THE HARBOR PORPOISE, *PHOCOENA PHOCOENA*, IN FISH HARBOUR, NEW BRUNSWICK, CANADA: OCCUPANCY, DISTRIBUTION, AND MOVEMENTS

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ABSTRACT

The distribution, movements, and relative population abundance of harbor porpoises were studied in the Fish Harbour region of New Brunswick, Canada (lat. 44°59′30″-45°01′00″N, long. 66°54′00″-66°57′00″W), from 1970 to 1978. In any given year numbers of this species were highest in the region between late July and early September. This is also the period during which surface temperatures attain a maximum (10°-12°C) and the largest herring, *Clupea harengus*, catches are usually made. During July-September the porpoise population of the inner (western) part of the study area contained 63% mothers with calves. Changes in relative population abundance were most strongly related with time of year (increasing from early July), tidal amplitude (most present when amplitude is 6.5 m or less), and wind phase (most present during onshore winds). Observation of recognizable individuals revealed consistent specific "territories" and patrolling patterns. A marked decrease in relative abundance in the latter half of the 1970s was noted. This decrease was coincident with a decline in mean midsummer surface temperature over 1974-78 of about 1°C. Unfortunately it was not possible to determine from existing data if major changes in availability of prey species also occurred in the inner Quoddy region during the same period.

Literature concerning ecology of the harbor porpoise, *Phocoena phocoena*, has been largely restricted to reports of nonquantitative or casual observations (Scheffer and Slipp 1948; Møhl-Hansen 1954; Amundin and Amundin 1974), although more recently Gaskin (1977), Prescott et al. (1981),[2] Flaherty and Stark (1982),[3] Kraus et al. (1983),[4] and Taylor and Dawson (1984) have presented information from surveys and some population estimates for limited areas of both east and west coasts of North America. A population estimate for the Copper River area of Alaska was provided by Matkin and Fay (1980). Habitat indices, relating occurrence of animals in coastal waters to various environmental factors have been given by Smith and Gaskin (1983) and Watts

and Gaskin (in press), and some radiotelemetric studies of distribution and movements by Gaskin et al. (1975) and Read and Gaskin (1983, in press).

In order to gain insight into the nature of local distributions and movements of *P. phocoena* over an extended period, we selected a semi-enclosed area of limited size in southern New Brunswick, Canada. Preliminary observations had already shown that the species was common in the area, and locality (about 8 km² maximum) bounded approximately by lat. 44°59′30″-45°59′00″N, long. 66°54′00″-66°57′00″W on the east coast of Deer Island (Fig. 1) was easily accessible for research and relatively sheltered. We were also aided by the occurrence in the area of several recognizable porpoises with surface disfigurements, large blemishes, or distinctive pigmentation patterns visible at some distance in favorable light; several of these animals were present in successive seasons.

CHARACTERISTICS OF THE STUDY AREA
(Figure 1)

Average depths range from about 8 m in Lords Cove to about 22 m in Simpson's Passage (respective maxima 20 m and 60 m) at mean low water. The region is subject to anomalistic, semidiurnal tides of
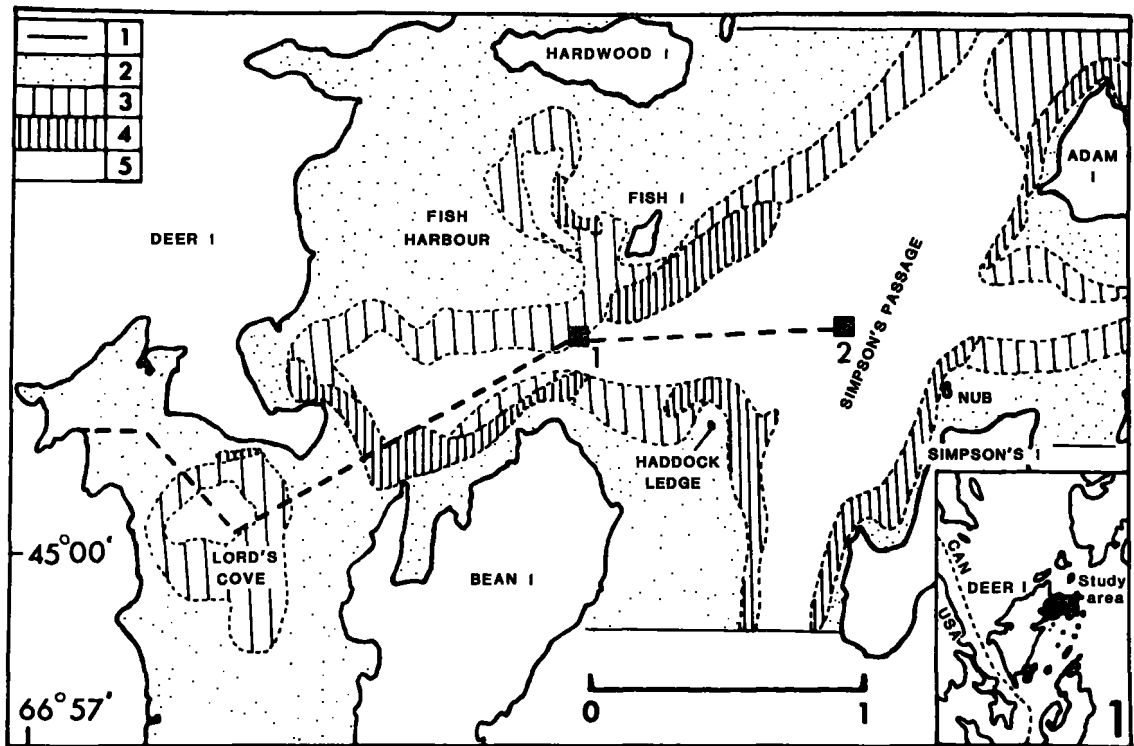
FIGURE 1. – The Fish Harbour region on the east coast of Deer Island region, New Brunswick, Canada (see inset). Legend: Straight solid lines indicate approximate limits of study area. Stipple indicates shallow shelf area (low water mark to 5 m); widely spaced vertical lines indicate areas of relatively gentle slope; narrowly spaced bars indicate steep scarps or slopes terminating in cliffs and the white areas (other than within island boundaries) are relatively deep basins and channels. Broken line shows regular track of boat with watch-stations 1 and 2. Place names are those used in the text. Scale = 1 km.

5.6-8.3 m (mean about 6.3 m) (Forrester 1960). Water turbidity is high (Secchi disk reading in July-August about 2 m). Most tidal flow from the area is by the northern end of Simpson's Passage. Salinities in the whole Quoddy region (Trites 1962) range from 29.5‰ (March-May) to 32.3‰ (September). Lower salinities in shallow inshore waters occur after heavy rain and may last for several days. While some year-to-year changes in mean surface temperature were recorded (Trites 1962, fig. 11), one of the most complete series (for 1978) provides a typical sequence of the relative changes from spring to autumn. Late May-early June surface temperatures ranged from 6.0° to 7.1°C, mid-July from 8.4° to 9.6°C, and mid-August-early September from 10° to 11.2°C. By early December the waters were 7°C again. Peak summer values of 11.3°-14.5°C were only obtained in mid-August at the head of Lords Cove in shallow water (< 5 m). At any given time surface temperatures were 0.5°-1.0°C warmer than those at 12 m despite the tidal mixing which obviously occurred. A general pattern of temperature profiles could be recognized in midsummer: The inner (western) part of Fish Harbour was vertically well-mixed throughout, but a rather steep horizontal gradient of about 1.0°C was maintained at all depths on the outer margin of this zone. In the central region (near Fish Island) the direction of water movement showed up to 90° variation at different depths at any given time of rapid tidal flow. The outer parts of Fish Harbour, and Simpson's Passage, tended to be well-mixed vertically, but were always about 0.5° cooler at the surface on the ebb. North of Adam Island there was a shift from horizonal gradients on flood to vertical gradients on the ebb. The inshore water is probably "trapped" in the bight of the harbor, i.e., with an extended residency time, while movement of water in and out the northern and southern entrances probably creates some mixing in the outer and central part of Fish Harbour. More detail of the static and dynamic characteristics of the study area and adjacent regions is provided by Smith et al. (1984).

METHODS

Most observations were made from a 5 m two-seater kayak (weather permitting), which appeared to exercise a negligible effect on the behavior of animals even at short distances (Watson 1976). A small fishing boat was used above Beaufort wind force 2, but this craft lacked the silent maneuverability of the kayak. Few publishable photographs were obtained because this species is an exceedingly difficult photographic subject. The method of making and maintaining contact was consistent throughout the study period (1 June 1970-10 September 1978). A central route from the head of Lords Cove was followed (Fig. 1); unless weather was too poor for optimal sighting in Simpson's Passage, or there was specific intent to track a group within Fish Harbour, the boat continued on track to watch-station 2 (Fig. 1). If no animals were present in Fish Harbour and conditions were less than Beaufort wind force 2, the boat would remain in the vicinity, but if the animals were already within Fish Harbour, the boat usually returned to watch-station 1 in outer Fish Harbour, from which point most of the study area normally used by porpoises could be kept under eye or binocular surveillance. As weather permitted, or presence and movements of animals dictated, this search pattern was usually repeated during the day at invervals of several hours. When porpoises were located either visually or from the sound of their expirations, the position of the boat and the initial positions of animals relative to the vessel were recorded to within a few tens of meters by taking 3-5 bearings from the many surrounding landmarks. Subsequent positions were noted in those cases when movements were tracked for extended periods, providing the animals surfaced long enough for accurate bearings to be taken and had moved to a significant distance (ca. 100 m) from the previous location. The time, location, size, and apparent composition of each porpoise group was recorded on and later transcribed from tape. The particular problems of quantifying sightings of this small cetacean have been considered by Gaskin (1977), Prescott et al. (footnote 2), Taylor and Dawson (1984), Kraus et al. (footnote 4, 1983), and Watts and Gaskin (in press). During the present study we used only data obtained in Beaufort Sea state 0-1, when visibility was unlimited within the study area and lighting was direct or diffuse, but uniform. In these ideal conditions some porpoises can be detected even from the air (250 m) at 650 m, although this is the least satisfactory method for sighting this species (Kraus et al. 1983). In a simultaneous comparison of effectiveness of stationary, mobile, and aerial observers (Kraus et al. 1983) the former, whether on land or stationary vessel, not only saw far more animals than the observers in the aircraft, but could detect them using binoculars in calm water at 1,000+ m. The probability of contact is enhanced when animals tend to surface repeatedly. The present authors found that porpoises working near the Nub close to the Simpsons Island (Fig. 1) could be clearly seen with binoculars from watch-station 1, at a distance of > 1 km in optimal conditions.

Some natural constraints on distribution of porpoises within the study area reduced the effective survey region to only 4 km². Virtually no animals ventured farther inshore than the shallow shelf edge (ca. 5 m) even during high water. Almost all ingress and egress was between Bean and Fish Islands (Fig. 1). Very few animals left by the southern passage from Lords Cove, and only two were ever noted to enter this way. Only one group of animals consistently visited Lords Cove in any case. No movement was noted through the narrow gut west of Hardwood Island, and only infrequent movement (≤ 5%) through the passage north of Fish Island.

Harbor porpoises in the Quoddy region appeared generally indifferent to boat traffic (Watts and Gaskin in press), with no noticeable attraction bias as noted for *Phocoenoides dalli* by Kasuya and Jones (1984). Because of the small size of the study area, the impossibility of making random transects, the highly clumped distributions, and nonrandom movements of animals (see latter), any kind of line-transect approach was inappropriate. From a combination of the initial strip census search and the stationary observations, we concentrated on obtaining a "best estimate" of the mean number of animals present during each observation period with reference to each hour of the day and each tide subphase within that period. All are minimum estimates because some animals were probably missed at the seaward periphery of the study area. We tried to avoid inclusion of repeat sightings in these estimates which would lead to an upward bias, except where we calculated simple sightings of individuals per hour. The "best estimate" data were used to give relative abundance with respect to various environmental conditions, while sightings per hour were more appropriate for time-based comparisons such as relative abundance from year to year.

When sighting conditions were particularly favorable, the movements of specific groups were plotted, either by observation from one or other watch-stations which commanded a wide view with many landmarks, or by discreetly following them in the

kayak on a parallel course at distances of 50-150 m. If only one observer was present in the kayak, these periods were only included in the main data base if very few animals were known to be in the study area.

STATISTICAL ANALYSIS

For statistical analyses of these data we considered the potential application of log-linear and multivariate models, principle component analysis (PCA), factor analysis (FA), and a categorical data (χ^2) procedure. Considerable differences in the magnitude of x-variate variances would make results from PCA or FA suspect (Maxwell 1977, ch. 4). Log-linear and multivariate approaches were initially attractive, but both have disadvantages. Tests for independence of x-variates are difficult in the latter, and while these are facilitated by the former, results obtained from log-linear models are often difficult to interpret (SAS Institute Inc. 1979, p. 222). Furthermore, statistical advisers noted that use of the whole data base was contraindicated in either method because 1) there was of necessity inclusion of linear, nonlinear, and enumeration data types, and 2) there were significant numbers of empty data cells usually resulting from poor weather when operation would have been pointless. The consultants recommended use of the categorical data procedure, not only for the reasons outlined above, but also because the very nature of the x-variates (e.g., lunar cycle and tidal cycle) precluded the existence of complete independence. From the ecological point of view it was considered more important to relate one dependent variable (relative abundance of porpoises) to a group of variables one at a time than to test for independence in the latter when the result would likely be spurious.

We first determined ($P = 0.13+$) that no data set from any x-variate was significantly associated with one part of the "range" of any other by a series of simple paired χ^2 tests. The main analyses were then carried out on an IBM[5] 360 mainframe computer using the PROC FREQ program (SAS Institute Inc. 1979) which used a generalized least squares model to generate χ^2 values for combinations of the categorical levels between variables. In this case the relative abundance was related to date, time of day, tidal amplitude, tidal phase, lunar phase, extant wind direction, and wind direction 24 h previously.

To examine changes in spatial distribution within

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

the study area, the location of 669 porpoise sightings collected in 1973-75 were plotted with respect to chronological time and time of tide. To avoid repeat sightings only the initial sighting was used in this context. To examine possible changes in distribution by depth and location, the study area was divided into three zones based on subsurface features: shallow shelving areas, subsurface slopes and scarps, and relatively deep basins and channels (Fig. 1). Such data cannot be used to deduce actual patterns of movement, but we were able to obtain some information on these through selective observations of identifiable individuals. Five of these were known to be females (consistently accompanied by calves), one a male (seen briefly copulating with a known female), and one of unknown sex. Each recorded sequential position was plotted for movements within a specific observation period, and for four of the known females data on all observations were plotted and the apparent ranges in consecutive seasons examined. In each case the master sheets had a grid with ordinates 100 m apart.

RESULTS

Hours of Observation of Porpoises in Fish Harbour Region

About 550 h of observation were made between June 1970 and September 1978, and 324 h of this were during an "intensive" study phase encompassing the summers of 1973-75. Estimates of changes in relative abundance with respect to environmental parameters were based on 181 h in optimal sighting conditions in this period (see section on Methods). Sporadic observations were maintained by our research group subsequent to 1975 or by auxilliary observers from Marine Research Associates of Lords Cove in most months except for late-December to mid-January.

Changes in Relative Abundance During the Year

From low relative abundance in the spring and late fall months, numbers of porpoises were highest during August or September in each year of the study period (Table 1). Highest values in ideal conditions were 8.00/h in Fish Harbour and 7.72/h in Simpson's Passage in September 1973 and August 1974 respectively. Observations by Marine Research Associates over the period 1971-77 in the same area, although largely of a casual nature, confirmed the animals can occur in small numbers in any month between Octo-

TABLE 1.—Sightings of harbor porpoises per hour in the Simpson's Passage and Fish Harbour areas, southern New Brunswick, 1970-78.

Month	1970	1971	1972	1973	1974	1975	1976	1977	1978
Simpson's Passage									
April	[1]0	—[2]	—	—	—	—	—	—	—
May	0.61 ± [3]0.07	0	—	0	—	—	—	—	—
June	0	0.90 ± 0.20	0.50 ± 0.15	0	—	—	—	0	0.94 ± 0.40
July	2.63 ± 0.30	1.91 ± 0.20	3.55 ± 0.40	3.55 ± 0.55	1.97 ± 0.65	1.68 ± 0.30	2.11 ± 0.30	0.76 ± 0.40	1.70 ± 0.25
August	4.42 ± 0.75	3.34 ± 0.60	6.44 ± 0.55	4.50 ± 0.60	7.72 ± 0.40	6.55 ± 0.40	3.37 ± 0.45	1.60 ± 0.25	1.93 ± 0.40
September	—	7.46 ± 1.15	6.33 ± 0.50	—	—	—	—	4.44 ± 1.00	7.47 ± 0.50
October	—	—	—	—	—	—	—	—	4.24 ± 0.02
November	—	—	—	—	—	—	—	—	0
Fish Harbour									
May	0	0	—	0	—	—	—	—	—
June	—	0	0	0.70 ± 0.01	—	—	—	0	0
July	0.93 ± 1.70	0.18 ± 0.05	3.44 ± 0.45	0.21 ± 0.04	0.46 ± 0.03	0.26 ± 0.04	0.92 ± 0.08	0.36 ± 0.15	0.22 ± 0.01
August	4.00 ± 0.78	1.04 ± 0.40	6.45 ± 0.40	4.48 ± 0.62	2.08 ± 0.70	1.94 ± 0.50	2.05 ± 0.30	1.17 ± 0.30	0.66 ± 0.08
September	—	2.41 ± 0.35	—	8.00 ± 1.80	5.22 ± 0.60	—	—	3.08 ± 1.12	0.89 ± 0.05
October	—	—	—	—	—	—	—	—	0
November	—	—	—	—	—	—	—	—	0

[1]No animals recorded.   [2]No search effort.   [3]Standard error of the mean.

ber and May, but probably rarely enter Fish Harbour (see next section).

Arrival and Departure of Porpoises Each Year in Relation to Sea Temperatures

First sightings in Fish Harbour were usually made in mid-late July when surface temperatures attained about 9°C, and never in Lords Cove until about mid-August despite 9°-11°C being reached at the surface in mid-late July. First regular sightings in Simpson's Passage varied from mid-May to late June. Determining the date of departure of the majority of animals from either sector was difficult because strong autumnal winds invariably interfered with observations from mid-September onwards when relative abundance was still high. In both 1977 and 1978, porpoises were still present in Fish Harbour until the last week of September and in Simpson's Passage until at least 15 October. Occasional animals may venture into the latter area in any month of the year since a very small population usually overwinters in the Quoddy region (Gaskin 1977), and one animal was sighted outside Fish Island on 7 December 1982 (B. M. Braune[6] and D. E. Gaskin, pers. obs.).

We could find no evidence that the distribution of porpoises was directly or indirectly influenced by the rather small daily local variations in sea temperatures within Fish Harbour. The most frequently observed known animal and her consorts would regularly traverse the width of the area (see Figure. 9) and their preferred locations appeared to have specific topographic rather than temperature characteristics.

Estimating Relative Abundance

Because the species does not make long dives (mean submergence 1 min 44 s, Watson and Gaskin (1983)), the required minimum period of observation needed to search the study area was not excessive. From our records we selected 3 wk in August 1972-75, when the probability of animals being present was high. In a random sample of 40 (i.e., above the minimum size for a "large" statistical sample (Bailey 1959)) search periods in optimum conditions of varying length (5 min to 2 h), the percentage of time that one or more animals was recorded increased from 50% for 10-min periods to well over 80% for 15-min periods. All observations of < 15 min were therefore discarded from the data set. If we were only interested in presence or absence, as in the case of simple locations at a given time of day or tide, observations from shorter periods or in Beaufort wind force 2+ were still of some value.

We have already outlined the methods for obtaining our "best estimates"; it is worth noting that various characteristics of the animals (e.g., short dive times, stereotyped movements, recognizable individuals) and of the study area (limited search area because of shallow water, many landmarks, shelter, and limited entry and exit points for animals) were of great assistance in reducing repeat sightings to a minimum.

[6]B. M. Braune, Department of Zoology, University of Guelph, Guelph, Ontario N1G 2W1, Canada.

Changes in Relative Abundance
Between 1970 and 1978

Table 1 gives sightings of individuals per hour by month for each year from 1970 to 1978. As some observation periods were eliminated (see above) the results sometimes differ slightly from values given by Gaskin (1977) for the earlier years. Results suggest a decline in relative abundance from 1972 onwards in Fish Harbour and from 1974 onwards in Simpson's Passage. Because the 1970 values were based on a relatively short series of observations, the apparent rise from 1970 to 1971 may be spurious. The slight increase in 1978 is also suspect as most observers were less experienced than the teams used in 1970-77. The overall trend however, seems unmis-

takable. Furthermore, a decline in each month of the July-September period is evident when data for the whole study area are pooled (Fig. 2).

Results of the categorical data procedure tests for relative abundance of porpoises against the set of environmental parameters are presented in Table 2 (Fish Harbour) and 3 (Simpson's Passage). As might be expected, large χ^2 and significant P values were generated from the sharp drop in overall numbers sighted per observation period (regardless of its length) from 1972 to 1975, and from the great increase occurring each year between July and September. Time of day appeared to exert no influence on relative abundance in either section (P = 0.45, 0.20), nor was any statistically significant relationship noted between relative abundance and
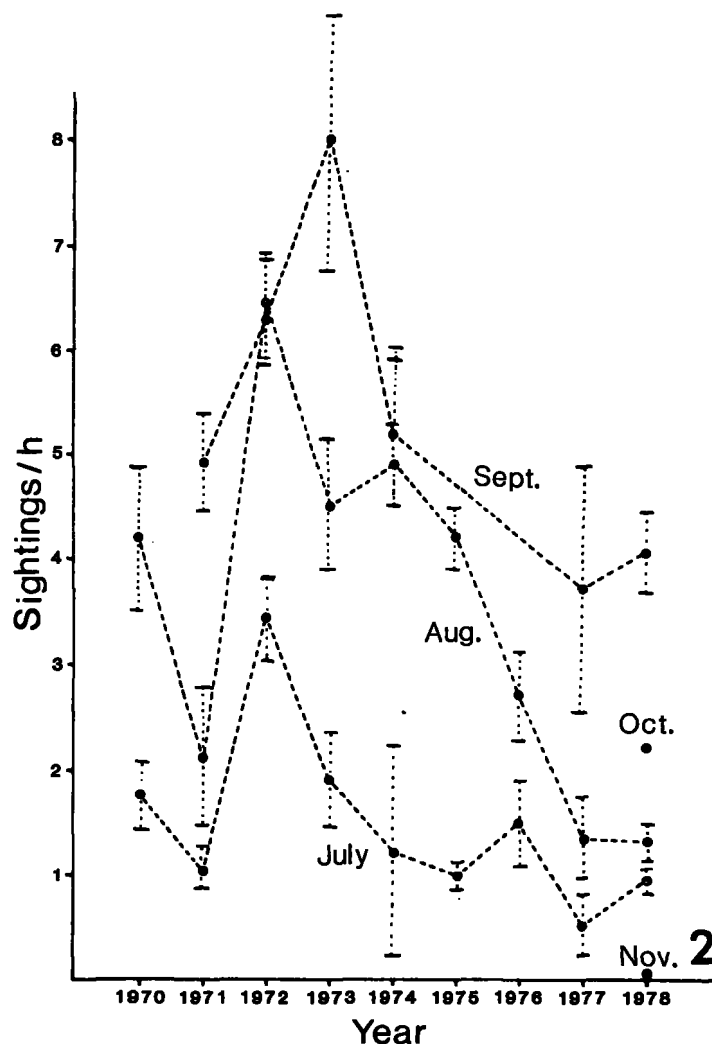

FIGURE 2. – Comparison of sightings per hour of porpoises in good condition in the Fish Harbour study area (Fish Harbour + Simpson's Passage), 1970-78 by month, from July to September. October and November values available for 1978 only. Vertical dots and bars represent standard error about the means.

TABLE 2.—Results of categorical data procedure tests for observed numbers of harbor porpoises in comparison to expected numbers with different environmental parameters in the Fish Harbour region of southern New Brunswick, 1972-75. I. Fish Harbour + Lords Cove (see Figure 1). n = observation periods; χ^2 = two-way table statistic.

Parameter measured	n	df	χ^2	P
Years (1972-75)	249	3	39.57	0.0001*
Time of year[1] (July to early September)	249	2	63.69	0.0001*
Time of day[2] (0600- + 1900)	249	4	3.67	0.4520
Tidal amplitude[3]	249	3	7.80	0.0500*
Tidal phases[4] (Start of falling tide to end of rising tide)	249	7	3.31	0.8450
Lunar phase[5] (New moon to full moon)	249	3	5.38	0.1450
Wind extant[6] (On shore, coastwise, or offshore)	249	2	17.58	0.003
Wind 24 h previous[6]	249	2	12.22	0.0094

[1]Categorical division of three periods (July, first 3 wk of August, last 1½ wk of August + early September) to balance effort.

[2]Four periods of 3 h each, post-1900 observations amalgamated.

[3]Four subphases (≥ 5.5, 5.6-6.5, 6.6-7.5, ≥ 7.6 m).

[4]The eight subphases given in Figure 4 were used.

[5]Three subdivisions used. More subdivision than these resulted in many empty data cells.

[6]Four subdivisions used. More subdivision than these resulted in many empty data cells.

*Statistically significant at 0.05 level or better.

TABLE 3.—Results of categorical data procedure tests for observed numbers of harbor porpoises in comparison to expected numbers with different environmental parameters in the Fish Harbour region of southern New Brunswick, 1972-75. II. Simpson's Passage. n = observation periods; χ^2 = two-way table statistic.

Parameter measured	n	df	χ^2	P
Years (1972-75)	132	3	7.58	0.050*
Time of year[1] (July to early September)	132	2	16.99	0.0002*
Time of day[2] (1600- + 1900)	132	4	5.98	0.201
Tidal amplitude[3]	132	3	2.54	0.468
Tidal phases[4] (Start of falling tide to end of rising tide)	132	7	9.97	0.190
Lunar phase[5] (New moon to full moon)	132	3	7.38	0.061**
Wind extant[6] (Onshore, coastwise or offshore)	132	2	0.95	0.620
Wind 24 h previous[6]	132	2	0.93	0.628

[1]Categorical division of three periods (July, first 3 wk of August, last 1½ wk of August + early September) to balance effort.

[2]Four periods of 3 h each, post-1900 observations amalgamated.

[3]Four subphase (≥ 5.5, 5.6-6.5, 6.6-7.5, ≥ 7.6 m).

[4]The eight subphases given in Figure 4 were used.

[5]Three subdivisions used. More subdivision than these resulted in many empty data cells.

[6]Four subdivision used. More subdivision that these resulted in many empty data cells.

*Statistically significant.

**Close to significance at 0.05 level.

magnitude of tidal amplitude in Simpson's Passage. In shallower, semi-enclosed Fish Harbour however, significantly more porpoises were present $(P = 0.05)$ at low tidal amplitudes (≤ 6.5 m) than high amplitudes (≥ 6.6 m). Data for the most commonly sighted individual (a female with a large dorsal scar) corroborated this general finding; about 78% of all sightings of this animals were made when the amplitude was 6.5 m or less.

Relative abundance did not alter $(P = 0.84, 0.19)$ in either zone of the study area during the tidal cycle. Similarly no significant change occurred relative to the lunar phase in Fish Harbour, although in Simpson's Passage the χ^2 value approached the arbitrary 0.05 level of significance $(P = 0.061; n = 249)$. No relationship between extant or previous wind direction was evident in Simpson's Passage $(P = 0.62, 0.63; n = 132)$, but there appeared to be a significant association between wind direction and relative abundance of porpoises in Fish Harbour $(P = 0.0003, 0.009; n = 249)$. In both cases far more animals were present during onshore wind directions than when winds were coastwise or offshore.

Distribution and movements of porpoises on the fine scale is likely to be correlated with the presence or absence of food species which, in the Quoddy region, consist largely of juvenile herring, *Clupea harengus*; mackerel; and small gadoids (Smith and Gaskin 1974). The dispersal of the former in this region is greatly influenced by current velocities (Jovellanos and Gaskin 1983). Unfortunately the beam width of available equipment was far too narrow to permit us to cover the study area by acoustic survey thoroughly, or even representatively, at any given time or tide phase. Because one of our major aims at the outset of the study was to avoid disturbing normal behavior of the porpoises, it was also rarely possible to acoustically scan in their immediate vicinity. We were however able to infer feeding behavior from diving patterns (e.g., "pattern B") carried out consistently in one location (Watson and Gaskin 1983). Sometimes fish were seen jumping at the surface in such areas (Fig. 3), and these zones were acoustically scanned on an opportunistic basis. Fish schools, recorded during bottom topographic acoustic mapping runs, tended to be concentrated at several locations in which porpoises were often sighted. Usually these traces were of herring schooltype. While this species predominates in the Quoddy region in the summer months (Jovellanos and Gaskin
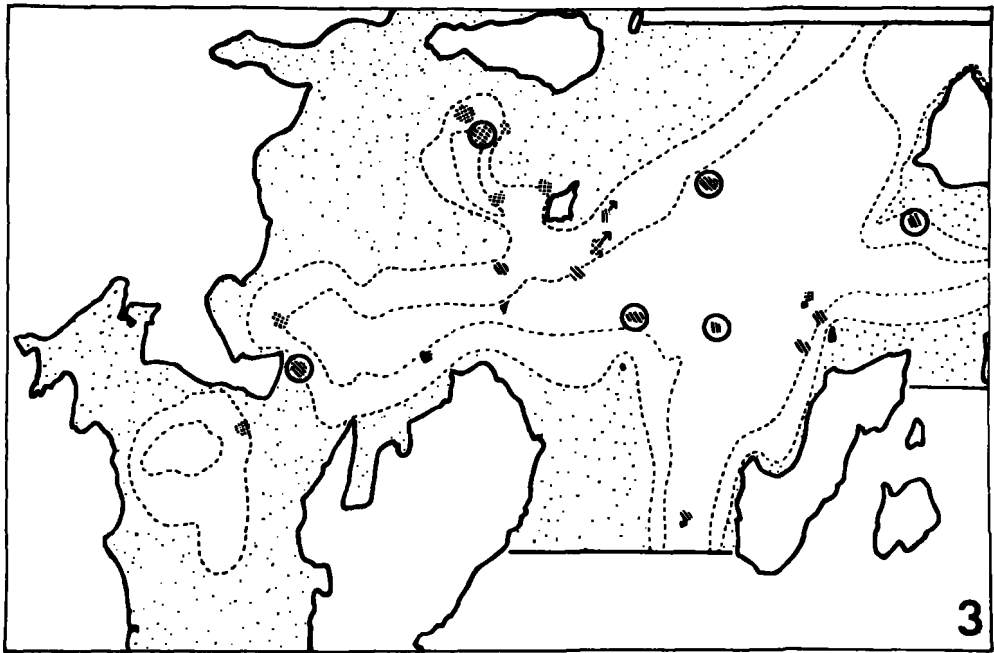
FIGURE 3. – Locations in Fish Harbour at which fish were detected visually or by sonar in 1973-78; opportunistic records only. Stipple: species not identified; vertical bars: Atlantic mackerel; diagonal bars: Atlantic herring; circles: one or more porpoises simultaneously present with record; arrows: direction of fish movement. The size of hatched areas indicates approximate size of the school.

1983), some could have been of harbor pollack, which are also taken by this species.

Changes in Distribution Within the Fish Harbour Region

No differences in distribution of the 669 recorded sighting positions for 1973-75 could be detected when they were plotted either by four or eight time periods from 0600-2200, but considerable differences were evident when they were plotted against eight subphases (slack low, slow flood #1, fast flood, slow flood #2, slack high, slow ebb #1, fast ebb, and slow ebb #2) of the tidal cycle. This analysis ignores for the moment the fact that many animals move in a rather regular manner through the study area, since useful information can be obtained simply from noting where they are at any given time of tide. The results (Fig. 4) showed that up to 80% of porpoises were congregated over the shallow shelf margins, slopes, and scarp areas between the onset of flood tide and high water. Conversely, about the same proportion became concentrated over the basin and channel areas between onset of the ebb, and slack low water.

The Nature of Movements Within the Fish Harbour Region

It became evident that when the recognizable animals returned each year they reestablished "specific ranges" (for lack of a better term) in virtually the same locations in Fish Harbour each summer (Figs. 5-8). There is some evidence that these "ranges" shifted progressively further east of Deer Island between 1973 and 1975, especially in the case of the scarred female mentioned earlier. Each of these areas in Fish Harbour, of which we were able to measure nine approximately, appeared to be about 1.0-1.5 km² in extent. Even the most distinctive animals would disappear from the study area for extended periods and then reappear again, just as Gaskin et al. (1975) noted for a female carrying a radiotelemetric package. The scarred female was once observed with a calf off the eastern coast of Simpson's Island, and on another occasion between Minke Ledges and Tinker Island, which lie between 1 and 3 km south of the main study area. This specimen was present in the Fish Harbour region for about half the days of excellent visibility in 1973-75, was well known to all observers, and yet was only
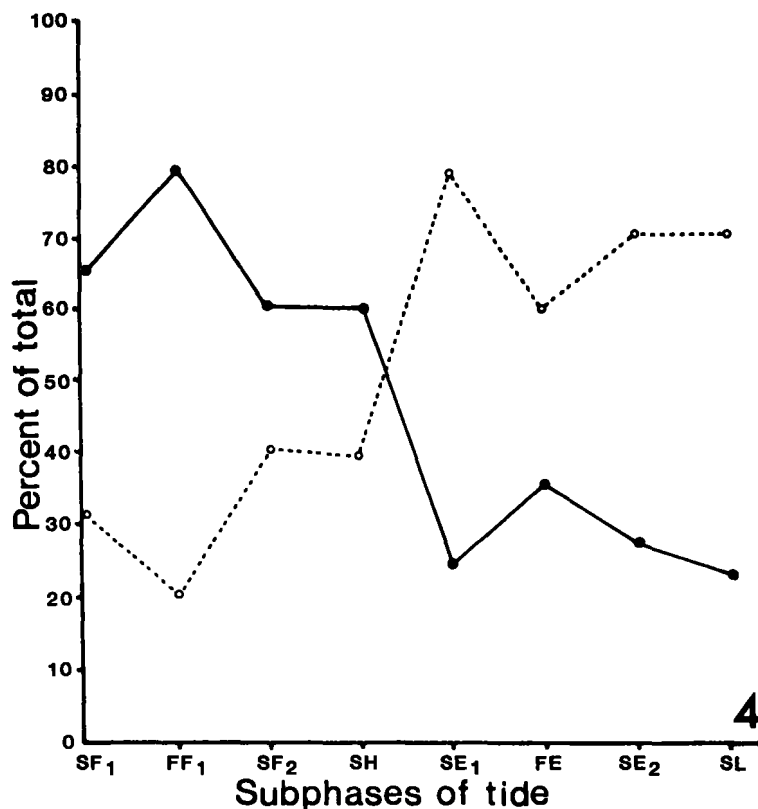
FIGURE 4.—Distributions of 669 harbor porpoises in Fish Harbour 1973-75 over subsurface topographic features, by eight subphases of the tide: Slack low water (SL), slow flood 1 (SF$_1$), fast flood (FF), slow flood 2 (SF$_2$), slack high water (SH), slow ebb 1 (SE$_1$), fast ebb (FE), and slow ebb 2 (SE$_2$). Solid line shows percentage over shallow shelf, scarps, and slopes; dotted line, percentage over basins and channels.

seen on the two above occasions during simultaneous surveys outside the present study area.

Only in the case of this particularly distinctive animal were we able to obtain enough observations to map some of her patterns of movement over extended periods. On 17 August 1973, for example, we tracked her for 2 h 12 min (57 position fixes, Fig. 9), noting that she tended to stay close to the slopes of the main basin-channel, with one foray around the small basin in Lords Cove. This kind of point-to-point travelling interspersed with short periods of submergences in one location is quite typical of this species. This animal repeated almost identical range movements on 13 and 29 August 1974. On 1 and 30 August 1974 (1 h 4 min and 3 h 3 min respectively) this animal spent far longer periods in relatively restricted locations (Fig. 10). Submergences were again of the "pattern B" type, and no surface resting was recorded. On 1 August many herring were seen jumping at the surface immediately after each submergence by the female. Her calf was often left at the surface during these bouts.

"Systematic patrolling" of small areas, often in the lee of ledges or small islets was also recorded (Fig.

10). The movements illustrated were carried out by a school of three medium-sized animals accompanied by one small one on 2 August 1974. The group sychronously dove repeatedly while moving back and forth in one restricted scarp location, then abruptly travelled to the second location shown and repeated the pattern.

DISCUSSION

The distribution of some small odontocetes is known to be correlated with sea surface temperatures (Gaskin 1968; Würsig and Würsig 1980), but the relationship is almost certainly indirect, the result of influences exerted one or more levels further down the food chain. The entry of the main summer population of harbor porpoises into the study area not only coincides with 9°-10°C surface temperatures, but also with the arrival of large numbers of juvenile herring which feed in the Quoddy region during the summer months (Battle et al. 1936; Jovellanos and Gaskin 1983). Although transport of relatively small fish into the study area might be expected to be at a maximum during spring tides,
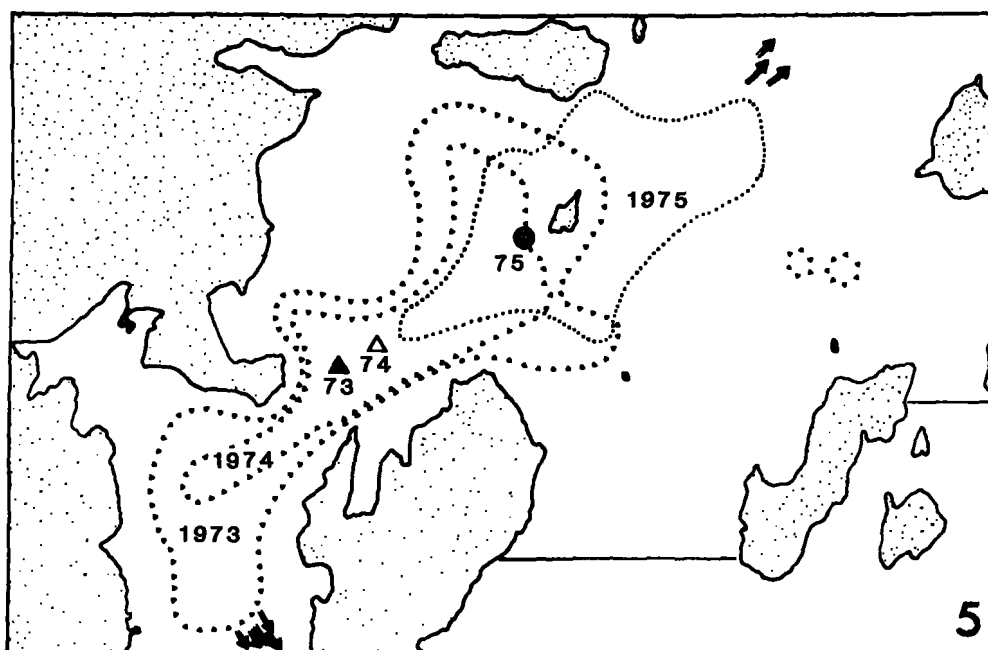
FIGURE 5. – Broken lines encompass all sightings of recognizable animal (#1, scarred mother). 1973: solid wedges; 1974: open wedges; 1975: dots. The solid triangle, open triangle, and solid circle respectively represent the center of the "range" as determined by the mean of the latitudes and longitudes of each position, excluding single isolated sightings. Arrows indicate number of times this animal (and any consorts) were observed leaving the "range". In each case they were swimming at 4 + knots and outdistancing the kayak.
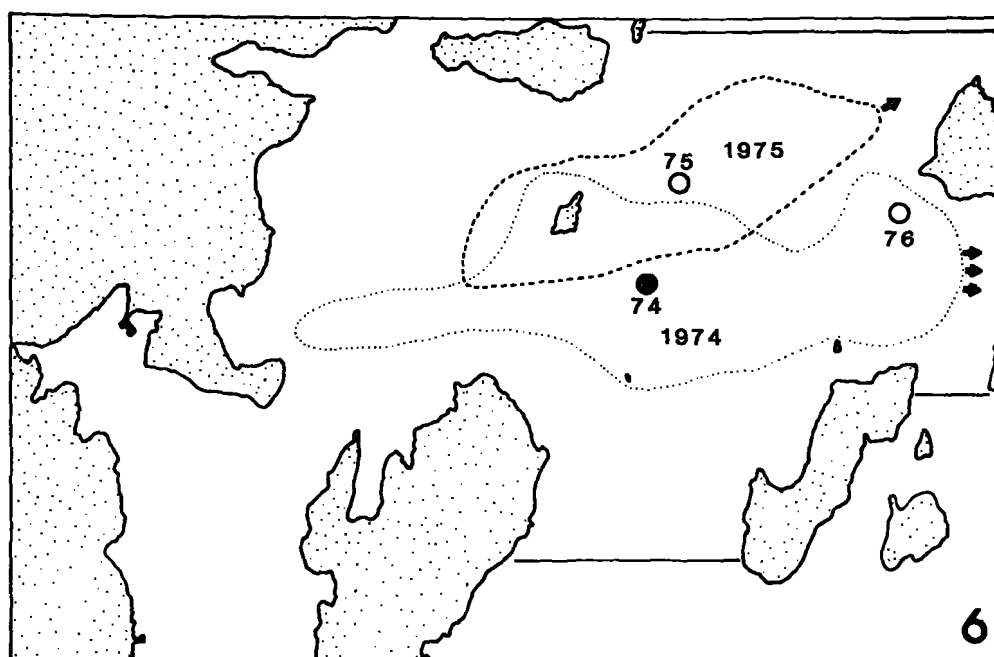
FIGURE 6. – Broken lines encompass all sightings of known animal #2 (clipped fin). 1974: dotted lines; 1974: dashes. Open circle and closed circle for 1974 and 1975 respectively, and arrows indicating animal leaving the area are as in Figure 5.
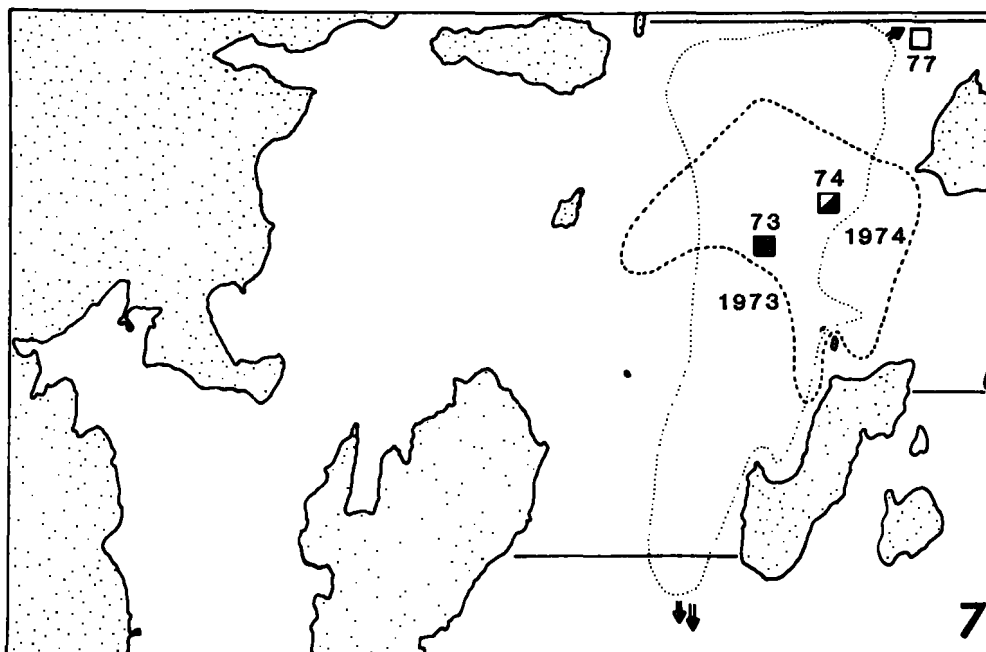
FIGURE 7. – Broken lines encompass all sightings of known animal #3 (Simpson's Passage mother) except for single 1977 sighting. 1973: dotted line; 1974: dashed line. Other symbols as in Figure 5.
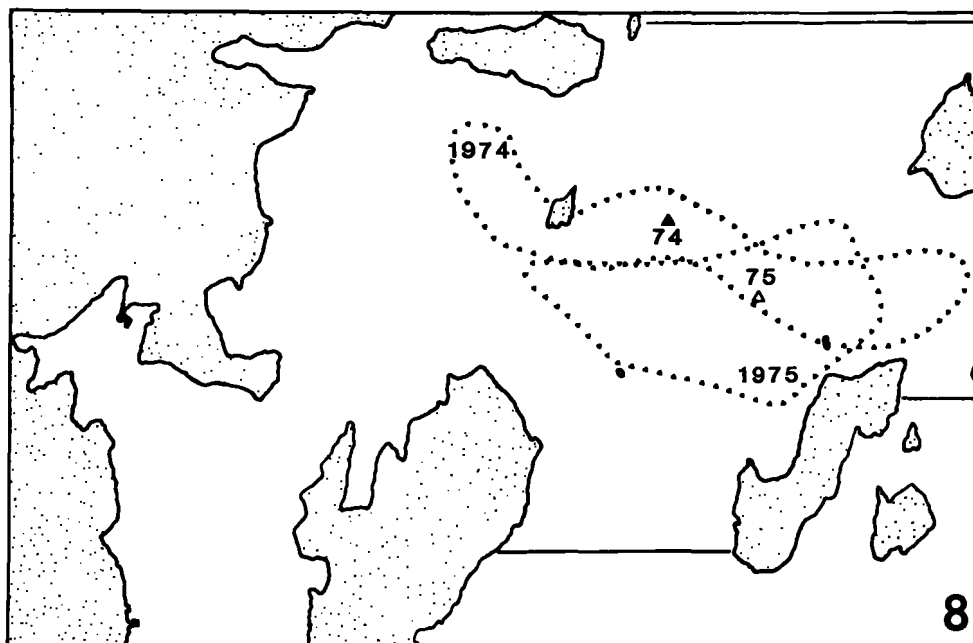

FIGURE 8. – Broken lines encompass all sightings of known animal #4 (Light brown mother). 1974: solid wedges; 1974: open wedges. Other symbols as in Figure 5.
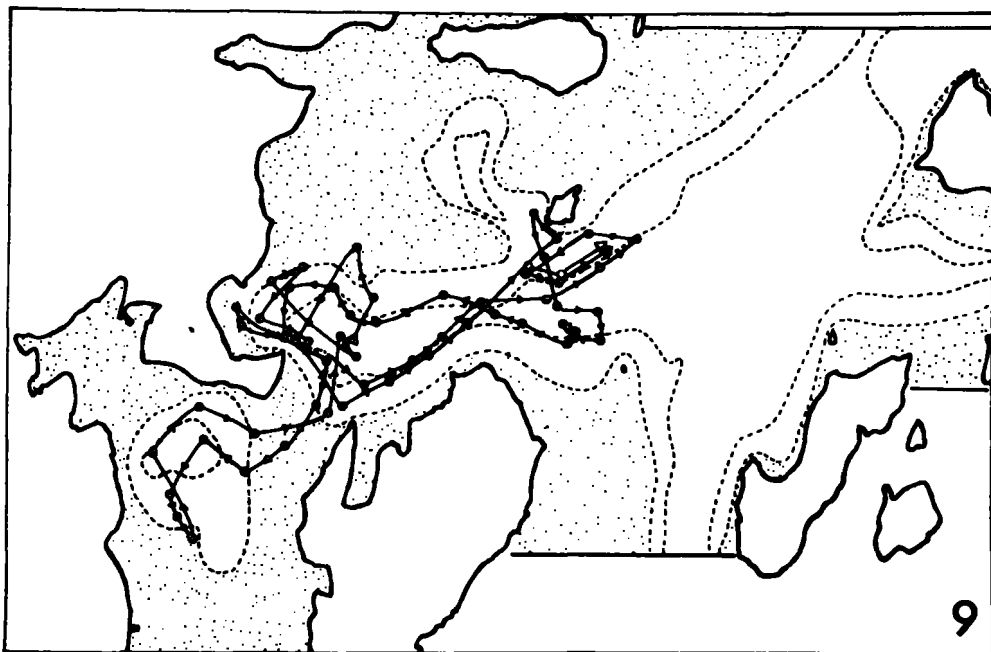
FIGURE 9.—Movements of scarred mother during 2 h 12 min period of 10 August 1973 accompanied by calf (57 position fixes). On some occasions they resurfaced close to an immediately previous position; about 75 surfacings are represented by these positions. Reverse arrow indicates initial contact point (just outside Lords Cove), solid arrow point where tracking was abandoned, and white circles position of a medium-sized animal which briefly joined the pair.

we found relative abundance of porpoises conversely to be greatest during neap tides. About 63% of the sightings in 1973-75 were of mothers and calves. Possibly these animals stay out of semi-enclosed areas during periods of maximum water transport, especially in areas with turbulent shallows such as the Fish Harbour region. On the other hand, if there are larger numbers of herring schools moving into the outer part of the Quoddy region it may not be necessary to forage in inshore waters. Once the animals are in the study area however, the observed changes in distribution during the tidal cycle confirm the earlier subjective comment (Watson 1976) that porpoises seemed to move inshore with the flood tide and offshore with the ebb.

The distribution of porpoise activity in the region appeared to be closely related to subsurface topography, particularly the margins of the basins and channels in areas of restricted water flow, the lee of islets, especially Fish Island and the Nub, and blind trench heads such as that just north of Hathaway Head. Because our meager acoustic records revealed fish traces in all these sites at one time or another (Fig. 3), we speculate that these may be areas of fish accumulation which the porpoises have

learned to exploit. Each may have subsurface eddies or areas of relatively slack water against the lee side of the slope or near the bottom, in which fish can shelter from strong currents, and in which zooplankton might also accumulate. In such areas fish could not only avoid being carried further inshore, but could also feed (Hamner and Hauri 1977). Dispersal from offshore areas into the coastal belt is likely to be augmented by onshore winds, which can increase significantly the flow of water in the immediate surface layers. Local fishermen believe that offshore winds serve to hold "feed" away from the coast, while coastwise winds might reduce the possibility of entry into Fish Harbour by increasing surface flow past the relatively narrow passages. We conclude that light or moderate winds are unlikely to affect any small cetacean directly; when winds were strong enough that behavior might conceivably be affected, we were not usually operating.

Large variation always occurs in data such as these, and it is to a large extent unpredictable. Such variation in relative abundance can be explained quite simply; these animals are large, highly mobile predators with sophisticated adaptations both for active and passive acoustic scanning for their equally
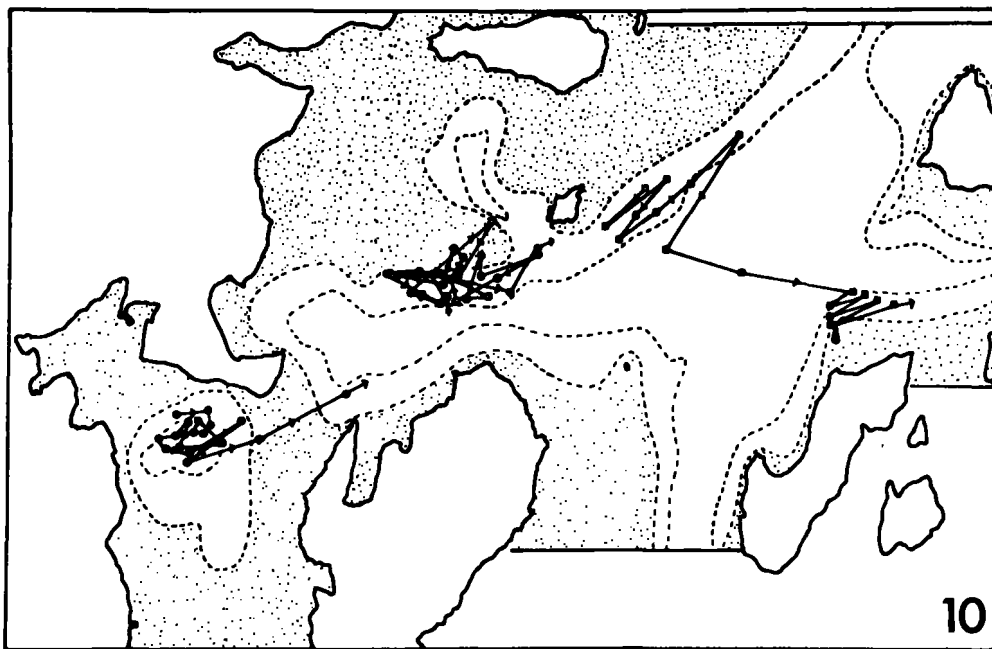
FIGURE 10. – Movements of scarred female on 30 August 1974 (solid circles at left of figure) and 29 August 1974 (solid circles in center of figure). Solid squares show "patrolling" behavior of school of four animals recorded on 2 August 1974. Qualifying comments on position fixes and surfacings in Figure 9 apply here also.

mobile prey. That the harbor porpoises in this area can shift tens of kilometers in a few hours cannot be questioned (Read and Gaskin in press); if few fish are present in one area, they may well move in a loosely synchronized group to forage in other localities. This degree of mobility and scanning ability is highly adapted not only to the mobility of their prey species, but also to the patchy nature of the distribution patterns of such fish; there is probably a significant random element in the dispersal of juvenile herring in the Quoddy region (Jovellanos and Gaskin 1983). The type of porpoise movement shown in Figure 9 was presumed to indicate that prey were dispersed, since the animal spent little time in any one location. In the other movement pattern (Fig. 10) the same animal was believed to be encountering prey in local concentrations that merited prolonged submergences in one area.

We have little evidence that the region might be significant either as a mating area or a calving ground. Females appear to have their calves offshore, since, although the latter may be very small in late June and July, they already accompany females sighted in the outer part of the Quoddy region (Smith and Gaskin 1983). Many females with calves appear to remain on tidal convergence streaks up to 20 km

offshore in the outer Quoddy region (Read 1983) and may not move into the coastal zone at all. It seems more likely that the study area functioned as a significant feeding area for this species rather than being a zone favoured for reproductive activity.

The demonstrated existence of "specific ranges" and annual returns by individual harbor porpoises in this study is not surprising. Rather similar patterns, although sometimes on very different geographical scales, have been recorded for *Delphinus delphis* by Martin et al. (1971), *Orcinus orca* by Bigg (1982), *Tursiops truncatus* by Wells et al. (1980) and Würsig and Würsig (1979), and *Lagenorhynchus obscurus* by Würsig and Würsig (1980). Periodic disappearances and abrupt reappearances of *T. truncatus* were also recorded by Würsig (1978), while studying the animal.

With respect to the progressive decline in relative abundance in the peak part of summer, lack of consistent observations through late September-late October (because of high winds) prevented us from determining whether or not this resulted from a real population decrease in the area, or simply a shift of peak abundance from mid-August to mid-September during the decade. Consequently we adopted an indirect approach to the problem, plotting sightings

439

per hour for each month of summer for each year with sufficient data (Fig. 2). This suggests that the decline resulted from a combination of both factors, with a general overall decline in relative abundance since about 1973 and a progressive retardation of the peak of numbers since about 1975. Unfortunately there is insufficient information in Department of Fisheries and Oceans records to decide if any change in food supply could have occurred during those years, especially with respect to juvenile herring abundance (T. D. Iles[7]). Nevertheless, our surface temperature records for the inner Quoddy region reveal a consistent decline in the mean summer value (centered on mid-August) from above 12°C in 1971 to below 11°C in 1977 (Gaskin et al. 1979). The temperature curve is compared with the pattern of relative abundance in Figure 11; there is close correspondence from 1972 onwards. Such a decline might result from increase in relative dominance of

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[7]T. D. Iles, Biological Station, Department of Fisheries and Oceans, New Brunswick, E0G 2X0, Canada, August 1980.

Nova Scotia current water in the Bay of Fundy (Sutcliffe et al. 1976) and perhaps a significant decline in the availability of zooplankton prey of juvenile herring. Alternatively the slightly cooler waters might be marginally less suitable for young porpoise calves.
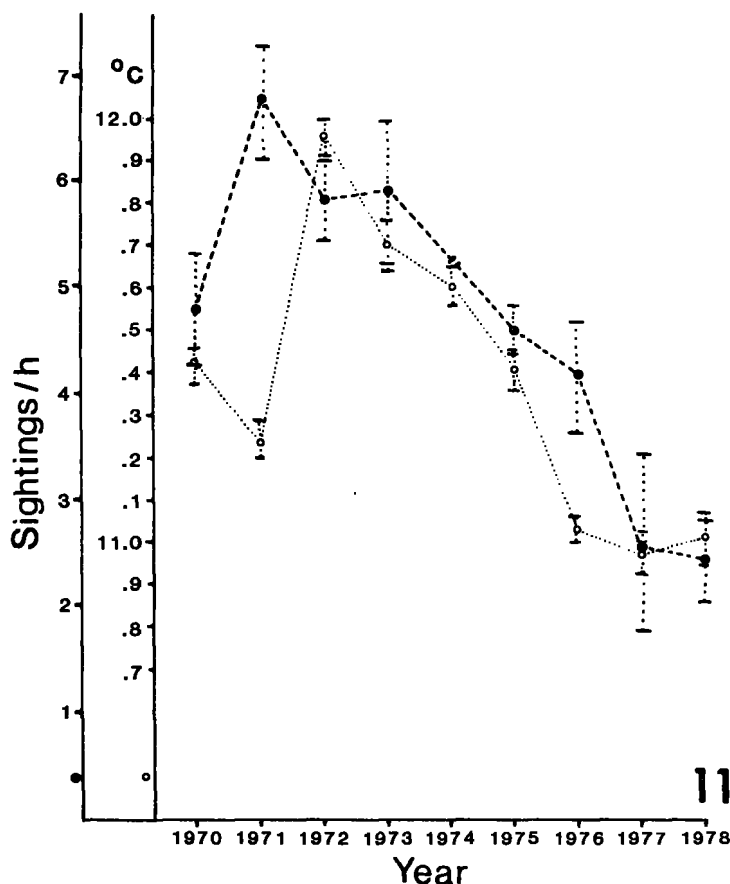
ACKNOWLEDGMENTS

FIGURE 11.—Comparison of midsummer (late July-early September) sightings per hour of harbor porpoises in the Fish Harbor region of New Brunswick between 1970 and 1978 with surface temperatures based on 8 stations (n = about 60/annum): Solid circles and dashed line (sightings per hour), open circles and dotted line (°C). Vertical dots and bars represent the standard error about the mean.

LITERATURE CITED

AMUNDIN, M., AND B. AMUNDIN.
    1974. On the behavior and study of the harbour porpoise, *Phocoena phocoena*, in the wild. *In* G. Pilleri (editor), Investigations on Cetacea, Vol. V, p. 317-328. Berne, Switzerland.
BAILEY, N. J. T.
    1959. Statistical methods in biology. Engl. Univ. Press, Ltd., Lond., 200 p.
BATTLE, H. I., A. G. HUNTSMAN, A. M. JEFFERS, G. W. JEFFERS, W. H. JOHNSON, AND M. A. McNAIRN.
    1936. Fatness, digestion and food of Passamaquoddy young herring. J. Fish. Res. Board Can. 2:401-429.
BIGG, M.
    1982. An assessment of killer whale (*Orcinus orca*) stocks off Vancouver Island, British Columbia. Thirty-second Rep. Int. Whaling Comm. SC/Jn81/KW4, p. 655-666.
FORRESTER, W. D.
    1960. Current measurements in Passamaquoddy Bay and the Bay of Fundy 1957 and 1958. J. Fish. Res. Board Can. 17: 727-729.
GASKIN, D. E.
    1968. Distribution of Delphinidae (Cetacea) in relation to sea surface temperatures off eastern and southern New Zealand. N.Z. J. Mar. Freshw. Res. 2:527-534.
    1977. Harbour porpoise *Phocoena phocoena* (L.) in the western approaches to the Bay of Fundy 1969-75. Rep. Int. Whaling Comm. 27:487-492.
GASKIN, D. E., G. J. D. SMITH, AND A. P. WATSON.
    1975. Preliminary study of movements of harbour porpoises (*Phocoena phocoena*) in the Bay of Fundy using radiotelemetry. Can. J. Zool. 53:1466-1471.
GASKIN, D. E., K. I. STONEFIELD, P. SUDA, AND R. FRANK.
    1979. Changes in mercury levels in harbour porpoises from the Bay of Fundy, Canada, and adjacent waters during 1969-1977. Arch. Environ. Contam. Toxicol. 8:733-762.
HAMNER, W. M., AND I. R. HAURI.
    1977. Fine-scale surface currents in the Whitsunday Islands, Queensland, Australia: Effect of tide and topography. Aust. J. Mar. Freshw. Res. 28:333-359.
JOVELLANOS, C. L., AND D. E. GASKIN.
    1983. Predicting the movements of juvenile Atlantic herring (*Clupea harengus harengus*) in the SW Bay of Fundy using computer simulation techniques. Can. J. Fish. Aquat. Sci. 40:139-146.
KASUYA, T., AND L. JONES.
    1984. Behavior and segragation of the Dall's porpoise in the Northwestern Pacific Ocean. Sci. Rep. Whales Res. Inst. No. 35, p. 107-128.
KRAUS, S. D., J. R. GILBERT, AND J. H. PRESCOTT.
    1983. A comparison of aerial, shipboard, and land-based survey methodology for the harbor porpoise, *Phocoena phocoena*. Fish. Bull., U.S. 81:910-913.
MATKIN, C. O., AND F. H. FAY.
    1980. Marine mammal-Fishery interactions on the Copper

River and in Prince William Sound, Alaska, 1978. U.S. Dep. Commer., N.T.I.S. Rep. PB80-159536, Springfield, VA, 81 p.
MAXWELL, A. E.
    1977. Multivariate analysis in behavioural research. Chapman and Hall, Lond., 164 p.
MØHL-HANSEN, U.
    1954. Investigation of reproduction and growth of the porpoise (*Phocoena phocoena* (L.)) from the Baltic. Vidensk Medd. Dan. Naturhist. Foren. Khobenh. 116:369-396.
READ, A. J.
    1983. Movements and distribution patterns of harbour porpoises (*Phocoena phocoena*) in the western Bay of Fundy. M.S. Thesis, University of Guelph, Guelph, Ontario, 87 p.
READ, A. J., AND D. E. GASKIN.
    1983. The application of radio tracking techniques to the study of harbour porpoises (*Phocoena phocoena*) in the Bay of Fundy. Proceedings of the 5th International Conference on Wildlife Telemetry, Halifax, N.S., Canada, August 1983, 7 p.
    1985. Radio tracking the movements and activities of harbour porpoise, *Phocoena phocoena* (L.), in the Bay of Fundy, Canada. Fish. Bull. U.S. 83(2).
S.A.S. INSTITUTE, INC.
    1979. SAS User's Guide. Edited by J. T. Helwig and K. A. Council. SAS Institute Inc., Raleigh, NC, 494 p.
SCHEFFER, V. B., AND J. W. SLIPP.
    1948. The whales and dolphins of Washington State with a key to the cetaceans of the west coast of North America. Am. Midl. Nat. 39:257-337.
SMITH, G. J. D., AND D. E. GASKIN.
    1974. The diet of harbour porpoises (*Phocoena phocoena* (L.)) in coastal waters of eastern Canada, with special reference to the Bay of Fundy. Can. J. Zool. 52:777-782.
    1983. An environmental index for habitat utilization by female harbour porpoises with calves near Deer Island, Bay of Fundy. Ophelia 22:1-13.
SMITH, G. J. D., C. L. JOVELLANOS, AND D. E. GASKIN.
    1984. Near-surface biooceanographic phenomena in the Quoddy region, Bay of Fundy. Can. Tech. Rep. Fish. Aquat. Sci. 1280, 124 p.
SUTCLIFFE, W. H., JR., R. H. LOUCKS, AND K. F. DRINKWATER.
    1976. Coastal circulation and physical oceanography of the Scotian Shelf and Gulf of Maine. J. Fish. Res. Board Can. 33:98-115.
TAYLOR, B. L., AND P. K. DAWSON.
    1984. Seasonal changes in density and behavior of harbour porpoise (*Phocoena phocoena*) affecting census methodology in Glacier Bay National Park, Alaska. Thirty-fourth Rep., Int. Whaling Comm., p. 479-483.
TRITES, R. W.
    1962. Temperature and salinity in the Quoddy region of the Bay of Fundy. J. Fish. Res. Board Can. 19:975-978.
WATSON, A. P.
    1976. The diurnal behavior of the harbour porpoise (*Phocoena phocoena*) in the coastal waters of the western Bay of Fundy. M.S. Thesis, University of Guelph, Guelph, Ontario, 94 p.
WATSON, A. P., AND D. E. GASKIN.
    1983. Observations on the ventilation cycle of the harbour porpoise *Phocoena phocoena* (L.) in coastal waters of the Bay of Fundy. Can. J. Zool. 61:126-132.
WATTS, P. W., AND D. E. GASKIN.
    In press. Habitat index analysis of harbour porpoise (*Phocoena phocoena* L.) in the southern coastal Bay of Fundy, Canada. J. Mammal. 64.
WELLS, R. S., A. B. IRVINE, AND M. D. SCOTT.
    1980. The social ecology of inshore odontocetes. *In* L. M. Herman (editor), Cetacean behavior: mechanisms and func-

tions, p. 263-317. Wiley-Interscience Publications, N.Y.

WÜRSIG, B.
1978. Occurrence and group organization of Atlantic bottlenose porpoises (*Tursiops truncatus*) in an Argentine bay. Biol. Bull. (Woods Hole) 154:348-359.

WÜRSIG, B., AND M. WURSIG.
1979. Behavior and ecology of the bottlenose dolphin, *Tursiops truncatus*, in the South Atlantic. Fish. Bull., U.S. 77: 399-412.
1980. Behavior and ecology of the dusky dolphin, *Lagenorhynchus obscurus*, in the South Atlantic. Fish. Bull., U.S. 77: 871-890.