patible with the distribution and behavior of Puget Sound ratfish.

While no quantitative measurements were made of light intensity or wavelength, to the human eye, the water in Puget Sound is quite dark at 25 m during the day, especially in winter. Considering that the fish is most abundant at about 75 m during the day and generally moves near shore only at night, McFarland's (1970) assessment that its retinal pigment might be appropriate for its depth distribution seems to be correct. Other aspects of its visual system, such as the apparently all-rod retina and nearly nonocclusible tapetum seem generally appropriate to its observed depth distribution. However, only more extensive studies of the feeding ecology, predators, and possible competitors of ratfish can explain why it moves onshore, why in some areas, such as Port Townsend Bay, it is found in shallow water during the day, and why in general it is found closer to shore in Puget Sound than in other areas in its range.

In summary, the data indicate that in Puget Sound, large ratfish predominate in shallow water, and smaller ones in deeper water. The species is most abundant in about 75 m of water, and tends to be in slightly shallower water in the spring and deeper water in the fall. Ratfish has a pronounced nocturnal onshore movement, which is composed primarily of smaller ratfish from deeper water.

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DETECTION OF PETROLEUM HYDROCARBONS BY THE DUNGENESS CRAB, *CANCER MAGISTER*

Behavioral responses that mitigate the effects of natural environmental perturbations may also be effective for contaminants from human activities, but the occurrence of any behavioral response, e.g., avoidance, first requires detection of the contaminant (Olla et al. 1980). To predict whether a behavioral response to a chemical pollutant will occur, one must ask whether the organism can detect the pollutant at concentrations likely to be encountered in field situations. Here we re-

port how antennular behavior was used to determine the concentrations at which the Dungeness crab, *Cancer magister* (Dana), detected petroleum hydrocarbons.

For decapod crustaceans the antennules have been considered the site of distance chemoreception (Hazlett 1971), and their flicking may be analogous to sniffing in vertebrates (Fuzessery 1978). Previous work has shown that in the blue crab, *Callinectes sapidus*, the antennular behavior indicating detection of food substances (Pearson and Olla 1977) also indicated detection of the petroleum hydrocarbon naphthalene (Pearson and Olla 1979, 1980) and the water soluble fraction of crude oil (Pearson et al. in press). In the Dungeness crab, similar antennular behavior, i.e., a change in orientation and increased flicking rate, also indicated detection of food substances (Pearson et al. 1979). Here we used these changes in antennular behavior to determine chemosensory detection thresholds in the Dungeness crab for naphthalene and the water soluble fraction (WSF) of Prudhoe Bay crude oil.

Materials and Methods

Dungeness crabs, trapped in the Strait of Juan de Fuca, Wash., were held outdoors in 1,200 l tanks under the conditions described by Pearson et al. (1979). The seawater temperatures (± SD) during the naphthalene and WSF experiments were 12.7° ± 0.6° C and 10.6° ± 0.3° C; the salinities, 31.6 ± 0.9‰ and 32.0 ± 0.0‰; the dissolved oxygen, 6.9 ± 0.7 mg/l and 7.3 ± 0.5 mg/l; and the pH, 8.12 ± 0.17 and 8.02 ± 0.16.

Experimental Solutions

Saturated solutions of naphthalene were prepared by adding naphthalene crystals to seawater filtered through a 0.4 μm Nucleopore[1] membrane. These stock solutions were stirred continuously at room temperature on a magnetic stirrer and were used after at least 18 h of stirring and no more than 5 d from first use. On each day of testing, a portion of the stock solution was siphoned off and passed through a 100 ml glass syringe fitted with a Millipore prefilter (Type A025) to remove any naphthalene crystals. Less than 1 h before testing, serial dilutions of this filtered stock naphthalene solution were made with seawater freshly filtered through a 0.4 μm membrane. An aliquot of the filtered seawater used for dilution served as the control solution. Experimental and control solutions were kept in a water bath at ambient seawater temperature during testing.

On each day of testing, samples of the stock solution and 10^{-1} dilution were analyzed for naphthalene content. Ten milliliters of hexane were vigorously shaken with 50 ml of sample solution for 1 min. This hexane was removed and analyzed for naphthalene content by capillary GC methods (Bean et al. 1978). The stock naphthalene solution was 22.9 ± 2.1 mg/l, and the 10^{-1} dilution was 2.2 ± 0.2 mg/l.

The WSF of Prudhoe Bay crude oil was prepared freshly each day by methods similar to Anderson et al. (1974). In a 19 l glass bottle, one part oil was gently poured over nine parts membrane-filtered seawater. Before the oil was added, a glass siphon tube inserted through a stopper covered with aluminum foil was placed in the filtered seawater. With the bottle stoppered, the seawater was slowly stirred on a magnetic stirrer for 20 h at room temperature. The stirring speed was adjusted so that the vortex did not extend more than 25% of the distance to the bottom of the bottle. After mixing, the oil and water phases were allowed to separate for 1 h. The water phase was then siphoned from below the oil phase and filtered through a prefilter under very low pressure to remove any remaining oil droplets. Serial dilutions of the resulting WSF were then immediately made with freshly membrane-filtered seawater and kept in a water bath at ambient seawater temperature during use. The membrane-filtered seawater used for dilution was the control solution. The stock WSF was analyzed by capillary gas chromatography for diaromatic and triaromatic hydrocarbons (Bean et al. 1978), and by gas partitioning analysis modified from McAuliffe (1971) for monoaromatics.

Chemosensory Threshold Determination

The apparatus and procedures of Pearson et al. (1979) were used here. In brief, glass testing chambers were arranged on four trays, 10 chambers to a tray, and the trays were surrounded by blinds. The experimental solutions were introduced into each testing chamber through an inlet manifold connected to a glass funnel. Seawater

[1] The use of trademarks does not imply endorsement by National Marine Fisheries Service, NOAA or Battelle, Pacific Northwest Laboratories.

from dripper arms entered each funnel at a rate of 1.0 l/min. A Teflon delivery tube carried the experimental solutions to the funnel from a buret calibrated to deliver 20 ml in 15 s.

To obtain a dilution factor for estimating the effective concentration of experimental solutions within a testing chamber, seawater solutions of ^{14}C-naphthalene (sp. act. 3.6 mCi/mmole, Amersham-Searle Corporation) were introduced and samples taken at timed intervals from the midpoint of the chamber and counted for radioactivity by liquid scintillation spectrometry. The chamber contained a crab model displacing 701 ml, a volume typical of the crabs tested. The maximum concentration in the chamber occurred 45 s after ^{14}C-naphthalene was added and was 0.0188 (± 0.0058 SD) times the concentration of the introduced solution. This dilution factor did not differ significantly from that found by Pearson et al. (1979) using a visible dye.

Approximately 24 h before testing, crabs were transferred to the testing chambers from the holding tanks where they had been fed an ad libitum diet of the blue mussel, *Mytilus edulis*. Because, in preliminary experiments, tidal phase was found to influence chemosensory responses (Pearson et al. 1979), testing was synchronized to begin and end within either a rising or falling tide. The seawater for the test dilutions and control was drawn and filtered 1 h after a tidal change. Testing then began as soon as possible and stopped before the next tidal change.

Each day a maximum of 40 crabs were presented individually with 20 ml of either one of nine dilutions of naphthalene stock solution, one of eight dilutions of WSF, or a control of filtered seawater. Molting and mating crabs were not tested. The order in which individual crabs were watched and the choice of experimental solution were randomized except that active crabs and ones with retracted antennules were passed over. The observer did not know the identity of any test solution. Individual crabs were observed for 1.0 min prior to introduction of the experimental solution, and their antennular flicking rate and other behavior recorded. The flicking rate of one antennule was measured using a hand-held counter. The solution was then introduced, and the observations continued for 1.0 min after the beginning of solution addition. The behavior was scored with the criteria used by Pearson et al. (1979).

To be scored as detecting an experimental solution, a crab had to exhibit an abrupt change in the orientation of the antennules within 30 s after solution introduction, and the ratio of the antennular flicking rate for 1.0 min after solution introduction to that for 1.0 min before had to be 1.50 or above. This value was determined previously by Pearson et al. (1979) from observations of crabs in the testing apparatus without any solutions present. Because 1.50 was the 95th percentile of these antennular flicking rate ratios, the a priori probability that a flicking rate ratio >1.50 represented a spontaneous increase rather than a reaction to the experimental solution was <5%.

Results

Composition of the WSF

The monoaromatic hydrocarbons by far dominated the WSF (Table 1) and composed 99.1% of the total hydrocarbons measured. The remaining aromatic hydrocarbons, mostly the naphthalenes, were present at concentrations 100 times less than that of the monoaromatics. The hydrocarbons partitioned into the WSF from the crude oil in proportion to their solubility in seawater (Clark and MacLeod 1977; Bean et al. 1978).

TABLE 1.—Composition of the water soluble fraction of Prudhoe Bay crude oil. Sample size was 3 for the di- and triaromatics and 6 for the monoaromatics.

Fraction	mg/liter
Total alkanes	<0.001
Naphthalene	.0851 ± 0.0088
Total methylnaphthalenes	.0766 ± 0.0080
Total dimethylnaphthalenes	.0269 ± 0.0015
Phenanthrene	.0006 ± 0.0004
Methylphenanthrene	<.0001
Dimethylphenanthrene	<.0001
Total polynuclear aromatics	.1892 ± 0.0175
Benzene	10.00 ± 0.29
Toluene	6.74 ± 0.42
Ethylbenzene	.30 ± 0.02
m- plus *p*-Xylene	1.12 ± 0.06
o-Xylene	1.12 ± 0.08
Total trimethyl benzenes	.46 ± 0.12
Total monoaromatics	19.75 ± 0.86
Total hydrocarbons measured	19.94

Detection Thresholds

Whereas Dungeness crabs detected both naphthalene and the WSF of Prudhoe Bay crude oil, the crabs detected the complex WSF mixture more readily and consistently. Because the percentage of crabs detecting naphthalene varied widely over

the range of concentrations presented, the regression equation relating percentage detection and the logarithm of concentration was not significant ($F = 1.3$, $P = 0.30$) (Figure 1). The curve for naphthalene detection was sawtooth-shaped with only four concentrations where the percentages of crabs detecting were above the upper 90% confidence limit about the control value. The sawtooth curve produced three concentrations at which 50% of the crabs could have detected naphthalene, 10^{-2}, 10^{-7}, and 10^{-9} mg/l. Because the factors producing the sawtooth curve are unknown, the most conservative approach is to consider the uppermost concentration, 10^{-2} mg/l, as the threshold for naphthalene detection. In contrast to naphthalene, the percentage of crabs detecting the WSF decreased in a consistent way with the WSF concentration (Figure 1). The regression equation was significant ($F = 60.4$, $P << 0.01$), and the variability was low ($R^2 = 91.0\%$). The 50% detection threshold from the regression equation was 4×10^{-4} mg/l, about 100 times lower than that for naphthalene.

When a crab detected naphthalene or WSF, the response was usually distinct. For crabs meeting the detection criteria, the median ratios of the antennular flicking rates did not vary with concentration (Median Tests, $\chi^2 = 2.38$, $P = 0.12$ for naphthalene; $\chi^2 = 9.07$, $P = 0.75$ for WSF), so that what varied with concentration was the percentage of crabs responding and not the magnitude of the response. Also, the magnitudes of the increase in antennular flicking were the same for both naphthalene and WSF. For naphthalene, the grand median of the antennular flicking rate ratios was 2.04; for the WSF, the grand median was 1.96.

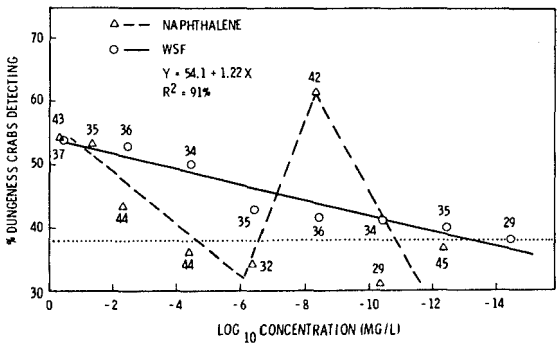

FIGURE 1.—Percentage of Dungeness crabs detecting naphthalene and the water soluble fraction (WSF) of crude oil as a function of the logarithm of concentration (mg/l). The percentage of crabs detecting a control of membrane-filtered seawater was 28.8% ($n = 66$) for naphthalene and 26.8% ($n = 41$) for WSF. The horizontal dotted line is the 90% confidence limit for the control values for both naphthalene and WSF (38%). The number beside each point is the number of trials at the concentration.

Discussion

When presented with naphthalene or WSF of crude oil, Dungeness crabs changed antennular orientation and flicking rate in the same manner as when presented with a clam extract. The blue crab also gives the same detection behaviors for hydrocarbons as for food (Pearson and Olla 1977, 1979, 1980; Pearson et al. in press). The similar findings in both species indicate that chemoreception by these crustaceans is not restricted to chemical cues for food and, thus, agree with Ache's (1975) suggestion that the chemical spectrum sensed by decapod crustaceans is really quite broad.

While the manner of antennular response to naphthalene and WSF was the same as that to a clam extract, the magnitudes of the flicking increase were slightly less and the chemosensory thresholds were 10^5 and 10^3 times higher than those found for the clam extract (Pearson et al. 1979). The grand median ratios of flicking rates for naphthalene and WSF, 2.04 and 1.96, were lower than that for the clam extract, 2.67. Also, the ranges of flicking ratios for the hydrocarbons were <30% of that for the clam extract. The slightly less intense response and much higher thresholds suggest that the petroleum hydrocarbons rank as much less potent chemical cues than sapid chemicals from a natural food.

Previously, Pearson and Olla (1980) had hypothesized that the chemical and chemosensory processes producing a higher detection threshold for a single petroleum hydrocarbon, naphthalene, than for a complex mixture of hydrocarbons, the WSF of crude oil, are analogous to the processes producing a similar relationship of thresholds for single amino acids and complex mixtures. Usually, food extracts and complex mixtures of amino acids and other chemicals have a lower detection threshold than that of a single amino acid (Mackie 1973; McLeese 1974). Indeed, with the Dungeness crab the detection threshold for WSF was about 100 times lower than that for naphthalene. Also, the variability in detection was much less for WSF than for naphthalene. This apparent greater dif-

ficulty in detecting the single hydrocarbon than the more complex WSF is presumptive evidence for the hypothesized analogy. With naphthalene constituting only 0.4% of the total hydrocarbons in the WSF, the crabs were probably responding primarily to other compounds or, perhaps, to some sort of odor medley.

One possible explanation for the extreme variability in naphthalene detection is that detection at high naphthalene concentrations was inhibited by some toxic, narcotic, or anesthetic action not present or much reduced at low concentrations. The blocking of chemosensory feeding and mating responses in the crab *Pachygrapsus crassipes* after 24-h exposure to naphthalene at 10^{-3} mg/l (Takahashi and Kittredge 1973) supports the possibility of such inhibition. If the threshold concentration for chemosensory inhibition was within the range of concentrations we presented, then a sharp increase in the percentage of crabs detecting naphthalene would be expected below the inhibition threshold and would produce the sawtooth-shaped curve seen for naphthalene in Figure 1. A sawtooth-shaped curve would also result if the sensitive antennular chemoreceptors were more impaired than the less sensitive body chemoreceptors on the dactyls, chelae, and mouthparts. If the antennular chemoreceptors were the more impaired at high naphthalene concentrations, detection would occur primarily through body chemoreceptors, and the antennular flicking increases would then derive from a reflex primarily involving the body chemoreceptors rather than one involving the antennular chemoreceptors. If the supposed chemosensory inhibition lessened or disappeared at low naphthalene levels, detection would switch to the more sensitive antennular chemoreceptors from the less sensitive body chemoreceptors. Whatever the explanation, the weak and inconsistent detection of naphthalene did not allow estimation of a threshold concentration by the method used here for WSF and elsewhere for food extracts (Pearson and Olla 1977; Pearson et al. 1979). Without more evidence concerning the mechanisms producing the particular shape of the naphthalene curve, the use of the apparently real peak in detection at 10^{-8} mg/l for estimating thresholds remains an open question. The most conservative approach for now is to consider 10^{-2} mg/l to be the naphthalene detection threshold.

For both food extract and petroleum hydrocarbons, the blue crab has exhibited more acute chemoreception than the Dungeness crab (Pearson and Olla 1977, 1979, 1980; Pearson et al. in press). Pearson et al. (1979) hypothesized that the lower detection threshold for clam extract seen in the blue crab was a consequence of the blue crab's greater ability to sample the chemical environment with its higher flicking rate and larger antennules. This hypothesis would apply equally to the differences between the two crabs in the hydrocarbon detection thresholds.

An important practical question is how the ability of the Dungeness crab to detect petroleum hydrocarbons compares with the range of hydrocarbon concentrations likely to be encountered by the crab. In the water column during an oil spill, McAuliffe et al. (1975) found concentrations of dissolved hydrocarbons ranging from 2×10^{-3} to 2×10^{-1} mg/l. Of these dissolved hydrocarbons about one-half were the monoaromatics dominating the WSF used here. During a spill from a North Sea platform, Grahl-Nielsen (1978) found petroleum hydrocarbon concentrations ranging up to 4×10^{-1} mg/l. In the open sea between Nova Scotia and Bermuda, Gordon et al. (1974) found petroleum hydrocarbon concentrations of 2.04×10^{-2}, 8×10^{-4}, and 4×10^{-4} mg/l at the surface, 1 m, and 5 m. These concentrations roughly agree with those given for relatively uncontaminated oceanic areas by Clark and MacLeod (1977), who also stated that chronically contaminated areas have hydrocarbon concentrations about two orders of magnitude higher than those of the open sea. Unfortunately, analytical difficulties in distinguishing petrogenic from biogenic hydrocarbons at low environmental concentrations make estimates of oil levels in chronically contaminated areas uncertain. For the North Sea, Grahl-Nielsen et al. (1979) found that despite considerable oil production there was no apparent standing crop of petroleum hydrocarbons, but rather petroleum contamination occurred as localized, transient patches. Thus, the petroleum hydrocarbon concentrations in uncontaminated (10^{-4} to 10^{-3} mg/l), chronically contaminated (10^{-4} to 10^{-2} mg/l), and oil spill (10^{-3} to 10^{-1} mg/l) situations are all at or above the WSF detection threshold (10^{-4} mg/l) so that Dungeness crabs can detect hydrocarbons readily at the concentrations found in oil spill situations, probably in chronically contaminated situations, and marginally in uncontaminated situations. In being able to detect the petroleum hydrocarbons at concentrations at and below those found in oil spill situations, Dungeness crabs can

achieve the first step to any subsequent behavioral response to petroleum.

Acknowledgments

We thank J. W. Anderson for his valuable discussions with us. The 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.

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