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Night behavior and ecology of humpback whales (Megaptera novaeangliae) in the western north atlantic

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NIGHT BEHAVIOR AND ECOLOGY OF

HUMPBACK WHALES (*Megaptera novaeangliae*)

IN THE WESTERN NORTH ATLANTIC

A Thesis

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ABSTRACT

Humpback whales (Megaptera novaeangliae) in the Gulf of Maine and Newfoundland, were radio tagged and tracked day and night. Gulf of Maine humpbacks were highly active most of the time, exhibiting only short periods of rest or play. Primary night activity was feeding on American sand lance (Ammodytes americanus) both within the water column and at the bottom. One form of bottom feeding apparently consisted of substrate disturbance by whales to elicit schooling of substrate-dwelling sand lance. Daytime behavior also included feeding, but other activities occurred slightly more frequently than feeding. Newfoundland humpbacks were active most of the time during the day but were relatively quiescent with some feeding at night.

Diel behavior and distribution changes of sand lance in the Gulf of Maine appeared to be light-level dependent and to be the main cause of the variety of humpback feeding methods there at night. Artificial light from the Boston vicinity skyline, as well as moonlight, appeared to greatly influence sand lance vertical distribution and, therefore, humpback feeding behavior and group structure. Humpbacks in the Gulf of Maine may have spent most of their time at night feeding to compensate for low prey densities in the Gulf of Maine or because of reduced feeding efficiency during the daytime due to the influence of high boat traffic.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

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INTRODUCTION

Nighttime observations of baleen whales have mostly been short term and there are no detailed published observations of whales made at these times. Watkins *et al.* (1981) and Baker *et al.* (1983) conducted short-term monitoring of radio tagged humpbacks in southeastern Alaska and found them to be relatively quiescent at night. However, other studies in southeast Alaska (Jurasz and Jurasz 1979, W. Dolphin, pers. comm.), and in Newfoundland (Whitehead 1981), indicated that some humpback whales were observed actively feeding at night under partial moonlight.

The lack of data on the night behavior and ecology of baleen whales is mainly due to limitations of the research methods which were available until recently for keeping track of individual whales during the night. However, radio telemetry allows for consistent and rapid re-identification of individual whales during darkness, and during inclement weather day and night. This study focuses on nighttime behavioral ecology of humpback whales in the southern Gulf of Maine off Cape Cod and off Newfoundland, based on direct observations and facilitated by a newly designed radio telemetry system for whales (Goodyear 1981).

From June through September each year, many humpback whales concentrate to feed in the study areas of both Newfoundland (Mitchell 1973, Lien 1980, and Whitehead *et al.* 1980) and the Gulf of Maine (Schevill and Backus 1960, Katona 1976). In the Gulf of Maine, the main prey for humpbacks, and also the most seasonally abundant small schooling fish, is the American sand lance *Ammodytes americanus* (Overholtz and Nicolas 1979, Hain *et al*. 1982, Kenney 1984, C. Mayo pers. comm.). In Newfoundland, humpbacks prey primarily on the seasonally abundant capelin (*Mallotus villosus*) (Mitchell 1973, Whitehead *et al*. 1980, Whitehead 1981, and Breden 1983).

The main objectives of this study were to: 1) elucidate the types and contrasts in behavior of humpbacks in the two study areas at night; 2) quantify diel changes in behavior and the level of activity in humpbacks in the southern Gulf of Maine; 3) determine how levels of activity and behavior change relative to diel differences in vertical distribution and behavior of prey; and 4) test a newly designed radio telemetry tag and small boat tracking system for large whales.

MATERIALS AND METHODS

Study Areas

Humpback whales were observed in Trinity Bay, Newfoundland in 1981 and 1982 (Figure 1), and in the southern Gulf of Maine (Figure 2) in 1983 and 1984. In the Gulf of Maine, I studied humpbacks within three to 54 km of shore with a 5.2 m Glastron motorboat operated from Provincetown Harbor and from Newburyport, Massachusetts. Most of the whales in the Gulf of Maine were on or in the vicinity of Stellwagen Bank (Figure 2), an area characterized by strong tidal influence, shallow depths (as little as 16 m), high concentrations of American sand lance, and consistent sitings of humpbacks since 1975 (Charles Mayo pers. comm.). The Newfoundland study area had near-shore water depths from 10 m to 400 m. Humpback whales there were easily and consistently found from the cliff-bordered rocky coastline to several kilometers offshore. Newfoundland whales were studied within 12 km of shore from a 25 Hp outboard powered Mark IV Zodiac inflatable.

Radio Tags

I used non-invasive radio tags which attached to the skin by suction cups (remora tag, Goodyear 1981, Figure 3). Each tag contained a two stage telemetry transmitter in the 151 Megahertz (VHF) band, and was purchased commercially from either Wildlife Materials, Inc., or AVM Instruments, Inc. The transmitters were fitted into a plexiglass or aluminum housing which provided protection, water proofing, and flotation. A single rubber suction cup was attached to each housing. Attached to each suction cup was a one-quarter wavelength antenna linked to the tag's transmitter. Each tag weighed approximately 150 gm and was balanced so that upon detachment from a whale (or if the whale was missed in a tagging attempt) the tag floated with antenna pointing vertically, and could be tracked and recovered.

To prepare a tag for deployment, a hollow fiberglass archery arrow was slipped through a retaining ring on the tag body (Figure 3) and forced into the stem hole of the suction cup. The suction cup was then folded back on itself and Dow Corning #111 silicone grease was applied to help seal the suction cup onto the whale's body. The tag-arrow combination was then loaded into a 67 kg pull Barnett crossbow.

Tagging and Tracking

Groups or individual humpback whales were approached for radio tagging, within guidelines of the National Marine Fisheries Service permit number 415. When we were within seven to 12 m of a whale, and as close to perpendicular to the whale's side as possible, a tag was shot. In the Gulf of Maine, shooting took place from a standing position on the forward deck approximately 2.6 m above the water. In Newfoundland, shooting took place from the front of the Zodiac and was approximately 1.8 m above the water. In both areas, more than one approach on a whale was sometimes necessary to achieve proper positioning for deployment. Aim was for as high up on the whale's dorsum as possible to provide the greatest exposure time of the tag when the whale surfaced. This would therefore provide the greatest number of radio signals at each surfacing. Once tagged (Figure 4), a Wildlife Materials Inc., Merlin 12, and an AVM Instruments, Inc., LA12 telemetry receiver were used to receive radio signals; signals were heard as beeps or viewed on the signal strength meter of the receivers.

Gulf of Maine trackings were done by boat only. The boat was equipped with a three element Yagi-Uda antenna mounted to a rotatable aluminum pole. A compass rose attached to the pole allowed the determination of relative bearings to a tagged whale. Antenna height was about four meters above the water. A whale's position relative to our boat was determined by manually panning the antenna back and forth in the general direction of the radio signals until the signal strength peaked. Directional accuracy of $\pm 5^0$ was easily obtained and was generally sufficient since a whale's position was usually verified by sight or sound. With practice, greater directional accuracy was achievable.

Boat positions were determined by combining bearings made on landmarks with a Ritchie hand compass, radio fixes made with an Airguide radio direction finder (RDF), identification of bottom topography using a Lowrance X-15A (192 kHz signal) recording echo sounder, and bearings made with the telemetry receiver system on telemetry transmitters which I had placed on buoys at the beginning of the study. Occasionally, nearby vessels provided us with LORAN numbers to verify our position.

Tagged whale monitoring during the Newfoundland trackings was done mainly from cliffs at elevations 10 to 200 m above sea level (Figure 1). Each cliff station consisted of a home-made null-peak antenna system (Banks et al. 1975) linked to a receiver, a CB radio, a cassette tape recorder, and a tent or the back of a Datsun pickup truck for refuge. Usually only one cliff station was manned at a time, and triangulation bearings from two points were infrequently obtained. Some tracking was conducted from the Zodiac with a hand-held antenna, but this was not usually practical due to high seas.

The occurrence and number of radio signals were spoken into a Panasonic RQ-342D cassette tape recorder in real time, or were recorded directly from the receiver by a Rustrak model 425A analog chart recorder. Radio signal patterns allowed identification of the tagged whale upon surfacing, its position relative to the observation point, and its general type of activity. Signals facilitated close approaches during boat tracking so that the tagged whale and associated whales could usually both be seen and heard even during the night. A tracking distance of 50 to 100 m was usually maintained. Often, close approaches were made: 1) in order to assess the vertical extent of fish and depth of the fish school next to the tagged whale with the echo sounder; 2) for whale sound recordings; 3) to verify the number of whales in the tagged whale group; 4) to identify the individuals associated with the tagged whale; 5) to observe and describe the behavior of the tagged whale and associated whales if it could not be deciphered from afar; 6) and by mistakenly drifting in too close. Close approaches were only used after I was confident that they had no or minimal observable influence on whale behavior.

The number of radio signals received from each tag varied among tagged whales mainly because precise positioning of a tag on a whale was difficult to achieve, and variation in signal reception quality and quantity occurred between whales. All tag signal repetition rates were standardized to 90 pulses per minute by adding up to 1.5 seconds to the time spent at the surface during each whale surfacing. A correction factor was not added to the time spent below the surface during each dive (dive duration). Dive durations lasted up to several minutes; therefore, correction factors were not considered important. Surface durations were determined by the number of radio signals received from tagged whales. Dive durations were calculated as the time between radio signal sequences.

In neither study area was the maximum range of the telemetry system tested. In the Newfoundland area, one whale was monitored to a maximum of about five km from a cliff station before it began heading back toward the shore. Monitoring whales from a boat in the Gulf of

Maine did not include range testing since the purpose was to remain relatively close to the tagged whale and its group. Whales were easily monitored (barring temporary equipment problems) even at the maximum distances they ranged (five km) from the boat.

During trackings in the Gulf of Maine, on an irregular basis, underwater sound recordings of whales were taken by a Y2, Ltd., Yack Yack hydrophone and a Sony TCD5M cassette recorder. Recordings were made to aid me in trying to interpret whale group interaction levels mainly during night feeding periods.

Whale Behavior, Activity Levels, and Group Structure

Observations of whales were coded into seven general behavior categories (Table 1) to facilitate analyses. I interpreted play to include breaching, splashing, tail slapping, tail swishing, tail breaching (tail and peduncle thrust above the water surface), and spy hopping (pitch poling). For example, when small whales breached near mothers while their mothers were quietly resting, I termed it play. The possibility that some of these behaviors served as threat or curiosity cannot be ruled out. Behaviors such as breaching can serve several functions (Whitehead 1985).

Transitory behavior (variable BEH7) included surfacings when a whale produced a normal blow or was engaged in slow travel but no other specific behavior was noted. Transitory behavior occurred when whales changed from an active mode such as lunge feeding to another type of feeding, to a less active mode (such as resting), or merely as a temporary break in a particular behavior, after which that same behavior was resumed.

Behaviors were further categorized into one of three levels of activity (qualitatively determined) from least energetic (ACTLEV1) to most energetic (ACTLEV3, Table 1). For example, resting at the surface (logging) and slow travel (less than 2 kph) were considered low level activities while breaching and fast travel were high level activities.

Whale activity levels (Table 1) were compared by time of day in seven Gulf of Maine trackings and in one Newfoundland tracking. Radio monitoring of whales from cliffs in Newfoundland prevented consistent direct observation of tagged whales, and therefore information on behaviors and activity levels is missing for most of the Newfoundland trackings.

Four group categories were formulated _a posteriori_: single whale, companion group, temporary tight group, and fluctuating extended group. A whale was considered single if it was separated from other whales by at least 100 m and did not exhibit synchrony in surfacing times or other behaviors except during observable feeding events at the surface. In the companion group, "companion" referred to one whale (at times a calf) which stayed with the tagged whale throughout an entire tracking. Temporary tight groups consisted of two or more whales which could be seen together on consecutive surfacings over several minutes or hours, engaged in the same activity with near synchrony. Fluctuating extended group was a very temporary grouping usually lasting about 30 min, which included several sub-groups of the other grouping types. Therefore, fluctuating extended groups developed only when many whale groups (usually three to eight) were in one area at the same time. Note that group types were not mutually exclusive. For example, each temporary tight group and fluctuating extended group could have been made up of several companion groups or single whales. Details of each group type are presented in Results.

Sex determination was made on eight of the nine Gulf of Maine tagged whales. Whales were individually identified from the Gulf of Maine humpback whale catalog (Mayo et al. 1985) which includes a brief history and sex of each whale listed.

Prey Abundance

An estimated 50% of the echo sounder recordings for determination of prey abundance were taken when the observation vessel was within 40 m of the tagged whale. Closer approaches were made to take echo sounder recordings whenever I believed that it was not likely to alter the whale's course of travel or other behaviors. Often, a whale surfaced next to the boat and we drifted or motored over the position where a whale last dove to take recordings. These activities did not appear to disturb the whales.

Prey abundance and water depth were recorded in seven of the Gulf of Maine trackings; no echo sounder data were available for the Newfoundland trackings. Prey abundance was based exclusively on vertical extent of schools of sand lance and included the total thicknesses of up to several separate fish schools seen on one echo sounder trace taken at one time and location. Generally, fish were concentrated as one school at a particular location. However, during crepuscular periods, the time when most sand lance were found to be vertically migrating, several separate schools were often seen. Therefore, when several schools could be discerned, their thicknesses were added together. Because of the difficulty of accurately determining horizontal extent of fish schools, which almost always was several times greater than the vertical extent, vertical extent alone was used as the prey abundance index. This is, therefore, a minimum prey abundance index. Distinction between A. americanus and other species was made by differences in individual fish size, school shape, direct observation of fish in the water, and school behavior. Ground truthing of echo sounder traces was done when fish could be directly observed near the surface and was often conducted with water visibilities up to 10 m looking down from the surface.

Movements of Tagged Whales

To determine movements of each tagged whale which was tracked an entire night, positions were plotted on a chart and lines were drawn to connect them (Figure 5). Precise positions of whales were not consistently achievable due to poor weather or visibility. Consequently, plots do not necessarily depict the precise track of each tagged whale. However, the movements of tagged whales were estimated to be no farther than 100 m from either side of the plotted track lines.

Data Processing

For analysis, some of the radio signal data were digitized directly from the chart recorder tapes with a SAC Graf-Pen sonic digitizer into a Prime mini-computer. All other observations which had been recorded into the cassette recorder were first transcribed onto data sheets and then manually typed into the computer.

Statistical analyses were conducted on the computer using SAS (SAS Institute, Statistical Analysis System) software. Assumptions and details of the specific tests referred to can be addressed by consulting "SAS User's Guides: Basics" (1982) and "SAS User's Guides: Statistics" (1982).

RESULTS

Behavior

Feeding: Daytime and Crepuscular Periods

Great variation in feeding methods occurred among whales and between day and night (Figure 6). Methods of feeding whales during daytime and crepuscular periods were indistinguishable. Feeding activities of Gulf of Maine whales focussed on sand lance. No other humpback whale prey species were seen on the echo sounder, in the mouths of birds diving at the site, observed directly, or reported caught by local commercial fisherman in the study area. Daytime feeding events were usually observable at the surface. However, subsurface feeding also occurred.

Lunge feeding without the use of bubble formations did not occur as often as did a variety of bubble feeding methods. The most common form of surface feeding included bubble cloud, bubble stream, or bubble net production just prior to the feeding lunge (for descriptions of these feeding types, see Hain et al. 1982 and Jurasz and Jurasz 1979).

Whales showed great individuality in how they bubble fed. For example, at the end of a bubble feeding event and just prior to diving, whale 284 consistently raised and then slammed her head with jaws closed, flat against the water before diving. Another whale (non-tagged) lunged through a bubble cloud and then turned on its side while simultaneously arching its flukes sharply forward, creating a splash which sent water and sand lance skyward. Another whale, Catspaw (see Mayo et al. 1985) always broached the surface through a bubble formation or a concentration of fish, in a vertical position, and extended itself nearly high enough to expose the flipper insertions. The whale then sank back into the water while maintaining a vertical attitude, re-surfaced with a high arched back, and then dove.

Some daytime feeding occurred totally below the surface. Evidence for this included: 1) formation of temporary tight groups (when feeding could be observed at the surface these groupings would always form and would break up once feeding stopped); 2) rapid travel by groups of whales back and forth across or within tightly restricted ranges (such as along the edge of Stellwagen Bank where much surface feeding occurs); 3) consecutive surfacings where whales produced emphatic blows (loud and of long duration indicating that the whales were being very active below the surface); 4) periods of surfacing when only one or two blows were made per sequence by each whale (when feeding and many sand lance were observable at the surface, whales produced few blows); and 5) simultaneous echo sounder traces in the areas where the whales last dove which showed concentrations of fish below the surface. Sand lance often stayed several meters below the surface on clear, bright, and calm days.

Daytime feeding methods used by Newfoundland whales were less diverse than those used by Gulf of Maine whales. Newfoundland whales fed primarily on capelin which were abundant until late July. After that, squid were in great abundance and appeared to become the primary prey target; much seasonal overlap occurred between these two prey species. Daily commercial fishing catches made in the study area showed the transition in abundance from capelin to squid. The most prevalent type of feeding was surface lunge feeding in groups of two to five whales. A simple form of bubble feeding was seen but was not common. Newfoundland whales commonly were seen feeding within meters of cliff faces, rocks, beaches, and along fishing nets. While whales progressed closer to these structures, capelin schools could usually be seen which appeared to become trapped and more concentrated.

Feeding: Nighttime

No Gulf of Maine whales were ever seen feeding at the surface at night. Much evidence was revealed, however, that suggested bottom feeding and feeding within the water column were occurring. Three forms of subsurface feeding were thought to have occurred at night. One of them, a form of bottom feeding, was suspected on the trackings of whales 283 and 383 and seemed to last for at least five hours on each of those nights (Figure 6A). The following conditions were observed: 1)temporary tight groups (one of the temporary tight groups included a tagged whale) remained tight together and very synchronous in their surfacings; 2) whale blows were emphatic or were trumpet blows (rapid, squealing sound); 3) these groups traversed or circled many times within restricted areas or along bank edges; 4) dive durations were uniform over long periods; 5) no fish could be seen on the echo sounder where these activities were taking place (sand lance burrow into the substrate at night, especially on dark nights) (Reay 1970, Winslade 1974, Pearson et al. 1984, Tom Meyer pers.comm.); 6) hydrophone recordings indicated that the whales produced few if any vocalizations; 7) no moonlight was seen and it was dark.

The second form of subsurface feeding (Figure 6B) took place several meters below the surface and appeared to be inextricably linked to, and probably the cause of, formations of fluctuating extended groups. Within the fluctuating extended group, the subgroups (companion groups, single whales, and temporary tight groups) dispersed to a radius of approximately two km after a reduction of vocal activity. Whales remained silent for up to 30 min while widely dispersed, then flurries of vocalizations developed again. The many whales making up the fluctuating extended group (spread over the two km radius) then congregated in another area. Vocalizations again subsided and whale dispersion recurred (Figure 6B).

Feeding by fluctuating extended groups was observed on two nights (whales 284 and 384) but I obtained echo sounder data for prey information on only one of the nights. Small, sparse, widely dispersed patches of fish, thought to be sand lance, were detectable at various depths below the surface to 37 m. This contrasts with no fish seen when bottom feeding was suspected (Figure 7). During both nights the skies were very bright with nearly a full moon, seas were calm, up to 25 humpbacks were estimated to be in one observable area, and whale behaviors were similar on the two nights.

The last type of presumed subsurface feeding (Figure 6C) occurred on one night (whale 483) when the following conditions were observed: 1) several independent temporary tight groups were seen traversing or circling within restricted areas for several minutes before moving on; 2) blows among the group members were consistently loud and of long duration, or were trumpet blows; 3) sand lance occurred in dense but widely separated patches (Figure 8) between one m and 37 m below the surface; 4) surfacing and dive arches were emphatic (rapid and with much flex); 5) whales were occasionally seen on the echo sounder within or near patches of fish (Figure 8); 6) whale vocalizations were infrequent; and 7) the sky was bright due to the reflection of Boston area lights off a low lying overcast (no moon was seen).

None of the Newfoundland tagged whales were seen feeding at night. This was perhaps because monitoring of tagged whales at night was limited and occurred only from cliff stations. Surfacings, which were very consistent in duration (determined by the radio signals), and the very limited movements of tagged whales (determined by antenna direction), indicated that they spent much of the time resting at night in protected water near shore. Prior to this study on two nights during bright moonlight, I drove the Zodiac offshore to about two km and observed humpbacks lunge feeding at the surface.

Structure of Whale Groups

Two of the Gulf of Maine tagged whales were males, six were female, and the companion to whale 683 was female (Table 2). Four of the six Gulf of Maine tagged females had calves which remained with them throughout the trackings. In three of the four cow-calf pairs, the calf was rarely seen more than 30 m away from the cow. The calf of whale 284, however, ventured as much as 100 m away and only occasionally was as close as 10 m.

None of the tagged whales was single. However, several non-tagged single whales were seen in the area during all trackings. All 12 trackings included a companion group; every tagged whale had one companion. Ten of the 12 companion groups were usually seen within 20 m of their respective partners and most often surfaced nearly synchronously with them. The calf of whale 284 and the companion to whale 181 appeared more loosely associated with their respective tagged whales. Each non-calf companion (Table 2), i.e., eight of the 12 companions, was of similar size to the tagged whale. Companion group was the only type of grouping which lasted throughout entire trackings. However, some temporary tight groups lasted throughout a night.

Temporary tight groups contained three to eight whales and were seen during the day or night or were maintained during a transition between periods before breaking up. The group of whale 284 was the smallest temporary tight group seen which included in addition to its calf, one very close similar sized associate whale which stayed with the group nearly the entire tracking and separated only after daybreak. In all five full night trackings in the Gulf of Maine (Table 2), temporary tight groups were formed. This occurred within one half to two h after dark, when one to several whales joined the tagged whale group to form a night feeding group (see feeding section for details).

The trackings of whales 283, 383, and 483, showed that these temporary tight groups/feeding groups remained intact until after daybreak. Whales 283 and 383 each maintained a group size of five and whale 483 a group size of four; the numbers of blows per surfacing by each group (which I could hear), and usually direct observations, allowed me to determine the number of whales in each group. Whale 384 was accompanied only by its calf until almost midnight when a third whale joined them and stayed with them until daybreak. Only whale 284 group did not increase in size after dark and in fact, the group lost its non-calf member sometime before daybreak.

Temporary tight groups were also common during the daytime. However, whale 284 group remained intact from day to night. Seven of the Gulf of Maine tagged whales were seen in a temporary tight group configuration for at least part of the daytime. Generally, these groupings were very temporary, usually lasting only a few minutes. As in the night, daytime temporary tight groups were seen almost exclusively during observed or presumed feeding activities. None of the Newfoundland tagged whales formed temporary tight groups, although I observed them in Newfoundland during daytime on occasions other than during trackings of tagged whales.

The fourth group configuration, fluctuating extended group (Figure 6B), occurred when several single whale, companion group, and/or temporary tight groups were seen in one area. Fluctuating extended groups were seen during two trackings (whales 284 and 384) and each lasted over five hours. These groups: 1) produced frequent underwater vocalizations, loud blows and/or trumpet blows (vocalizations were all of short duration and classified as social sounds; see Silber 1984); 2) engaged in the same type of activity; 3) showed detectable synchrony in surfacings over the observation range (sometimes over two km radius at night); 4) were seen converging and diverging several times; and 5) formed as an integral part of subsurface feeding activities. Each convergence-divergence cycle took as long as 30 min. Convergences followed flurries of short duration vocalizations. Divergences followed reduction in vocalization activity.

Movements of Tagged Whales

Plots of tracks of tagged whales in the Gulf of Maine, except for whale 483 (Figure 5), show that whale movements were near, and usually parallel to, shallow bank edges; the 37 m depth contour serves as a depth reference. Track of whale 483 occurred at a greater distance offshore than tracks of the other Gulf of Maine whales, and it was not in the vicinity of any notable bank formation.

Newfoundland tracks all occurred within a few kilometers of shore (Figure 1). Many of the positions of tagged whales during those tracks were within meters of shallow exposed rocky shoals or cliff edges. Water depths were often less than the body length of the tagged whale.

An estimate was made that ranges of tagged whales were within about 100 m on both sides of the plotted track lines (Figures 1 and 5). Determination of a greater number of accurate positions would have allowed determination of range area, which would have been a more useful indicator of extent of whale movements than one dimensional track lines.

Diel Changes in Behavior and Activity Levels

Whale activity levels varied significantly across time (General Linear Models Procedure, SAS ANOV for unbalanced design, degrees of freedom (DF) from 5 to 18, N from 110 to 727, $P<F$ at 0.0001 in all cases). In four of the five Gulf of Maine trackings which included a complete night period (Table 2), Tukey's multiple comparisons test (MCT) showed that differences were mostly between crepuscular (dawn to dusk lumped, 18:00 to 20:00 h and 04:00 to 06:00 h) or daytime and nighttime. In one of the five latter trackings, the MCT indicated no particular patterns in differences in activity levels among periods. In other words, in one of the trackings, differences were not necessarily due to day, crepuscular, or night influences. However, some differences fell within a night, day, or crepuscular period. Six categories of behavior (Table 1; general feeding category was not included in this comparison) varied significantly dielly (SAS FUNCAT procedure, Chi-Square ranged from 56.8 to 318.2, DF from 40 to 72, P from 0.042 to 0.0001). However, it was difficult to identify diel trends.

Frequency distributions of the occurrence of each category of behavior and activity level for each tracking were established and were separated into the three time periods (Figure 9-11). Frequencies of the lumped category of night feeding ranged from 32% to 99% of total observations and represented 60% (N=578) of all night observations (Figure 9A). These percentages exceed those accounted for by combining the frequencies of play and rest.

Nighttime observations of play and rest combined had totals for each tracking which ranged from 0% to only 16%, with an overall combined total of 6.9% (N=67). Percent of observations attributed to rest and play were 2.9% and 4%, respectively. Only five of the 28 observations of rest were obtained between the hours of 21:00 and 04:00; 23 observations were obtained during the hour of 20:00-21:00.

Percent of nighttime observations of transitory behavior was greater than the combined feeding category in only one of the six whale comparisons but represented 34% (N=333) of the total among whales. Transitory behavior does not necessarily indicate departures from feeding activities; after a short feeding break of transitory behavior, feeding may resume (Figure 9A).

Of the total 978 nighttime behavioral observations, only 2.9% (N=28) were assigned to low level activity (range from 0% to 16 % among trackings, Figure 9B). Occurrence of medium level activity ranged from 0% to 64%, but overall 34% (N=333) were assigned to that category. Most observations (N=617, 63%) were assigned to the highest activity level (range 36% to 100%). On only one night (whale 284) was a greater number of observations recorded as medium level activity than high level. Observation distances were sufficiently close so we were confident we were not missing occurrences of the lower level activity behaviors.

Frequencies of behavioral observations made during daytime and crepuscular periods were treated similarly to those for nighttime. The daytime combined feeding category represented the highest percentage of the observations in three of the six trackings (Figure 10A). Overall, combined daytime feeding category was responsible for only 439 observations out of 1302 or 33.7% of the total. Individually, both play and rest represented greater percentages of the total daytime observations than they did during the night, with 3.8% and 8.8%, respectively (N=163). The highest percentage of daytime observations was assigned to transitory behavior with an overall total of 53.8% (N=700).

Daytime activity levels also differed from those at night (Figure 10B). Low level activity represented a higher percentage of the daytime observations but was still only 8.8% (N=114) of the total. Medium level activity was the dominant daytime category (N=700, 53.8%). High level activity was still frequent but occurred only about half as often as it did during the night (N=488, 37.5%).

Last in these frequency comparisons is consideration of observations made during crepuscular periods, Gulf of Maine data only. Overall, total percentages of observations assigned to the combined feeding and transitory categories were nearly equal with 44.1% (N=301) and 47.6% (N=325) respectively (Figure 11A). Most of the observations were assigned to transitory behavior during crepuscular periods. Whales were traveling slowly and sand lance were going through their diel vertical migration, rising toward the surface at dawn and diving to the bottom at dusk.

During crepuscular periods, play and rest occurred least frequently among behaviors (N=38, 5.6%, and N=19, 2.8%). Combined, play and rest occurred 8.4% of the time (N=57) during crepuscular periods.

Occurrences of medium and high levels of activity during crepuscular periods were nearly equal (N=325, 47.6%, and N=339, 49.6%, Figure 11B). Low level activity was infrequent (N=19, 2.8%).

By combining observation data from the three periods, standardized percentage daily totals for the behavior and activity level categories were calculated (Figure 12). Overall, whales fed (45.6%) or were in transitory behavior (45.1%) more often than other behaviors. Play and rest were infrequent and together made up only 9.3% of the observations. Humpbacks were highly active half of the time (50.0%), and conducted low level activity only 5.0% of the time. Medium level activity accounted for 45.0% of their time, which was represented by transitory behavior.

Surface and Dive Durations

Considering all tagged whales, surface durations ranged from one second (seen at least once in all taggings) to 660 seconds (whale 683 while logging (resting at the surface) during the day). The highest mean surface duration for any given hour was 109 seconds (N=17, SE=48.4) by whale 683 (between 11:00 and 12:00 h) which exhibited long durations of logging under flat seas and sunny skies. Short surface durations were most common and were particularly short during rapid traveling and feeding sequences which took place near the surface.

There were significant differences in surface durations between hours in 10 of the 12 taggings (Kruskal Wallace, $P \leq 0.006$ in all cases). However, no temporal trends could be detected. Whale 182 showed significant differences in surface durations by hour only at the

P=0.064 level. In the remaining tracking whale 284, a narrow range of surface durations (2 to 7 seconds) over the course of the 14 hour tracking produced tied values in the comparison.

Dive durations ranged from one second to 462 seconds with the highest and lowest means being 96 seconds (N=31, SE=26.6, whale 483) and 23 seconds (N=74, SE=1.4, whale 283), respectively. Since calculations of dive durations included shallow dives during blow sequences, highest values may seem low. Deep dives of whales after blow sequences were often several minutes long. However, during observation at night, it was sometimes difficult to determine and mark which was the final dive in a sequence. Therefore, calculations of dive durations included all dives, not just the deep dive at the end of a sequence. In 10 of the 12 whale comparisons there were significant differences in dive durations among hours (KW, $P \leq 0.02$ in all cases). As with means of surface durations, trends in differences between means of dive durations were difficult to see (Figure 13).

Significant differences in dive durations with behavior categories were found in only four of the ten whales tested (Kruskal Wallace, $P \leq 0.012$). In five of the 10 whales (nine Gulf of Maine whales and one Newfoundland whale) surface durations varied significantly among behavior categories (Kruskal Wallace, $P \leq 0.003$ in all cases). In two of the above tests, all values were tied.

In four of the 10 comparisons where surface and dive durations were tested against activity level, surface durations varied significantly with activity level (Kruskal Wallace, $P \leq 0.0002$) and two of the 10 had tied values. Dive durations varied significantly with activity level in one of 10 trackings (KW) at the $P \leq 0.024$ level, and nearly so on two others at P=0.057 and P=0.072. Trends in where these differences were present were not clear.

Changes in Whale Behavior and Activity Level Related to Diel Changes in Abundance, Distribution, and Behavior of Prey

Prey Distribution and Behavior

Prey abundance (added vertical thicknesses of sand lance schools seen on the sonar) ranged from 0 to 30.5 m with hourly means from 0 to 18.3 m. Crepuscular periods provided consistently high hourly mean fish school sizes with the dawn period means generally greater than those at dusk. However, highest hourly means occurred at the end of the night period when I could first detect sunlight (up to 04:00 h). The highest hourly mean prey abundance of 18.3 m (whale 283) was seen just before 04:00 h when sand lance began their rapid upward migration.

Nighttime fish school sizes were generally small (Figure 14). On only one night was a high abundance of sand lance detected by the sonar in the water column, and verified by sight from the surface. Those observations were during the tracking of whale 483 in the Thatcher Island area (Figure 2), when Boston area lights reflected off a low lying cloud layer producing unusually bright light conditions at sea (Figure 6C). I estimated that the sand lance were about 10 cm apart, spread over at least a seven meter diameter horizontal surface area, and extended from the surface down for several meters. The only other night trackings within which notable yet generally lower abundances of sand lance were seen on the sonar were those of whales 283 and 284 on

Stellwagen Bank. During the latter tracking, the bright moon conditions were such that whales could be visually observed from distances as far as one km. Light and sea conditions, and whale behaviors seen during the track of whale 384 were the same as those during the whale 284 tracking, but no fish data were recorded (due to a broken sonar).

Eight of the nine Gulf of Maine trackings occurred in the Stellwagen Bank area (Figure 2). Water depth on the bank ranged from 16.8 m to 33.0 m while the outlying areas ranged from 40.2 to 86.0 m. Eighteen to 30 km north of the northern tip of Stellwagen Bank where whale 483 tracking occurred (Figure 2), depth ranged from 33.0 to 134.0 m. Mean depths, calculated by hour for each whale range, varied from 22.3 to 100 m. Also, mean depths over the each entire tracking were calculated. Of the six Gulf of Maine tagged whales on which water depth data were recorded, the range of mean depths was was 17.2 m (whale 282) to 52.2 m (whale 384).

Changes in Whale Behavior and Activity Levels

Of the seven trackings in which fish data existed, a significant difference in surface duration in relation to fish school size was seen in only whale 583 (Kruskal Wallace, DF=3, Chi-Square, $P<0.009$). Dive duration also varied significantly with fish school size in only one tracking, whale 284 (Kruskal Wallace, DF=8, Chi-Square, $P<0.001$). Level of activity of tagged whales varied significantly with fish school size in three of the seven trackings at $P\leq0.018$ (SAS FUNCAT Procedure).

Radio Tags, Tagging, and Tracking

Responses by humpback whales to deployment and deployment attempts of remora tags were usually minimal and no long term changes in behaviors were seen. In 49 tagging attempts in the Gulf of Maine (tagging attempt was either a missed shot or the tag did not attach) immediate responses by the whales ranged from no reaction (69%) to a detectable reaction (31%). Detectable reactions included quickened dive, high back arch, tail swish, or breaching. Only one breach was seen in over 100 tagging attempts (both study areas included) which was by a very active calf. Within five minutes of that calf breach, it and its mother approached the boat, I tagged the mother, and the two whales stayed alongside for several minutes. In all of the tagging attempts, approached individuals and their associated whales either resumed behaviors engaged in prior to the tagging attempt, became curious and approached the tagging vessel, or were easily approachable within five minutes after the tagging attempt.

Radio tags stayed on whales from less than five hours to nearly 80 hours (Table 2). In the Gulf of Maine, tags remained attached for generally shorter duration than they did on Newfoundland whales with a maximum of 20 hours. A total monitoring time of 186 hours was conducted in the Gulf of Maine (Table 2). Approximately 600 hours were spent searching for whales, and recording data before, during, and after radio monitoring.

The suction cup attachment technique does not appear to harm the whale's skin. On several whales which lost a tag, the shiny spot caused by the silicone grease used to help seal the suction cup could easily be seen. The skin there appeared normal.

The monitoring of tagged whales, even from close distances, did not appear to alter their behavior or the behavior of their associated whales. During feeding activities, for example, whales often swam below the boat en-route to making a feeding lunge or bubble cloud. On several occasions it was necessary for us to immediately relocate because we became surrounded by the bubble net of a humpback.

DISCUSSION

General Behavior

Humpback whales in the lower Gulf of Maine spent more time feeding, both day and night, than in any other general activity. Furthermore, nearly twice as much time was spent feeding at night than during the day. This extent of night feeding activity was particularly surprising. Observations by Baker et al. (1983) and Watkins et al. (1981) on radio tagged Alaskan humpback whales and Jurasz and Jurasz (1979) on non-tagged humpbacks in Alaska, indicated that those whales were relatively quiescent at night. William Dolphin (pers. comm.) thought that some feeding occurred in Alaskan waters at night, particularly under bright moonlight. Nighttime observations of humpbacks in Newfoundland--radio tagged and non-radio tagged-- are consistent with those of Alaskan humpbacks; humpbacks were generally quiescent at night. The level of night activity by those Alaskan and Newfoundland whales appeared to be dependent on the ambient brightness. Whitehead (1981) believed that some feeding occurred by humpbacks in Newfoundland during moonlit nights.

Non-feeding activities of Gulf of Maine humpbacks occurred much less frequently than feeding activities. However, transitory behavior represented a major portion of humpback's diel time budget. Much transitory behavior occurred between feeding bouts and likely represented a time when whales allowed prey within patches to regroup as observed for Newfoundland humpbacks (Whitehead 1981) and when humpbacks could regain energy and complete ingestion of food previously captured. Therefore, transitory behavior often related to feeding behavior. Considering all behaviors, humpbacks were highly active most of the time.

Little time was spent by humpbacks in rest or play behavior. Surprisingly, these behaviors were not common at night. There are two possible ways to account for this. If the whales sensed decreases in the abundance or changes in distribution of sand lance, they may have increased their total daily feeding time to achieve at least a minimum food intake threshold. A second possibility is due to intensive whalewatching and the high level of boat traffic in the area which may also affect the daytime foraging efficiency of humpbacks.

Boats approach and often temporarily displace whales from feeding for variable lengths of time. Night feeding might therefore be the way that southern Gulf of Maine humpbacks compensate for loss of feeding time during some other period of the day. If this is so, it might be assumed that these Gulf of Maine humpbacks were forced to revert to less efficient feeding modes (such as when light was low) in order to maximize food intake.

If either of the above reasons for the occurrence of night feeding is true, then one might predict that humpbacks in the southern Gulf of Maine would change their distribution in subsequent seasons to improve their chances of meeting food requirements. Although in the summer of 1985, the year following this study, humpbacks were plentiful in the study area, they were very scarce in 1986 and 1987 (Mayo et al. 1987, pers. obs.). A paucity of sand lance was also observed there in those years (Mayo et al. 1987, pers.obs.). In 1988, both sand lance and humpbacks were very abundant in the study area (C. Mayo pers.comm., pers. obs.). Therefore, it appears that sand lance distribution and abundance influences the distribution and seasonal abundance of humpbacks in the Gulf of Maine. The sensory and behavioral mechanisms by which humpbacks detect and respond to changes in their prey status are still in question.

Night Feeding

The duration of night activity, primarily feeding, by Gulf of Maine humpbacks did not seem to be dependent on the level of available light, although patterns of feeding and whale groupings did (qualitatively determined). Three patterns of night feeding and two specific group configurations by Gulf of Maine humpbacks are hypothesized: bottom feeding in temporary tight groups (Figure 6A); feeding in fluctuating extended groups on sparsely distributed, sparse patches of sand lance (Figure 6B); and feeding in temporary tight groups on sparsely distributed, dense patches of sand lance (Figure 6C). The latter two occurred under moonlight or artificial light. These feeding patterns and group configurations appeared to be related to the behavior and response to light levels of their main prey, American sand lance. Sand lance are highly responsive to light and usually burrow into the substrate at low light levels (Reay 1970, Winslade 1974, Pearson et al. 1984, Tom Meyer pers. comm.). Intuitively, therefore, it would seem that when it is dark, sand lance would become more difficult for foraging whales to locate.

However, it appears likely that humpbacks are able to bottom feed on sand lance, which might proceed in two ways. SCUBA divers at night on Stellwagen Bank observed that sand lance suddenly left the substrate and concentrated just above the sea bottom when the divers swam above it (Meyer et al. 1979) or when the sea bottom was illuminated by flashlights (Tom Meyer pers. comm.). One or several humpbacks cruising just above the bottom would create bow wave effects (water disturbances) greater than those produced by a few human divers and therefore should elicit the escape response by sand lance (Figure 6A). Bottom cruising humpbacks should be able to detect escaping sand lance either by bioluminescence created by water disturbance or possibly by hearing low frequency sounds produced by the sand lance when they quickly depart the substrate (H. Winn pers. comm.) to form dense schools. An even greater water disturbance effect would be produced when several whales worked synchronously together. Therefore, a stronger stimulus for eliciting substrate escape response by sand lance would result. Group coordination by humpbacks during feeding under these circumstances (in other words, when sand lance are buried in the substrate during low light conditions) would therefore be likely. In support of this, under these conditions, whales behaved synchronously and were conducting activities as temporary tight groups.

Another possible way for humpbacks to bottom feed is by lightly plowing through the substrate with one side of their mouths, capturing sand lance before they can escape. John Oliver (pers. comm.) suggested that instead of lightly plowing through the substrate for prey, the whales more likely "blow and suck" as he has found gray whales to do when bottom feeding. Many humpbacks observed in the study area have had some of the skin abraided off the top surface of one side of the lower jaw (C. Mayo pers. comm., pers. obs.). Also, a substantial but unmeasured volume of sandy gravel and sand lance was observed in the stomach of one humpback whale which stranded and died in Nova Scotia (J. Conologue pers. comm.). It is likely that some substrate material becomes ingested in the bottom feeding process and temporarily resides in the stomach. Gray whales (Nerini and Oliver 1983; Oliver et al. 1984) and bowhead whales (Wursig et al. 1983) have also been shown to bottom feed by disturbing the substrate in some fashion.

There are some advantages of bottom feeding on sand lance. Sand lance distributed in a two dimensional plane shallowly buried in the substrate, instead of as sparsely distributed three dimensional balls within the water column, would be more easily found in the dark. Three dimensional concentrated volumes of fish from within the water column redistributed as a two dimensional plane in the surface substrate layer would cover a greater area; this would occur as a result of their diel vertical migration. Therefore, the location of the prey should be more predictable. This type of feeding by any balaenopterid has not been reported elsewhere and therefore it may be specific to feeding on sand lance. No other prey species of balaenopterids have been reported to burrow and temporarily reside in the surface layers of the substrate.

Bottom feeding may have other advantages for humpbacks since it is thought that mysticetes, including humpbacks, rely heavily on vision (Jansen and Jansen 1969, Madsen and Herman 1980) and probably lack food finding sonar (Beamish 1978); Eberhardt and Evans (1962) came to a similar conclusion for gray whales. Bottom feeding humpbacks might merely have to detect where the bottom is in order to locate prey in areas generally productive for prey. Reduced visual navigation efficiency during darkness would seem to make foraging for water column dwelling prey impractical at night. This theory depends on the ability of humpbacks to be able to determine when they are just at the bottom; this may be considered a major assumption (K. Norris pers. comm.). It is likely that the back-pressure wave or ground effect created as whales cruise the bottom would be detectable to them, and therefore allow them to maintain their relative positions above the substrate. Humpbacks may also be able to determine the precise bottom location tactilely with a pectoral fin (K. Norris pers. comm.).

Two other types of night feeding by Gulf of Maine humpbacks which I thought occurred also appeared to be linked to sand lance behavior and the level of light. Subsurface feeding by whales as fluctuating extended groups, occurred during a nearly full moon. Presumed feeding within the water column in the form of temporary tight groups occurred under conditions of artificial light caused by the Boston vicinity skyline. Few data were used to formulate these feeding types. However, wide ranges in the distribution and abundance of sand lance, were clearly observable on the sonar or directly.

The apparent influence of intense Boston area sky light (qualitatively determined) on sand lance and humpback behavior was not expected. The greatest concentrations of sand lance within the water column at night and the only occurrence of them observable at the surface at night, took place under the glow of artificial light from the Boston skyline; there was no moonlight seen. Sand lance exhibit the unusual behavior of burrowing into the substrate when it's dark and rise up into the water column on introduction of light (Winslade 1974). It is not assumed here, and is physically unlikely, that the artificial light of the Boston skyline was penetrating to the ocean bottom and eliciting upward vertical migration of sand lance. However, what does seem possible is that in areas when and where high levels of artificial light overlap and follow daylight as nighttime approaches, sand lance within the water column may not experience darkness. Sand lance might stay high up in the water column as if "fooled" by the abnormally bright conditions. Further documentation of similar responses of sand lance to what might be termed light pollution may indicate the potential for a significant effect on sand lance and species which prey on them.

The occurrence of vocalizations by humpbacks appeared to vary widely with nighttime light levels, prey distributions and abundance, and humpback feeding patterns. Humpbacks were most vocal when prey were widely dispersed in sparse schools and when fluctuating extended groups formed. Vocalizations were nearly absent when sand lance were in the substrate and bottom feeding by whales was suspected.

Presumably, the nighttime vocalizations communicate basic information about locations of feeding conspecific individuals or groups and the general location and size of prey patches, especially when they are sparsely distributed in the water column. Whales contributing useful information to others might in the future benefit by becoming more readily accepted into the feeding groups of those initial recipients. This system, if real, has characteristics of reciprocal altruism as defined by Trivers (1971). Contributors or reciprocators (vocalizers of prey and feeding information) would in turn increase their own potential and the potential of others to locate prey in the water column at night. In order for this system to have evolved, mechanisms would have to have developed which guarded against cheating or at least made the long term benefits of reciprocating outweigh the short term benefits of cheating (Trivers 1971, and Connors and Norris 1982). Humpbacks taking advantage of the broadcasted prey information, but ones whom remain quiet when they locate prey (cheaters) might be recognized by vocalizers. They might not enjoy the same degree of acceptance into feeding groups awarded to true reciprocal altruists. Without this basic communication exchange, humpbacks might not succeed in locating any prey within the water column when sand lance are distributed there at night. It is possible that Gulf of Maine humpbacks which feed during the night under what appear to be poor prey conditions may in fact feed effectively by incorporating a system of reciprocal altruism. Additional support for this hypothesis is that during the daytime when sand lance were in huge dense concentrations at or near the surface (Figure 15) and presumably easily located, humpbacks rarely vocalized. Experiments to test for the presence of reciprocal altruism in humpbacks in the Gulf of Maine and how the necessary communications are made could provide significant insight into how North Atlantic humpback whales satisfy their annual food requirements under the ever-changing prey conditions there.

Further observation and quantification of light levels and prey distribution might reveal a gradient between the extremes of feeding types observed in this study. These types of feeding are likely only examples of a more extensive foraging repertoire of which humpbacks are capable. Just as humpbacks utilize a great variety of prey types (Matthews 1937, Nemoto 1959 and 1970, Mitchell 1973, and Jurasz and Jurasz 1979) they also have several ways of reaching their goal of feeding.

Radio Telemetry

Humpback whales were easily approached and radio tagged from a small boat. The remora-suction attached-radio tags allowed tagged individuals to be monitored for up to several days (Table 2). Tag attachment duration was somewhat variable within each study area (southern Gulf of Maine and Newfoundland) but more so between areas. Tags and tagging attempts did not appear to change whale behavior for more than one or two minutes.

Most attachments of radio tags on Gulf of Maine whales were of shorter duration than on Newfoundland whales. Surface waters in the Gulf of Maine were typically about two to five degrees C warmer than Newfoundland waters. It is possible that the temperature differences affected skin sloughing rates or the development of an algae or diatom layer on the skin of the whales. These factors could possibly limit maximum duration of suction, and therefore attachment duration of remora tags.

Because the boat was small (5.2 m), quiet, and could quickly be relocated, it was relatively easy to keep track of tagged whales and their associates both by radio and visually. Even at night, once observers' eyes adjusted to the low light levels, the number of whales associated with the tagged whale and their general behaviors could easily be seen and assessed. On occasion at night, it was possible to identify individual humpbacks by markings or fluke patterns (Katona et al. 1980). Boat approaches to pass over whales to obtain sonar traces of whales and fish may have occasionally and temporarily altered their sub-surface course. However, whales appeared to continue with their present behavior.

The manually rotatable Yagi-Uda antenna system was inexpensive, simple to use, and sufficiently accurate to allow me to determine a whale's position rapidly. An automatic direction finding (ADF) system might have made direction finding of a surfacing tagged whale slightly more rapid (Bruce Mate pers. comm.). However, ADF systems which were available were expensive and would not have provided adequate signal transmission range with the low antenna heights typically achievable from the small boat. Also, transmitter life (given the small battery size used in the remora tags) would be reduced in order to make transmission signals compatible with an ADF system, due to signal pulse-width requirements.

LITERATURE CITED

Baker, C.S., L.M. Herman, B.G. Bays, and G.B. Bauer. 1983. The impact of vessel traffic on the behavior of humpback whales in Southeast Alaska: 1982 season. Report to National Marine Fisheries Service, National Marine Mammal Lab, Seattle, WA., May 17, 1983. 30 pp.

Banks, E.M., R.J. Brooks, and J. Schnell. 1975. A radio tracking study of home range and activity of the brown lemming (Lemmus trimucronatus). J. Mamm. 56:888-901.

Beamish, P. 1978. Evidence that a captive humpback whale (Megaptera novaeangliae) does not use sonar. Deep-Sea Res. 25(5):469-472.

Breden, K. 1983. Foraging ecology of humpback whales off Newfoundland. In: Abstracts of the Fifth Biennial Conference on the Biology of Marine Mammals, Boston, MA. p 12.

Connor, R.C., and K.S. Norris. 1982. Are dolphins reciprocal altruists? Am. Nat. 119(3):358-374.

Eberhardt, R.T., and W.E. Evans. 1962. Sound activity of the California gray whale Eschrictius glaucus. J. of the Audio Eng. Soc. 10:324-328.

Goodyear, J. 1981. Remora tag effects the first tracking of an Atlantic humpback. In: Abstracts of the Fourth Biennial Conference on the Biology of Marine Mammals, San Francisco, CA. p 46.

Hain, J.H.W., G.R. Carter, S.D. Kraus, C.A. Mayo, and H.E. Winn. 1982. Feeding behavior of the humpback whale, Megaptera novaeangliae, in the western North Atlantic. Fish. Bull. 80(2):259-268.

Jansen, J. and J.K.S. Jansen. 1969. The nervous system of Cetacea. In: "The Biology of Marine Mammals", H.T. Anderson, editor, Academic Press, New York. pp. 175-252.

Jurasz, C.M., and V.P. Jurasz. 1979. Feeding modes of the humpback whale, Megaptera novaeangliae, in southeast Alaska. Sci. Rep. Whales Res. Inst. (31):69-83.

Katona, S.K. 1976. Whales in the Gulf of Maine: 1975 Report of the Gulf of Maine Whale Sighting Network, College of the Atlantic, Bar Harbor, Maine 04609. 45 pp.

Katona, S.K., P. Harcourt, J.S. Perkins, and S.D. Kraus. 1980. Humpback whales: a catalogue of individuals identified by fluke photographs. Second Edition, July 1980. College of the Atlantic, Bar Harbor, Maine 04609. 169 pp.

Kenney, R.D. 1984. Distributional biology of the cetacean fauna of the northeastern United States continental shelf. Ph.D. dissertation, Univ. of Rhode Island, Kingston, R.I. 158 pp.

Leatherwood, S., and W.E. Evans. 1979. Some recent uses and potentials of radiotelemetry in field studies of cetaceans. In: "Behavior of Marine Animals, Vol. 3", H.E. Winn, and B.L. Olla editors. Chap. 1. Plenum Publishing Corp. pp. 1-31.

Lein, J. 1980. Whale entrapment in inshore fishing gear in Newfoundland, Final Report to Canadian Government.

Madsen, C.J., and L.M. Herman. 1980. Social and ecological correlates of cetacean vision and visual appearance. In: "Cetacean Behavior: Mechanisms and Functions", L. M. Herman, editor, John Wiley and sons, N.Y. pp. 101-147.

Matthews, L.H. 1937. The humpback whale, Megaptera nodosa. Disc. Rept. 17(7):7-92.

Mayo, C., C. Carlson, P. Clapham, and D. Mattila. 1985. Humpback whales of the southern Gulf of Maine. Shankpainter Press, Provincetown, MA. 59 pp.

Mayo, C.A., D.K. Mattila, S. Pittman, and L. Baraff. 1987. Abundance distribution, and habitat use of large whales in the southern Gulf of Maine: May 1-September 30, 1986. Center for Coastal Studies, Provincetown, MA, Report to National Marine Fisheries Service, Northeast Fisheries Center, Woods Hole, MA. 34 pp.

Meyer, T.L., R.A. Cooper, and R.W. Langton. 1979. Relative abundance, behavior, and food habits of the American sand lance, Ammodytes americanus, from the Gulf of Maine. Fish. Bull. 77(1):243-253.

Mitchell, E. 1973. Draft report on humpback whales taken under special scientific permit by eastern Canadian land stations, 1969-1971 to the International Commission on Whaling, June, 1972. pp. 138-154.

Nemoto, T. 1959. Food of baleen whales with special reference to whale movements. Scient. Rep. Whales Res. Inst., Tokyo, (16):89-103.

Nemoto, T. 1970. Feeding pattern of baleen whales in the ocean. In: "Marine Food Chains", J.H. Steel, editor, Univ. Calif. Press, Berkeley, and L.A. pp. 241-252.

Nerini, M.K., and J.S. Oliver. 1983. Gray whales and the structure of the Bering Sea benthos. Oecologia. 59:224-225.

Oliver, J.S., P.N. Slattery, M.A. Silberstein, and E.F. O'Connor. 1984. Gray whale feeding on dense ampeliscid amphipod communities near Bamfield, British Columbia. Can. J. Zool. 62(1):41-49.

Overholtz, W.J., and J.R. Nicolas. 1979. Apparent feeding by the fin whale, Balaenoptera physalus, and humpback whale, Megaptera novaeangliae, on the American sand lance, Ammodytes americanus, in the Northwest Atlantic. Fish. Bull. 77(1):285-287.

Pearson, W.H., D.L. Woodruff, P.C. Sugarman, and B.L. Olla. 1984. The burrowing behavior of sand lance, Ammodytes hexapterus: effects of oil-contaminated sediment. Mar. Envir. Res. 11:17-32.

Reay, P.J. 1970. Synopsis of biological data on North Atlantic sand-eels of the genus Ammodytes: A. tobianus, A. dubius, A. americanus, and A. marinus. Fishery Synopsis F.A.O. 82:42 pp.

SAS Institute Inc. 1982. SAS User's Guide: Basics. SAS Institute Inc., Cary, N. Carolina. 923 pp.

SAS Institute Inc. 1982. SAS User's Giude: Statistics. SAS Institute Inc., Cary, N. Carolina. 584 pp.

Schevill, W.E., and R.H. Backus. 1960. Daily patrol of a megaptera. J. Mamm. 41(2):279-281.

Silber, G.K. 1984. Non-song phonations and associated surface behavior of the Hawaiian humpback whale (Megaptera novaeangliae). M.A. Thesis, San Jose State University, San Jose, CA.

Trivers, R.L. 1971. The evolution of reciprocal altruism. Q. Rev. Biol. 46:35-57.

Watkins, W.A., K.E. Moore, D. Wartzok, and J.H. Johnson. 1981. Radio tracking of finback (Balaenoptera physalus) and humpback (Megaptera novaeangliae) whales in Prince William Sound, Alaska. Deep-Sea Research. 28A(6):589-599.

Whitehead, H. 1985. Why whales leap. Sci. Am. 252(3):84-89.

Whitehead, H.P. 1981. The behavior and ecology of the humpback whale in the Northwest Atlantic. Ph.D. Dissertation, Christ College, Cambridge, England, June, 1981. 180 pp.

Whitehead, H.P., P. Harcourt, K. Ingham, and H. Clark. 1980. The migration of humpback whales past the Bay-de-Verde Peninsula, Newfoundland, during June and July, 1978. Can. J. Zool. 58(5):687-692.

Winslade, P. 1974. Behavioral studies on the lesser sandeel *Ammodytes marinus* (Raitt): II. The effect of light intensity on activity. J. Fish. Biol. 6(5):577-586.

Würsig, B., E.M. Dorsey, M.A. Fraker, R.S. Payne, W.J. Richardson, and R.S. Wells. 1984. Behavior of bowhead whales, *Balaena mysticetus*, summering in the Beaufort Sea: surfacing, respiration, and dive characteristics. Can. J. Zool. 62(10):1910-1921.

Table 1. Seven categories of behavior (variable BEH) and three categories of activity level (variable ACTLEV) were established. Note, BEH 1 represents all feeding categories combined.

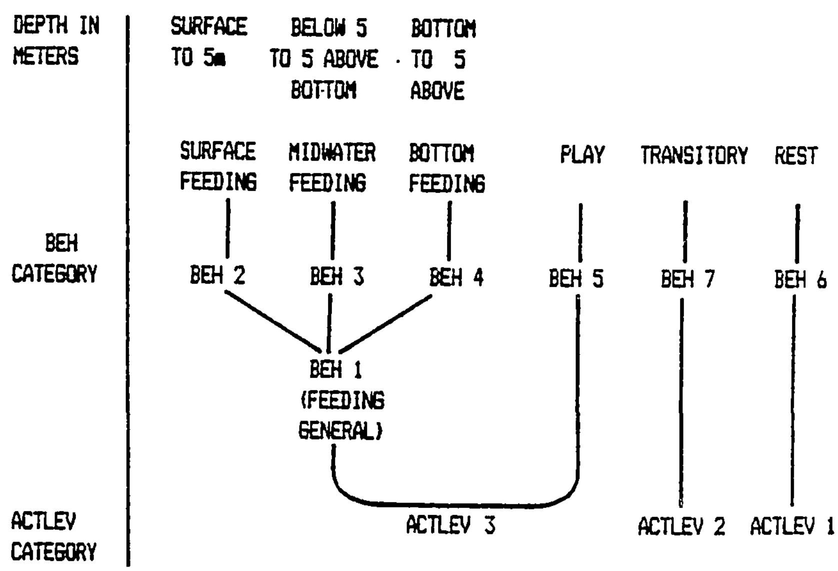


Table 2. Descriptions of tagged whales and trackings from Newfoundland and the Gulf of Maine. Names of Gulf of Maine whales are from Mayo et al. (1985). Asterisks identify whales on which monitoring stopped but the tag remained attached.

WHALE #	WHALE NAME	SEX	LENGTH IN METERS	CALF YES/NO	NON-CALF COMPANION Y/N	COMPANION SIZE IN METERS	LOCATION OF TAGGING	BEGINNING TIME AND DATE	ENDING TIME AND DATE	HOURS OF MONITORING
181	BEEPER	?	9.8	N	Y	10.8	NORTHERN COVE NFLD.	07:11 7/29/81	13:24 8/01/81	78.2*
182	BARSTOW	?	13	N	Y	12.7	OFF CATALINA NFLD.	17:45 7/23/82	23:13 7/23/82	5.5*
282	T'TIA	?	12.5	N	Y	13.3	OFF CATALINA NFLD.	11:33 7/26/82	05:41 7/27/82	18.1*
183	SINESTRA	F	14	Y	N	8.5	OFF GLOUCESTER MA.	11:07 6/13/83	17:36 6/13/83	6.5*
283	SCYTHE	M	10.7	N	Y	10.5	STELLWAGEN BANK	18:54 7/17/83	07:20 7/18/83	12.4
383	OLYMPIA	F	15	Y	N	8.5	STELLWAGEN BANK	18:46 7/19/83	05:20 7/20/83	10.6
483	ROPE	M	12.8	N	Y	13	OFF THATCHER ISL. MA.	12:54 8/10/83	08:58 8/11/83	20
583	COMET	M	12.7	N	Y	12.9	STELLWAGEN BANK	19:27 8/16/83	21:55 8/16/83	2.3*
683	APPALOOSA	F	10.7	N	Y	10.9	STELLWAGEN BANK	11:20 8/21/83	16:02 8/21/83	4.7*
184	SILVER	F	15.3	N	Y	15	STELLWAGEN BANK	14:17 7/02/84	19:13 7/02/84	4.9
284	JANUS	F	14.7	Y	N	?	STELLWAGEN BANK	18:56 7/10/84	07:43 7/11/84	12.8
384	MARS	F	14.4	Y	N	?	STELLWAGEN BANK	19:32 7/12/84	05:24 7/13/84	9.9

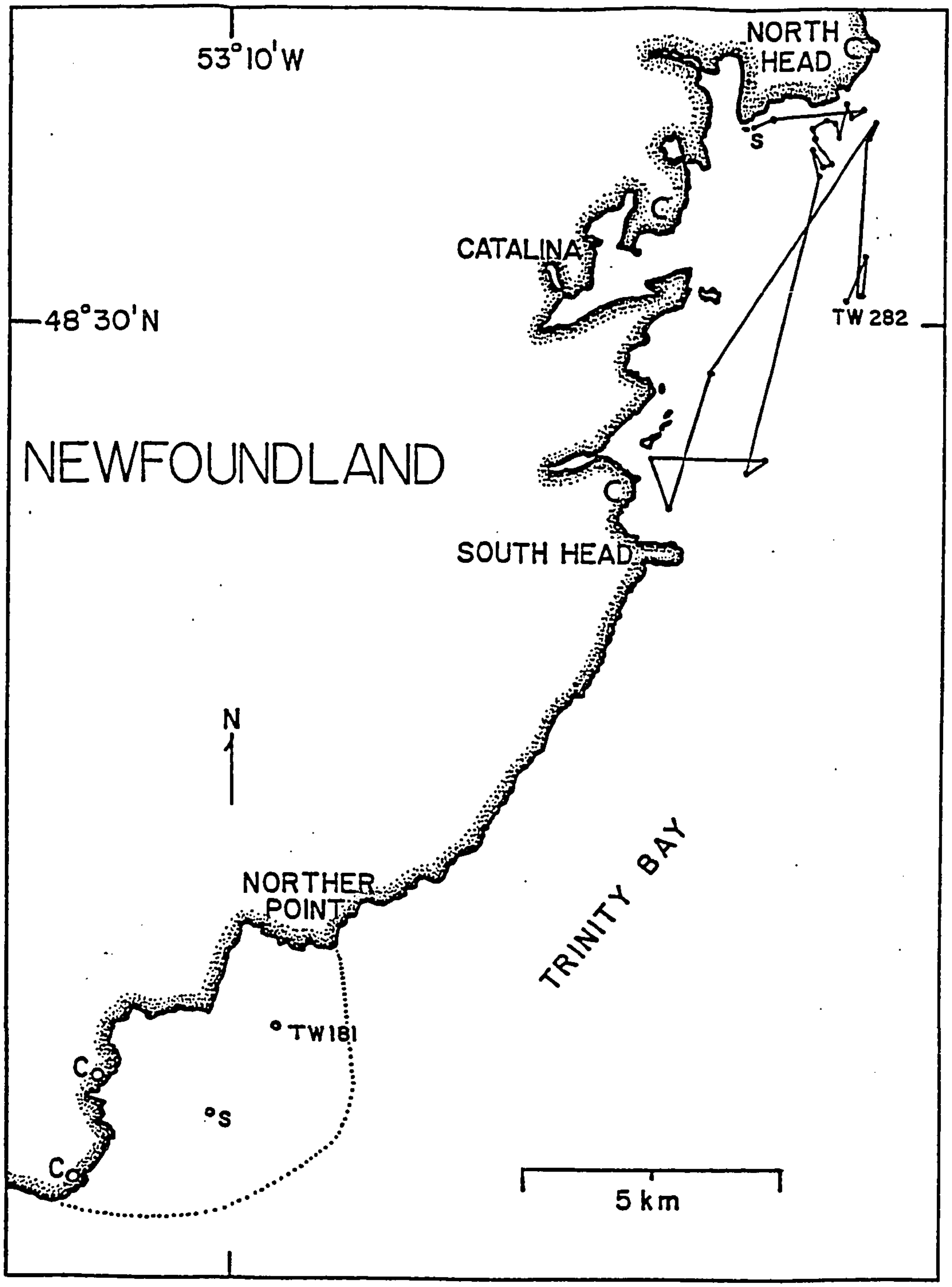


Figure 1. Newfoundland study area. Sites of tagging (TW) and end of tracking (S) of each tagged humpback are marked; "C" marks locations of cliff monitoring stations (see also Table 2).

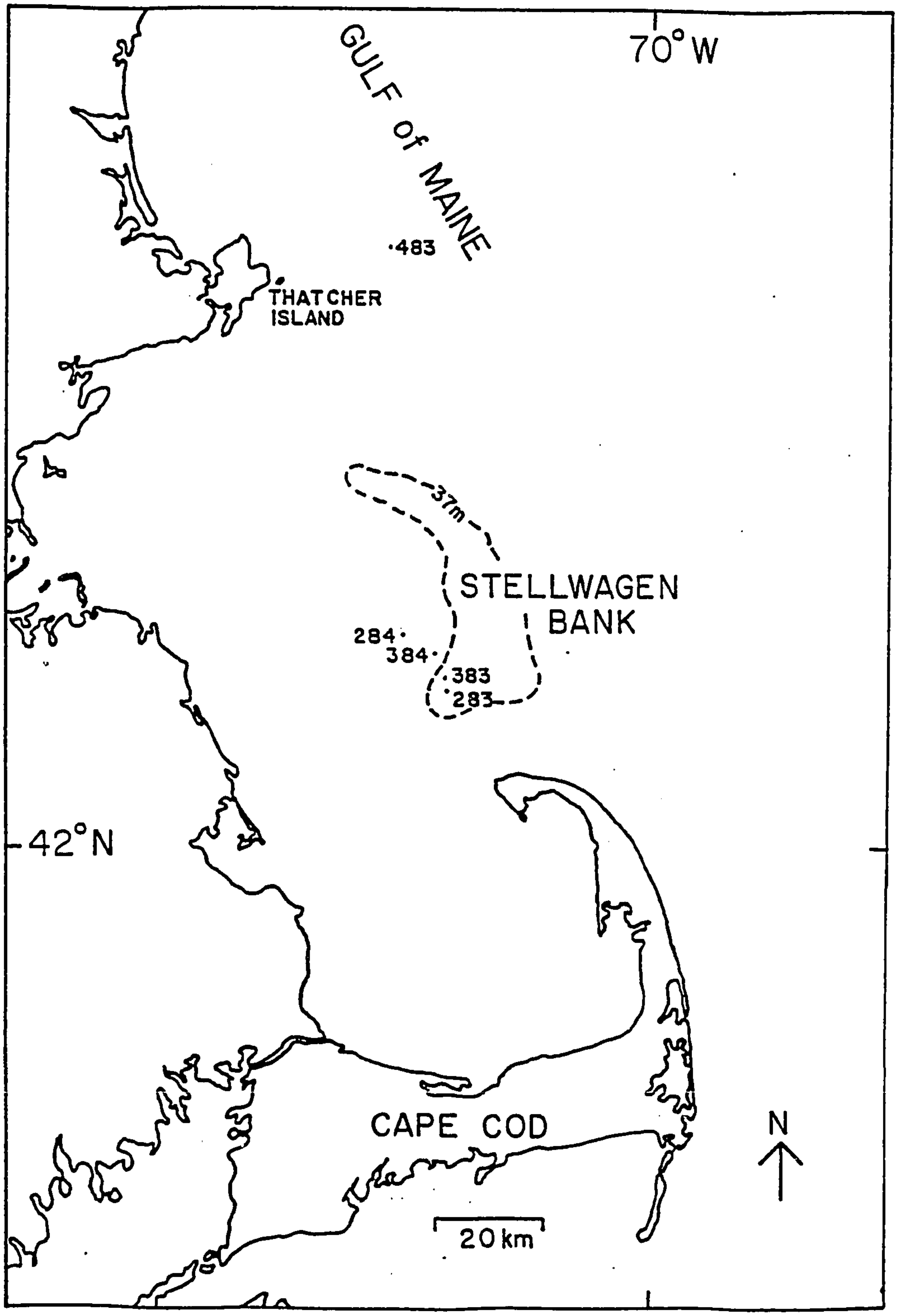


Figure 2. Lower Gulf of Maine study area. Tagged humpbacks were numbered (see Table 2). Tagging site for each humpback is marked.

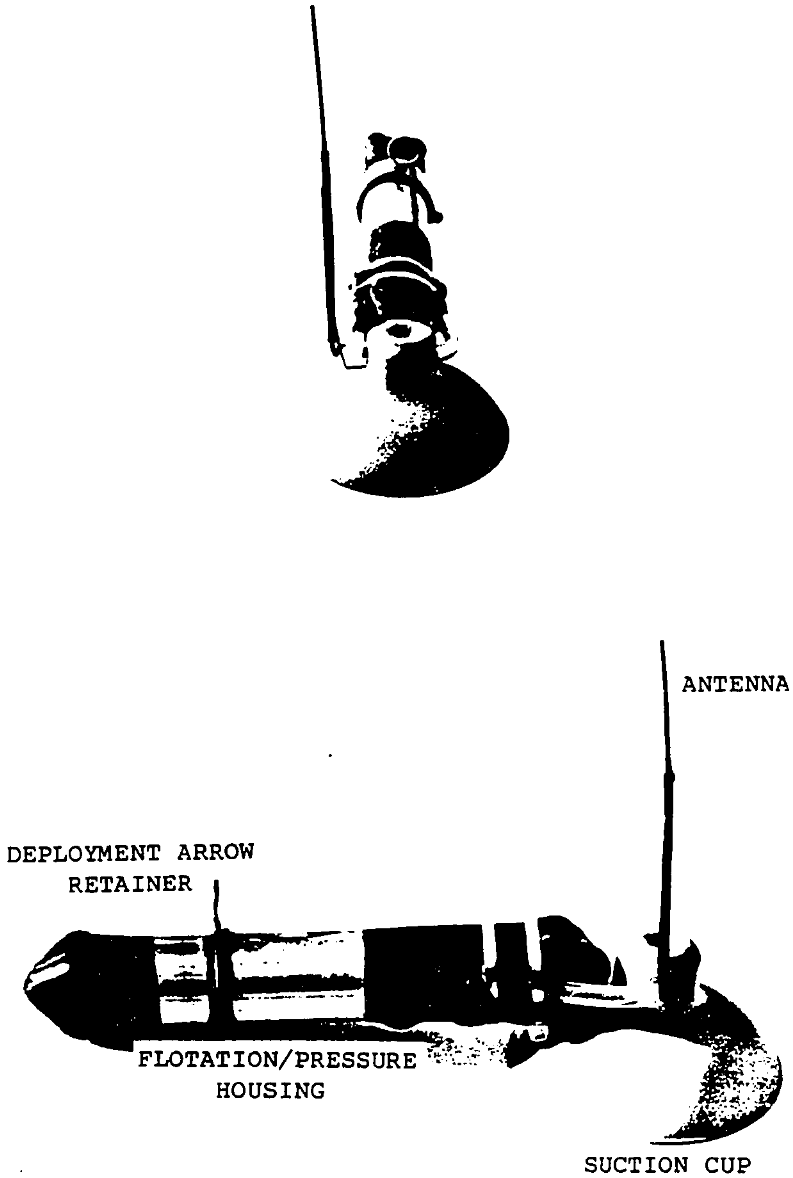


Figure 3. Remora suction attached radio tag. Parts are labelled.
Housing length is 14 cm.

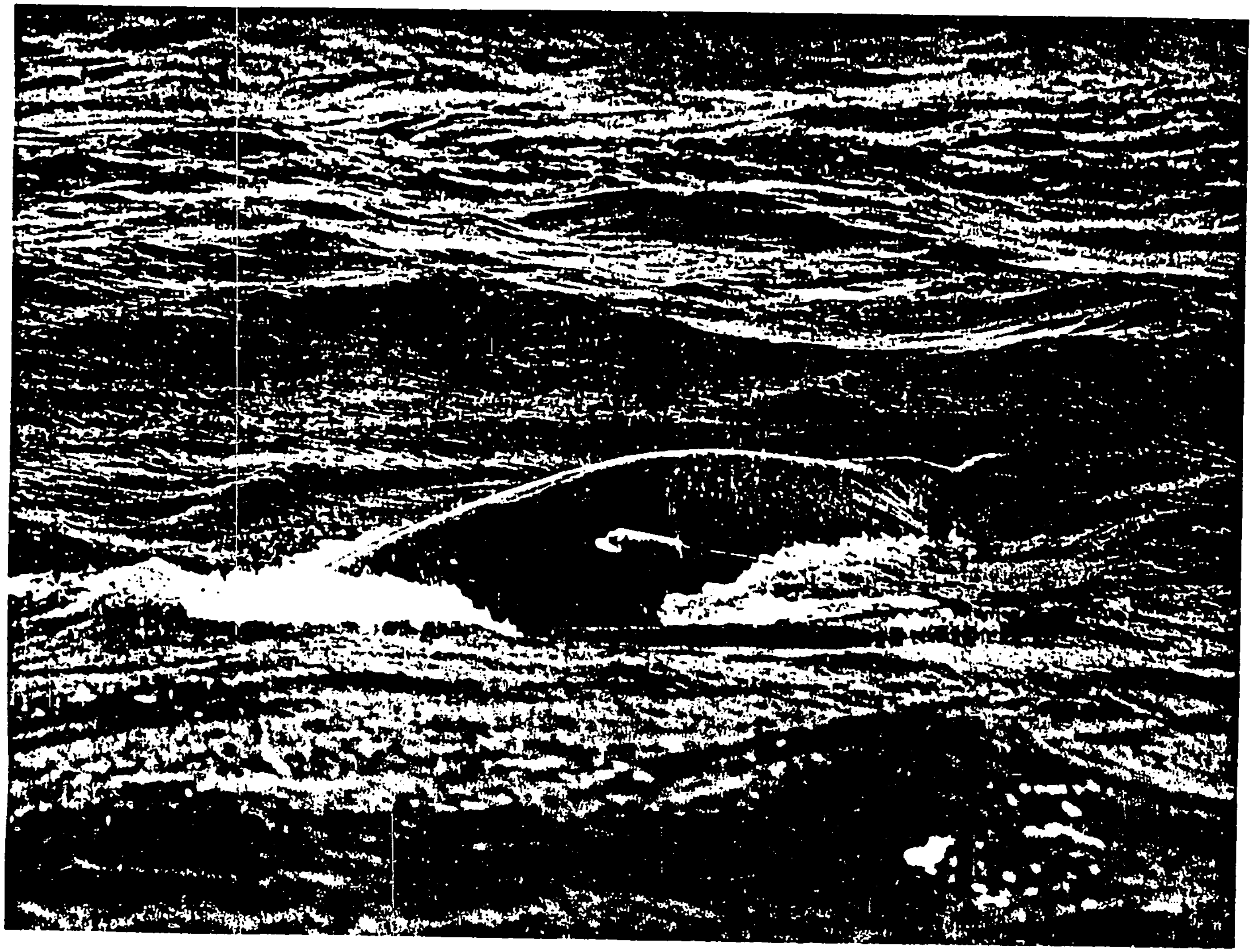


Figure 4. Remora radio tag on Newfoundland humpback number 282.

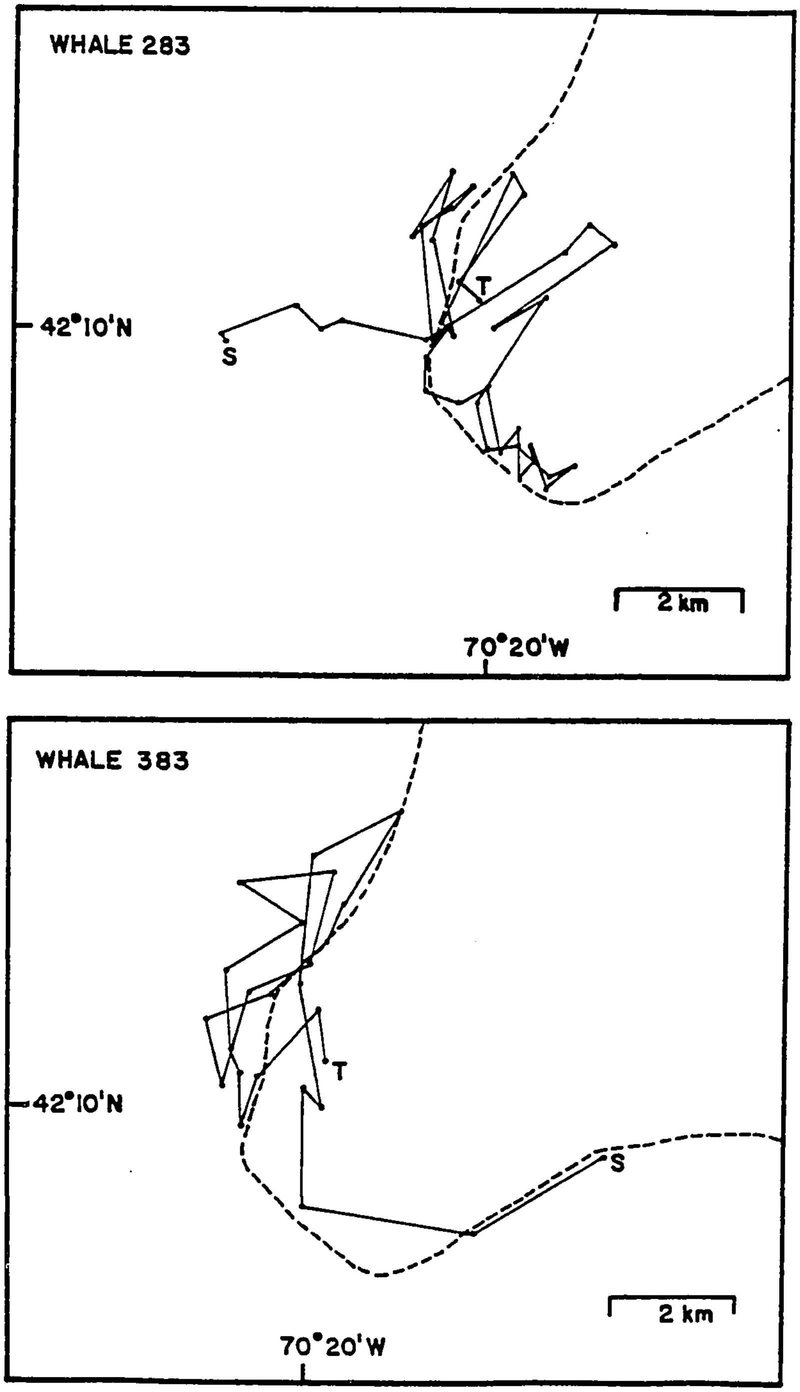


Figure 5. Tracks of lower Gulf of Maine humpbacks followed at least an entire night. Tagging and end of tracking sites are marked T and S respectively. Hatched line is Stellwagen Bank 37 m contour; track of whale 384 required two maps.

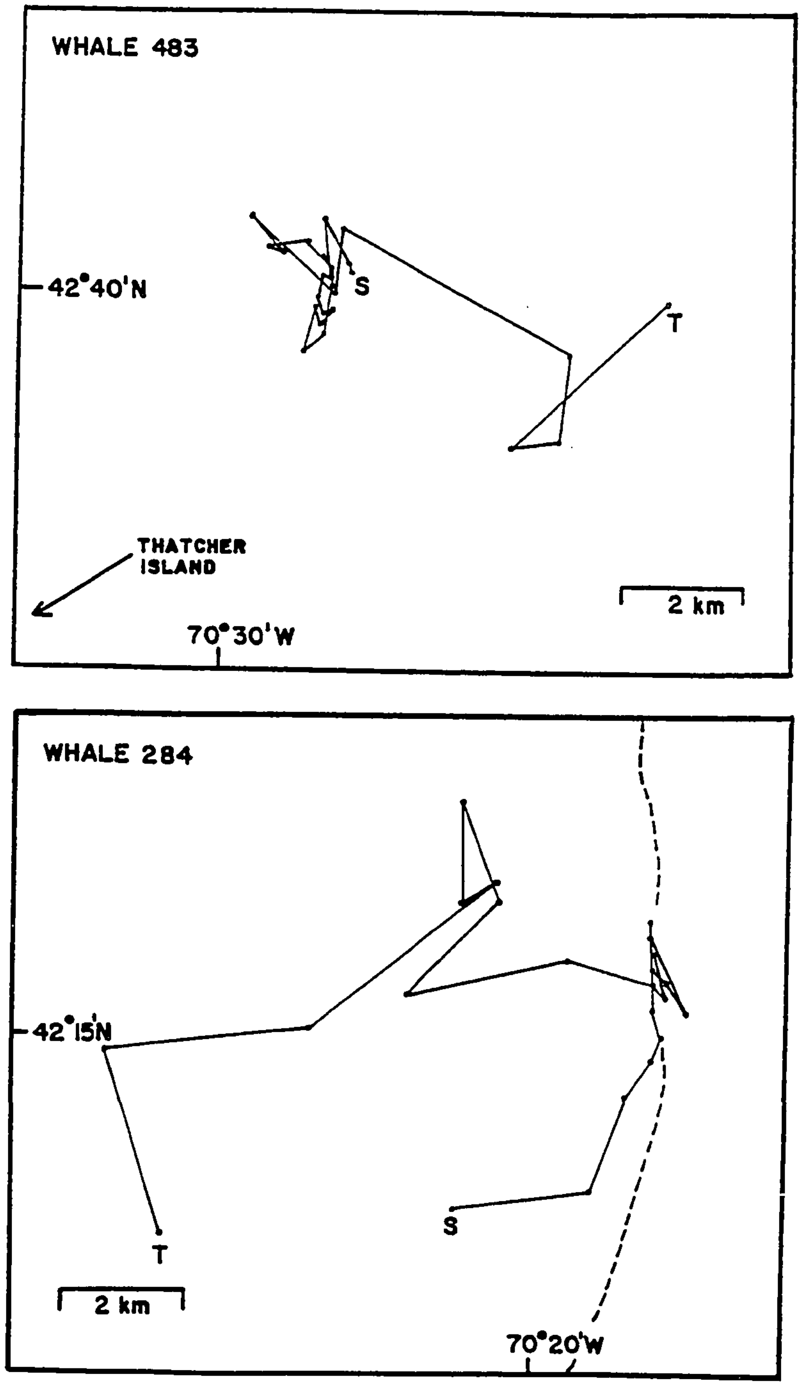


Figure 5. (continued)

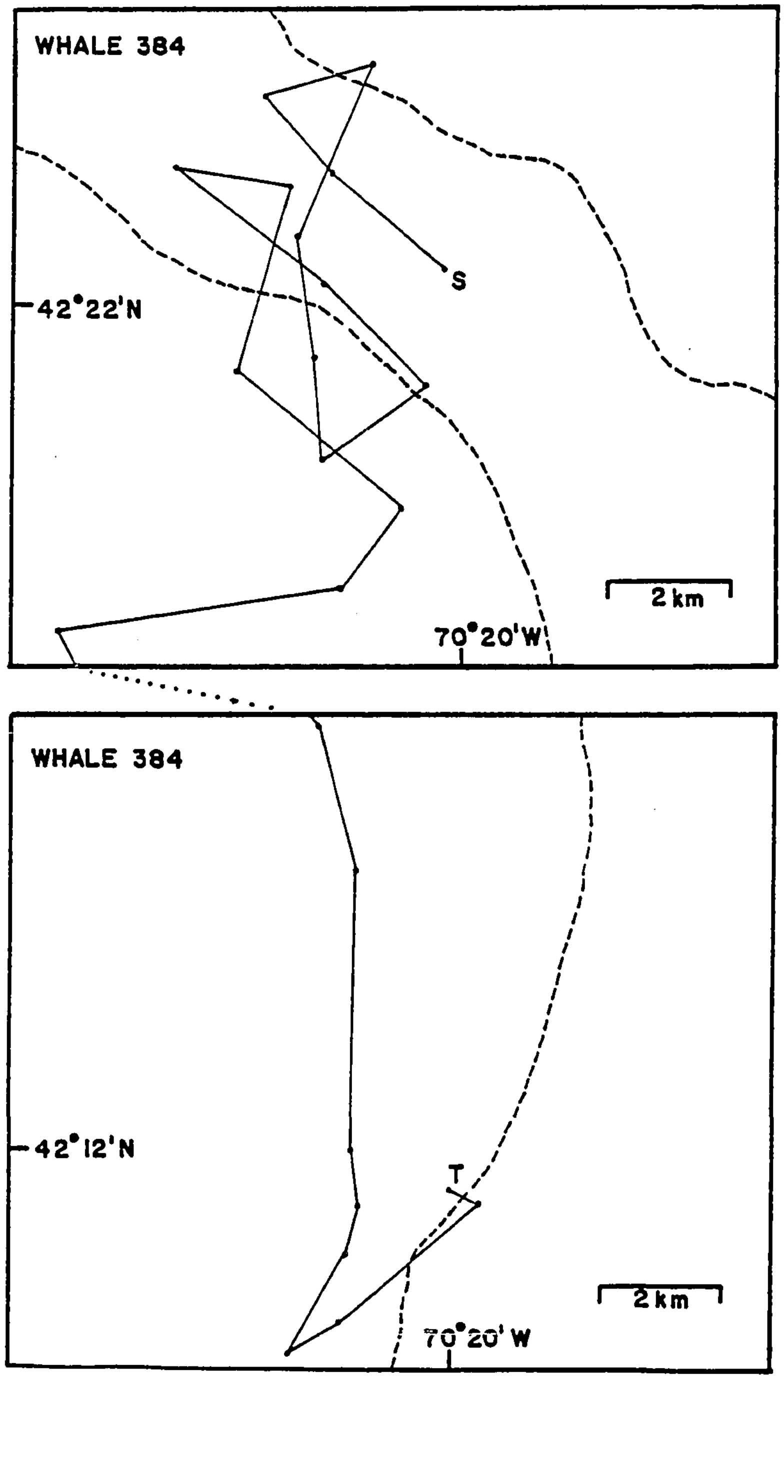


Figure 5. (continued)

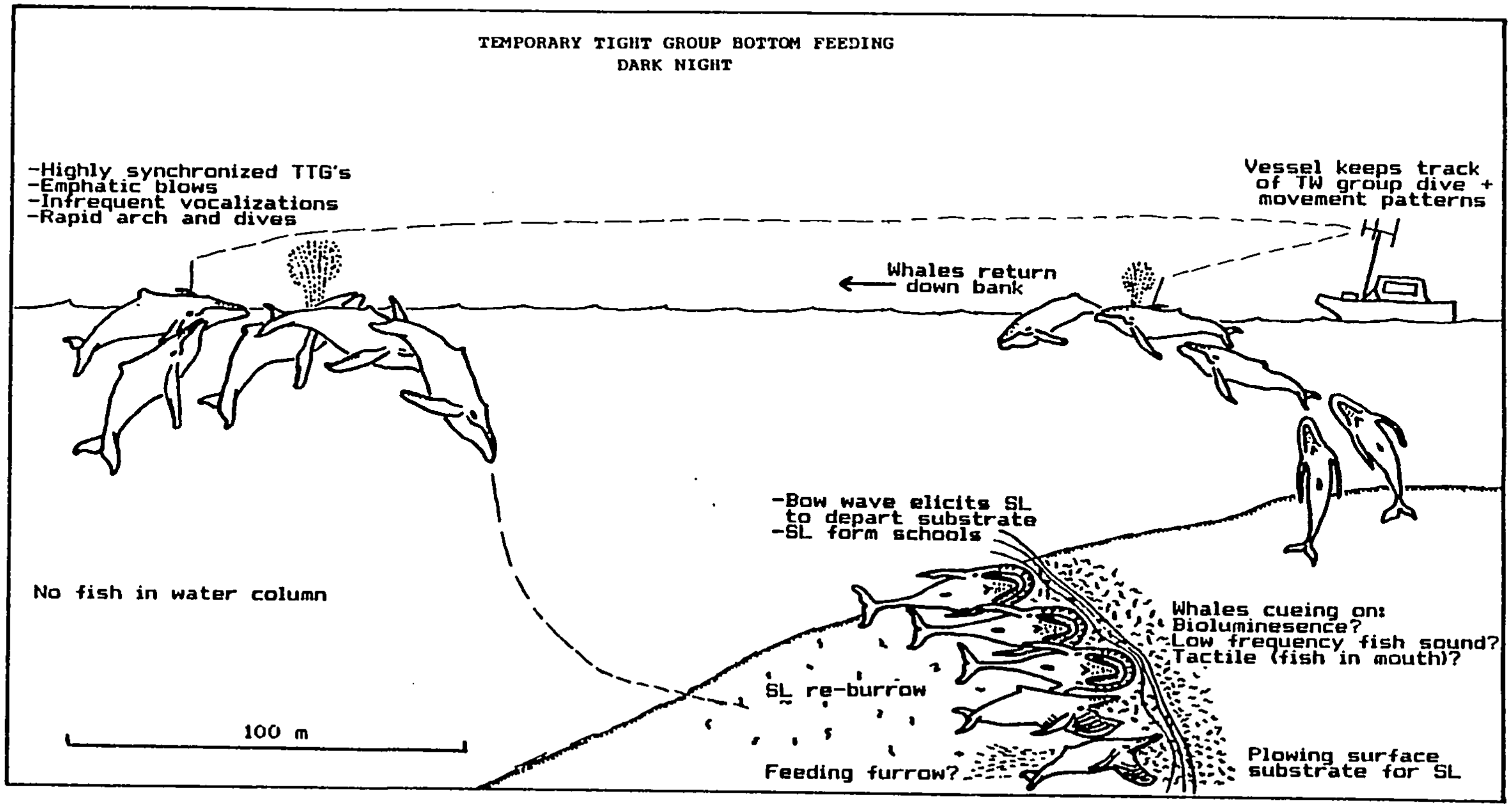


Figure 6A. Hypothetical bottom feeding by temporary tight groups (TTG) of humpbacks on sandlance (SL). Distinction is shown between bow-wave elicitation of sand lance escape from the substrate, and plowing.

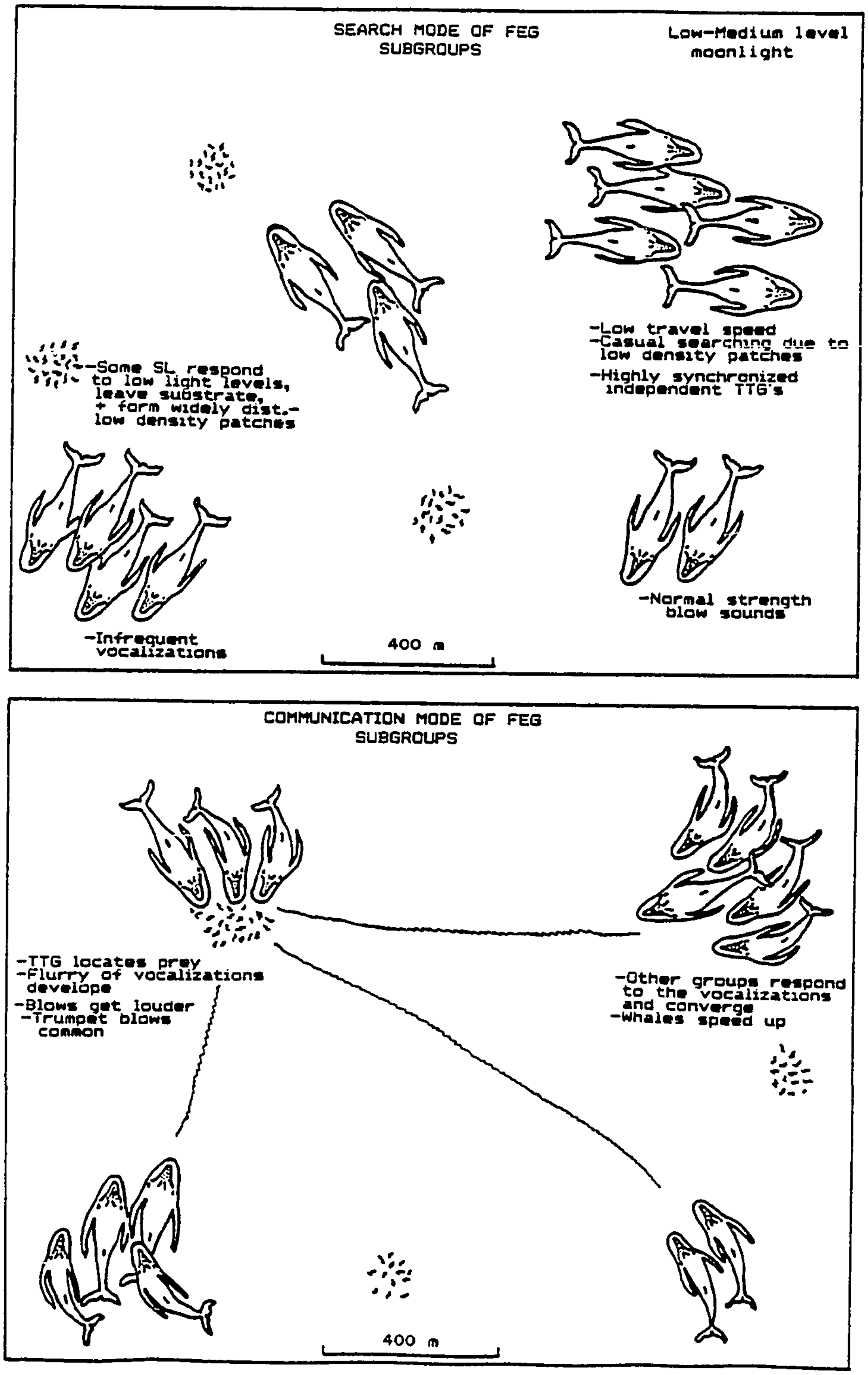


Figure 6B. Formation and activities of fluctuating extended groups of humpbacks (FEG). These groups formed under low to medium level moonlight. Sequence is from top to bottom and continues on next page.

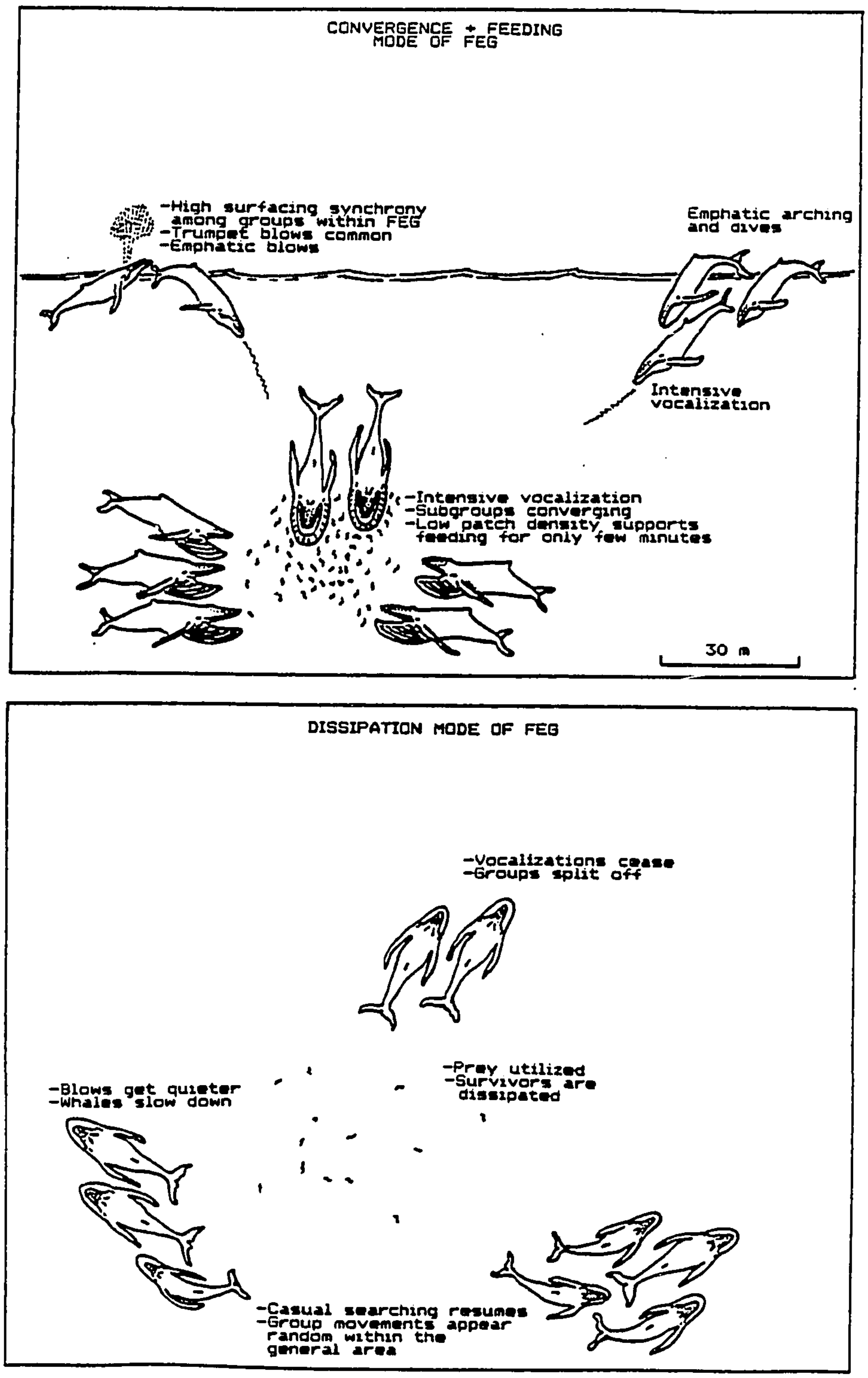


Figure 6B. (continued)

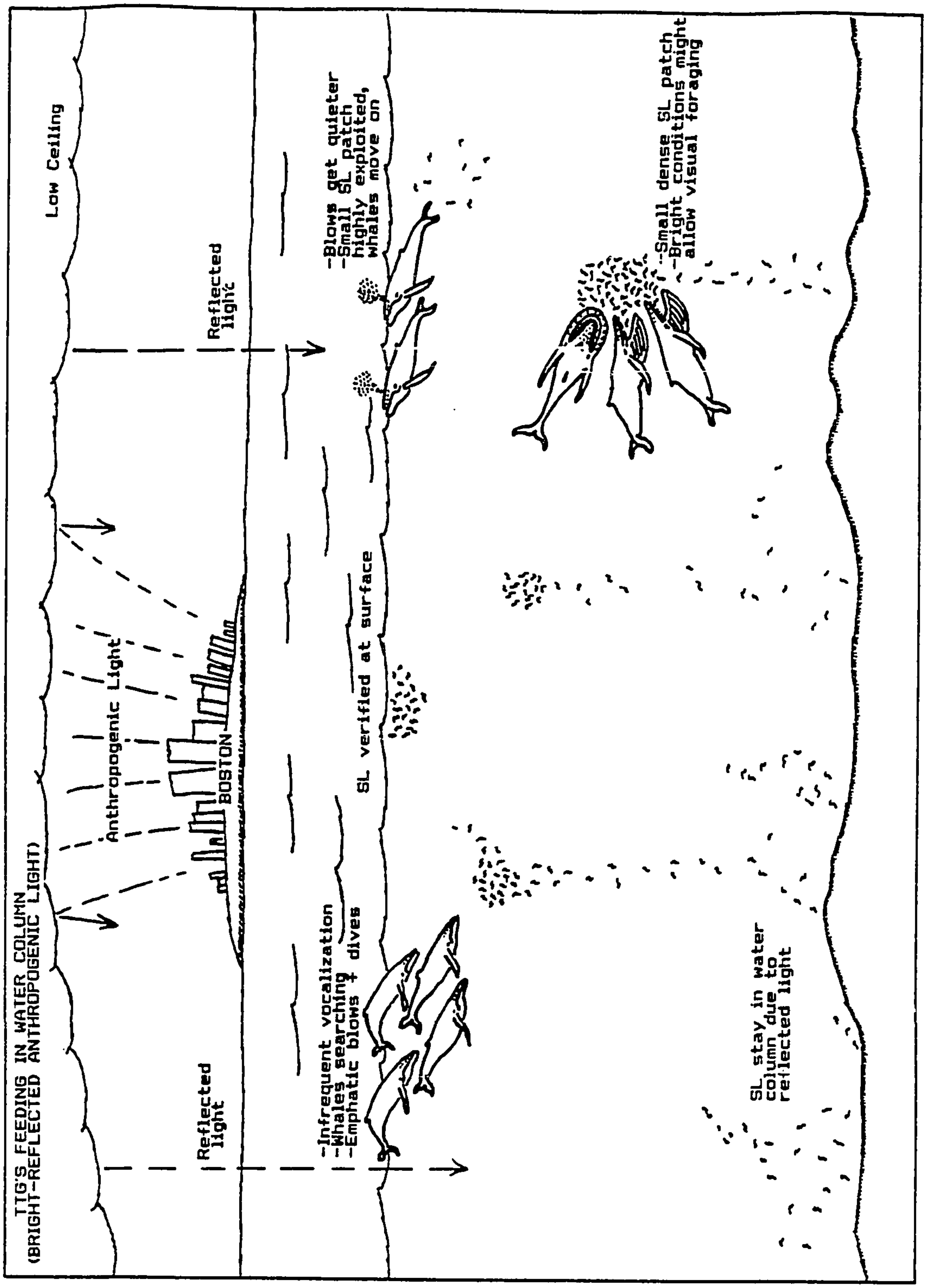


Figure 6C. Night feeding by temporary tight groups (TTG) within the water column when anthropogenic light reflects off a low cloud ceiling.

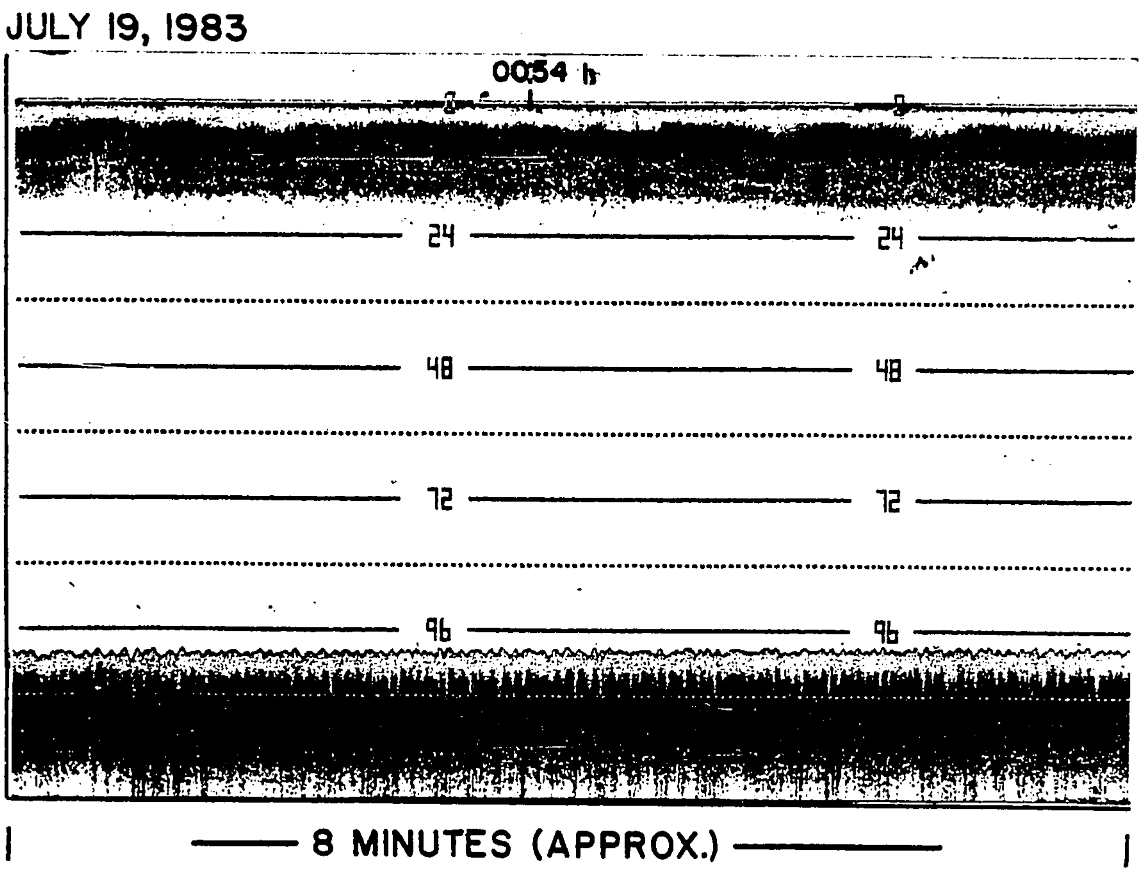


Figure 7. A typical sonar trace made during a dark night in the Gulf of Maine study area showing no prey; sand lance burrow into the substrate when it is dark. Dark area at the top of the trace is surface noise.

AUGUST 11, 1983

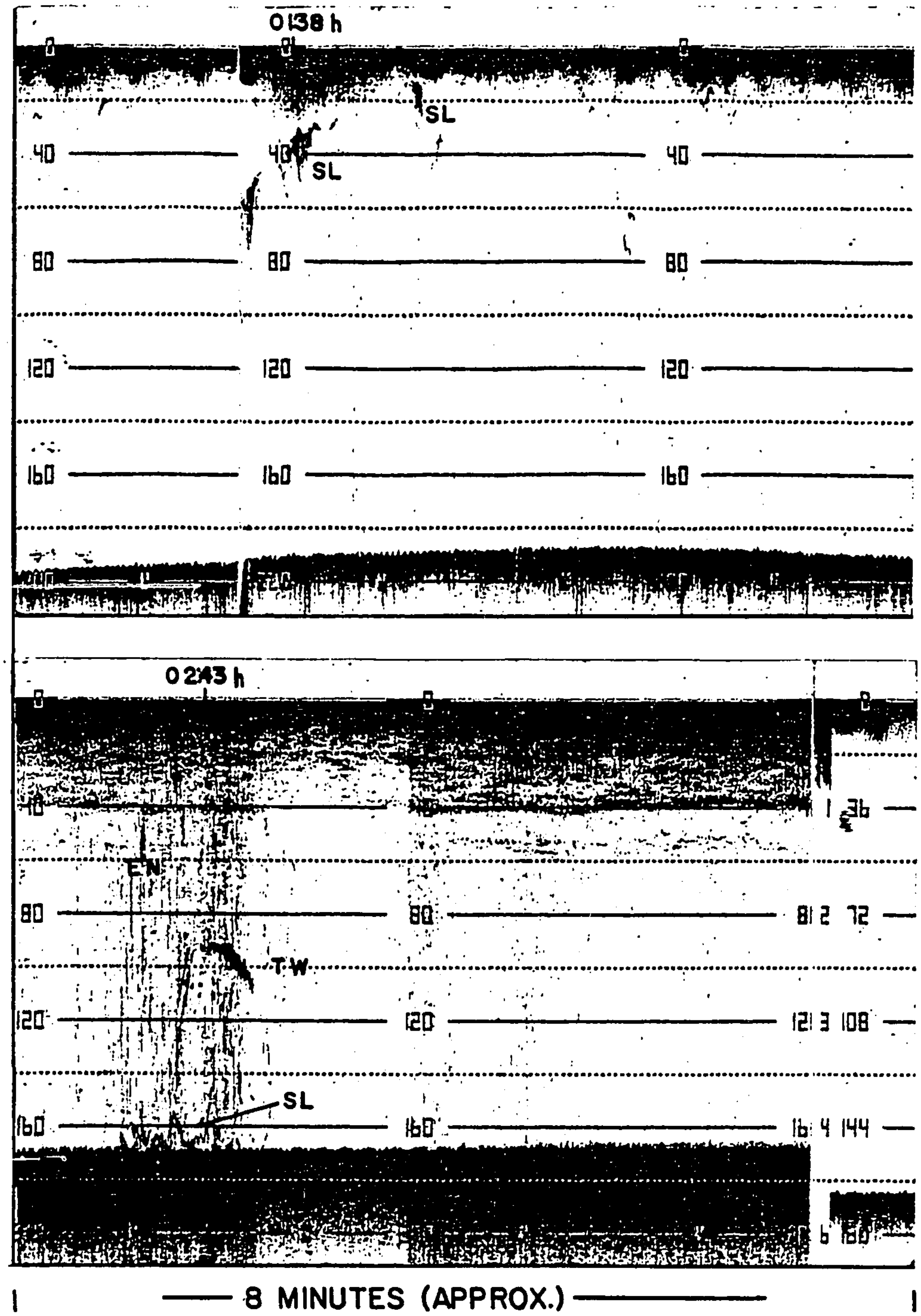


Figure 8. Sonar trace showing sand lance (SL) and a humpback (W) seen when Boston area lights reflected off a low cloud ceiling (see also Figure 6C). Sand lance patches were dense but widely separated; "EN" identifies engine noise.

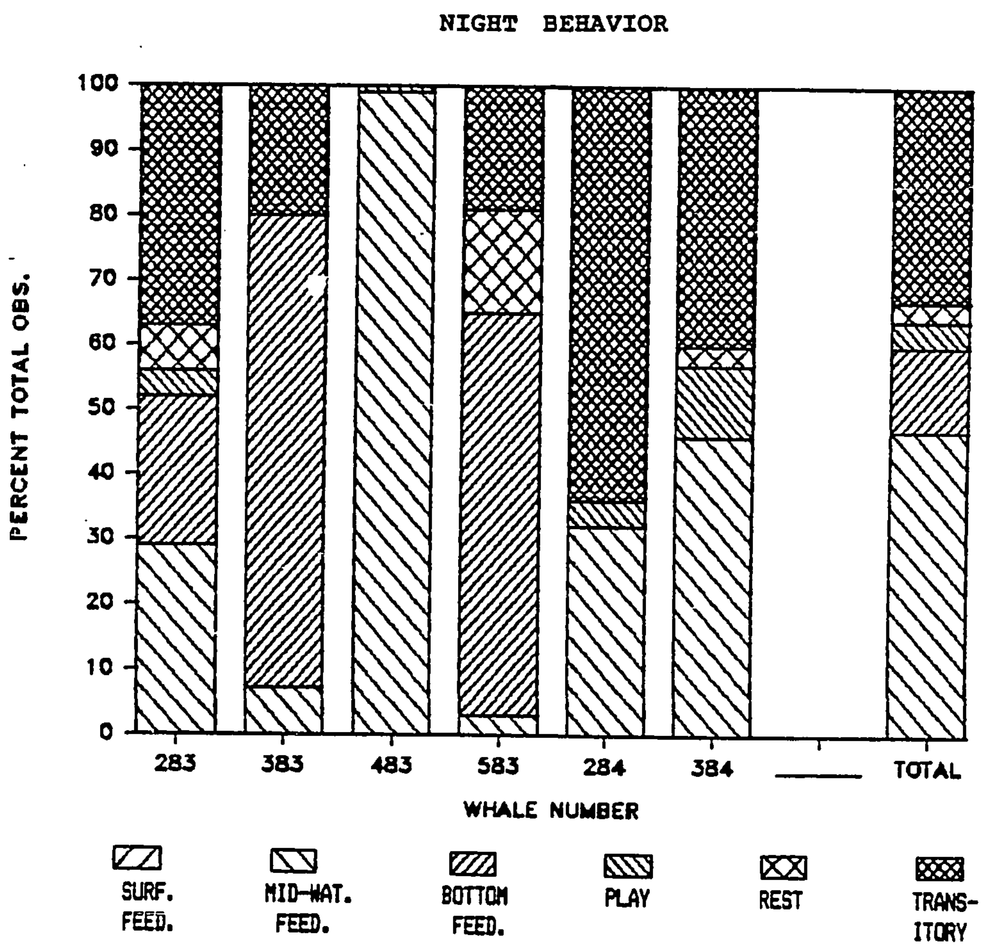


Figure 9A. Percent of night observations assigned to each behavior category. Only whales followed an entire night are included.

NIGHT ACTIVITY LEVEL

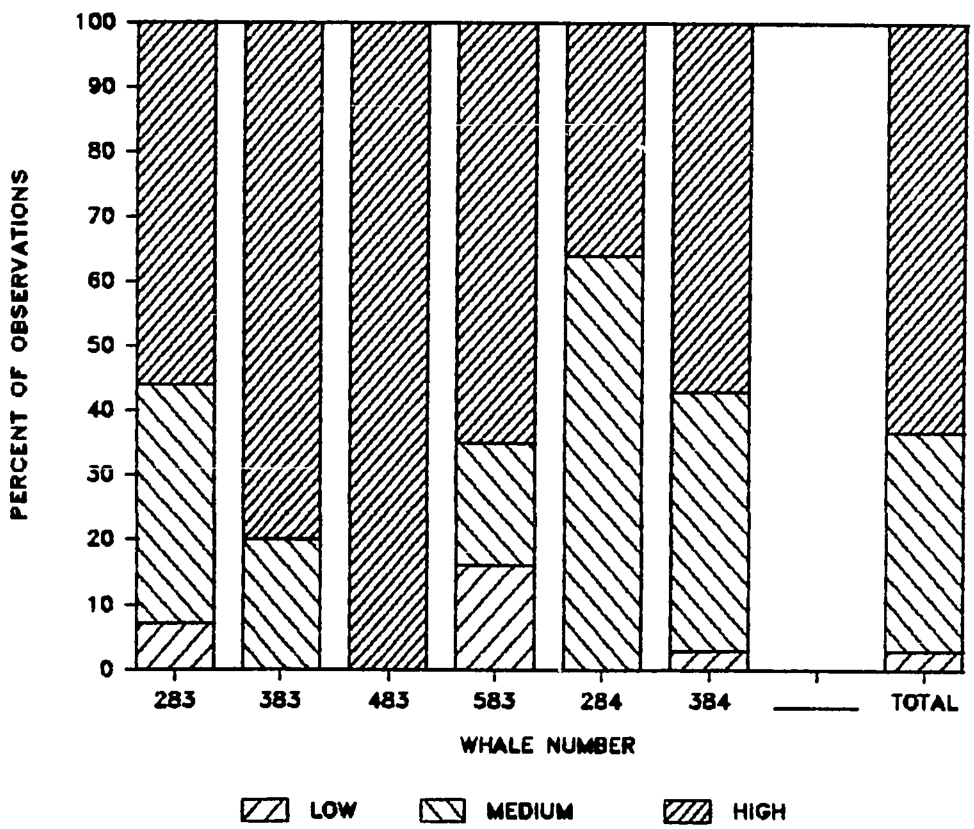


Figure 9B. Percent of night observations assigned to each activity level category. Only whales followed an entire night are included.

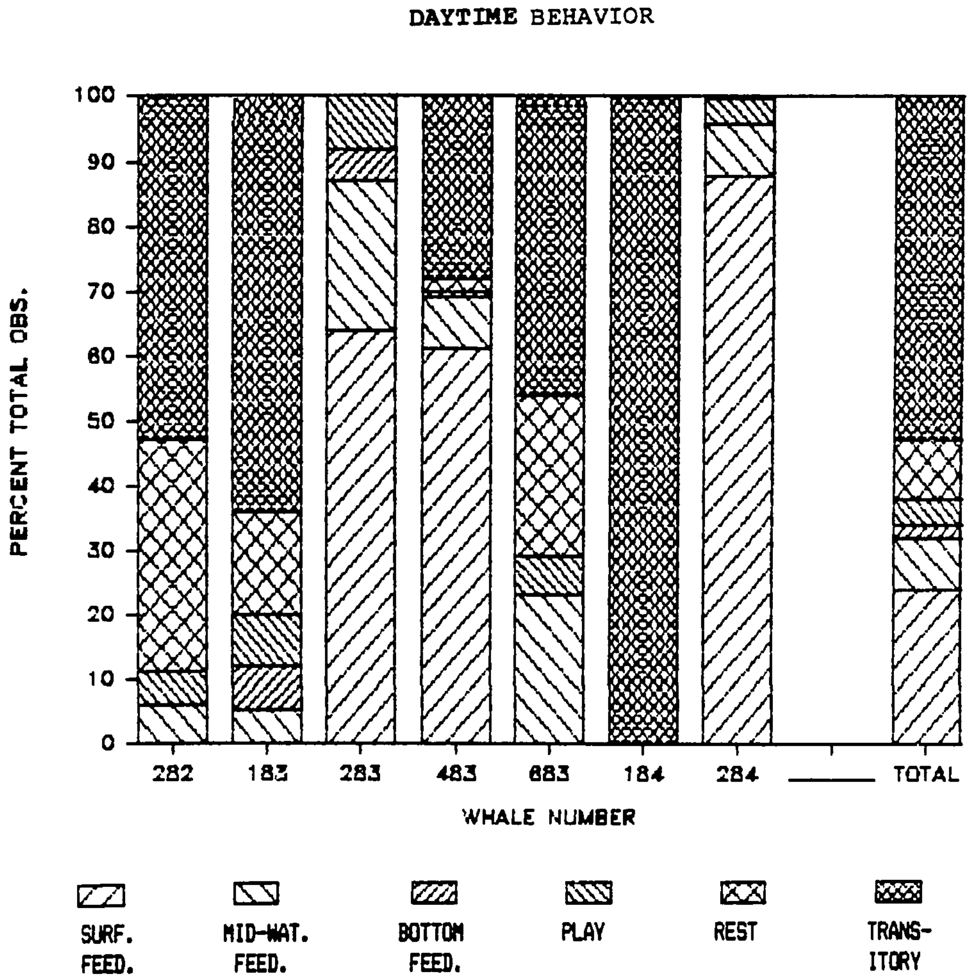


Figure 10A. Percent of daytime observations assigned to each behavior category. Only whales followed an entire night are included.

DAYTIME ACTIVITY LEVEL

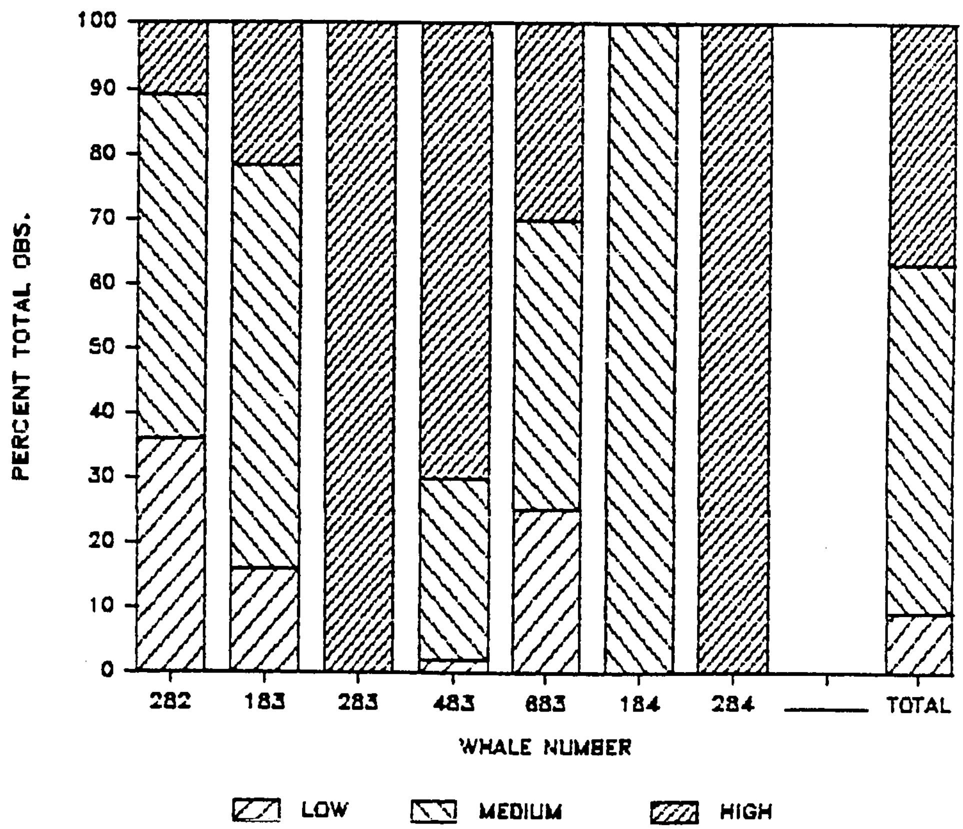


Figure 10B. Percent of daytime observations assigned to each activity level category. Only whales followed an entire night are included.

CREPUSCULAR BEHAVIOR

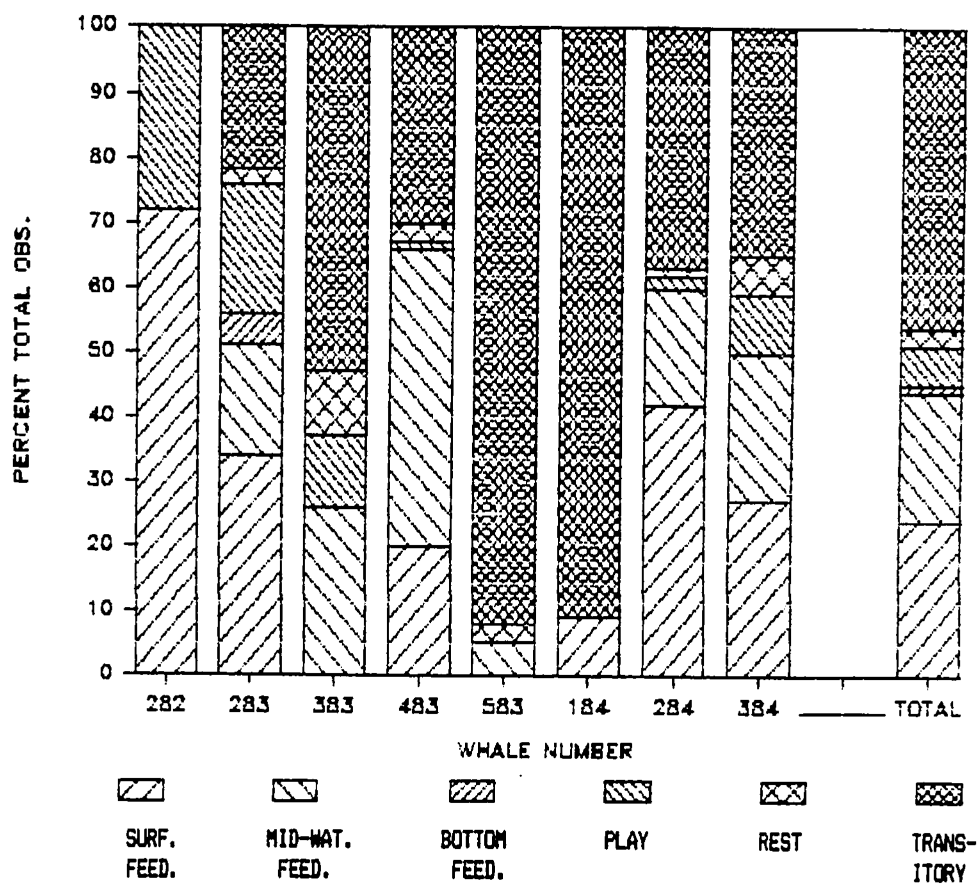


Figure 11A. Percent of crepuscular period observations assigned to each behavior category. Only whales followed throughout the night are included.

CREPUSCULAR ACTIVITY LEVEL

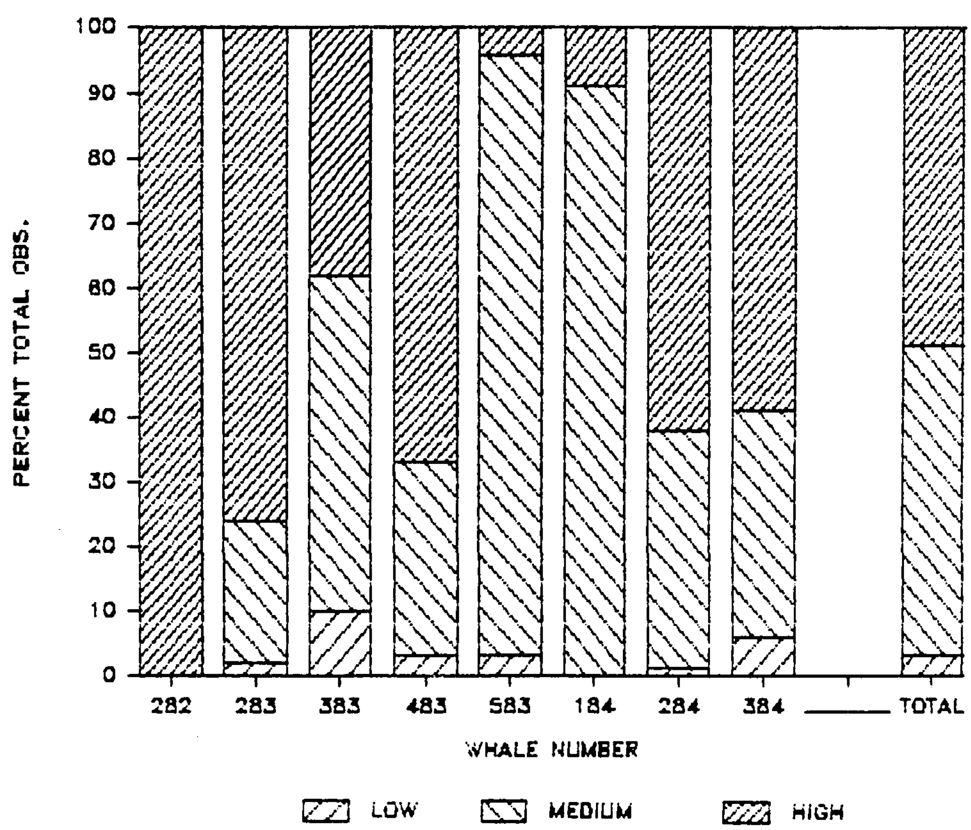
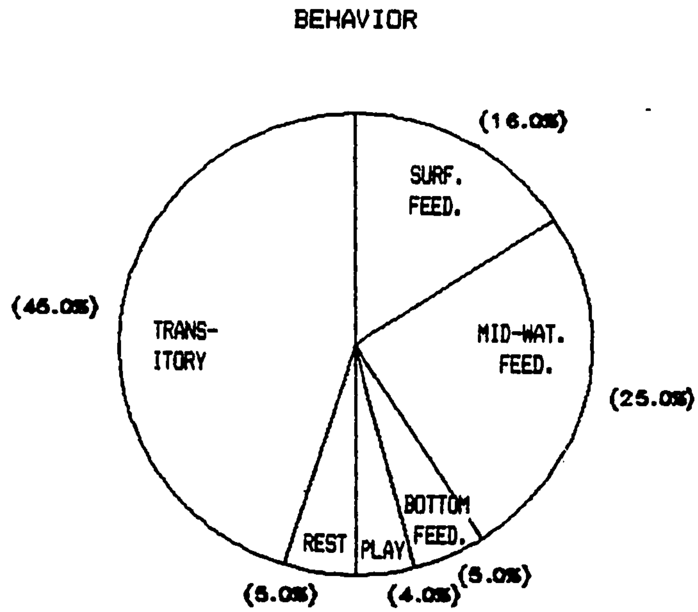


Figure 11B. Percent of crepuscular period observations assigned to each activity level category. Only whales followed throughout the night are included.



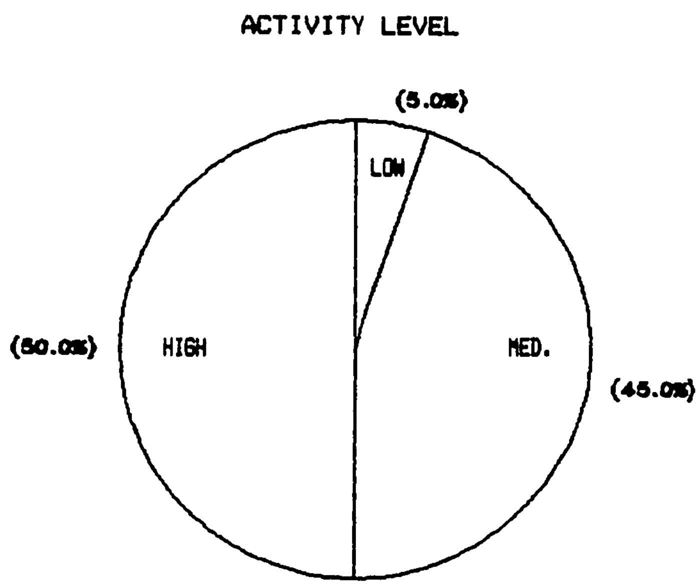


Figure 12. Percent of observations of tagged whales of each behavior and activity level category considering all time periods.

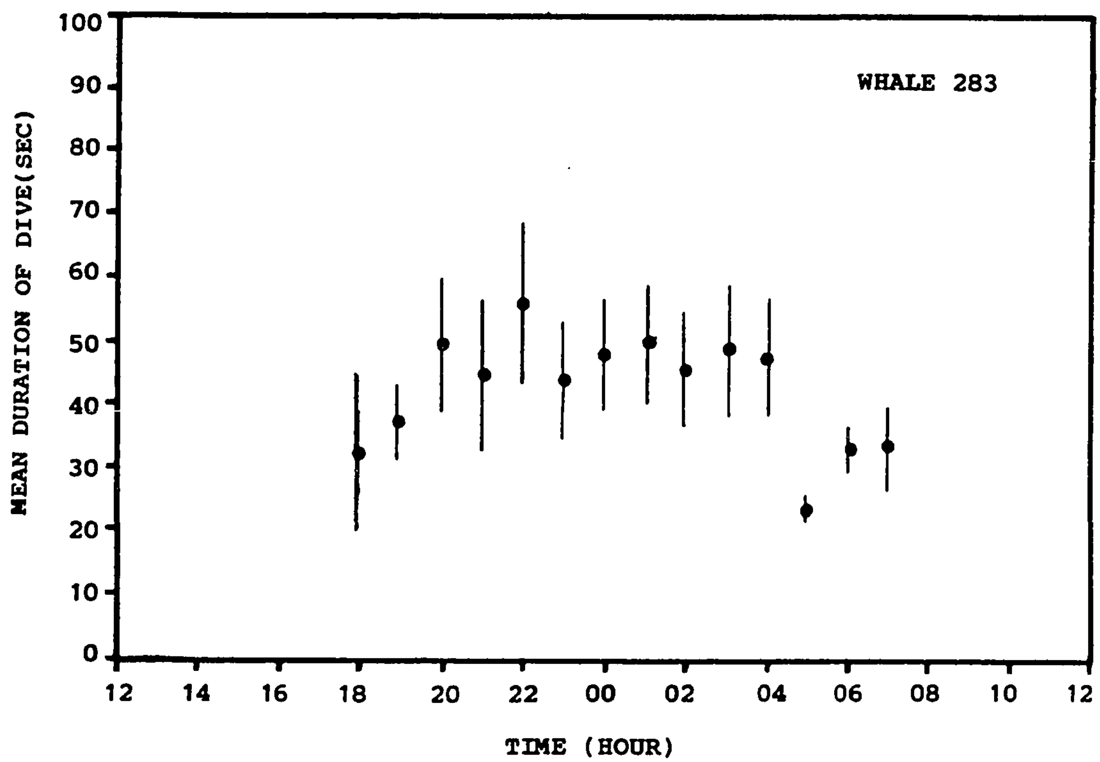


Figure 13A. Hourly mean time in seconds tagged whale 283 spent during each dive (± Std. Error, N ranged from 9 to 92 among hours).

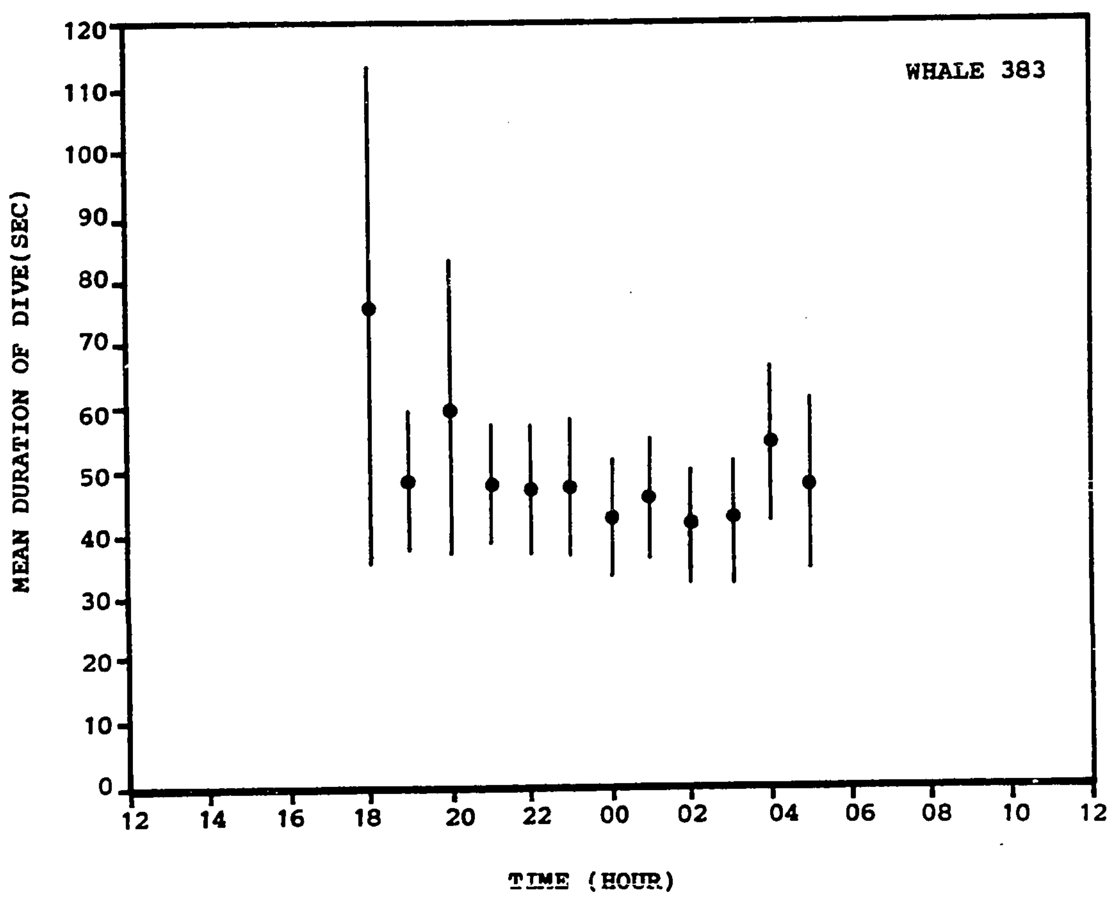


Figure 13B. Hourly mean time in seconds tagged whale 383 spent during each dive (± Std. Error, N ranged from 10 to 78 among hours).

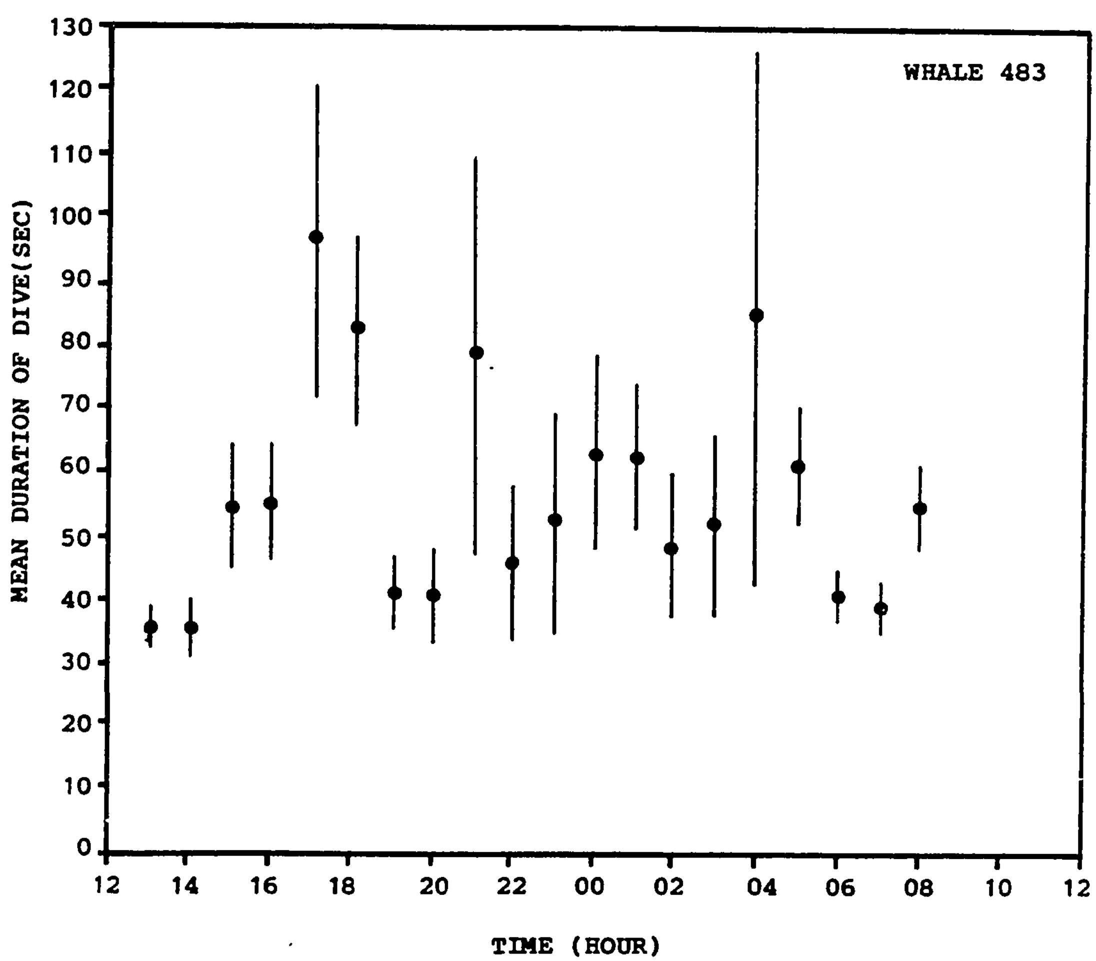


Figure 13C. Hourly mean time in seconds tagged whale 483 spent during each dive (± Std. Error, N ranged from 11 to 97 among hours).

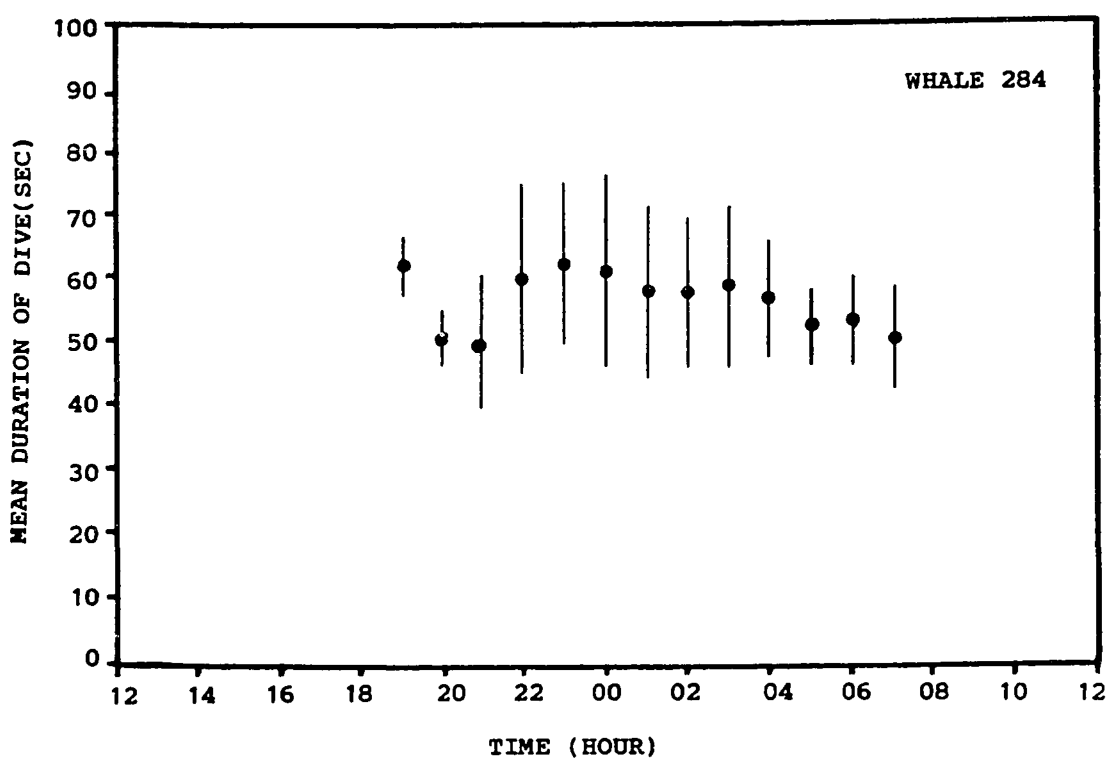


Figure 13D. Hourly mean time in seconds tagged whale 284 spent during each dive (± Std. Error, N ranged from 50 to 90 among hours).

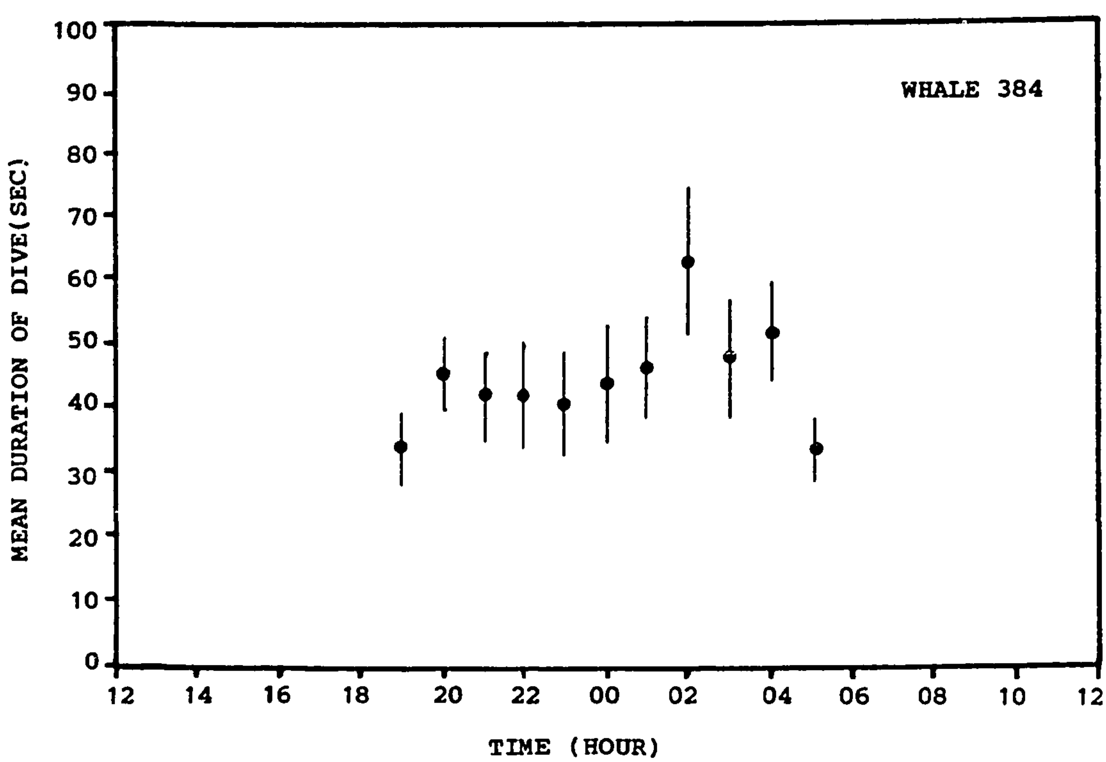


Figure 13E. Hourly mean time in seconds tagged whale 384 spent during each dive (± Std. Error, N ranged from 38 to 81 among hours).

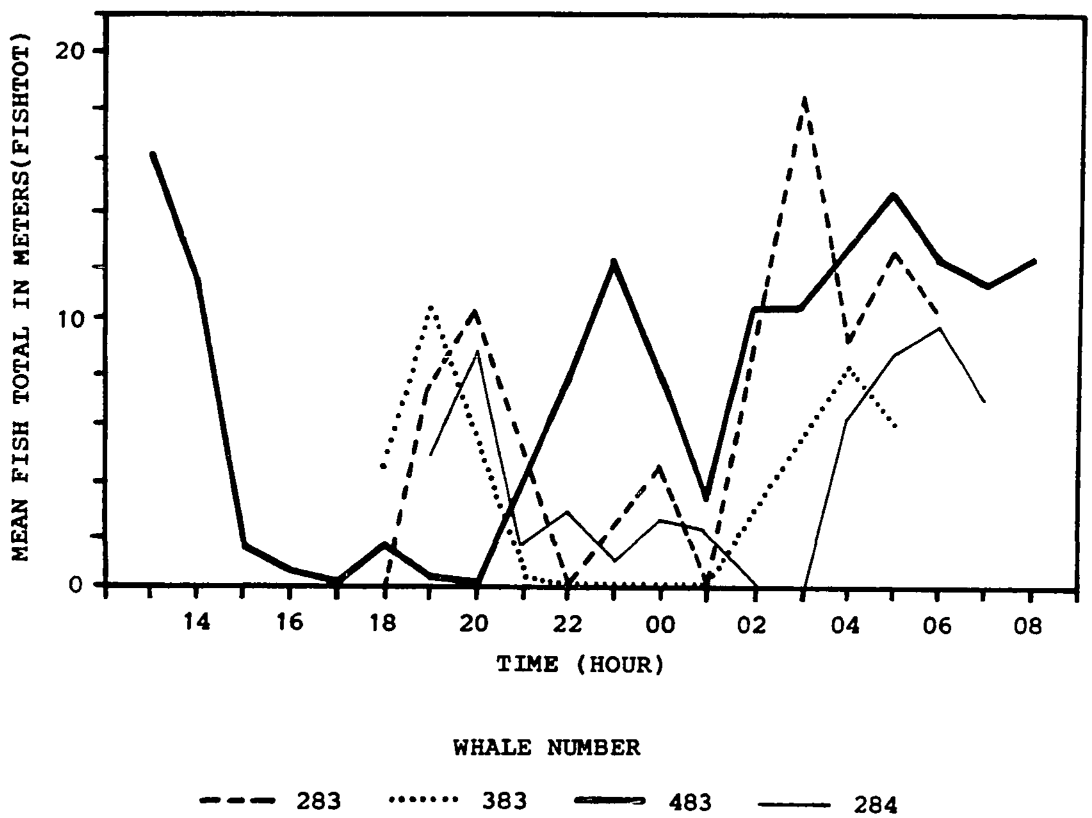


Figure 14. Hourly mean prey abundance (sand lance) in meters (variable FISHTOT; see text) seen on sonar during tracking of Gulf of Maine whales; only whales followed an entire night are included.

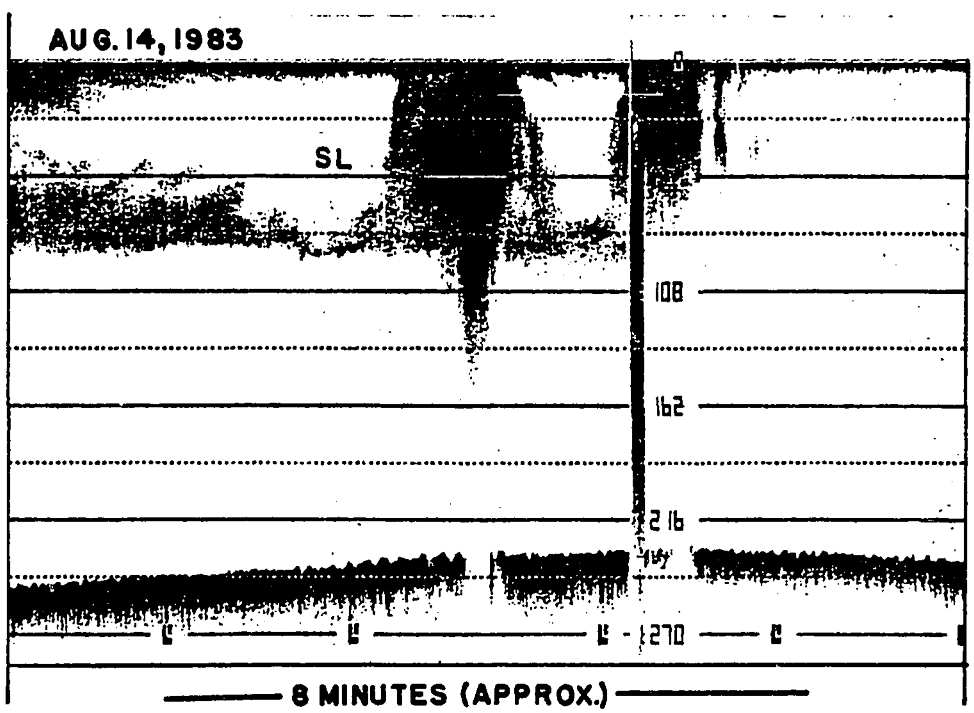


Figure 15. Sonar trace showing extensive but typical daytime sand lance (SL) concentrations in the lower Gulf of Maine.