IMPAIRMENT OF THE CHEMOSENSORY ANTENNULAR FLICKING RESPONSE IN THE DUNGENESS CRAB, *CANCER MAGISTER*, BY PETROLEUM HYDROCARBONS

WALTER H. PEARSON,[1] PETER C. SUGARMAN,[1] DANA L. WOODRUFF,[1] AND BORI L. OLLA[2]

ABSTRACT

After exposing Dungeness crabs in a continuous-flow system to seawater contaminated with Prudhoe Bay crude oil (0.27 parts per million), we observed the behavior of crabs presented with a clam extract. In response to seawater solutions of clam extract, Dungeness crabs change antennular orientation and increase antennular flicking rate. After 24-hour exposure and with oil still present, the proportion of crabs showing the changes in antennular behavior indicating detection of chemical food cues was significantly reduced. In contrast, the proportion showing chelae probing was not. Within 1 hour after return to clean water the antennular response recovered. Such rapid recovery indicates that the chemosensory impairment probably did not derive from structural damage to sensory cells but does not indicate which of several other possibilities was the most likely mechanism. By impairing the chemosensory antennular flicking response of Dungeness crabs, petroleum hydrocarbons could cause crabs some difficulty in finding food.

For marine organisms, disruption of chemoreception by oil is viewed as both likely and of important ecological consequence (Blumer 1969; Olla et al. 1980). Chemosensory disruption by various petroleum hydrocarbons and oil fractions has been reported in snails (Jacobson and Boylan 1973; Hyland and Miller 1979), lobsters (Atema and Stein 1974), and in shore crabs (Takahashi and Kittredge 1973). In some of these early studies the exposure regime was not well defined and did not always compare well with the length and level of exposure likely to be encountered in oil spills. Here we report on the ability of the Dungeness crab, *Cancer magister* Dana, to detect and respond to a food extract after 24-h exposure to seawater contaminated with Prudhoe Bay crude oil in a continuously flowing seawater system.

The antennules of many decapod crustaceans are a site for chemoreception of water-borne chemical cues (Hazlett 1971a). Antennular flicking may be analogous to sniffing in vertebrates (Fuzessery 1978) and enhances the ability of crustaceans to detect changes in their chemical environment (Schmitt and Ache 1979). Behavioral observations of antennular flicking rate indicate that detection of a clam extract occurs at 10^{-15} g/l in the blue crab, *Callinectes sapidus* (Pearson and Olla 1977), and at 10^{-10} g/l in the Dungeness crab (Pearson et al. 1979).

To determine whether exposure to petroleum hydrocarbons impaired this acute detection ability, we exposed Dungeness crabs to oil-contaminated seawater for 24 h, presented them with a clam extract in the presence of the oil-contaminated seawater, and recorded the percentages of crabs showing the changes in antennular behavior indicative of detection and of those showing the chelae probing indicative of food searching. At 24 h and 48 h after stopping the flow of oil-contaminated seawater, we retested the crabs to determine the time necessary for recovery of detection ability. Because this first experiment indicated rapid recovery, we performed a similar second experiment in which we presented the clam extract to Dungeness crabs 1 h after stopping the flow of contaminated seawater.

MATERIALS AND METHODS

Animal Collection and Maintenance

Dungeness crabs trapped in the Strait of Juan de Fuca, Wash., were held under the conditions described by Pearson et al. (1979). Seawater temperatures during the two experiments were 8.9 ($\pm$2.7 SD)° C (n = 16) and 9.2 ($\pm$0.5)° C (n =

[1]Battelle Pacific Northwest Laboratories, Marine Research Laboratory, Washington Harbor Road, Sequim, WA 98382.
[2]Northeast Fisheries Center Sandy Hook Laboratory, National Marine Fisheries Service, NOAA, Highlands, NJ 07732.

Manuscript accepted June 1981.
FISHERY BULLETIN: VOL. 79, NO. 4, 1981.

16); salinities, 31.8 (±0.4)‰ (n = 5) and 32.0 (±0.0)‰ (n = 4); and dissolved oxygen 7.6 (±0.7) mg/l (n = 16) and 8.0 (±0.3) mg/l (n = 9). Clumps of the blue mussel, *Mytilus edulis*, and the littleneck clam, *Protothaca staminea*, provided an ad libitum diet.

Experimental Apparatus

We coupled the oil delivery system developed by Vanderhorst et al. (1977), and used extensively by Anderson et al. (1979, 1980), to the chemosensory testing apparatus of Pearson et al. (1979). Seawater contaminated with Prudhoe Bay crude oil was delivered to 20 of the 40 chemosensory testing chambers from dripper arms situated along manifolds connected to the oil delivery system. Contaminated water entered each exposure chamber at 0.1 l/min while clean water entered at 0.9 l/min. Control chambers received clean water at 1.0 l/min. Seawater entered each chamber through a glass funnel connected to a slotted inlet tube within the chamber. Teflon[3] tubes carried seawater solutions of the clam extract to the funnels from burets calibrated to deliver 20 ml within 15 s. Previous dye studies of Pearson et al. (1979) showed that the maximum concentration of an introduced solution within a chamber occurs 10 s after introduction and is 0.011 (±0.003) times the concentration of the introduced solution.

The delivery system produced oil-contaminated seawater that was largely a water-soluble fraction with some finely dispersed droplets. The chemical composition of this oil-contaminated seawater has been well characterized by Bean et al. (1978) and reported by Anderson et al. (1980). Here we sampled seawater in the testing chambers by the resin column absorption technique of Bean et al. (1978) and analyzed the samples by infrared (IR) spectrophotometry. The data of Bean et al. and Anderson et al. show the correlations between the values determined by IR and the concentration of specific hydrocarbons determined by other methods for the same system. To determine how rapidly hydrocarbon concentrations dropped after stopping the flow of oil-contaminated water in the second experiment, we supplemented IR analyses with analyses for monoaromatic hydrocarbons by a helium gas partitioning technique modified from McAuliffe (1971).

[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

Experimental Solutions

The experimental solutions were seawater solutions of freeze-dried clam extract (FDCE) of littleneck clam prepared following Pearson et al. (1979). Stock solutions averaging 1.89 (±0.12) g FDCE/l (n = 6) for the first experiment and 2.06 (±0.22) g FDCE/l (n = 5) for the second were refrigerated and used within 5 d. A 10^{-6} dilution of the stock FDCE solution was made 1 h before testing with seawater freshly filtered through a 0.4 μm membrane. An aliquot of the filtered seawater used for dilution was used as the control solution. All solutions were held in a water bath at ambient seawater temperature.

Procedures

After the oil delivery system had been operating for several days and the hydrocarbon concentrations measured, a single Dungeness crab was added to each of the 20 exposure and 20 control chambers. Chemosensory testing was synchronized to begin and end within either a rising or falling tide and after 24-h exposure to oil-contaminated seawater. In the first experiment, the FDCE solutions were presented with oil-contaminated seawater still flowing through the chambers. Each crab was presented with either one of two dilutions of FDCE or a control of filtered seawater. After correction for dilution within a chamber, these FDCE concentrations were 10^{-2} and 10^{-8} g/l. The choice of dilution and the order of presentation were randomized except that active crabs and those with retracted antennules were passed over. The observer did not know the identity of any solution. An individual crab was observed for 60 s prior to introduction of experimental solution, and the antennular flicking rate and other behavior recorded. The observer depressed a switch of an event counter for each flick of one antennule. The solution (20 ml) was then introduced and observation continued for another 60 s from onset of introduction.

The criteria of Pearson et al. (1979) were used to score the behavior. Detection was indicated when a crab abruptly changed antennular orientation and increased antennular flicking rate so that the ratio of the rate after solution introduction to that before was 1.50 or higher. Previous observations indicate that the a priori probability that such an increase in antennular flicking is spontaneous, rather than in response to the solution, is <5%

(Pearson et al. 1979). The onset of food searching was indicated when a crab probed the substrate with its chelae or exhibited the capture response described by Pearson et al. (1979).

To examine recovery of detection ability, we stopped the flow of oil-contaminated water after the first presentation of FDCE. Clean seawater then entered the chambers at 0.9 l/min. After 24 h and 48 h both exposed and control crabs were again presented with experimental solutions and their behavior observed and scored.

Because the first experiment indicated rapid recovery, we wished to see if such recovery was quick as 1 h and, therefore, repeated the exposure phase of the first experiment. Instead of presenting FDCE with oil-contaminated water still present, we turned off the contaminated water and presented the FDCE 1 h later. The start and finish of exposure for individual crabs was staggered to achieve this 1-h clearance of oil from the chambers.

Statistical Analysis

The experiments were run until 28-33 crabs had been tested under each experimental condition. The numbers of crabs detecting and not detecting the various experimental solutions were totaled for exposed and control conditions. Although data is presented as the percentage of crabs detecting the FDCE, chi-square analysis was done on 2 × 2 contingency tables of the number of crabs detecting or not detecting under control or exposed conditions. Data for crabs showing chelae probing were treated similarly.

RESULTS

Hydrocarbon Concentrations

During the first experiment, where the clam extract was presented in the presence of oil-contaminated seawater, the total hydrocarbon concentrations by IR analyses were 0.27 (±0.04) ppm (n = 22) during the 24-h exposure and 0.013 (±0.004) ppm (n = 6) 24 h after the oil-contaminated water was stopped. During the second experiment, where the clam extract was presented 1 h after stopping the oil-contaminated seawater, the total hydrocarbon concentration by IR averaged 0.34 (±0.07) ppm (n = 10). Also, in the second experiment after 1 h the concentration of monoaromatic hydrocarbons (Table 1) fell to 0.008 times the exposure level.

TABLE 1.—The concentrations (parts per billion) of monoaromatic hydrocarbons in the testing chambers. Determined by helium gas partitioning, n = 4.

	Hydrocarbon concentrations			
	During 24 h of continuous flow		1 h after flow stopped	
Hydrocarbon	$\bar{X}$	SD	$\bar{X}$	SD
Benzene	50.1	10.8	0.13	0.24
Toluene	85.0	12.7	.16	.31
Ethylbenzene	13.8	2.8	.74	.95
m- plus *p*-Xylene	38.0	5.2	.94	1.36
o-Xylene	19.5	3.4	.90	1.22
Total trimethylbenzenes	40.6	11.9	<.01	
Total	247.0	34.7	1.98	3.76

Impairment and Recovery of Chemosensory Detection

After 24-h exposure to and still in the presence of oil-contaminated seawater, the percentage of exposed crabs detecting the clam extract was about half that of control crabs (Table 2). In contrast, the percentage of crabs probing with chelae did not differ significantly between control and exposed conditions (Table 3). Of the exposed crabs that probed the substrate with their chelae after presentation of 10^{-2} g FDCE/l, 48% (n = 25) did so without the normally preceding increase in the antennular flicking rate to above the criterion ratio of 1.50. One control crab (3%, n = 31) probed with the chelae without the normal increase in the antennular flicking rate. For crabs showing chelae probing, the antennular flicking rate ratio was significantly higher for control individuals (median = 2.36, range = 1.46-17.50, n = 31) than for exposed individuals (median = 1.56, range = 0.76-6.82, n = 25; median test, χ^2 = 9.19, df = 1, P = 0.998). Previously, no Dungeness crab (n = 89) presented with high levels of clam extract (10^{-3} to 10^{-6} g/l) showed chelae probing without first increasing the antennular flicking rate (Pearson et al. 1979).

Recovery of detection ability occurred rapidly. In the first experiment the percentage of crabs detecting FDCE at both levels did not differ between control and exposed conditions for both 24 h and 48 h (Table 2). In the second experiment, where the FDCE was presented 1 h after the flow of oil-contaminated seawater was stopped, again the percentage of crabs detecting did not differ significantly between control and exposed conditions (Table 4).

Whereas the antennular response to the clam extract was reduced under exposure and recovered after return to clean water, the basic rate of

TABLE 2.—Percentage of Dungeness crabs detecting the clam extract (FDCE) after exposure to continuously flowing seawater contaminated with Prudhoe Bay crude oil.

FDCE (g/l)	Treatment	After 24-h exposure				After 24 h in clean water				After 48 h in clean water			
		No. tested	Detecting (%)	χ^2	P	No. tested	Detecting (%)	χ^2	P	No. tested	Detecting (%)	χ^2	P
10^{-2}	Control	32	97	16.0	0.999	37	95	1.18	0.723	31	97	1.96	0.838
	Exposed	30	53			31	87			31	87		
10^{-8}	Control	34	32	3.46	.937	38	42	.05	.177	31	36	1.06	.697
	Exposed	31	13			33	39			31	48		
Control	Control	18	17	.40	.473	17	35	.13	.282	16	40	1.97	.840
	Exposed	20	25			22	41			17	18		

TABLE 3.—Percentage of Dungeness crabs probing with the chelae upon presentation of a clam extract (FDCE) after exposure to continuously flowing seawater contaminated with Prudhoe Bay crude oil.

FDCE (g/l)	Treatment	After 24-h exposure				After 24 h in clean water				After 48 h in clean water			
		No. tested	Probing (%)	χ^2	P	No. tested	Probing (%)	χ^2	P	No. tested	Probing (%)	χ^2	P
10^{-2}	Control	32	97	2.18	0.860	37	84	0.114	0.265	31	84	2.20	0.862
	Exposed	30	87			31	81			31	68		
10^{-8}	Control	34	6	.329	.434	38	5	.395	.470	31	0	1.02	.687
	Exposed	31	10			33	9			31	3		
Control	Control	18	0	.924	.664	17	0	.793	.627	16	6	1.10	.705
	Exposed	20	5			22	4			17	0		

TABLE 4.—Percentage of Dungeness crabs responding to a clam extract (FDCE) presented in clean water 1 h after 24-h exposure to oil-contaminated seawater.

FDCE (g/l)	Treatment	No. tested	Crabs detecting			Crabs chelae probing		
			%	χ^2	P	%	χ^2	P
10^{-2}	Control	28	96	0.002	0.040	89	0.952	0.671
	Exposed	30	97			80		
10^{-8}	Control	33	42	.551	.542	0	1.118	.710
	Exposed	30	33			3		
Control	Control	19	37	.681	.591	0		
	Exposed	13	23			0		

antennular flicking was not affected by exposure. The antennular flicking rate during the minute before introduction of the clam extract did not vary under exposure, control or recovery conditions over both experiments (median test, $\chi^2 = 2.62$, df = 7, $P = 0.08$). The overall grand median flicking rate was 33 flicks/min ($n = 653$). The median antennular flicking rate for resting Dungeness crabs was previously found to be 30 flicks/min (Pearson et al. 1979).

DISCUSSION

Whereas our exposure regime was low, brief, and well-characterized compared with most of the oil effects studies to date, we must clarify the circumstances to which our exposure is applicable. We exposed Dungeness crabs for 24 h to oil-contaminated seawater (0.27 ppm total hydrocarbons by IR) in which dissolved monoaromatic hydrocarbons (0.247 ppm) predominated. Our system produced this oil-contaminated seawater by continuous mixing of fresh oil with flowing seawater (9° C) followed by separation of floating oil and diversion of nonfloating mixture to the exposure chambers (Vanderhorst et al. 1977).

For a study of its kind we believe our exposure regime to be the best characterized to date, but the exposure regime is not representative of all, or perhaps even most, oil spill situations. Concentrations of total oil in the water ranging from 0.1 to 1.0 and lasting several days have indeed been reported (Grahl-Nielsen 1978; Calder and Boehm in press), but in such cases detection of substantial amounts of alkane (saturate) hydrocarbons indicated that an unknown but substantial amount of oil was emulsified, i.e., present as droplets. Because only 2% of the total hydrocarbons in our oil-contaminated seawater were saturates (Anderson et al. 1980), our exposure regime did not mimic situations where emulsified oil and high proportions of saturate hydrocarbons exist. The chemosensory effects of emulsified oil remain to be studied. Our results are most applicable to situations where dissolved monoaromatic hydrocarbons predominate in the water column.

When oil is spilled, monoaromatic hydrocarbons usually do not attain high concentrations in the water column but rather are rapidly lost by evaporation (McAuliffe 1977a, b). During the last 3 d of a 21-d platform spill in the Gulf of Mexico McAuliffe et al. (1975) measured total low molecular weight (C_1-C_9) hydrocarbons in the water column using a gas equilibration method similar

to ours and found concentrations ranging from 0.002 to 0.010 ppm at 5 and 10 m. Near-surface concentrations ranged from a maximum of 0.200 ppm near the platform (230 m) to 0.002 ppm at a distance (1.5 km). About half these C_1-C_9 hydrocarbons, i.e., 0.100 ppm, were the monoaromatics predominating in our oil-contaminated seawater. During four 10.5-barrel experimental spills concentrations of C_2-C_{10} aromatic hydrocarbons ranged from 0.002 to 0.050 ppm at 1.5 m within 20 min after the spill and were not detectable after 1 h (McAuliffe 1977b). Because the low temperature (9° C) of our seawater and perhaps other system properties slow evaporative loss, our system produced oil-contaminated seawater with a monoaromatic concentration 2.5 to 5 times higher than those reported in the water column during spills. While our higher concentration has not been reported, it is conceivable that subsurface leakage of fresh oil from pipelines or sunken vessels into cold water could produce exposures similar to ours.

One example of how cold temperature and other hydrographic conditions may combine to prevent evaporative loss and allow monoaromatic concentrations more persistent and higher than those cited above for oil spills is found in Valdez Arm, Alaska. Because of the stratification of the water column typical of a fjord, effluent from the oil tanker ballast water treatment facility at Valdez does not mix uniformly but instead is confined to a lens near the bottom. The treatment facility releases about 4.5×10^7 l (12×10^6 gal) daily (Lysyj et al. 1979) with average concentrations of monoaromatic hydrocarbons between 5.1 and 6.4 ppm (Lysyj et al. 1979, 1981; Rice et al. 1981). The distribution of monoaromatics in the receiving body was studied by Lysyj et al. (1981) who found the monoaromatics trapped within a narrow (10 m) zone of maximum concentration that spread horizontally 2 to 3 km in a thin pancake shape. Depth of the pancake varied with season from 50 to 65 m and approached the bottom. A monoaromatic concentration of 0.021 ppm was found 2 m off the bottom, and the maximum monoaromatic concentration observed was 0.127 ppm, half of the exposure concentration used here. Our exposure regime then may be most applicable to situations where there is chronic release of monoaromatic hydrocarbons under hydrographic conditions, e.g., low temperatures and stratification of the water column, that prevent evaporative loss.

The observed chemosensory impairment under oil exposure could have derived from several possible mechanisms, structural damage to chemoreceptor cells, anesthesia of chemoreceptors or other neurons, masking of food cue odor by oil, oil-induced changes in motivation, or coating or matting of the sensory hairs of the antennule by oil. The rapid recovery of the antennular flicking response eliminates only direct structural damage to the chemoreceptor cells as a possibility. Cellular damage would have required a recovery period of days whereas other mechanisms, such as masking or anesthesia, would have been rapidly reversible upon return to clean seawater (Johnson 1977). Anesthesia of the chemoreceptor or higher level neurons remains possible because our oil-contaminated seawater contained several aromatic and saturate hydrocarbons known to produce anesthesia or reversible narcosis in barnacle larvae (Crisp et al. 1967). Dungeness crabs do detect the water-soluble fraction of Prudhoe Bay crude oil at 10^{-4} ppm (Pearson et al. 1980) so that masking of the clam extract by the odor of oil was also possible. Odor masking by oil was also suggested by Atema and Stein (1974) as one possible mechanism behind a longer food finding time in the northern lobster, *Homarus americanus*. A change in feeding motivation was also suggested by Atema and Stein, but the observation in our first experiment of no difference between exposed and control conditions in the proportion of Dungeness crabs showing the chelae probing indicative of food searching argues against a change in motivation having occurred here. Antennular flicking enhances the ability of crustaceans to detect changes in the chemical milieu by splaying out the sensory hairs and increasing the passage of stimulative chemicals to the sensory neurons (Schmitt and Ache 1979), and oil might impair chemosensory function by slowing the passage of stimulating chemicals through coating or matting of the sensory hairs. Because our system produced oil-contaminated seawater with only 2% saturate hydrocarbons (Anderson et al. 1980) and thus little oil existed as emulsified droplets rather than dissolved hydrocarbons, we feel that in our system coating of the sensory hairs was not as likely as one of the other mechanisms. In a spill like the *Amoco Cadiz* where large amounts of oil are emulsified by turbulence (Calder and Boehm in press) physical blockage of chemical cues by the coating of sensory hairs is a possibility that needs study. Whereas

our behavioral results indicate direct structural damage to chemosensory cells was unlikely, which of the other mechanisms actually produced the observed chemosensory impairment remains an open question.

Decapod crustaceans have two chemoreceptor systems, one seated in the antennules and another in the dactyls, chelae, and mouth parts (Luther 1930; Case and Gwilliam 1961; Levandowsky and Hodgson 1965; Hazlett 1968, 1971a, b). The observation that after presentation with a clam extract a significant proportion of exposed crabs showed chelae probing without the normally preceding increase in antennular flicking suggests that 24-h exposure to our oil-contaminated seawater depressed the functioning of the antennular system in Dungeness crabs while, at least as far as we can determine, not significantly affecting the dactyl chemoreceptor system. Perhaps longer exposure would have affected the dactyl system.

The practical implication that needs further investigation is how the observed impairment of the chemosensory antennular flicking response would affect food foraging by the Dungeness crab. Whereas the exact role of the antennules in food finding is not fully understood, abundant evidence exists for the involvement of the antennules in food searching. Upon water-borne chemical stimulation, increases in antennular flicking rate precede food searching behaviors in the Dungeness crab (Pearson et al. 1979) and the blue crab (Pearson and Olla 1977). Because the electrophysiological work of Schmitt and Ache (1979) demonstrated that antennular flicking enhances perception of changes in the chemical milieu, increased flicking would presumably further enhance detection of rapid chemical changes. In the spiny lobster, *Panulirus argus*, chemical stimulation of the antennules usually initiated feeding behavior although chemical-tactile stimulation of the dactyl was more effective (Maynard and Sallee 1970). In hermit crabs intact antennules were necessary to sustain feeding behavior when contact with food is not direct and immediate (Hazlett 1968). Ablation of the antennules impaired the ability of the pelagic shrimp, *Acetes sibogae australis*, to follow food scent trails although antennular ablation did not prevent the detection of scent trails (Hamner and Hamner 1977). The ablation experiments of Reeder and Ache (1980) showed that chemosensory input from the lateral aesthetasc hair tufts of the antennules triggers food searching by *P. argus* and guides the spiny lobster to a distant odor source. Our observation of an impaired chemosensory antennular flicking response coupled with the good evidence of antennular involvement in food finding indicated that difficulty in finding food in the presence of petroleum hydrocarbons is a possibility for Dungeness crabs. If the antennular chemoreceptor system is as critical to successful guidance to distant odor sources in the Dungeness crab as the results of Reeder and Ache (1980) showed it is for the spiny lobster, then we particularly need to investigate whether entry to baited traps is affected when dissolved aromatic or other hydrocarbons are present.

ACKNOWLEDGMENTS

This work was supported by the National Oceanic and Atmospheric Administration of the U.S. Department of Commerce under the Interagency Energy-Environment Program of the U.S. Environmental Protection Agency.

We thank J. W. Anderson for his valuable discussions. Chemical analyses were performed by J. W. Blaylock and J. Webster.

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