92	
59	9		1.62	
26	6		1.30	
37	7		2.00	
54	14		2.15	
44	14			
94	14			
87	17		2.25	
75	15		2.33	
127	47			
61	11		2.08	
59	19			
90	20			
104	24			

Appedix 1.3. Wet weight (g) and carapace length (mm) of crabs used in the handling study. Treatment code: 1 = handled once, 2 = handled twice, 3 = handled three times, 4 = modified handling, 5 = control. Sex categories: 1 = ovigerous female, 2 = juvenile female, 3 = sublegal male.

Treat.	Sex	Wt (g)	CL (mm)	Treat.	Sex	Wt (g)	CL (mm)
1	1	791.4	100.5	2	1	1074.8	115.7
1	1	884.8	107.6	2	1	1131.0	117.0
1	1	930.1	111.6	2	1	1208.4	118.3
1	1	1194.8	112.9	2	1	1209.4	119.9
1	1	1029.2	113.6	2	2	257.7	70.3
1	1	1018.9	114.7	2	2	336.2	77.4
1	1	1170.1	118.8	2	2	369.7	77.5
1	1	1079.4	119.5	2	2	493.3	84.8
1	1	1217.4	122.7	2	2	563.9	88.1
1	2	289.0	72.9	2	2	509.5	90.6
1	2	335.6	78.2	2	2	563.9	90.6
1	2	466.5	83.2	2	2	594.8	93.0
1	2	421.1	83.5	2	2	746.5	100.3
1	2	509.6	86.9	2	3	420.4	80.9
1	2	531.4	88.2	2	3	501.2	86.5
1	2	586.9	93.7	2	3	640.4	91.5
1	2	734.9	98.8	2	3	763.2	99.3
1	2	920.4	104.8	2	3	874.6	102.5
1	3	458.9	83.7	2	3	1016.4	102.5
1	3	582.9	89.0	2	3	928.7	104.7
1	3	553.1	93.1	2	3	1278.5	116.5
1	3	810.6	98.0	2	3	1440.9	121.6
1	3	673.2	98.9	3	1	816.1	102.2
1	3	966.6	104.7	3	1	1067.3	102.7
1	3	1044.3	108.3	3	1	777.4	102.9
1	3	1172.0	114.2	3	1	933.8	106.7
1	3	1467.8	125.1	3	1	1057.8	112.1
2	1	746.3	98.2	3	1	1007.4	112.2
2	1	837.4	106.7	3	1	1104.7	114.3
2	1	953.3	108.8	3	1	1202.3	120.9
2	1	982.3	110.5	3	1	1292.9	120.9
2	1	1050.6	114.9	3	2	310.9	75.8

Appendix 1.3 (page 2)

Treat.	Sex	Wt (g)	CL (mm)	Treat.	Sex	Wt (g)	CL (mm)
3	2	364.9	78.9	4	3	370.7	78.8
3	2	400.1	79.6	4	3	577.3	89.3
3	2	459.4	85.5	4	3	587.7	90.4
3	2	507.4	88.3	4	3	642.2	95.5
3	2	541.5	88.7	4	3	829.1	100.2
3	2	582.5	89.0	4	3	929.2	103.5
3	2	727.9	98.9	4	3	1146.6	110.9
3	2	823.7	103.2	4	3	1297.2	116.2
3	3	381.3	78.2	4	3	1473.7	119.3
3	3	488.4	86.1	5	1	579.9	88.0
3	3	626.6	93.6	5	1	835.0	98.4
3	3	762.3	96.7	5	1	894.4	112.5
3	3	863.4	103.3	5	1	1068.8	112.5
3	3	932.5	106.9	5	1	1166.1	114.1
3	3	1046.1	107.0	5	1	911.1	116.5
3	3	1188.9	110.1	5	1	1051.3	116.8
3	3	1481.4	122.0	5	1	1205.7	120.4
4	1	638.5	91.7	5	1	1419.0	125.0
4	1	861.4	102.8	5	2	314.5	75.3
4	1	922.6	106.7	5	2	369.8	79.0
4	1	1040.1	109.6	5	2	406.1	80.8
4	1	1023.4	112.3	5	2	365.0	80.9
4	1	1059.7	113.2	5	2	495.7	84.0
4	1	1150.7	117.7	5	2	517.6	88.8
4	1	1188.7	118.2	5	2	576.5	91.2
4	1	1413.9	123.4	5	2	631.7	93.5
4	2	317.8	74.2	5	2	816.2	97.9
4	2	343.9	75.1	5	3	527.8	87.3
4	2	444.4	84.5	5	3	662.4	92.7
4	2	463.7	85.7	5	3	638.6	93.2
4	2	495.9	87.4	5	3	681.7	95.2
4	2	563.1	87.4	5	3	620.6	97.7
4	2	575.6	90.7	5	3	787.2	98.4
4	2	685.4	95.3	5	3	910.1	104.2
4	2	860.0	103.8	5	3	1055.4	105.7

Appendix 1.4. Carapace length (mm) and carapace width (mm) before and after molt for molted male crabs.

		Carapace length			Carapace width		
Date	Crab	Before	After	Increase	Before	After	Increase
18-Sep	1M30	105.0	110.7	5.7	118.2	133.2	15.0
1-Oct	1M22	98.1	112.8	14.7	108.4	126.1	17.7
1-Oct	4M1	78.9	91.8	12.9	84.8	99.7	14.9
4-Oct	4M23	99.9	110.8	10.9	113.1	126.6	13.5
6-Oct	1M36	114.2	124.6	10.4	127.0	>135	>8
9-Oct	5M21	95.4	107.4	12.0	106.5	121.9	15.4
27-Oct	3M33	106.4	115.0	8.6	120.0	133.2	13.2
27-Oct	5M26	103.6	119.2	15.6	116.7	131.3	14.6
30-Oct	2M03	80.7	93.6	12.9	89.0	102.6	13.6
31-Oct	3M24	102.9	112.7	9.8	114.0	121.4	7.4
31-Oct	4M16	95.6	104.2	8.6	104.5	116.7	12.2
1-Nov	5M08	87.5	100.4	12.9	95.4	113.5	18.1
2-Nov	3M19	96.7	102.5	5.8	100.9	118.3	17.4
3-Nov	3M13	93.8	105.8	12.0	104.2	119.1	14.9
4-Nov	4M35	110.4	121.1	10.7	120.4	>133.5	>13.1
7-Nov	5M17	92.7	105.3	12.6	103.5	119.6	16.1
8-Nov	1M17	88.8	98.6	9.8	100.4	113.7	13.3
17-Nov	3M37	110.6	121.6	11.0	124.2	139.2	15.0
18-Nov	4M43	119.1	130.9	11.8	138.2	151.5	13.3
19-Nov	1M04	84.0	91.0	7.0	93.7	102.9	9.2
19-Nov	1M18	98.5	109.5	11.0	106.5	120.0	13.5
21-Nov	3M02	75.7	85.6	9.9	81.1	91.1	10.0
22-Nov	4M10	89.2	98.8	9.6	96.8	109.8	13.0
24-Nov	2M07	86.6	98.7	12.1	93.2	107.8	14.6
29-Nov	2M15	91.1	100.0	8.9	101.1	113.6	12.5
19-Dec	2M39	115.7	130.3	14.6	131.7	147.4	15.7

Appendix 1.5. Wet weight (g) increases and growth rate ($g.kg^{-1}$) for molted male crabs.

Crab #	Before molt	After molt	Increment	Growth rate
1M09	553.1	786.0	232.9	421.1
1M18	673.2	907.8	234.6	348.5
1M22	810.6	1211.6	401.0	494.7
2M03	420.4	667.0	246.6	586.6
2M07	501.2	743.5	242.3	483.4
2M39	1278.5	1709.2	430.7	336.9
3M13	626.6	916.0	289.4	461.9
3M19	762.3	1023.0	260.7	342.0
3M24	863.4	1125.5	262.1	303.6
3M37	1188.9	1574.5	385.6	324.3
4M10	577.3	815.6	238.3	412.8
4M16	642.2	874.4	232.2	361.6
4M23	829.1	1116.1	287.0	346.2
4M43	1473.7	1923.0	449.3	304.9
5M08	1146.6	1498.9	352.3	307.3
5M17	527.8	840.5	312.7	592.5
5M21	662.4	992.0	329.6	497.6
4M35	681.7	969.8	288.1	422.6
5M26	910.1	1344.5	434.4	477.3

Appendix 2.1. Increase in antenular flicking rate in one minute. Bait code: 1 = squid, 2 = herring, 3 = mussle, 4 = king crab muscle, 5 = king crab ovary. Crab group: 1 = juvenile female, 2 = ovigerous female, 3 = small male (≤ 110 mm CL), 4 = large male (>110 mm CL). Solution concentration was in $\log_{10}$ g.L^{-1}.

			IFR		
Bait	Group	Concentration	Mean	SD	n
1	1	-17.85	1.0	4.73	6
1	1	-15.85	2.8	4.62	6
1	1	-13.85	1.9	6.96	7
1	1	-11.85	0.3	9.12	7
1	1	-9.85	2.1	7.52	7
1	1	-7.85	6.1	8.18	10
1	1	-5.85	8.0	4.27	9
1	1	-4.85	7.8	4.29	10
1	1	-3.85	10.6	7.62	10
1	1	-2.85	10.1	11.53	10
1	1	-1.85	27.1	11.48	9
1	2	-17.85	3.7	6.55	7
1	2	-15.85	9.0	5.06	6
1	2	-13.85	2.3	5.22	7
1	2	-11.85	4.9	9.96	7
1	2	-9.85	4.1	5.21	7
1	2	-7.85	5.3	5.44	10
1	2	-5.85	6.0	6.80	10
1	2	-4.85	6.7	6.75	9
1	2	-3.85	8.5	5.56	10
1	2	-2.85	17.5	10.42	10
1	2	-1.85	31.7	6.37	7
1	3	-17.85	3.2	5.22	5
1	3	-15.85	5.2	4.12	6
1	3	-13.85	1.8	5.34	6
1	3	-11.85	4.0	2.28	6
1	3	-9.85	4.8	6.34	6
1	3	-7.85	4.6	3.83	11
1	3	-5.85	2.2	5.58	11
1	3	-4.85	4.6	5.63	11
1	3	-3.85	9.5	6.07	11

Appendix 2.1 (page 2)

Bait	Group	Concentration	IFR		
			Mean	SD	n
1	3	-2.85	13.3	4.42	9
1	3	-1.85	23.8	8.24	10
1	4	-15.85	3.8	4.53	8
1	4	-13.85	3.3	4.10	8
1	4	-11.85	1.8	4.65	8
1	4	-9.85	4.0	7.78	8
1	4	-7.85	3.2	6.32	9
1	4	-5.85	7.7	5.22	9
1	4	-4.85	8.7	5.29	9
1	4	-3.85	9.4	5.22	9
1	4	-2.85	17.8	6.88	8
1	4	-1.85	27.4	11.25	10
2	1	-17.85	4.5	6.75	6
2	1	-15.85	5.2	5.64	6
2	1	-13.85	5.0	5.69	6
2	1	-11.85	4.8	7.83	6
2	1	-9.85	5.8	5.95	6
2	1	-7.85	4.0	3.71	10
2	1	-5.85	6.7	7.42	10
2	1	-4.85	10.6	6.83	10
2	1	-3.85	13.7	8.14	10
2	1	-2.85	17.3	7.90	10
2	1	-1.85	26.1	11.07	9
2	2	-17.85	1.6	2.70	5
2	2	-15.85	5.6	3.10	7
2	2	-13.85	4.3	4.27	7
2	2	-11.85	2.3	4.07	7
2	2	-9.85	4.4	5.62	7
2	2	-7.85	-0.1	5.28	10
2	2	-5.85	3.5	4.38	10
2	2	-4.85	5.2	8.19	10
2	2	-3.85	8.9	7.05	10
2	2	-2.85	16.5	5.28	10
2	2	-1.85	26.1	10.92	8
2	3	-17.85	3.8	2.32	6
2	3	-15.85	3.0	4.90	6

Appendix 2.1 (page 3)

Bait	Group	Concentration	IFR		
			Mean	SD	n
2	3	-13.85	4.5	5.17	6
2	3	-11.85	4.7	5.13	6
2	3	-9.85	1.3	5.89	6
2	3	-7.85	1.6	4.90	10
2	3	-5.85	5.6	5.23	10
2	3	-4.85	7.9	3.30	9
2	3	-3.85	9.2	6.12	10
2	3	-2.85	15.5	6.64	10
2	3	-1.85	27.0	10.56	9
2	4	-15.85	1.9	2.42	8
2	4	-13.85	3.4	2.40	9
2	4	-11.85	2.1	4.54	9
2	4	-9.85	2.9	3.98	9
2	4	-7.85	3.4	6.88	9
2	4	-5.85	6.7	4.03	9
2	4	-4.85	8.8	3.38	9
2	4	-3.85	12.6	6.97	9
2	4	-2.85	17.7	6.98	9
2	4	-1.85	24.9	5.55	7
3	1	-17.85	3.5	4.36	4
3	1	-15.85	1.0	3.58	6
3	1	-13.85	3.8	2.79	6
3	1	-11.85	2.7	2.50	6
3	1	-9.85	5.5	3.21	6
3	1	-7.85	2.8	5.41	10
3	1	-5.85	5.5	5.23	10
3	1	-4.85	5.5	5.19	10
3	1	-3.85	11.9	5.69	10
3	1	-2.85	17.5	6.93	10
3	1	-1.85	28.1	10.23	9
3	2	-17.85	3.6	5.09	7
3	2	-15.85	-0.7	5.09	7
3	2	-13.85	4.0	5.39	7
3	2	-11.85	3.1	5.93	7
3	2	-9.85	-0.3	5.65	7
3	2	-7.85	3.5	6.50	10

Appendix 2.1 (page 4)

Bait	Group	Concentration	IFR		
			Mean	SD	n
3	2	-5.85	4.0	5.03	10
3	2	-4.85	5.7	4.42	10
3	2	-3.85	7.1	6.87	10
3	2	-2.85	15.5	6.13	10
3	2	-1.85	23.0	8.02	8
3	3	-17.85	4.3	2.34	6
3	3	-15.85	5.0	3.87	7
3	3	-13.85	-1.0	5.51	7
3	3	-11.85	6.1	4.26	7
3	3	-9.85	4.6	4.35	7
3	4	-5.85	3.7	9.17	9
3	4	-4.85	6.0	5.29	9
3	4	-3.85	7.6	7.30	9
3	4	-2.85	14.3	9.55	9
3	4	-1.85	23.1	7.18	9
4	1	-17.85	-0.5	4.18	6
4	1	-15.85	4.5	8.96	6
4	1	-13.85	1.2	6.62	6
4	1	-11.85	7.2	3.76	6
4	1	-9.85	6.7	6.47	6
4	1	-7.85	5.4	4.70	10
4	1	-5.85	5.3	4.99	10
4	1	-4.85	15.0	6.18	9
4	1	-3.85	14.6	8.58	10
4	1	-2.85	24.9	12.68	10
4	1	-1.85	30.3	11.51	9
4	2	-17.85	3.4	5.65	7
4	2	-15.85	5.0	4.80	7
4	2	-13.85	2.3	5.96	7
4	2	-11.85	7.0	6.11	7
4	2	-9.85	8.4	5.13	7
4	2	-7.85	4.8	6.30	10
4	2	-5.85	11.8	6.63	10
4	2	-4.85	10.6	5.40	10
4	2	-3.85	16.0	5.10	10
4	2	-2.85	19.3	8.08	9

Appendix 2.1 (page 5)

			IFR		
Bait	Group	Concentration	Mean	SD	n
4	2	-1.85	22.1	10.67	8
4	3	-17.85	2.7	3.93	6
4	3	-15.85	3.9	4.74	7
4	3	-13.85	1.4	6.80	7
4	3	-11.85	3.6	2.88	7
4	3	-9.85	6.6	5.77	7
4	3	-7.85	6.5	4.66	11
4	3	-5.85	6.2	5.40	11
4	3	-4.85	9.8	6.32	11
4	3	-3.85	15.6	6.33	11
4	3	-2.85	16.3	7.02	11
4	3	-1.85	28.2	11.58	11
4	4	-15.85	1.0	5.71	8
4	4	-13.85	4.6	2.97	8
4	4	-11.85	6.5	4.50	8
4	4	-9.85	2.1	4.94	8
4	4	-7.85	7.8	5.36	9
4	4	-5.85	9.6	6.80	9
4	4	-4.85	11.3	7.53	9
4	4	-3.85	10.3	6.71	9
4	4	-2.85	14.4	7.16	9
4	4	-1.85	22.1	8.28	9
5	1	-17.9	-0.6	5.73	5
5	1	-15.9	3.5	8.78	6
5	1	-13.9	0.8	5.45	5
5	1	-11.9	6.3	6.89	6
5	1	-9.85	2.8	7.19	6
5	1	-7.85	4.8	4.87	10
5	1	-5.85	8.4	6.92	10
5	1	-4.85	8.4	3.10	10
5	1	-3.85	12.5	9.79	10
5	1	-2.85	16.2	6.23	10
5	1	-1.85	21.2	10.30	10
5	2	-17.9	0.9	6.28	7
5	2	-15.9	1.0	3.61	7
5	2	-13.9	1.7	5.77	7

Appendix 2.1 (page 6)

			IFR		
Bait	Group	Concentration	Mean	SD	n
5	2	-11.9	2.0	5.77	7
5	2	-9.85	0.7	3.35	7
5	2	-7.85	2.5	6.88	10
5	2	-5.85	5.0	5.94	10
5	2	-4.85	8.3	5.92	9
5	2	-3.85	7.1	7.68	8
5	2	-2.85	14.4	8.62	10
5	2	-1.85	15.0	9.83	10
5	3	-17.9	2.2	3.87	6
5	3	-15.9	1.1	7.52	7
5	3	-13.9	-0.3	5.47	6
5	3	-11.9	3.4	5.29	7
5	3	-9.85	4.6	5.00	7
5	3	-7.85	5.0	5.39	11
5	3	-5.85	6.6	4.80	11
5	3	-4.85	9.9	8.38	11
5	3	-3.85	9.9	6.47	11
5	3	-2.85	17.9	9.04	11
5	3	-1.85	20.5	13.00	11
5	4	-17.9	4.0	5.00	8
5	4	-15.9	2.9	4.12	8
5	4	-13.9	4.9	4.88	8
5	4	-11.9	2.8	4.53	8
5	4	-9.85	2.8	4.13	8
5	4	-7.85	6.6	5.96	9
5	4	-5.85	4.3	3.94	9
5	4	-4.85	6.4	5.94	9
5	4	-3.85	6.9	6.05	9
5	4	-2.85	17.4	8.06	9
5	4	-1.85	22.0	9.17	9

Appendix 2.2. Response rate of red king crabs to five bait extracts. Bait code: 1 = squid, 2 = herring, 3 = mussle, 4 = king crab muscle, 5 = king crab ovary. Solution concentrations were in $\log_{10}$ g.mL^{-1}. Crab group: JF = juvenile female, OF = ovigerous female, SM = small male (≤ 110 mm CL), LM = large male (>110 mm CL).

Bait	Log C	JF	OF	SM	LM	Mean
1	-7.85	0.30	0.40	0.09	0.22	0.25
1	-5.85	0.40	0.30	0.18	0.44	0.33
1	-4.85	0.10	0.60	0.18	0.56	0.35
1	-3.85	0.60	0.30	0.73	0.56	0.55
1	-2.85	0.60	0.90	0.73	0.78	0.75
1	-1.85	0.90	1.00	1.00	0.89	0.95
2	-7.85	0.10	0.00	0.09	0.33	0.13
2	-5.85	0.60	0.10	0.36	0.44	0.38
2	-4.85	0.60	0.40	0.55	0.33	0.48
2	-3.85	0.70	0.70	0.73	0.67	0.70
2	-2.85	0.80	1.00	0.64	0.89	0.83
2	-1.85	1.00	1.00	1.00	1.00	1.00
3	-7.85	0.20	0.40	0.18	0.33	0.28
3	-5.85	0.30	0.20	0.09	0.11	0.18
3	-4.85	0.30	0.20	0.36	0.22	0.28
3	-3.85	0.70	0.50	0.27	0.33	0.45
3	-2.85	0.80	0.70	0.64	0.78	0.73
3	-1.85	0.90	0.80	1.00	1.00	0.93
4	-7.85	0.20	0.30	0.36	0.44	0.33
4	-5.85	0.40	0.60	0.36	0.56	0.48
4	-4.85	0.70	0.40	0.64	0.78	0.63
4	-3.85	0.80	0.80	0.91	0.67	0.80
4	-2.85	0.90	0.70	0.91	0.67	0.80
4	-1.85	1.00	0.70	1.00	1.00	0.93
5	-7.85	0.30	0.40	0.27	0.33	0.33
5	-5.85	0.50	0.40	0.27	0.22	0.35
5	-4.85	0.30	0.70	0.27	0.22	0.38
5	-3.85	0.70	0.30	0.73	0.44	0.55
5	-2.85	0.80	0.70	0.82	0.89	0.80
5	-1.85	1.00	0.70	0.73	0.89	0.83

Appendix 2.3. Response rate of red king crab feeding behavior. Bait code: 1 = squid, 2 = herring, 3 = mussle, 4 = king crab muscle, 5 = king crab ovary. Index: 1 = leg movement, 2 = body elevation, 3 = cheliped probing, 4 = maxilliped movement. Crab groups are as in Appendix 2.1. C = Solution concentration in $\log_{10}$ g.L^{-1}.

Bait	Index	Group	C	Rate
1	1	1	-3.85	0.10
1	1	1	-2.85	0.10
1	1	1	-1.85	0.60
1	1	2	-3.85	0.10
1	1	2	-2.85	0.20
1	1	2	-1.85	0.80
1	1	3	-3.85	0.00
1	1	3	-2.85	0.18
1	1	3	-1.85	0.36
1	1	4	-3.85	0.00
1	1	4	-2.85	0.11
1	1	4	-1.85	0.44
1	2	1	-3.85	0.00
1	2	1	-2.85	0.00
1	2	1	-1.85	0.20
1	2	2	-3.85	0.10
1	2	2	-2.85	0.10
1	2	2	-1.85	0.70
1	2	3	-3.85	0.00
1	2	3	-2.85	0.09
1	2	3	-1.85	0.18
1	2	4	-3.85	0.00
1	2	4	-2.85	0.00
1	2	4	-1.85	0.22
1	3	1	-3.85	0.10
1	3	1	-2.85	0.10
1	3	1	-1.85	0.30
1	3	2	-3.85	0.10
1	3	2	-2.85	0.40
1	3	2	-1.85	1.00
1	3	3	-3.85	0.09
1	3	3	-2.85	0.27
1	3	3	-1.85	0.55
1	3	4	-3.85	0.00
1	3	4	-2.85	0.22
1	3	4	-1.85	0.67
1	4	1	-3.85	0.00
1	4	1	-2.85	0.10
1	4	1	-1.85	0.60
1	4	2	-3.85	0.10
1	4	2	-2.85	0.70
1	4	2	-1.85	0.90
1	4	3	-3.85	0.00
1	4	3	-2.85	0.45
1	4	3	-1.85	0.91
1	4	4	-3.85	0.22
1	4	4	-2.85	0.33
1	4	4	-1.85	0.78
2	1	1	-3.85	0.10
2	1	1	-2.85	0.40
2	1	1	-1.85	0.60
2	1	2	-3.85	0.10
2	1	2	-2.85	0.40
2	1	2	-1.85	0.80
2	1	3	-3.85	0.00
2	1	3	-2.85	0.55
2	1	3	-1.85	0.82
2	1	4	-3.85	0.22
2	1	4	-2.85	0.33
2	1	4	-1.85	0.56
2	2	1	-3.85	0.00
2	2	1	-2.85	0.30
2	2	1	-1.85	0.40
2	2	2	-3.85	0.10

Appendix 2.3 (page 2)

Bait	Index	Group	C	Rate
2	2	2	-2.85	0.40
2	2	2	-1.85	0.80
2	2	3	-3.85	0.00
2	2	3	-2.85	0.18
2	2	3	-1.85	0.73
2	2	4	-3.85	0.00
2	2	4	-2.85	0.11
2	2	4	-1.85	0.33
2	3	1	-3.85	0.10
2	3	1	-2.85	0.40
2	3	1	-1.85	0.60
2	3	2	-3.85	0.10
2	3	2	-2.85	0.60
2	3	2	-1.85	0.80
2	3	3	-3.85	0.00
2	3	3	-2.85	0.73
2	3	3	-1.85	0.91
2	3	4	-3.85	0.00
2	3	4	-2.85	0.67
2	3	4	-1.85	0.78
2	4	1	-3.85	0.00
2	4	1	-2.85	0.40
2	4	1	-1.85	0.70
2	4	2	-3.85	0.40
2	4	2	-2.85	0.70
2	4	2	-1.85	0.90
2	4	3	-3.85	0.09
2	4	3	-2.85	0.73
2	4	3	-1.85	0.91
2	4	4	-3.85	0.22
2	4	4	-2.85	0.67
2	4	4	-1.85	0.89
3	1	1	-3.85	0.10
3	1	1	-2.85	0.30
3	1	1	-1.85	0.40
3	1	2	-3.85	0.20
3	1	2	-2.85	0.00
3	1	2	-1.85	0.30
3	1	3	-3.85	0.00
3	1	3	-2.85	0.09
3	1	3	-1.85	0.18
3	1	4	-3.85	0.00
3	1	4	-2.85	0.00
3	1	4	-1.85	0.22
3	2	1	-3.85	0.10
3	2	1	-2.85	0.10
3	2	2	-3.85	0.00
3	2	2	-2.85	0.00
3	2	2	-1.85	0.20
3	2	3	-3.85	0.00
3	2	3	-2.85	0.00
3	2	3	-1.85	0.00
3	2	4	-3.85	0.00
3	2	4	-2.85	0.00
3	2	4	-1.85	0.00
3	3	1	-3.85	0.10
3	3	1	-2.85	0.10
3	3	1	-1.85	0.40
3	3	2	-3.85	0.00
3	3	2	-2.85	0.20
3	3	2	-1.85	0.40
3	3	3	-3.85	0.00
3	3	3	-2.85	0.09
3	3	3	-1.85	0.36
3	3	4	-3.85	0.00
3	3	4	-2.85	0.00
3	3	4	-1.85	0.33
3	4	1	-3.85	0.10
3	4	1	-2.85	0.00
3	4	1	-1.85	0.80
3	4	2	-3.85	0.30
3	4	2	-2.85	0.60
3	4	2	-1.85	0.90
3	4	3	-3.85	0.18

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Bait	Index	Group	C	Rate
3	4	3	-2.85	0.36
3	4	3	-1.85	0.91
3	4	4	-1.85	0.89
3	4	4	-3.85	0.00
3	4	4	-2.85	0.22
4	1	1	-3.85	0.00
4	1	1	-2.85	0.30
4	1	1	-1.85	0.30
4	1	2	-3.85	0.10
4	1	2	-2.85	0.00
4	1	2	-1.85	0.20
4	1	3	-3.85	0.27
4	1	3	-2.85	0.09
4	1	3	-1.85	0.45
4	1	4	-3.85	0.11
4	1	4	-2.85	0.22
4	1	4	-1.85	0.11
4	2	1	-3.85	0.00
4	2	1	-2.85	0.10
4	2	1	-1.85	0.20
4	2	2	-3.85	0.10
4	2	2	-2.85	0.00
4	2	2	-1.85	0.10
4	2	3	-3.85	0.18
4	2	3	-2.85	0.09
4	2	3	-1.85	0.27
4	2	4	-3.85	0.11
4	2	4	-2.85	0.11
4	2	4	-1.85	0.00
4	3	1	-3.85	0.00
4	3	1	-2.85	0.10
4	3	1	-1.85	0.20
4	3	2	-3.85	0.20
4	3	2	-2.85	0.40
4	3	2	-1.85	0.30
4	3	3	-3.85	0.09
4	3	3	-2.85	0.18
4	3	3	-1.85	0.27
4	3	4	-3.85	0.00
4	3	4	-2.85	0.11
4	3	4	-1.85	0.22
4	4	1	-3.85	0.00
4	4	1	-2.85	0.10
4	4	1	-1.85	0.50
4	4	2	-3.85	0.10
4	4	2	-2.85	0.90
4	4	2	-1.85	0.80
4	4	3	-3.85	0.18
4	4	3	-2.85	0.18
4	4	3	-1.85	0.45
4	4	4	-3.85	0.00
4	4	4	-2.85	0.00
4	4	4	-1.85	0.22
5	1	1	-3.85	0.00
5	1	1	-2.85	0.10
5	1	1	-1.85	0.20
5	1	2	-3.85	0.00
5	1	2	-2.85	0.10
5	1	2	-1.85	0.20
5	1	3	-3.85	0.36
5	1	3	-2.85	0.18
5	1	3	-1.85	0.27
5	1	4	-3.85	0.00
5	1	4	-2.85	0.11
5	1	4	-1.85	0.00
5	2	1	-3.85	0.00
5	2	1	-2.85	0.00
5	2	1	-1.85	0.00
5	2	2	-3.85	0.00
5	2	2	-2.85	0.00
5	2	2	-1.85	0.00
5	2	3	-3.85	0.09
5	2	3	-2.85	0.00
5	2	3	-1.85	0.18

Appendix 2.3 (page 4)

Bait	Index	Group	C	Rate
5	2	4	-3.85	0.00
5	2	4	-2.85	0.11
5	2	4	-1.85	0.00
5	3	1	-3.85	0.00
5	3	1	-2.85	0.10
5	3	1	-1.85	0.20
5	3	2	-3.85	0.10
5	3	2	-2.85	0.20
5	3	2	-1.85	0.80
5	3	3	-3.85	0.09
5	3	3	-2.85	0.09
5	3	3	-1.85	0.18
5	3	4	-3.85	0.00
5	3	4	-2.85	0.11
5	3	4	-1.85	0.00
5	4	1	-3.85	0.00
5	4	1	-2.85	0.20
5	4	1	-1.85	0.20
5	4	2	-3.85	0.10
5	4	2	-2.85	0.80
5	4	2	-1.85	0.80
5	4	3	-3.85	0.09
5	4	3	-2.85	0.00
5	4	3	-1.85	0.36
5	4	4	-3.85	0.00
5	4	4	-2.85	0.22
5	4	4	-1.85	0.33

Appendix 3.1. Summary of red king crab responses to pots in two hours. Data are shown in the number of responses.

	Ovigerous Female				Juvenile Female				Legal Male				Sublegal Male			
Trial	Appr.	Leave	Enter	Exit	Appr.	Leave	Enter	Exit	Appr.	Leave	Enter	Exit	Appr.	Leave	Enter	Exit
1	5	5			3	2	1		4	4			6	6		
2	1	1			0				1	1			0			
3	11	9	2		7	6	1		10	9	1		0			
4	1	1			0				4	4			0			
5	16	15	1	1	2	2			2	0	3	1	3	2	1	
6	6	6			1	1			8	8			0			
7	4	4			1	1			0				0			
8	1	1			0				0				1	1		
9	1	1			0				4	4			0			
10	0				7	7			2	2			1	1		
11	2	2			4	4			1	1			3	3		
12	2	2			4	4			2	2			0			
13	5	3	2		8	7	1		3	1	2		6	6		
14	0				0				0				7	5	2	
15	0				8	7	1		0				0			
16	9	9			3	3			2	2			4	3	1	
17	6	6			1	1			1	1			1	1		
18	12	12			9	9			0				3	3		
19	2	2							0				0			
Sum	84	79	5	1	58	54	4	0	44	39	6	1	35	31	4	0

Appendix 3.2. Number of approaches per crab and number of crabs that made that number of approaches. Crab group: OF = ovigerous female, JF = juvenile female, LM = legal male, SM = sublegal male. No. app = number of approaches.

Crabs did not enter the pot					
No. app	OF	JF	LM	SM	Total
1	5	6	10	5	26
2	4	3	1	2	10
3	0	4	3	3	10
4	2	1	2	0	5
5	1	2	0	1	4
6	3	0	0	0	3
7	0	0	0	0	0
8	1	0	0	0	1
9	0	0	0	0	0
10	0	0	0	0	0
11	1	0	0	0	1
Sum	17	16	16	11	60

Crabs entered the pot					
No. app	OF	JF	LM	SM	Total
1	1	1	3	0	5
2	0	0	1	1	2
3	0	0	0	1	1
4	1	0	0	1	2
5	2	1	0	1	4
6	1	1	0	0	2
7	0	0	0	0	0
8	0	1	0	0	1
9	0	0	0	0	0
10	0	0	1	0	1
Sum	5	4	5	4	18

Appendix 3.3. Approach direction and number of sector searched before entering or leaving. One sector = 45°. Sector I was right downstream. Crab group codes are the same as in Appendix 3.2.

	Number of approaches				
Sector	OF	JF	LM	SM	Total
I	40	25	27	17	109
II	11	16	9	9	45
III	2	0	1	2	5
IV	1	0	0	0	1
V	1	1	0	2	4
VI	1	1	1	1	4
VII	7	4	2	1	14
VIII	21	11	4	3	39
Sum	84	58	44	35	221

	Number of sectors searched				
No. sect	OF	JF	LM	SM	Total
1	33	20	21	14	88
2	30	23	20	12	85
3	16	8	2	4	30
4	1	5	0	1	7
5	2	2	1	3	8
6	0	0	0	1	1
7	2	0	0	0	2
8	0	0	0	0	0
Sum	84	58	44	35	221

Appendix 3.4. Entering behavior. Crab group codes are the same as in the Appendix 3.2. Entering sector = sector where the crab entered. Search duration (min) was the duration from touching the pot to entering the pot. Entering direction: F = front, RF = right front, R = right, L = left. Entering time (min) was from when the first was leg inserted into the entrance to when the crab was in the pot.

Crab group	No. of approaches	Entering sector	No. Sect searched	Search duration	Entering direction	Entering time
OF	5	6	1	1	F	0.27
OF	5	2	3	1	F	0.22
OF	4	6	2	8	RF	0.33
OF	6	2	3	12	F	0.67
OF	1	5	7	66	R	0.85
JF	6	1	4	15	F	0.50
JF	8	2	4	10	F	0.37
JF	1	1	1	1	L	
JF	5	1	2	10	F	0.33
LM	10	2	2	4	R	3.02
LM	1	1	1	2		
LM	1	1	1	2	R	0.67
LM	1	2	2	4	L	1.50
LM	2	2	5	25	F	1.75
SM	1	5	2	6	F	0.31
SM	2	6	2	0	R	0.28
SM	3	2	2	3	R	2.63
SM	6	2	1	2	F	1.25

Appendix 3.5. Escape attempt rate (Number of escape attempts.h^{-1}.$crab^{-1}$) in 6 h periods. Crab group: OF = ovigerous female, JF = juvenile female, LM = legal male, SM = sublegal male.

Time (h)	OF	JF	LM	SM
6	0.07	0.08	0.01	0.10
12	0.12	0.14	0.02	0.08
18	0.19	0.07	0.02	0.08
24	0.08	0.10	0.03	0.11
30	0.10	0.08	0.02	0.09
36	0.05	0.03	0.02	0.10
42	0.00	0.13	0.03	0.02
48	0.00	0.00	0.02	0.12

Appendix 3.6. Escape behavior from the escape experiment. Exit entrance (the entrance where a crab exited) and Starting panel: 1 = downstream, 2 = upstream, A = closest to the center of the tank, B = closest to the tank wall, F = floor panel, T = top panel. Exit duration (min) was from when the first leg inserted into the entrance to when the crab was completed out of the entrance.

Crab group	Exit entrance	Starting panel	Exit direction	Exit duration
OF	1B	B	Right	0.43
OF	1B	B	Right	1.28
OF	2B	B	Front	0.95
OF	2B	B	Front	0.50
OF	2B	B	Left	1.62
OF	2B	B	Left	0.35
OF	2B	B	Left	2.78
OF	2B	B	Right	1.23
OF	2B	B	Right	0.50
JF	1A	A	Right	1.67
JF	1A	A	Left	0.63
JF	1A	A	Right	3.32
JF	1B	B	Right	1.83
JF	1B	B	Right	0.53
JF	1B	B	Right	1.97
JF	2A	A	Right	1.67
JF	2B	B	Left	0.95
JF	2B	B	Right	0.68
JF	2B	B	Right	0.67
LM	2B	F	Right	0.42
LM	2B	F	Left	1.48
SM	1A	A	Left	1.05
SM	1A	A	Right	4.75
SM	1B	B	Right	4.50
SM	2A	B	Left	0.45
SM	2B	B	Left	0.83
SM	2B	B	Left	1.33
SM	2B	B	Left	1.00
SM	2B	T	Left	0.48

Appendix 4.1. Data sets of catch per trap versus soak time.

Sinoda 1969

Time (d)	Catch
0	0
1	19.5
2	31
3	36

Kennelly 1989

Time (min)	Catch
0	0
15	3.78
60	9.78
120	11.56

Miller 1979

	Bait exposed	Bait enclosed
Time (d)	Catch	Catch
0	0	0
2	8.8	3.6
4	9.6	5
6	14.2	7.2
8	17.4	8.2
10	17.6	10.4
12	19.2	8.8

Somerton and Merritt 1986

Entry only pots

Time (d)	Catch
0	0
1	20.33
2	26.33
3	27.67
4	28
5	29.67
6	30.67
7	32.67

Auster

	1985	1986
Time (d)	Catch	Catch
0	0	0
1	0.36	0.306
2	0.56	0.476
3	0.63	0.53
4	0.84	0.472
5	0.7	0.485
6	0.9	
7	0.42	

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Munro 1974

Time (d)	Catch
0	0
1	24.8
2	28
3	29
4	21.3
5	21

Sloan and Robinson 1985

Time (h)	Catch
0	0
6.2	4.5
13.3	8.2
23.8	11.9
24.1	14.9
44.7	26.6
95.4	17.7

High & Worlund 1978

Time (d)	Catch
0	0
1	44
3	71
7	17
10	12
15	6

Skud 1979

Time (d)	March-May Catch	June-Sept catch
0	0	0
1	2.2	3.3
2	3.8	5.4
3	4.5	6.9
4	5.2	7.6
5	5.5	7.5
6	5.4	7.8
7	4.9	7.7
8	4.8	7.2
9	4.5	6.3
10	4	6

Somerton 1986

Time (d)	Pot 1~5 Catch	Pot 6~8 Catch
0	0	0
1	13.2	31.33
2	15	23.67
3	12.2	
4	10.8	25
5	10	20
6	9.2	19
7	8.8	14.67

Appendix 4.1. (page 3)

Zhou and Shirley, unpublished data

	Catch			Catch	
Time (h)	Legal male	Sublegals	Time (h)	Legal male	Sublegals
0	0.0	0.0	25	1.6	0.3
1	1.3	1.1	26	1.6	0.3
2	1.7	1.0	27	1.6	0.2
3	1.8	1.0	28	1.4	0.2
4	2.1	0.9	29	1.4	0.1
5	2.2	0.8	30	1.3	0.1
6	2.1	0.8	31	1.3	0.2
7	2.2	0.6	32	1.3	0.1
8	2.1	0.7	33	1.3	0.1
9	1.9	0.6	34	1.3	0.1
10	2.0	0.4	35	1.2	0.2
11	1.9	0.4	36	1.1	0.1
12	1.9	0.4	37	1.3	0.1
13	2.0	0.3	38	1.3	0.2
14	2.0	0.3	39	1.3	0.1
15	1.8	0.3	40	1.3	0.3
16	1.8	0.4	41	1.3	0.3
17	1.9	0.3	42	1.3	0.3
18	1.9	0.3	43	1.3	0.3
19	1.8	0.4	44	1.3	0.2
20	1.9	0.4	45	1.3	0.2
21	1.8	0.3	46	1.3	0.3
22	1.8	0.3	47	1.3	0.2
23	1.7	0.3	48	1.3	0.2
24	1.6	0.4			