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[Article]

Horizontal and Vertical Odor Plume Trapping of Red King Crabs Explains the Different Efficiency of Top- and Side-Entrance Pot Designs

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Abstract.—Interactions between the food search behavior of the red king crab *Paralithodes camtschaticus* and pot design and the consequences for entry success were studied in situ with a square pot with two funnels on opposite sides and a conical pot with one vertical funnel at the top. Red king crabs that approached the pots upcurrent were chemically stimulated and appeared to be locked onto the odor plume, whereas those that approached the pots across-current showed more flexible search behavior. The location of the funnels meant that entry also requireed a vertical search phase. Forty percent of the red king crabs encountering the pots performed vertical searches on each type of pot, but the probability of entry once a vertical search had commenced was 20 times as high for the square pot as for the conical pot. Chemically stimulated red king crabs limited their vertical search to the bait plume. The location of the bait relative to the entrance may have caused chemically stimulated rheotaxis to lead red king crabs all the way into the square pots, in contrast to the conical pots for which the entrance is higher than the extension of the plume. These results demonstrate the importance of including both horizontal and vertical dimensions in behavioral studies of the catch efficiency of crab pots.

Interactions between the food-search behavior of the target species and pot design determine the catching success of crab pots. The orientation of the funnel relative to current direction is crucial to the efficiency of red king crab pots, as red king crabs *Paralithodes camtschaticus* generally tend to approach pots and enter funnels upcurrent through the odor plume (Zhou and Shirley 1997a). When a pot has been encountered entry requires vertical movements, and the position and design of the funnel greatly influences the probability of entry (Miller 1990).

There are several sensory modalities involved in the catch process. During the attraction phase, red king crabs encounter olfactory stimuli and at closer range they also perceive visual stimuli (Miller 1979; Zhou and Shirley 1997a). Moreover, red king crabs already feeding in the pot may produce sounds to which other red king crabs can respond (Tolstoganova 2002), and once they are in physical contact with the pots, red king crabs are exposed to tactile stimuli from the net (Zhou and Shirley 1997b). Thus, red king crabs are successively or simultaneously exposed to a multitude of stimuli that may interact and either compete or reinforce each other. The outcome of the catch process may be influenced by which stimulus is dominant and the order in which red king crabs are exposed to different stimuli.

Two different types of pots have been used in making stock estimates of the red king crab, which was introduced in the Barents Sea in the 1960s (Orlov and Ivanov 1978); initially, conical pots with the vertical entrance at the top and later collapsible square pots with horizontal entrances on two sides. Comparative fishing trials have demonstrated that catch rates of square pots are three times higher than those of conical pots (Stiansen et al. 2008). Both when combining different stock estimate time series and when exploiting marine resources, it is crucial to know the efficiency and selective properties of the fishing gear used. Insight into how red king crabs interact with different types of pots is therefore essential.

We observed the horizontal and vertical movements of red king crabs encountering square and conical pots in situ to better understand the capture process of the

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TABLE 1.—Overview of the video recordings of red king crab behavior at conical and square pots. The observations of the conical pot were made with artificial light, while no light was used during the observations of the square pot.

Pot type	Date	Start time (hours)	Duration (min)	Depth (m)	Approaches	Entries
Conical	22 Aug 1997	2130	120	140	9	1
Conical	23 Aug 1997	2354	720	140	30	0
Conical	7 Jul 2000	1450	525	125	30	0
Square	18 Jul 2001	1203	272	47	38	9
Square	19 Jul 2001	1500	330	43	28	10
Square	20 Jul 2001	1338	262	55	45	8

two pot designs. As the inner funnel openings are above the seabed and placed at different heights relative to the bait, vertical search movements ought to have a profound effect on the catch efficiency of these pots. To enter the conical pot, a red king crab must climb to the top of the pot above the bait odor plume and then descend into the funnel. For the square pot, where the bait is at the same height as the funnel, red king crabs can follow the odor plume up the funnel and into the pot when the current is aligned with the entrance. There have been a number of studies on the behavior of crustaceans in relation to pots (e.g., Miller 1990; Vienneau et al. 1993; Zhou and Shirley 1997a, 1997b), but to the best of our knowledge this is the first quantitative study of the vertical dynamics involved.

Methods

The behavior of red king crabs vis-à-vis a baited conical pot was observed in the Bugøyfjord (Finnmark, northern Norway) in August 1997 and July 2000 (Table 1), with an underwater video camera (SIMRAD SIT OE1324; sensitivity, 2×10^{-4} lx) mounted in a frame to which the pot was attached (Figure 1). The observations were made at depths of 125–140 m and a low-intensity (9 W) artificial red light was used. Real-time video recordings were transmitted by radio link from a surface buoy to the research vessel and videotaped for later analysis (see Svellingen et al. 2002 for further technical details on the instrument platform).

The current direction was determined from a plastic streamer attached to the pot and from drifting particles. The angle of dispersion of the odor plume from a bait located off the bottom was assumed to be 30° (15° on either side of the current direction), both horizontally (Miller 1980) and vertically. Periods of very low current, determined by the streamer being vertical, and periods of unstable current were excluded from the analyses.

The conical pot was 80 cm tall, had lower and upper diameters of 140 and 85 cm, respectively, and weighed 17 kg in air (Figure 1). Its steel frame consisted of three horizontal circular frames joined by six evenly spaced vertical bars. The frame was lined with 4-mm polyethylene netting with a mesh size (inside length of stretched mesh) of 150 mm. The pot's vertical conical-shaped funnel was made of plastic, had outer and inner diameters of 45 and 40 cm, respectively, and a length of 30 cm. It was placed on the top of the pot, giving an entrance sector of 360°. The 20-cm-long bait bag was made of 20-mm-mesh polyamide netting and placed in the center of the pot, about 10 cm below the inner funnel opening. Each pot was baited with about 1 kg of chopped (~2-cm pieces), thawed Atlantic herring *Clupea harengus*.

A red king crab's activities related to a pot were categorized into five categories: approach, entrance search, leaving, entry, and exit (see Zhou and Shirley 1997b for detailed definitions). The entrance search was further divided into a horizontal phase and a vertical phase. Movements on the seabed after the red king crab made physical contact with the pot were categorized as horizontal search, and the horizontal search sector displayed by a crab was defined as the sector of the pot circumference that was searched. Movements on the pot with no physical contact with the seabed lasting at least 5 s were defined as vertical search.

The direction of movement of red king crabs approaching the pot was recorded relative to the current direction. Red king crabs moving upcurrent within a sector of 90° (i.e., 45° to either side of the current direction) were categorized as approaching the pot upcurrent. Similarly, red king crabs encountering the pot within the other 90° sectors were categorized as approaching the pot down-current or across-current.

Similar behavioral observations of red king crabs as those collected for the conical pot were made with a square pot type in July 2001 (Table 1). These observations were also made in the Bugøyfjord, but at a shallower site with a depth of 43–55 m and without the use of artificial light.

The square pot was collapsible and made from 3-mm polyethylene netting with mesh size of 100 mm, and was attached to an upper aluminum frame and a lower steel frame (Figure 1). The pot weighed 37 kg out of

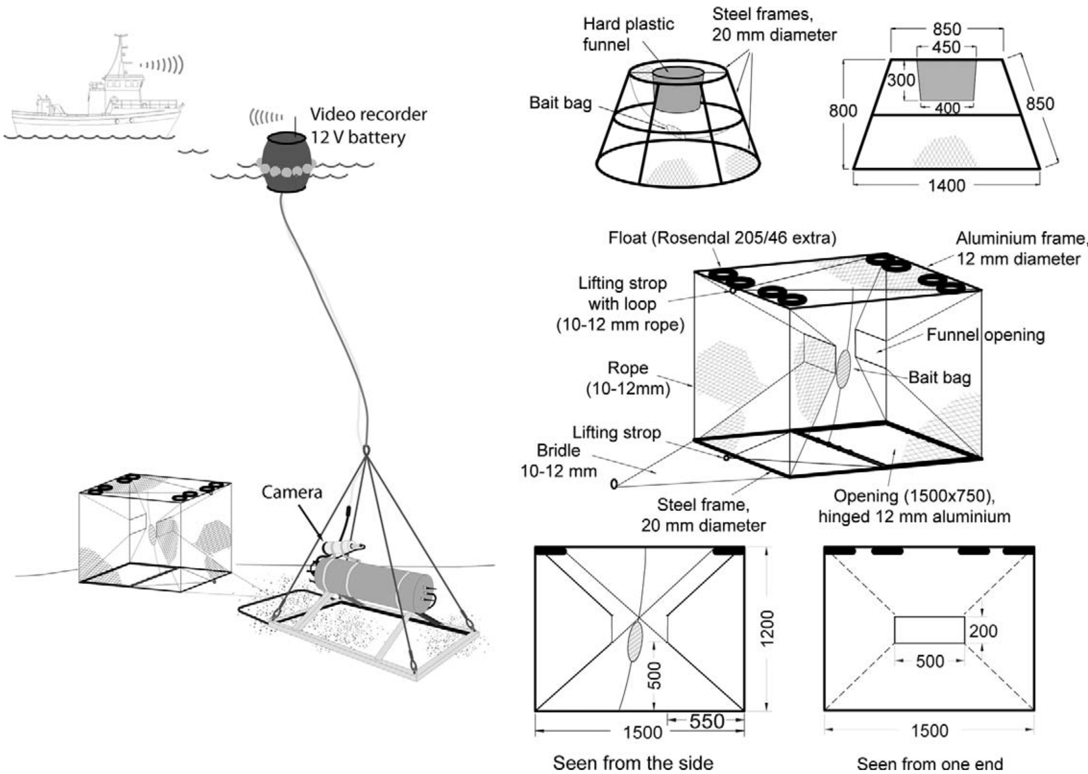

FIGURE 1.—Experimental setup used to study the search behavior of red king crabs vis-à-vis baited square and conical pots. Design details are given in the right-hand portion of the figure. Dimensions are in millimeters.

the water. When unfolded in the sea by the floats attached to the upper frame, the dimensions of the pot were 150 × 150 × 120 cm. The pot had two opposed funnels (entrances), and thus an entrance sector of 180°. The funnels were made of netting similar to that lining the frames and the inner funnel opening was rectangular, measuring 50 cm wide × 20 cm high. A herring-baited bag similar to that used for the conical pot was placed in the center of the pot at the height of the lower part of the inner end of the funnels.

When red king crab movements relative to the square pot were being quantified, it was also noted whether the crab encountered the pot on a side with or without an entrance, and how the pot was oriented relative to the current direction.

Standard errors of estimated proportions of red king crabs ($\hat{r}$) displaying a specific behavior were calculated assuming a binomial experiment with n red king crabs as follows:

$$\mathrm{SE}(\hat{r}) = \sqrt{\hat{r}(1-\hat{r})/n}.$$

Frequency data arising from the categorization of red king crab behavior related to the two pot designs were tabulated in contingency tables and a Fisher exact test was used to test the null hypotheses that behavior (e.g., distribution of approach angle) was independent of pot type.

Results

For both pot types the majority of red king crabs approached upcurrent (Table 2) but the proportion of upcurrent approaches was significantly higher for the conical (84 ± 5% [mean ± SE]) than for the square pot (62 ± 6%) (Fisher's exact test: $P = 0.014$). For the

TABLE 2.—Direction of approach of red king crabs at conical and square pots. Pot orientation is the orientation of the square pot relative to the current (i.e., 0 = the axis through the entrances is parallel to the current, 90 = the axis through the entrances is perpendicular to the current).

			Direction of approach (%)		
Pot type	Pot orientation	Number of crabs	Up-current	Across-current	Down-current
Conical		63	84.1	12.7	3.2
Square	0	43	74.4	23.3	2.3
Square	90	34	47.0	41.2	11.8

TABLE 3.—Percentage distributions of the horizontal sector of the pot circumference searched by red king crabs after arriving at conical and square pots. In parentheses are the number of red king crabs entering the pot/the number in the search sector.

Pot type	Pot orientation	Approach direction	Horizontal search sector (°)				
			<45	[45, 90)	[90, 135)	[135, 180)	>180
Conical		Up	32.1 (0/17)	47.2 (1/25)	9.4 (0/5)	5.7 (0/3)	5.7 (0/3)
		Across	12.5 (0/1)	37.5 (0/3)	25.0 (0/2)	12.5 (0/1)	12.5 (0/1)
Square	0	Up	46.9 (11/15)	43.8 (2/14)	9.4 (1/3)	0	0
		Across	30.0 (0/3)	20.0 (1/2)	10.0 (1/1)	40.0 (1/4)	0
	90	Across	71.4 (7/10)	21.4 (0/3)	7.1 (0/1)	0	0
		Up	56.3 (0/9)	12.5 (0/2)	18.8 (0/3)	12.5 (0/2)	0

square pot, the approach angle depended on the orientation of the pot relative to the current direction (Fisher's exact test: $P = 0.04$), with a higher proportion of red king crabs performing upcurrent approaches when the current direction was parallel to the pot entrances (74 ± 7%) than when it was across the current (47 ± 9%). When the current was parallel to the entrances of the square pot, the distributions of approach angles were similar for conical and square pots (Fisher's exact test: $P = 0.36$).

About three-quarters of the red king crabs encountering the pots displayed a horizontal search sector of less than 90° of the pot circumference (Table 3), irrespective of pot type (conical: 75 ± 4%; square: 81 ± 4%). Of the red king crabs that approached the square pot upcurrent, the proportion with a search sector less than 90° was not significantly different (Fisher's exact test: $P = 0.10$) for those that encountered the sides with (91 ± 5%) and without (69 ± 12%) an entrance. However, for the red king crabs approaching the square pot across the current, this proportion was significantly higher for those red king crabs that encountered the sides with an entrance (93 ± 7%) than that of those that encountered the sides without an entrance (50 ± 16%) (Fisher's exact test: $P = 0.05$).

TABLE 4.—Proportion of crabs that started a vertical search for each of the three approach directions (upcurrent, across-current, and downcurrent).

Pot type	Pot orientation	Number of crabs	Direction of approach (%)		
			Up-current	Across-current	Down-current
Conical		63	60.4	12.5	0
Square	0	43	59.4	60.0	0
Square	90	34	0	57.1	25.0

The percentage of red king crabs that started a vertical search did not differ significantly between the conical (52 ± 6%) and square pots (44 ± 6%) (Fisher's exact test: $P = 0.40$). The initiation of vertical search on the conical pot was dependent on the direction of approach relative to the current direction ($P < 0.01$; Table 4), with red king crabs approaching upcurrent searching vertically more often (60 ± 7%) than red king crabs approaching across current (13 ± 12%). Vertical search on the square pot was dependent on the orientation of the pot relative to the current direction ($P < 0.01$; Table 4). Red king crabs that approached upcurrent and encountered the side without an entrance did not display vertical search, whereas vertical search was observed in about 60% of the red king crabs in the other three categories of upcurrent and across-current approaches.

The probability that the vertical search would lead the red king crab to the funnel area was significantly ($P < 0.01$) higher for the square (0.88 ± 0.05) than for the conical (0.52 ± 0.09) pot. Furthermore, once a vertical search had been initiated, the probability of entry was 20 times higher for the square (0.68 ± 0.07) than for the conical (0.03 ± 0.03) pot.

Red king crabs making vertical searches on the conical pot spent most of the time at heights corresponding to the vertical extension of the odor plume, although the majority (88 ± 5%) occasionally explored higher (Figure 2). Six minutes after they started the vertical search, only 40 ± 9% of the red king crabs had terminated their search and left the pot, and one-third of the red king crabs (SE, 8%) were still at the pot after 15 min. None of the red king crabs making vertical searches on the square pot extended their search above the upper reach of the odor plume, and red king crabs that were not caught terminated their vertical search in less than 6 min (Figure 3).

The single red king crab caught in the conical pot

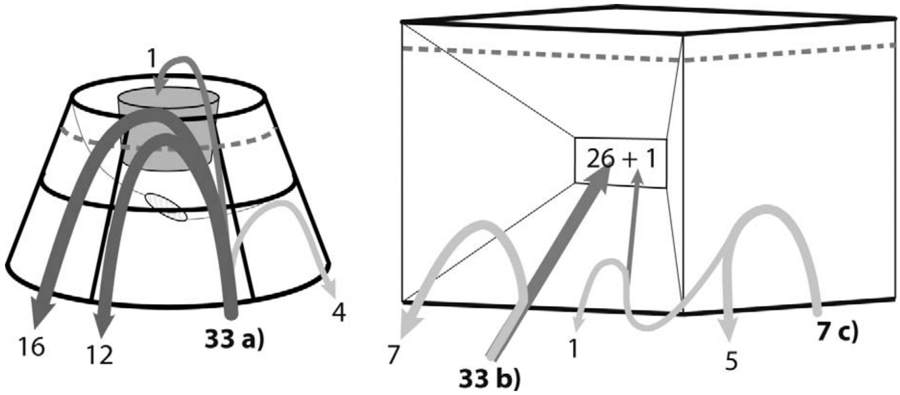

FIGURE 2.—Movements of red king crabs initiating vertical searches at conical and square pots. The movements are illustrated by arrows; the dotted lines indicate the upper vertical extensions of the odor plumes at the pot sides, assuming a vertical angle of dispersion of 30°. For the conical pot, 33 red king crabs initiated a vertical search (a), and 1 was caught. For the square pot, 33 crabs initiated a vertical search at the side with an entrance (b) and 7 on the side without an entrance (c); of these, 26 and 1, respectively, were caught.

entered after having spent 11 min on its vertical search, while four red king crabs entered the square pot within 30 s of starting their vertical search, and 15 of the 27 red king crabs captured had entered within 90 s of the start of their vertical search.

Discussion

In situ studies provide realistic observations of how red king crabs interact with baited pots. Despite their potentially powerful effect on the catch efficiency of pots, movements in the vertical plane have never before been quantified in crustaceans. Our study on the behavior of red king crabs vis-à-vis different pot designs provides novel observations on their vertical dynamics.

Ideally, the pots should have been studied in the same year, and at the same time of day and depth. The difference in the time of day of our observations is unlikely to have affected the results, as Tarverdieva (1978) observed that red king crabs continued to feed throughout the 24-h cycle, and red king crabs tagged with acoustic transmitters showed no diel activity rhythm during the arctic summer (Jørgensen et al. 2007). The two pot types were observed at different depths, with artificial light used to study the conical pot. If visual stimuli from captured red king crabs influenced crabs that were approaching pots, the light level, and therefore the depth, might have had an effect. In comparative fishing trials, however, neither catch nor size distribution was found to differ across the depth range from 50 to 250 m (Stiansen et al. 2008). The proportion of red king crabs that performed vertical searches did not differ between the pots, and the observation that the vertical (and horizontal) movements were mostly restricted to within the odor plume strongly suggests that the foraging behavior of the red king crabs was guided primarily by olfactory stimuli. The angle of dispersion of the odor plume can be modified by current velocity (Stanley et al. 1985) and bait distance from bottom (Webster and Weissburg 2001). We assumed that the bait odor plume had a vertical angle of dispersion of 30° (see Miller 1980) but moderate deviations from this assumption are not crucial to our conclusions.

The probability of red king crabs entering the square pot was much higher than for the conical pot. Movements in the horizontal plane cannot explain this difference, as the less effective conical pot had an entrance sector of 360°. However, the vertical dynamics influenced the probability of entering the pot. Although similar proportions of the red king crabs encountering the two pots initiated vertical searches, which were a prerequisite of capture, the probability of entry once a vertical search had been initiated was 20 times higher for the square pot than for the conical pot. The red king crabs tended to remain within the odor plume of the bait after encountering a pot. The upper funnel opening in the conical pot was located 40 cm above the bait and thus outside the odor plume. Although half of the red king crabs initiating a vertical search climbed onto the roof of the conical pot, they then moved undirected and descended back into the odor plume (except for one red king crab that was caught), apparently "locked" in the plume (Miller 1978a, 1978b). In contrast, red king crabs in the odor plume of the square pot, where the bait was placed at the same height as the inner opening of the funnel, were able to follow the odor plume all the way through

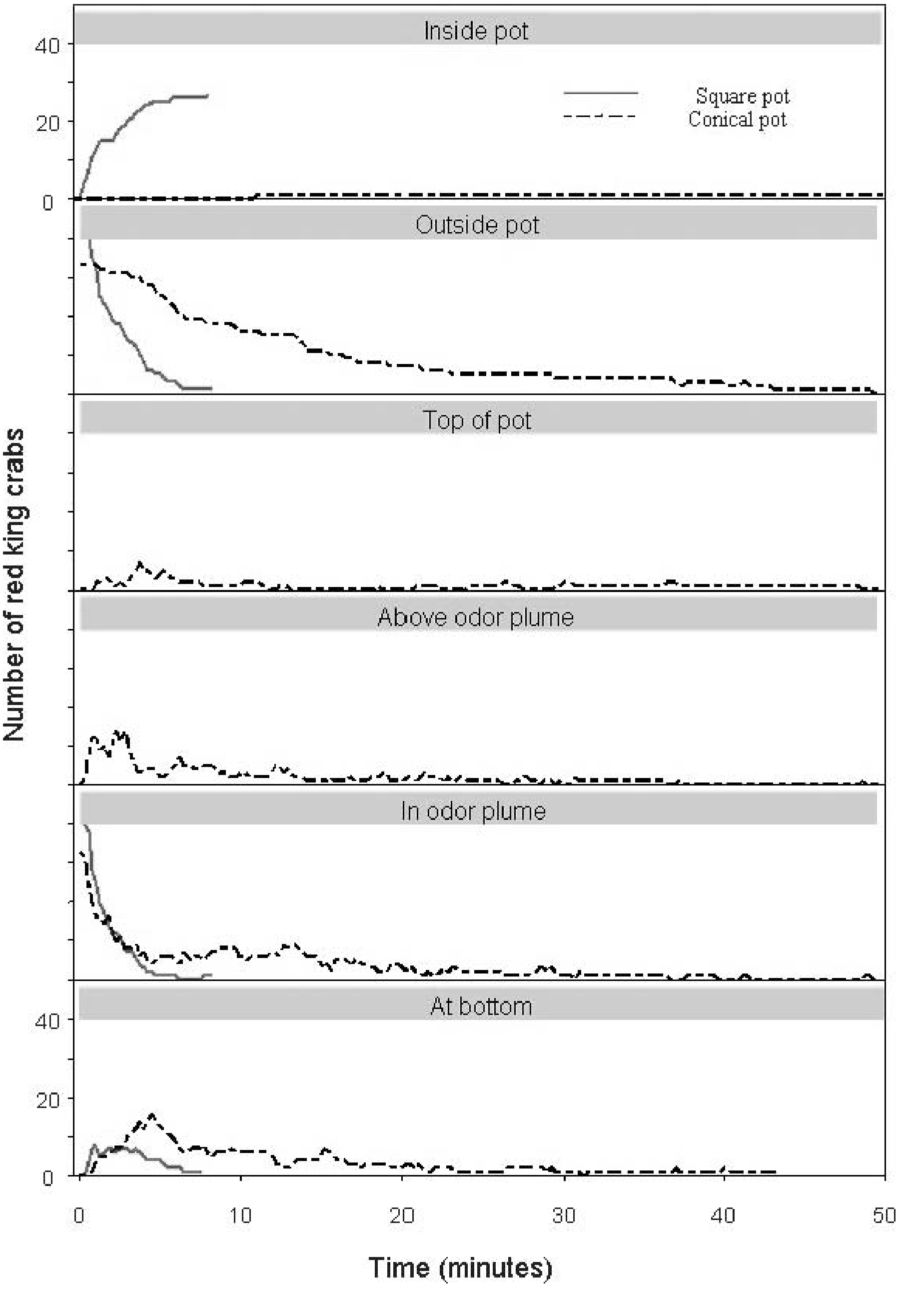

FIGURE 3.—Locations of red king crabs that made vertical searches at conical ($n = 33$) and square pots ($n = 40$). The curves show the locations of the crabs every 15 s after the vertical search was initiated. The panel labeled "outside pot" represents the total number of crabs in the bottom four panels. The panel labeled "inside pot" shows the number actually trapped.

the funnel provided they had encountered the pot when the current was aligned with the entrance. The position of the funnel entrance relative to the bait most likely explains the difference in probability of entry, although the two pot designs also differed in other aspects.

A large proportion of the red king crabs that approached the square pot upcurrent when the current was parallel to the funnel entered the pot. However, red king crabs that entered the observation field upcurrent when the current was perpendicular to the funnel did not enter the square pot. These red king crabs encountered a side without a funnel and kept butting against the netting of the pot for some time, and never initiated a vertical search. Chemically stimulated rheotaxis therefore appears to "lock" the red king crabs in the odor plume, and our observations suggest that chemical stimulation triggers a specific search strategy with limited flexibility.

In contrast, when red king crabs approached the square pots across the current, a surprisingly high proportion entered. Some of these red king crabs were able to enter the funnel by just continuing to move in the same direction as that when they approached the pot. In addition, red king crabs encountering a side without a funnel often made a wider horizontal search that allowed them to localize the odor plume and the funnel. This demonstrates that continuous chemical stimulation is not a prerequisite for red king crabs to enter baited pots, and suggests that auditory stimuli from red king crabs feeding on the bait bag (Tolstoganova 2002) or visual stimuli from the pot or captured red king crabs may attract other red king crabs (Miller 1979). Thus, responses of red king crabs to baited pots may be more flexible than has previously been observed in tanks (Zhou and Shirley 1997a).

An initial response to olfactory stimuli may present red king crabs with a challenge, as they appear to rely mainly on the chemical sensory modality. If the current does not pass out of the funnels of the square pot, the chemically stimulated red king crabs need to solve a detour problem to enter the pot, a capacity that red king crabs seem to lack in a situation that is presumably seldom encountered under natural conditions. Red king crabs that approach the bait across the current (i.e., not chemically stimulated) seem to employ a more complex search strategy that involves auditory or visual stimuli, and includes a wider vertical and horizontal search pattern. These red king crabs may be individuals that have had previous contacts with the pot and the odor plume. After moving away from the pot and odor plume following an unsuccessful upcurrent approach, red king crabs may switch their search strategy. We observed that red king crabs more often approached the pot across the current when the current direction was perpendicular to the entrance than when parallel to it. This suggests that red king crabs that approached the pot upcurrent when the current direction was perpendicular to the entrance modified their search behavior upon eventually leaving the pot, and later reentered the observation field from a different direction.

In conclusion, this study suggests that the low catch efficiency of conical pots compared with square pots (Stiansen et al. 2008) can be explained by the low probability of red king crabs locating and entering the funnel of conical pots. As red king crabs are usually "locked onto" the odor plume in both horizontal and vertical dimensions, the current direction and position of the bait relative to the funnels have an important influence on catch efficiency. This study demonstrated how crucial vertical movements are for the efficiency of a pot, and that they need to be studied if we wish to fully understand differences in efficiency between pots. Our study also elucidates the role of chemical stimuli vis-à-vis other types of stimuli. In crustaceans, chemical stimulation is crucial in food search, and in red king crabs, chemical stimuli seemed to override subsequent auditory and visual stimulation. The order in which a red king crab encounters different stimuli as well as earlier experience may influence its search strategy and thereby affect the efficiency of baited pots. If the order in which crabs encounter different stimuli influences their behavior, this should have consequences for our general understanding of how aquatic organisms interact with different types of fishing gear.

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