Chemoreception and feeding responses of red king crabs to potential bait extracts

Shijie Zhou and Thomas C. Shirley

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. The median effective concentration at which 50% of crabs detected the solution 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 the most sensitive. The median effective concentration at which 50% of crabs showed feeding responses 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 was detected between the sexes for chemosensation.

Introduction

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 & Olla, 1977; Pearson *et al.*, 1979; Rittschof & Buswell, 1989; Zimmer-Faust & Case, 1983), how-

ever, no chemosensory study on red king crabs, *Paralithodes camtschaticus*, one of the most important commercial species in Alaska, has been published.

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 & Grant, 1980; McLeese, 1970; Miller, 1990; Zimmer-Faust & Case, 1982, 1983). Also, artificial baits have been developed (Hunter *et al.*, 1990; Mackie & Grant, 1980; McLeese, 1970). Despite the many studies on other decapods, however, there have been no bait efficiency studies on red king crabs.

The objectives of present work were: 1) to investigate the chemosensory behavior and feeding behavior of red king crabs; 2) to compare the efficiency of potential baits; and 3) to compare sensitivity between red king crabs of different sexes and sizes. Behavioral responses to food and test solutions were observed and described. Antennular flicking pattern was used as an indicator of chemoreception. The movements of maxillipeds, chelipeds, walking legs, and body were employed as indicators of feeding behavior. The results of this study will provide information for bait selection in the commercial fishery of

red king crabs.

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 aquaria supplied with flowing sea water. Frozen salmon and squid were provided as food twice a week. The aquaria were covered with green fiberglass 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 $31 \times 22 \times 17$ cm with a volume of 11.6 L each. The aquarium was opaque but covered with a transparent plexiglass board to permit observations (Fig. 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 $\times$ 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

Fig. 1. A schematic diagram of the experimental apparatus.

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 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 (Fig. 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 it 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 the 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 of 5 ml water 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} ($\pm 0.46 \times 10^{-3}$ SD), and this factor was used for adjustment of test solutions.

Test solutions

Mollusca, crustaceans, and fish are important foods for red king crab in nature (Jewett & Feder, 1982). In this study, opal squid (*Loligo opalescens*), Pacific herring (*Clupea harengus*), and blue mussel (*Mytilus trossulus*) were selected as potential baits. In addition, extracts from female red king crab muscle and ovary were tested to examine for avoidance response to conspecific chemicals or attraction of male crabs. Therefore, a total of 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 mm 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 $\text{Wet weight} = a \times \text{Dry weight}$. 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} wet weight. 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 mm membrane was used as control.

Response indexes

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, $P=0.135$, $df=3$, $N=112$). The change of flicking rate between the first 30 s and the following 30 s ranged from 0 to ± 9 with a mean of $-0.07 (\pm 3.46 \text{ SD}, N=96)$. The 95% tolerance interval was: mean $\pm 1.98 \times \text{SD} = 6.7$. A crab was considered to have detected a test solution if the antennular IFR of either side was ≥ 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%. The solution concentration at which 50% of the crabs responded (IFR ≥ 7 in 30 s) was called the median effective dose, ED_{50} , and was used as a measure of sensitivity of chemoreception.

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 median effective dose (ED_{50}), the concentration at which 50% of the crabs displayed any of the above feeding behaviors, was also used as a measure of feeding sensitivity.

Test procedures

Preliminary observations indicated that the feeding behavior of red king crabs was not disturbed by the presence of an observer. 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, and antennular flicking counting began 10 s after the introduction. The counting was made separately for the left and right 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 ($10^{-15} \text{ g l}^{-1}$) 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 and food

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 lowered antennules.

The behavioral responses of red king crabs to test solutions were similar to their responses to food. 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. These behaviors were also observed at the initial stage when food was provided, and 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 test 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 $-0.55 \text{ flicks min}^{-1}$ ($\pm 5.1 \text{ SD}$, $N=56$). 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 ($\pm 6.6 \text{ SD}$, $N=56$) was recorded for the 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: concentrations below 1.4×10^{-8} , and above $1.4 \times 10^{-8} \text{ g l}^{-1}$ (Fig. 2). The mean IFR fluctuated between 2 and 4 min^{-1} at concentrations from 1.4×10^{-18} to $1.4 \times 10^{-8} \text{ g l}^{-1}$. 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, hermit, 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 $1.4 \times 10^{-8} \text{ g l}^{-1}$ was also significantly higher than the spontaneous IFR (Scheffe's test, $P < 0.0001$).

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 $1.4 \times 10^{-14} \text{ g l}^{-1}$ (Scheffe's test, $P=0.123$, $N=477$). Nevertheless, the IFR for crab extract was significantly higher

Fig. 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.

than other extracts and sea water when the concentration was between 1.4×10^{-12} and $1.4 \times 10^{-8} \text{ g l}^{-1}$ (Scheffe's test, $P = 0.001$, $N = 535$, Fig. 2).

At solution concentrations above $1.4 \times 10^{-8} \text{ g l}^{-1}$, 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 with mussel extract, where juvenile females displayed a higher IFR than OF and SM ($P = 0.046$).

Chemoreception sensitivity

Loglinear analysis was applied to examine the effects of extract type, crab

Fig. 3. The relationship between the percentage of crabs detecting the five extracts and the solution concentration. The dashed line indicates a 50% responding rate.

group, and solution concentration on the responding rate, the percentage of crabs that detected the solution. 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. Therefore, 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

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

	<i>a</i>	<i>b</i>	R^2	ED_{50}
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

parameters. The median effective concentration at which 50% of the crabs detected the solution was then calculated (Table 1, Fig. 3).

Crabs were most sensitive to the extract from king crab muscle. The estimated ED_{50} of -5.83 logarithmic unit ($1.4 \times 10^{-6} \text{ g l}^{-1}$) 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 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 concentrations greater than $1.4 \times 10^{-3} \text{ g l}^{-1}$ (Fig. 3).

Indexes for feeding behavior and feeding sensitivity

Movements of the second and third maxillipeds, probing and grasping of chelae, moving and walking movements of legs, and body elevation were readily observed at high concentrations. Since these four feeding activities only occurred at concentrations from 1.4×10^{-4} to 1.4×10^{-2} , only these three concentrations were used for 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, $P = 0.402$, $df = 7$, Fig. 4). These indexes significantly differed from each other, except probing by chelae and leg movement (Relative median potency comparison, Norusis, 1993). The median effective concentration at which 50% of the crabs exhibited feeding behavior showed that the 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).

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 $b = .96$ (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 (Fig. 5). Comparison of relative potency indicated that juvenile females had a significantly lower feeding sensitivity than others, and large males also had a significantly lower sensitivity than ovigerous

Fig. 4. Responding rate after logit transformation with regard to four feeding behavior indexes and solution concentration. The dashed line indicates a 50% responding rate.

females (Table 2).

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 conspecific muscle and ovary in the other. 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 (Fig. 6, Table 2).

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

Table 2. Median effective 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. ED₅₀ was the log₁₀ solution concentration at which 50% of the crabs responded.

Behavior	Maxillip.	Chelae	Legs	Body
ED ₅₀	-2.75	-2.18	-1.97	-1.41
±95% CI	0.16	0.16	0.13	0.20

Crabs	JF	OF	SM	LM
ED ₅₀ ¹⁾	-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
ED ₅₀	-2.62	-3.03	-2.64	-2.06	-1.92
±95% CI	0.41	0.41	0.40	0.42	0.42

¹⁾ Feeding behavior was movement of maxillipeds.

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 (Fig. 5). 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

Chemosensation behavior of red king crabs is similar to other decapods. The antennules, the pereopod dactyls, and the mouthparts have been considered as the primary chemosensory organs of decapods (Ache, 1982). While mouthparts and dactyls are considered analogous to verte-

brate tongues, antennules are believed to be analogous to vertebrate noses (Carr & 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 & Derby, 1991; Pearson & Olla, 1977; Pearson *et al.*, 1979, 1981; Rebach *et al.*, 1990; Zimmer-Faust & Case, 1983). Our study verifies that antennular flicking is also an appropriate indicator of chemoreception for red king crabs.

Feeding behavior involved movement of maxillipeds, grasping by chelipeds, probing by legs, and locomotion (Derby & Atema, 1982). Red king crabs also share similar feeding behavior with other decapods (Derby & Atema, 1981; Fine-Levy *et al.*, 1989; McLeese, 1970; Pearson & Olla, 1977; Pearson *et al.*, 1979; Zimmer-Faust & Case, 1983). In red king crab, the onset of maxilliped movements, probing by chelipeds and walking legs, and body elevation required different concentrations. We inspected these behaviors and found that the maxilliped movements were the most

Fig. 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.

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.

Red king crabs had the most sensitive chemosensation to the extract made from muscle of their conspecifics. The median effective concentration of crab muscle extract was one or more orders of magnitude

lower than that of other extracts. The antennular flicking rate to crab extract at concentrations as low as 10^{-12} g l⁻¹ was significantly higher than responses to sea water. Red king crabs may 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

Fig. 6. The relationship between responding rate for movement of maxillipeds after logit transformation and solution concentration for five extracts. The dashed line indicates a 50% responding rate.

were very sensitive to conspecific muscle extracts, the median effective concentration 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 & 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 & Worlund, 1979).

Some results are contradictory. In our laboratory, when king crabs were fed with newly killed conspecifics, initially many crabs avoided it, but later might feed on the crab meat. Cannibalism occurred commonly during molting among juveniles (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, we assume that muscle of conspecifics may contain chemicals both functioning as alerting signals and as food. The characteristic response, either positive or negative, depends on quality and quantity of these chemicals, and the adaptation by crabs to these chemicals.

Among the three potential baits, herring, squid, and mussel, red king crabs are most sensitive 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 & Derby, 1986). Amino acids and amines have been considered the major feeding attractants (Daniel & Bayer, 1989; Zimmer-Faust & Case, 1982). Carr *et al.* (1996) reported that great differences in relative concentrations of these compounds of low molecular weight exist between extracts of tissues from fish and molluscs, but similarities are evident within each group (fish or molluscs). Although herring contains a lower concentration of total stimulants than mussel and squid, some stimulants have a higher concentration (Carr *et al.*, 1996). 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).

Juvenile female, ovigerous female, small male, and large male king crabs had similar chemosensory sensitivities. However, the four crab groups had differences in their feeding sensitivities. Ovigerous females had the highest feeding sensitivity while juvenile females had the lowest. We 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 days pre- and 34 days 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 responses of male crabs more effectively than that of females. Ovigerous females had a higher feeding sensitivity to ovary extract than the other crab groups. This difference was basically the same as for other extracts. An attempt to change catchability of the different sexes by using any of these tested baits appears to be unsuccessful.

Acknowledgments

Thanks are due to T. Koeneman, C. Botelho, K. Imamura, W. Loofbourrow of Alaska Department of Fish Game, and the crew of the R/V MEDEAE, for assistance with the collection of king crabs used for this study. We gratefully acknowledge Drs. R. Fagen, L. Haldorson, C. O'Clair, A. Paul, and A. Tyler for their reviews of the manuscript. Funded by

Alaska Department of Fish and Game, Commercial Fisheries Management and Development Division, partly under Cooperative Agreement NA37FL0333 with National Oceanic and Atmospheric Administration, National Marine Fisheries Service. The views expressed herein are those of the authors and do not necessarily reflect the views of NOAA or any of its sub-agencies.

Literature Cited

- Ache, B. W., 1982. Chemoreception and thermoreception. In: H. L. Atwood & D. C. Sandeman, (ed.) *The Biology of Crustacea* Vol. 3. Neurobiology: Structure and Function. pp. 369–398, Academic Press, New York.
- Breen, P. A., Carolsfeld, W., & Narver, D., 1985. Crab gear selectivity studies in Departure Bay. In: G. S. Jamieson, (ed.), *Invertebrate Management Advice*, Pacific Region, Canada. Manuscript Report of Fisheries and Aquatic Sciences, 1848: 21–39.
- Brodersen, C. C., 1992. Rearing red king crabs from the first benthic stage. Proceeding of the International Crab Rehabilitation and Enhancement Symposium, Alaska Department of Fish and Game and Kodiak College, 30–38.
- , Rounds, P. M., & Babcock, M. M., 1989. Diet influences cannibalism in laboratory-held juvenile red king crabs (*Paralithodes camtschatica*). In: *Proceedings of the International Symposium on King and Tanner Crabs*, Nov. 1989, Anchorage, Alaska. pp. 377–382, Univ. of Alaska Fairbanks.
- Carr, W. E. S., & Derby, C. D., 1986. Chemically stimulated feeding behavior in marine animals. *Journal of Chemical Ecology*, 12: 989–1011.
- , Netherton, J. C. III, Gleeson, R. A., & Derby, C. D., 1996. Stimulants of feeding behavior in fish: analyses of tissues of diverse marine organisms. *Biological Bulletin*, 190: 149–160.
- Daniel, P. C., & Bayer, R. C., 1989. Fish byproducts as chemo-attractant substrates for the American lobster (*Homarus americanus*): concentration, quality and release characteristics. *Fisheries Research*, 7: 367–383.
- , & Derby, C. D., 1991. Mixture suppression in behavior: the antennular flick response in the spiny lobster toward binary odorant mixtures. *Physiology and Behavior*, 49: 591–601.
- Derby, C. D., & Atema, J., 1981. Selective improvement in responses to prey odors by the lobster, *Homarus americanus*, following feeding experience. *Journal of Chemical Ecology*, 7: 1073–1080.
- , & ———, 1982. The function of chemo- and mechanoreceptors in lobster (*Homarus americanus*) feeding behavior. *Journal of Experimental Biology*, 98: 317–327.
- Fine-Levy, J. B., Daniel, P. C., Girardot, M. N., & Derby, C. D., 1989. Behavioral resolution of quality of odorant mixtures by spiny lobsters: differential aversive conditioning of olfactory responses. *Chemical Senses*, 14(4): 503–524.
- Hancock, D. A., 1974. Attraction and avoidance in marine invertebrates—their possible role in developing an artificial bait. *Journad du Conseil International Pour L'exploration de la Mer*, 35: 328–331.
- Hazlett, B. A., 1971. Antennule chemosensitivity in marine decapod Crustacea. *Journal of Animal Morphology and Physiology*, 18: 1–10.
- , 1990. Source and nature of disturbance-chemical system in crayfish. *Journal of Chemical Ecology*, 16: 2263–2275.
- Heatwole, D. W., Hunt, J. H., & Kennedy, F. S. Jr., 1988. Catch efficiencies of live lobster decoys and other attractants in the Florida spiny lobster fishery. Florida Marine Research Publications. Florida Department of Natural Resources, Bureau of Marine Research, 44, 15 pp.
- High, W. L., & Worlund, D. D., 1979. Escape of king crab, *Paralithodes camtschatica*, from derelict pots. NOAA Technical Report. U.S. Department of Commerce, National Marine Fisheries Service, NMFS-734, 11 pp.
- Hunter, J. V., Pfister, V. A., Romaine, R. P., & Baum, T. J., 1990. Effectiveness of commercially formulated and fish baits in trapping cambarid crawfish. *Journal of the World Aquaculture Society*, 21: 288–294.
- Jewett, S. C., & Feder, H. M., 1982. Food and feeding habits of the king crab *Paralithodes camtschatica* near Kodiak Island, Alaska. *Marine Biology*, 66: 243–250.
- Mackie, A. M., & Grant, P. T., 1980. The relative efficiencies of natural and artificial baits for the lobsters, *Homarus gammarus*: laboratory and field trials. *Journal du Conseil International Pour L'exploration de la Mer*, 39: 123–129.
- McLeese, D. W., 1970. Detection of dissolved

- substances by the American lobster (*Homarus americanus*) and olfactory attraction between lobsters. *Journal of Fisheries Research Board of Canada*, 27: 1371-1378.
- Miller, R. J., 1990. Effectiveness of crab and lobster traps. *Canadian Journal of Fisheries and Aquatic Sciences*, 47: 1228-1251.
- Norusis, M. J., 1993. *Advanced Statistics. SPSS for Windows*, Release 6.0. 578 pp., SPSS Inc., Chicago.
- Pearson, W. H., & Olla, B. L., 1977. Chemoreception in the blue crab, *Callinectes sapidus*. *Biological Bulletin*, 153: 346-354.
- , Sugarman, P. C., & Woodruff, D. L., 1979. Thresholds for detection and feeding behavior in the Dungeness crab, *Cancer magister* (Dana). *Journal of Experimental Marine Biology and Ecology*, 39: 65-78.
- , ———, ———, & Olla, B. L., 1981. Impairment of the chemosensory antennular flicking response in the Dungeness crab, *Cancer magister*, by petroleum hydrocarbons. *Fisheries Bulletin*, 79: 641-647.
- Rebach, S., French, D. P., von Staden, F. C., Wilber, M. B., & Byrd, V. E., 1990. Antennular sensitivity of the rock crab *Cancer irroratus* to food substances. *Journal of Crustacean Biology*, 10: 213-217.
- Richards, R. A., & Cobb, J. S., 1987. Use of avoidance responses to keep spider crabs out of traps for American lobsters. *Transactions of the American Fisheries Society*, 116: 282-285.
- Rittschof, D., 1992. Chemosensation in the daily life of crabs. *American Zoologist*, 32: 363-369.
- , & Buswell, C. U., 1989. Stimulation of feeding behavior in three species of fiddler crabs by hexose sugars. *Chemical Senses*, 14: 121-130.
- Zimmer-Faust, R. K.; & Case, J. F., 1982. Odors influencing foraging behavior of the California spiny lobster, *Panulirus interruptus*, and other decapod Crustacea. *Marine Behavior and Physiology*, 9: 35-58.
- , & ———, 1983. A proposed dual role of odor in foraging by the California spiny lobster, *Panulirus interruptus* (Randall). *Biological Bulletin*, 164: 341-353.
- , Tyre, J. E., & Case, J. F., 1985. Chemical attraction causing aggregation in the spiny lobster, *Panulirus interruptus* (Randall), and its probable ecological significance. *Biological Bulletin*, 169: 106-118.
- Zoutendyk, P., 1988. Consumption rates of captive cape rock lobster *Jasus lalandii*. *South Africa Journal of Marine Sciences*, 6: 267-271.
- Addresses: (SZ) Alaska Department of Fish and Game, Commercial Fisheries Management and Development Division, P. O. Box 25526, Juneau, Alaska 99802, U.S.A.; (TCS) Juneau Center, School of Fisheries & Ocean Sciences, University of Alaska Fairbanks, 11120 Glacier Highway, Juneau, Alaska 99801, U.S.A.
E-mail: (SZ) shijiez@fishgame.state.ak.us