Further evidence for olfactory foraging by Sooty Shearwaters and Northern Fulmars

by Larry V. Hutchinson, Bernice M. Wenzel, Kenneth E. Stager, and Bruce L. Tedford
Department of Physiology, University of California, Los Angeles, CA, USA 90024

1. Abstract

Our earlier work showed that certain procellariiform species off the central California coast are selectively attracted from downwind to various food-related odours, including cod-liver oil. We here compare the attractiveness of a volatile fraction of cod-liver oil to that of the whole oil, and of homogenates of squid and of krill. All birds in the study area were identified to species, and data are presented here for the Northern Fulmar (*Fulmarus glacialis*) and Sooty Shearwater (*Puffinus griseus*). Comparative data are presented for the Western Gull (*Larus occidentalis*), Common Loon (*Gavia immer*), and Common Murre (*Uria aalge*). The fulmars and shearwaters arrived sooner and more reliably with the cod-liver-oil fraction than with the whole oil, suggesting that volatility was an important factor. Shearwaters also flew upwind to squid and krill. Neither procellariid was sighted when seawater or heptane controls were used alone. Nonprocellariids showed no differential behaviour with respect to stimulus or wind direction. These data, collected with careful controls from October to May throughout a range of weather conditions, strengthen the conclusion that some procellariiform species are attracted by odours related to their natural prey.

2. Résumé

Nos travaux précédents ont montré que certaines espèces de procellariiformes au large de la côte du centre de la Californie étaient attirées de façon sélective sous le vent par différentes odeurs associées à la nourriture, y compris l'huile de foie de morue. Dans le présent article, nous comparons l'attirance d'une fraction volatile de l'huile de foie de morue à celle de l'huile entière et d'homogénats de calmars et d'euphausiacés. Tous les oiseaux dans la zone d'étude ont été identifiés à l'espèce, et les données sont présentées ici pour le Fulmar boréal (*Fulmarus glacialis*) et le Puffin fuligineux (*Puffinus griseus*). Des données comparatives sont fournies pour le Goéland de l'Ouest (*Larus occidentalis*), le Huard à collier (*Gavia immer*) et la Marmette commune (*Uria aalge*). Les fulmars et les puffins étaient attirés plus tôt et de façon plus sûre avec la fraction de l'huile de foie de morue qu'avec l'huile entière, ce qui laisse croire que la volatilité était un facteur important. Les puffins volaient aussi au vent en direction des calmars et des euphausiacés. Nous n'avons vu aucun procellariidé quand nous utilisions, seuls, des témoins faits d'eau de mer ou d'heptane. Les non-procellariidés ne montraient pas de comportement différenciel selon le stimulus ou la direction du vent. Ces données, recueillies avec minutie d'octobre à mai sous tout un éventail de conditions météorologiques, renforcent la conclusion que certaines espèces de procellariiformes sont attirées par des odeurs rappelant leurs proies naturelles.

3. Introduction

In studies of the feeding ecology of seabirds, less attention has been given to how birds find prey than to the types of prey eaten and to where and how they are taken. The dominant guidance is assumed to be visual (e.g. Sealy 1973, Hoffman *et al.* 1981), with possible auditory cues from prey and other birds, but the literature is relatively silent not only on this specific application but also on visual and auditory physiology of seabirds in general.

The specialized interior nasal anatomy and unusually large olfactory mucosae, nerves, and bulbs in many procellariiforms (Bang 1966) suggest olfactory guidance in feeding, a possibility supported by early anecdotal accounts and field notes (reviewed by Wenzel 1980). Recent research has provided direct evidence. Grubb (1972) reported that Leach's and Wilson's storm petrels (*Oceanodroma leucorhoa*, *Oceanites oceanicus*) and Greater Shearwaters (*Puffinus gravis*) made upwind approaches to a sponge soaked in cod-liver oil more often than they did to one soaked in seawater. The very few Sooty Shearwaters (*P. griseus*) sighted did not approach either sponge. Four other species (*Fratercula arctica*, *Larus argentatus*, *Morus bassanus*, and *Sterna paradisaea*) were seen once and showed no systematic reactions to the sponges. In a more extensive study (Hutchison and Wenzel 1980), procellariiforms common off the central California coast were attracted from downwind in daylight by odours of fish oils and vegetable oil but not by mineral oil, seawater, or petroleum oil. By contrast, nonprocellariiforms were not affected and appeared as frequently upwind as downwind. Once attracted from downwind, procellariiforms were more likely to fly close to the source, sometimes repeatedly. Many of their approaches followed a zigzag course, narrowing closer to the odour source, as if following a trail. Close approaches and landings by non-procellariiforms occurred regularly when popcorn or puffed cereal was spread on the water but such visual stimuli had little effect on procellariiform behaviour.

The present study extends information learned from our earlier observations by documenting birds' responses to odours of their own prey and to the volatile portion of cod-liver oil, a readily available material of proven attractiveness but not associated with fish normally eaten by fulmars and shearwaters. Greater potency of the volatile fraction would emphasize the significance of an airborne stimulus.

4. Methods

Tests were conducted with whole cod-liver oil; the volatile fraction of cod-liver oil collected in heptane; homogenized squid (*Loligo opalescens*); homogenized krill (*Euphausia superba*) made from frozen krill obtained from Sea World in San Diego, California; heptane; and seawater as controls. The behavioural responses to each stimulus were analysed for the most plentiful species throughout the testing period, *viz.*, Northern Fulmar (*Fulmarus glacialis*), Sooty Shearwater, Western Gull (*L. occidentalis*), Common Loon (*Gavia immer*), and Common Murre (*Uria aalge*).

All testing was done during daylight in Estero Bay off Morro Bay, California, the same area as we used for our earlier work. Locations varied from 4 to 64 km from shore between longitudes 120 and 122°W and latitudes 35 and 36°N (Fig. 1). Data were collected under a wide range of weather conditions during 50 cruises evenly distributed from October 1980 through May 1981, aboard either of two boats — a 9-m sailboat or a 17-m commercial fishing vessel. Whole cod-liver oil was presented in 49 tests on 40 cruises, cod-liver-oil fraction in 24 tests on 17 cruises, squid homogenate in 20 tests on 19 cruises, and krill homogenate in 11 tests on 10 cruises. For experimental controls, seawater was used in 17 tests on 17 cruises, and heptane in 9 tests on 9 cruises. Tests with whole cod-liver oil, squid homogenate, and seawater were made each month of the study; tests with the other stimuli occurred during the last 4 months.

In the present tests, unlike our earlier ones (Hutchison and Wenzel 1980), we used one method of presenting stimuli, which was a standardized refinement of the final technique developed in the previous study. Odour diffused from a cotton wick on a wire frame that protruded about 3 cm from a 400-mL bottle mounted in a gimbal atop a pole 3.5 cm in diameter and 1 m high. The pole was attached to a float made of an inflated tire inner tube, 110 cm in diameter, with a wooden floor (Fig. 2). One to six hours before testing, whole cod-liver oil, squid homogenate, and krill homogenate were put into bottles. Seawater was bottled at sea shortly before each test, and the highly volatile cod-liver-oil fraction and heptane were transferred from their tightly-sealed containers to bottles immediately before releasing the float. The sample size for each test substance was 150 mL.

To start a test, we uncapped the bottle, inserted a wick, placed the bottle in the gimbal, and put the float overboard when no birds were visible. The boat moved approximately 100 m away in the crosswind direction and a sea anchor was deployed to minimize drift of the vessel. Most tests lasted 90 min. We recorded all species sighted, their locations relative to the wind, the distance of the closest approach to the wick, the direction of departure, and other behaviour patterns of interest. The position, date, time, weather, sea conditions, and bottom characteristics were noted. We stored all data on floppy discs using a Sol micro-computer, for subsequent analysis on an IBM 3033 computer.

At least three observers were present on all trips; any discrepant opinions about species identification or behaviour were settled after each test. We identified birds with

Figure 1
Map of the study area

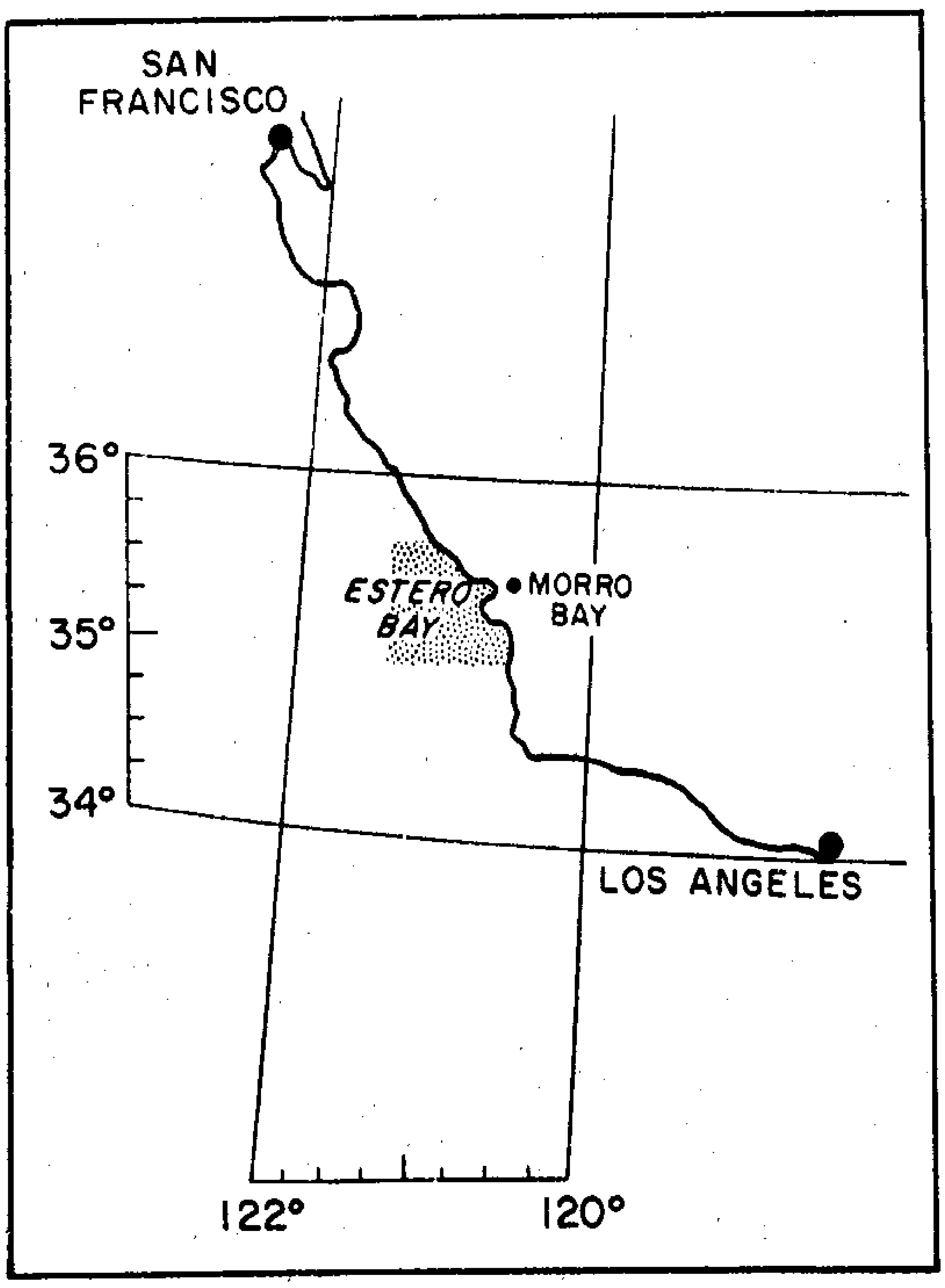
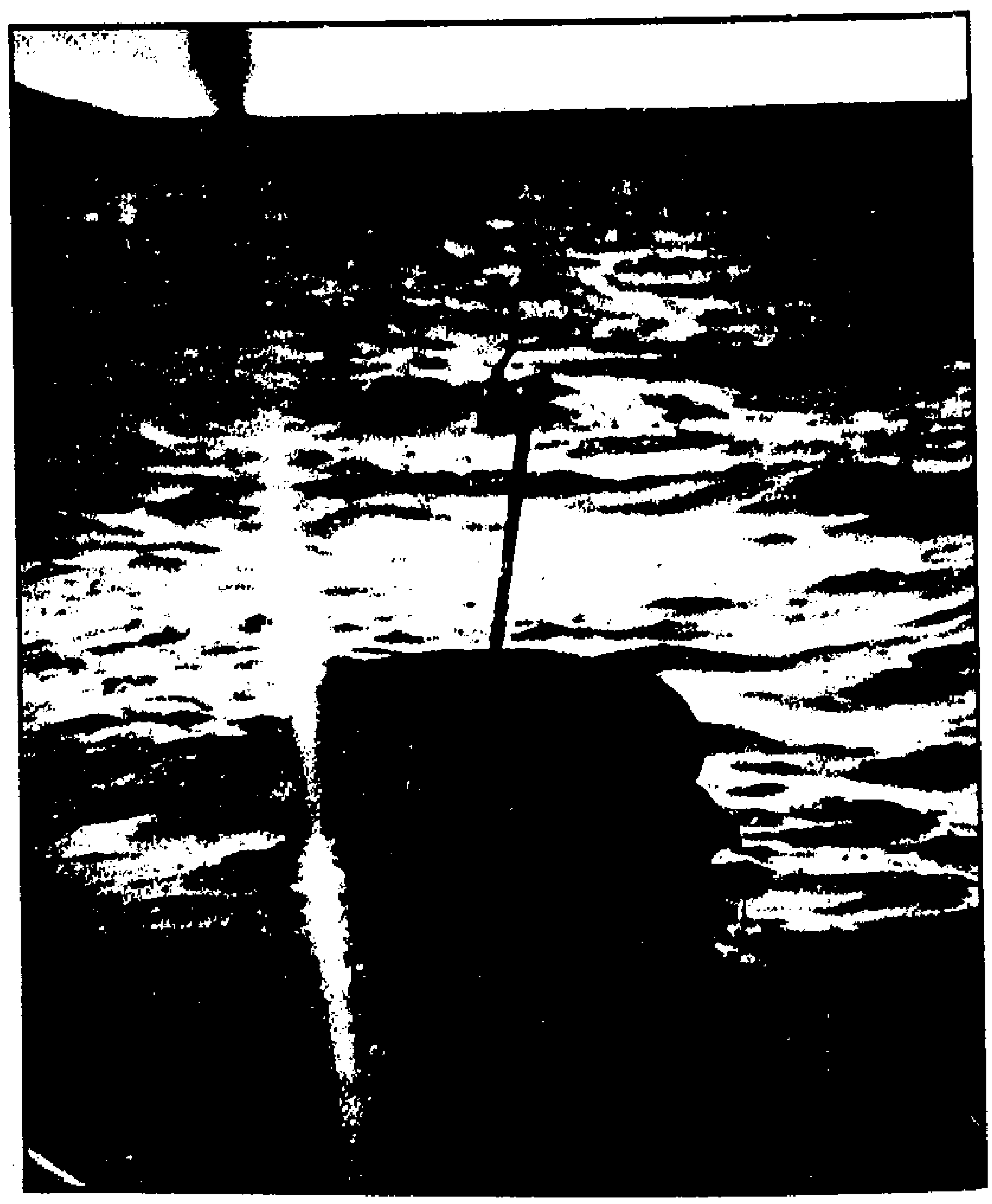


Figure 2
Float with stimulus bottle and wick attached



the aid of binoculars and took photographs of anything of special interest, including close approaches. Successive tests were separated by 20–90 min depending on the presence of birds, condition of equipment, and special problems. Whenever possible, seawater and heptane were presented at the same locations as the experimental odours. Some cruises were interrupted by poor weather, mechanical problems, or minor accidents so test schedules had to be flexible.

Squibb or Nature's Best whole cod-liver oil was used for the early tests in this series; for the later majority of experiments, oil was obtained in 3–4 gallon amounts from J.A. Sanborn Co., Boston, Massachusetts. The volatile fraction was prepared from the whole oil by vacuum extraction and collected in reagent-grade heptane as solvent. Each 150 mL of solvent included approximately 0.5% cod-liver-oil volatiles. Squid homogenate was made from fresh or freshly thawed animals in a heavy-duty Waring blender. The krill was homogenized in a different blender.

5. Results

In close agreement with our earlier results (Hutchison and Wenzel 1980), approaches of Northern Fulmars and Sooty Shearwaters were almost entirely (77–100%) downwind of the wick after release of all four experimental stimuli (Table 1, Figs. 3–6), and were sighted only once or not at all during control tests with heptane and seawater (Table 1, Figs. 7 and 8). Chi-square tests of the distributions of sightings by wind direction showed that the shearwaters were sighted significantly more often downwind than either upwind or crosswind in the tests with whole cod-liver oil and the fraction ($p<0.001$). With squid homogenate, 29 of 30 shearwater sightings were downwind and with krill homogenate, 21 of 26 sightings were so; crosswind and upwind frequencies were thus too low for a chi-square test.

Table 1
Total number of each species sighted with each stimulus, the percent downwind (*% DW*), and the mean number sighted per test (*M*/test)

Stimulus	Northern Fulmar	Sooty Shearwater	Western Gull	Common Loon	Common Murre
Cod-liver oil					
Whole					
Sightings	23	60	124	48	223
% DW	83	77	32	25	37
M/test	0.5	1.2	2.5	1.0	4.6
Fraction					
Sightings	7	43	60	26	29
% DW	100	84	25	92	10
M/test	0.3	2.0	2.9	1.2	1.4
Squid					
Sightings	4	30	41	16	99
% DW	100	97	51	25	63
M/test	0.2	1.5	2.0	0.8	5.0
Krill					
Sightings	1	26	25	20	9
% DW	100	81	40	85	0
M/test	—	2.2	2.1	1.7	0.8
Heptane					
Sightings	0	0	20	2	6
% DW	—	—	26	50	67
M/test	0	0	2.2	0.2	0.7
Seawater					
Sightings	1	1	42	20	67
% DM	0	0	60	90	34
M/test	—	—	2.5	1.2	3.9

Fulmar counts were high enough to permit statistical analysis only for the tests with whole cod-liver oil when their downwind approaches were significantly more frequent than either of the other directions ($p<0.05$). In seawater tests, one fulmar and one shearwater were sighted, each crosswind, and no sightings of either species occurred in tests with heptane.

No consistent pattern of direction related to our experimental or control stimuli was seen in the three species of nonprocellariiforms (Table 1, Figs. 3–8). During the tests with cod-liver-oil fraction, most Common Loons were sighted downwind, which corresponded to their migratory path

Figure 3
Direction of sighting and closest approach for each species during all tests with whole cod-liver oil. Numbers of birds are depicted as percentages for comparability; absolute totals sighted are shown below each chart. The float is at the centre, the inner circle is 10 m away from it, the outer circle 50 m. To illustrate interpretation, of the 23 Northern Fulmars sighted during 49 tests, 39% were downwind and approached within 11–49 m of the float, 52% were downwind and approached within 10 m, and 9% were crosswind and approached within 10 m.

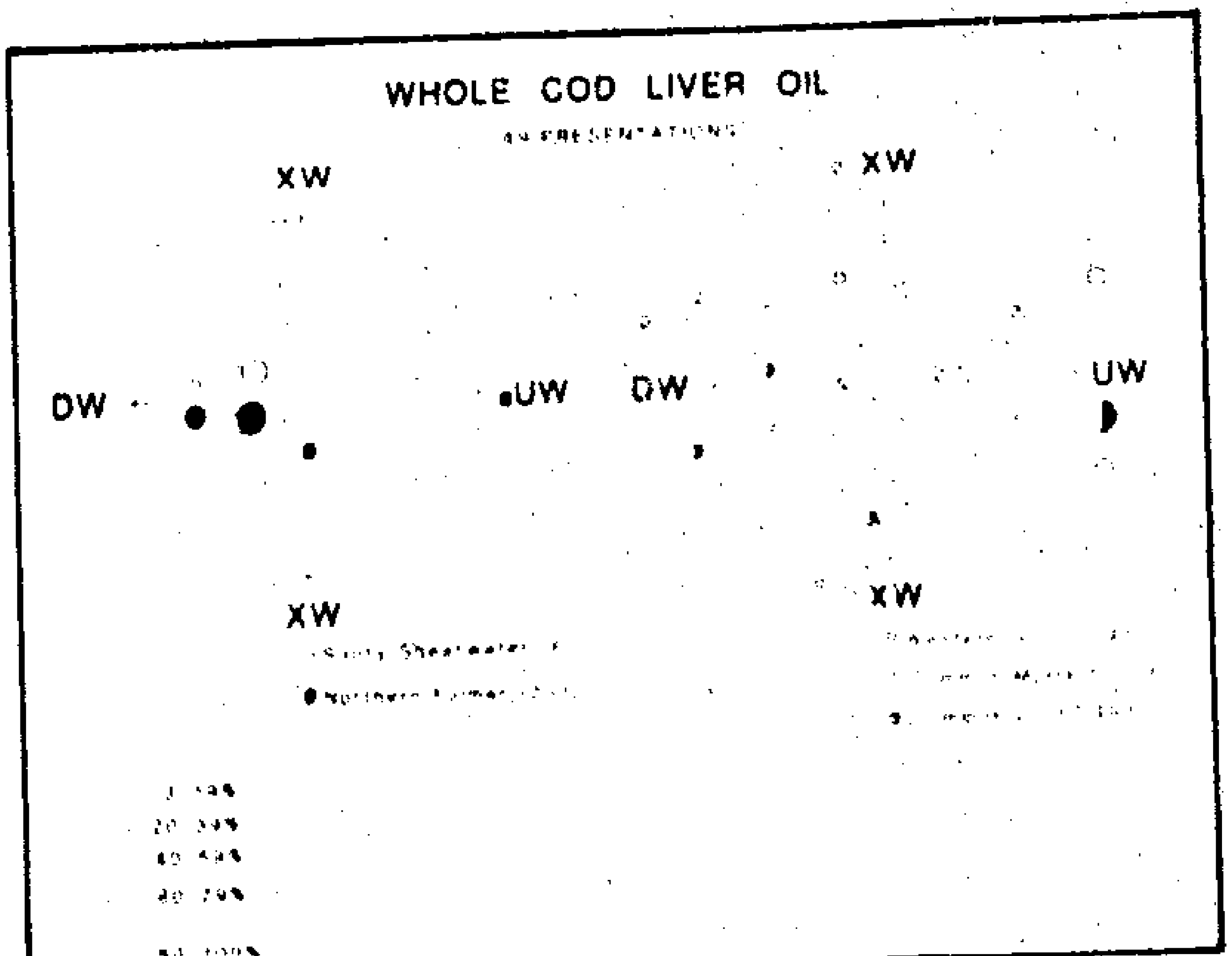
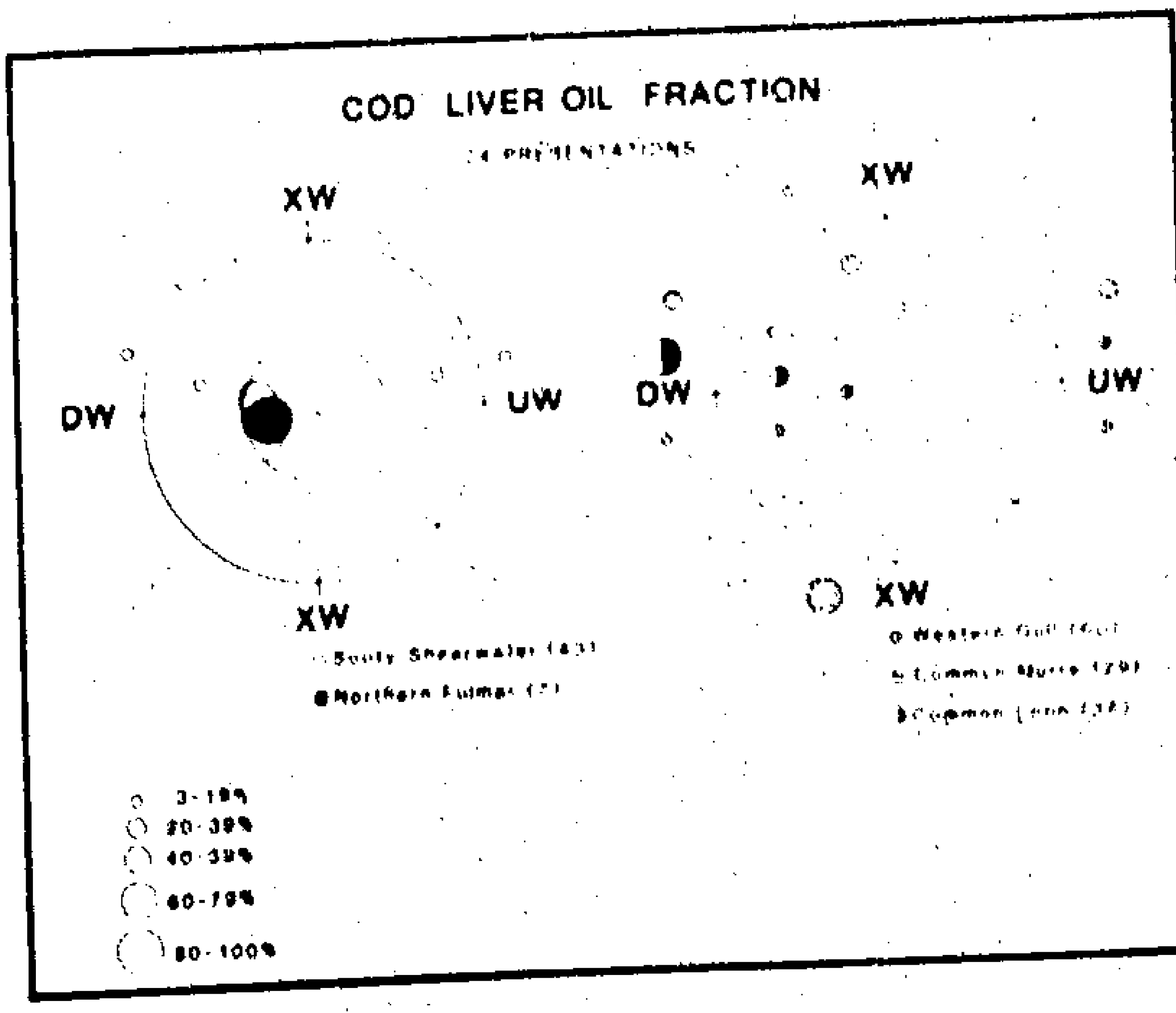


Figure 4
Direction of sighting and closest approach for each species during all tests with cod-liver-oil fraction in heptane. See legend of Fig. 3.



through our study area. So few loons were seen flying in other directions that no chi-square could be calculated for directional differences. Conversely, during tests with whole cod-liver oil, Common Loons were sighted significantly most frequently upwind of the stimulus ($p<0.01$). The same reversal occurred for Western Gulls (whole cod-liver oil, upwind most frequent, $p<0.001$; cod-liver-oil fraction, downwind most frequent, $p<0.05$). Common Murres were either evenly distributed across directions or so densely located in only one that statistical analysis was meaningless.

In further verification of the attractiveness of our test materials, the fulmars and shearwaters flew close to the wick when food-related stimuli were being released (Figs. 3–6). With whole cod-liver oil, the fulmar's approaches from downwind to within 10 m were significantly more frequent than all other combinations of distance and direction (chi-square test, $p<0.05$). Frequencies for fulmars in tests with other odours were too low for analysis, although all seven fulmar approaches to the cod-liver-oil fraction were from downwind and within 10 m. Their four approaches to squid were from downwind but only one was within 10 m. The one fulmar sighted during tests with krill was downwind and approached closer than 50 m. The shearwaters' close approaches from downwind were significantly greater than all other combinations with each of the four experimental stimuli (whole cod-liver oil, $p<0.001$; cod-liver-oil fraction, $p<0.001$; squid homogenate, $p<0.01$; krill homogenate, $p<0.05$).

By contrast, nonprocellariiforms seldom flew closer than 50 m to the wick. Loons most commonly passed at 50 m or more from both the whole oil and the fraction ($p<0.01$ each). With squid homogenate, all of their flights were at these distances; with krill homogenate the frequencies were too scattered for analysis. Western Gulls also passed at the outer distance. No gull made a close approach from any direction with krill homogenate and only one did so, crosswind, with cod-liver-oil fraction. With the other two food-related stimuli, also, 50 m or more was their most frequent distance (whole cod-liver oil, $p<0.001$; squid homogenate, $p<0.01$). Common Murres made only five close approaches out of 359, none from downwind, and these five involved three different stimuli.

The procellariids' close approaches often followed the zigzag path described earlier (Hutchison and Wenzel 1980). Rather than flying straight toward the float, they crisscrossed the area downwind of it with progressively shorter traverses, as if following an odour trail. Upon

Table 2
Average ambient wind velocity (km/h) and approach latency (min) to whole cod-liver oil and cod-liver-oil fraction in heptane by Northern Fulmars and Sooty Shearwaters, and the correlation of wind velocity and the birds' approach latency (VL), their mean number of circuits around the float, and the correlation of their circling frequency with wind velocity (VC)

	Velocity (km/h)	Latency (min)		Circuits	
	Mean ± SD	Mean ± SD	r_{VL}	Mean ± SD	r_{VC}
Whole oil					
Fulmars	13.2 ± 8.7	21.5 ± 2.0	−0.04	1.4 ± 1.3	0.16
Shearwaters	14.2 ± 7.7	20.4 ± 2.3	−0.03	1.3 ± 1.1	0.28
Oil fraction					
Fulmars	18.5 ± 8.4	7.3 ± 1.4	−0.24	3.6 ± 1.3	−0.55
Shearwaters	15.8 ± 10.9	7.4 ± 2.2	−0.21	1.8 ± 1.5	0.25

Figure 5
Direction of sighting and closest approach for each species during all tests with squid homogenate. See legend of Fig. 3

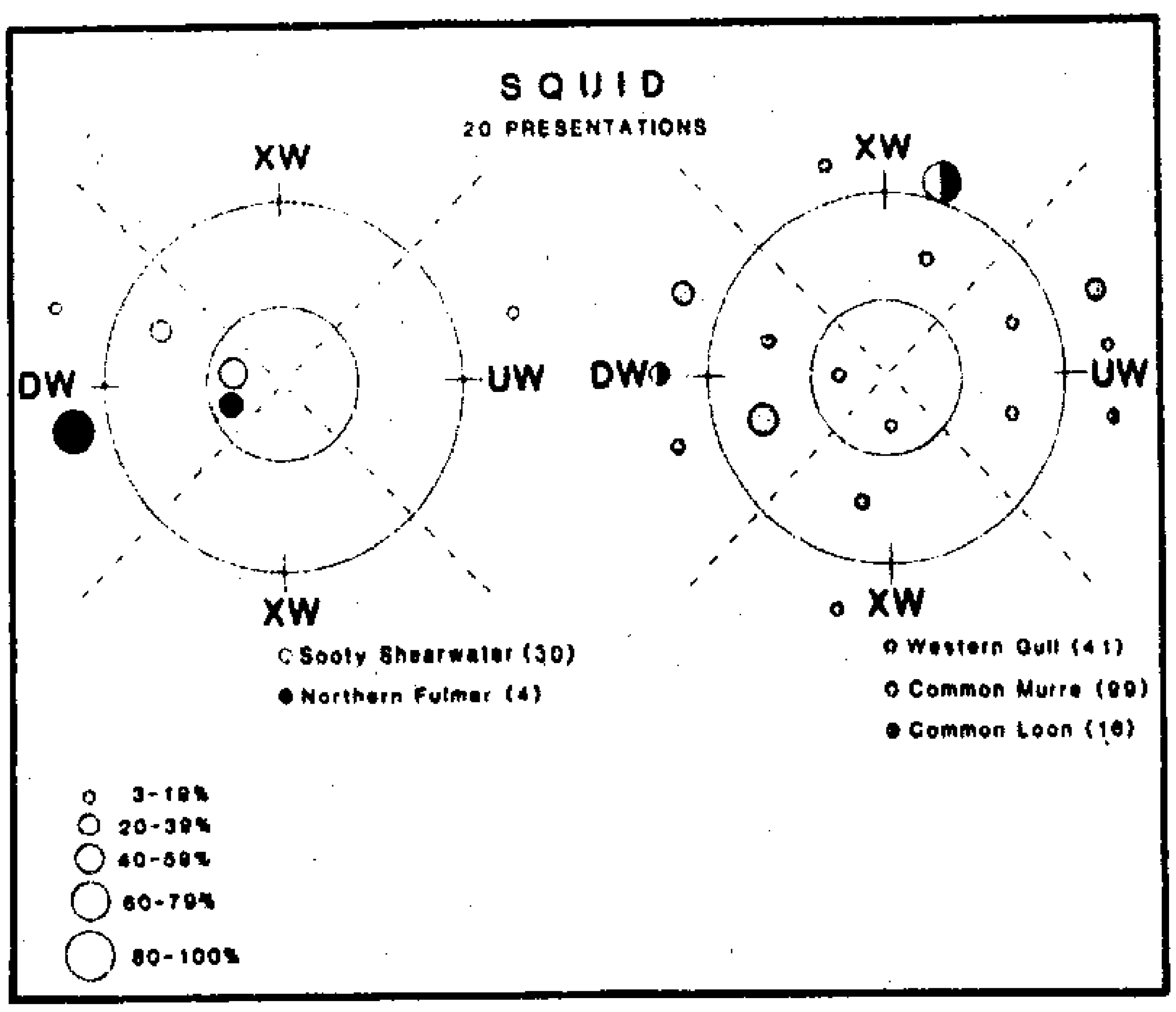
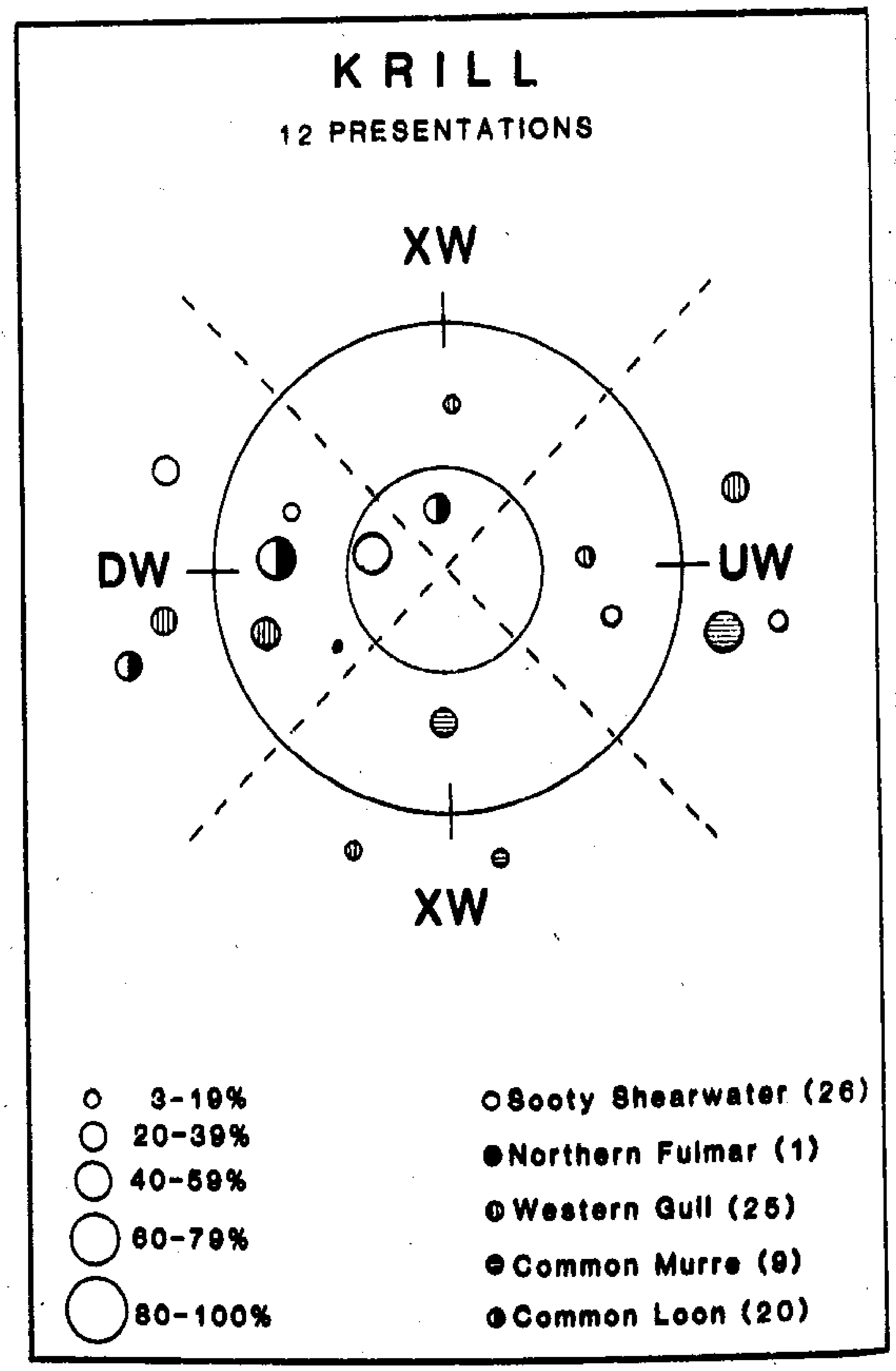


Figure 6
Direction of sighting and closest approach for each species during all tests with krill homogenate. See legend of Fig. 3



reaching the float, birds usually circled it from one to five times before flying away. They never landed on the float or flew directly toward the observation boat. Occasionally, a bird would land on the water, 10–20 m downwind of the float and stay for 5–10 min.

The cod-liver-oil fraction was a more potent attractant than the whole oil. Fulmars or shearwaters approached on 91% of the tests with the fraction compared to 47% of tests with the whole oil, and approaches within 10 m were more common (Figs. 3 and 4). Table 2 shows the mean latencies of downwind sightings of fulmars and shearwaters that approached within 50 m during tests with both stimuli. Frequency distributions of latencies were normalized by logarithmic conversion of each score and differences between stimuli were tested by the t-test. For each species, the latency was significantly shorter with the fraction than with whole oil ($p<0.001$). Mean wind velocities during these tests were comparable (Table 2) and could not account for the differences. We have no direct measure of the diffusion rates of the two preparations but greater volatility insures faster vaporization, resulting in earlier arrival of molecules at a given distance downwind. Neither latency nor circling behaviour was correlated with wind velocity for either species with either preparation (Table 2). The mean number of circuits flown around the wick by fulmars was significantly ($p<0.01$) greater with the cod-liver-oil fraction (Table 2). Every fulmar sighted during tests with the fraction not only approached closely but also circled at least twice and every shearwater circled at least once. With the whole oil, shearwaters failed to circle on 28% of their close approaches and fulmars made no circles on 38% of such approaches.

The mean visibility was 25 km for all cruises, with the great majority at 16 or better. The lowest values were 5–10 km, accompanied by light to medium fog. These conditions occurred when fulmars were in the study area, during tests in January, February, and March, and they were most frequently attracted to the food-related odours on such days. Shearwaters, on the other hand, showed an opposite effect, being most likely to approach on days with high visibility ($p<0.01$).

Fulmars made almost no approaches to squid or krill homogenate, although tests with krill did not start until shortly before they usually leave our study area. They approached the cod-liver-oil stimuli in the same period, however. Shearwaters were strongly attracted to both. They

Figure 7
Direction of sighting and closest approach for each species during all tests with heptane. See legend of Fig. 3

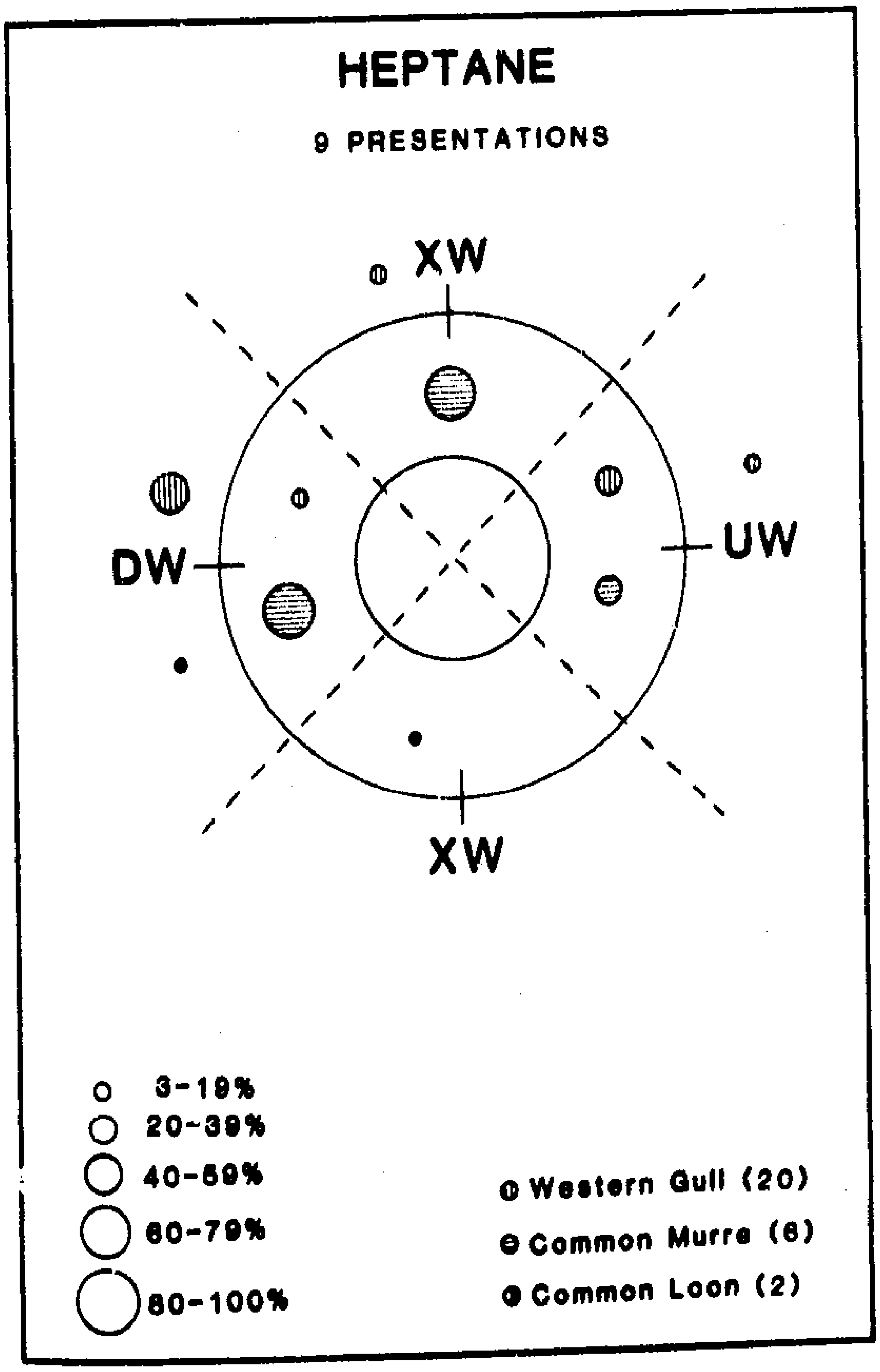
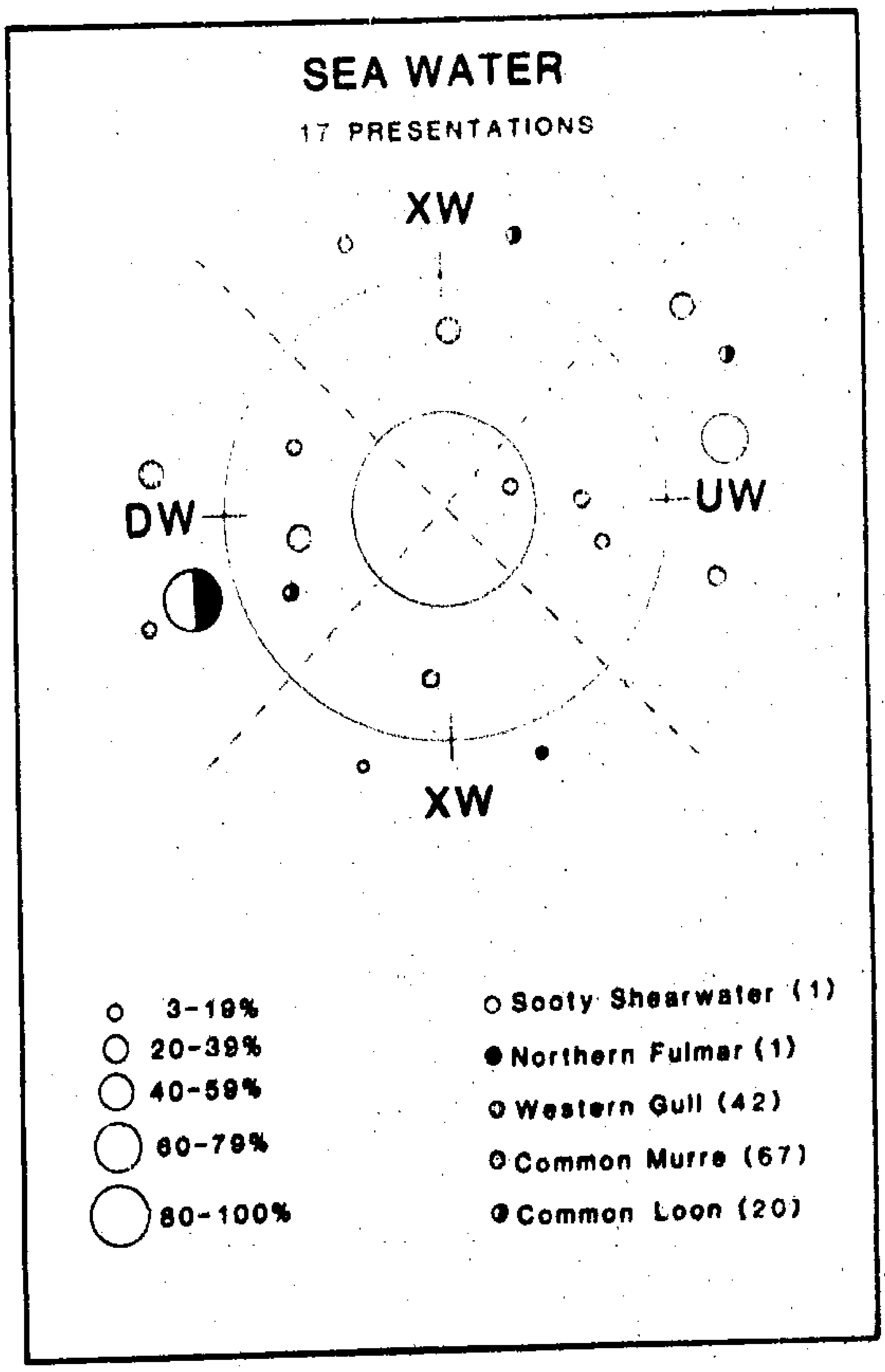


Figure 8
Direction of sighting and closest approach for each species during all tests with seawater. See legend of Fig. 3



approached closely on 75 and 73%, respectively, of the tests with squid and krill. In these tests, also, they appeared predominantly on days with high visibility. Their mean approach latencies were 16.6 and 21.5 min, comparable to their latencies with whole cod-liver oil (Table 2). They averaged 2.2 and 2.8 circuits on each close approach, significantly ($p<0.01$) more than with whole cod-liver oil (Table 2).

The prevailing wind in Estero Bay is from the northwest, and throughout the test period winds were in the quadrant between west and north 70–80% of the time. The fact that the procellariids' upwind approaches to our stimuli were oriented generally northwest through the test period means that they were not simply migrating.

6. Discussion

These data confirm and extend our previous work (Hutchison and Wenzel 1980) showing reliance on olfaction in foraging by Northern Fulmars and Sooty Shearwaters. The faster and closer approaches to the volatile fraction of cod-liver oil compared to the whole oil support the conclusion that airborne stimuli are used for guidance by these species. Furthermore, the attractiveness of odours of squid and krill for Sooty Shearwaters, two dietary components for these birds (Chu, this volume), strongly suggests that olfactory guidance is normally used to find prey. Such conclusions imply that foraging would be better in areas with enough wind to disperse odorous molecules over a significant distance. Our lack of correlation between wind velocity and both approach latency and circling, however, shows that high winds do not necessarily increase investigative behaviour. Odour quality is probably as important as the intensity.

Other sensory systems may also be important to fulmars and shearwaters in foraging. In their extensive pelagic habitat, with its infinite variations of weather and visibility, however, it would be highly advantageous to have well-developed detection systems for smell as well as sight. Olfaction may be especially helpful when visibility is low. Several times fulmars approached our experimental stimuli from downwind during fog and limited visibility, and many procellariids are known to feed at night (Gould 1967, Wenzel 1980). The use of olfaction is not restricted to poor visibility, however, as shown by our present results when visibility was generally much better than previously (Hutchison and Wenzel 1980). The greater tendency of fulmars than shearwaters to approach during lower visibility may be due partly to greater frequency of such conditions in the months when Northern Fulmars are plentiful off central California. This explanation does not account for their scarce appearances on completely clear days in the same period, but the impression persists that they were more responsive to odours during limited visibility.

Our high rate of success in attracting Sooty Shearwaters to odours of squid and krill suggests a resemblance to natural foraging. We do not know what odours are associated with these prey in nature. Under our conditions, these crude preparations were as effective as whole cod-liver oil as measured by latency of approach, and as effective as the volatile fraction of cod-liver oil as measured by the number of circles flown around the wick. Sooty Shearwaters have been identified as a principal catalyst of seabird feeding flocks in Alaska (Hoffman *et al.* 1981). It may be that they are aided by smell in locating plentiful supplies of fish or euphausiids and the sight of their feeding behaviour then attracts other birds. Black-legged Kittiwakes (*Rissa tridactyla*) are also said to start feeding flocks (Sealy 1973, Hoffman *et al.* 1981). Their olfactory anatomy has never been examined; possibly they, too, have large amounts of primary olfactory tissue. Procellariids may not be alone among seabirds in olfactory ability.

7. Acknowledgements

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8. Literature cited

Bang, B.G. 1966. The olfactory apparatus of tubenosed birds. Acta Anat. 65:391–415.

Chu, E.W. This volume. Sooty Shearwaters off California: diet and energy gain.

Gould, P. 1967. Nocturnal feeding of *Sterna fuscata* and *Puffinus pacificus*. Condor 69:529.

Grubb, T.C., Jr. 1972. Smell and foraging in shearwaters and petrels. Nature 237:404–405.

Hoffman, W.; Heinemann, D.; Wiens, J.A. 1981. The ecology of seabird feeding flocks in Alaska. Auk 98:437–456.

Hutchison, L.V.; Wenzel, B.M. 1980. Olfactory guidance in foraging by procellariiforms. Condor 82:314–319.

Sealy, S.G. 1973. Interspecific feeding assemblages of marine birds off British Columbia. Auk 90:796–302.

Wenzel, B.M. 1980. Chemoreception in seabirds. Pages 41–67 *in* Burger, J.; Olla, B.L.; Winn, H.E. eds. Behavior of marine animals. Vol. 4. Plenum. New York. 515 pp.