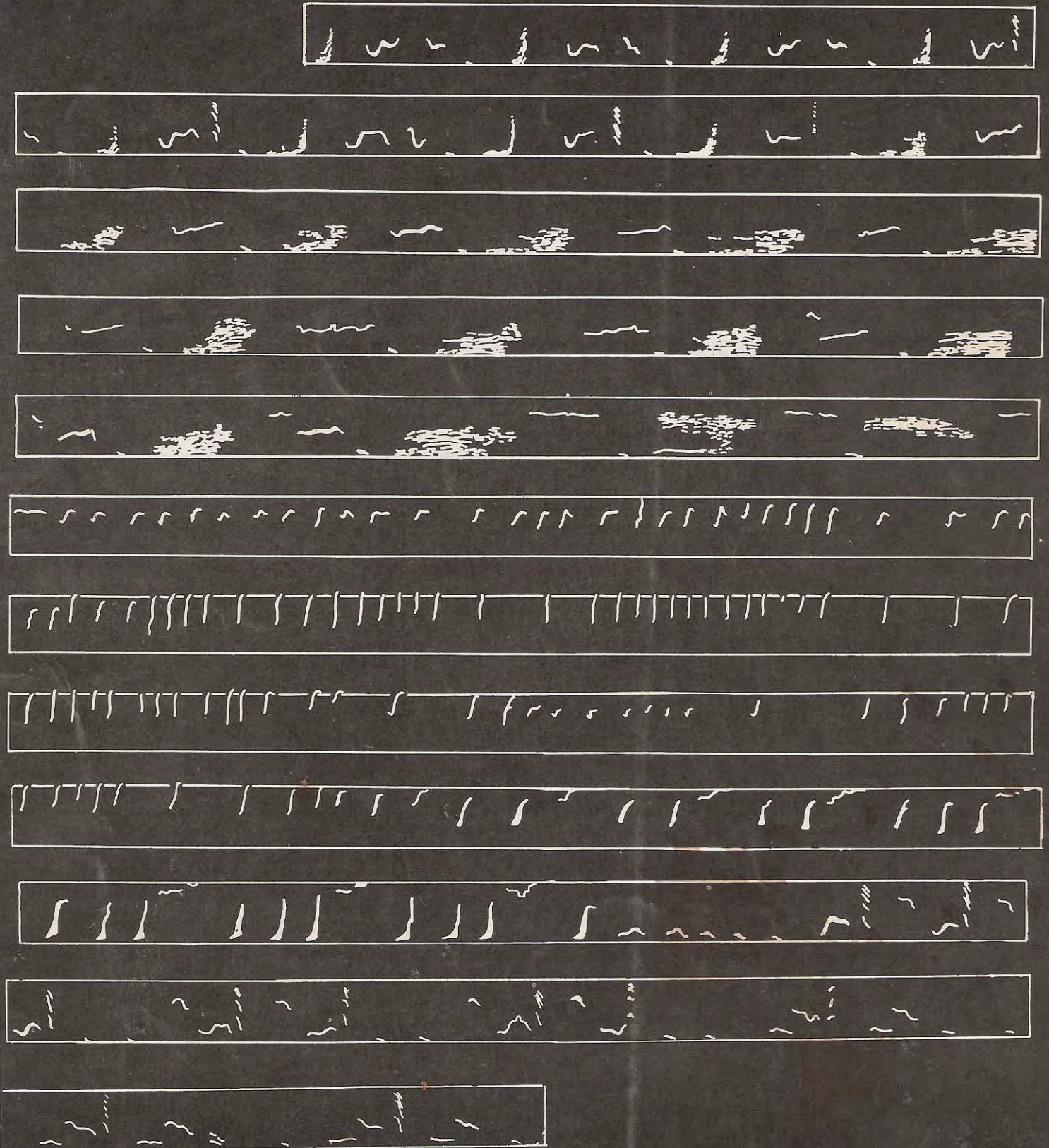


Songs of Humpback Whales

Roger S. Payne and Scott McVay



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Humpbacks emit sounds in long, predictable patterns ranging over frequencies audible to humans.

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During the quiet age of sail, under conditions of exceptional calm and proximity, whalers were occasionally able to hear the sounds of whales transmitted faintly through a wooden hull (1). In this noisy century, the widespread use of propeller-driven ships and continuously running shipboard generators has made this a rare occurrence. Not until World War II, when research in sonar and antisubmarine warfare fostered major efforts and facilities for listening underwater, did it become generally known that many species of whales are vocal. At this time the first whale recordings were made.

Of the 25 or more species of whales that have been recorded, most are Odontocetes (toothed whales). Their sounds fall into three rough categories: short broad-band clicks, longer narrow-band squeals, and complex sounds (2). The complex sounds usually consist of rapidly repeated clicks. Most authors assume that both clicks and complex sounds serve principally for echolocation and that whistles are primarily for communication. However, there is little direct proof of either assumption (2). There seems to be no evidence that the sort of sound-patterning with which this article is concerned occurs among Odontocetes, but there are good reasons to suppose that it might.

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Mysticete (baleen whale) sounds are varied and complex, consisting, for the most part, of lower and longer sounds than have yet been recorded from Odontocetes. The fin whale (*Balaenoptera physalus*) makes very low moans (at a fundamental frequency around 20 hertz) that are monotonously repeated in a regular pattern (3, 4). To date, the most vocal Mysticete that has been studied is the humpback whale (*Megaptera novaeangliae*).

Humpback whales, like sperm whales, are found in all oceans of the world. However, while the sperm whale has been, and remains, the most numerous large cetacean on earth, the humpback has never been very plentiful. The principal concentration of humpback whales is in the Antarctic Ocean (5), where they have probably never numbered more than 34,000 at any one time. However, the intense whaling of the past 40 years has reduced the number of humpbacks there to no more than a few percent of the original numbers.

The International Whaling Commission has called for full protection of the humpback. Yet, even if this moratorium is honored, the number of humpbacks in the Southern Hemisphere seems dangerously low, perhaps too low to provide the pool of genetic variability needed to survive the next natural or man-made crisis.

Though they have also been seriously overhunted in the Northern Hemisphere, small herds of humpbacks ap-

pear in a few areas during natural periods of concentration (that is, for feeding, migration, delivering young, and the like). The waters near Bermuda are well known as such an area. Humpbacks are found to the south of Bermuda in considerable numbers during their annual spring migration from winter breeding grounds in the south to summer feeding grounds in the north (2, 3, 6). It is from studies of the herd sojourning in these waters that we have become aware of what we believe to be the humpbacks' most extraordinary feature—they emit a series of surprisingly beautiful sounds, a phenomenon that has not been reported previously in more than a passing way. We describe here one part of the humpbacks' sonic repertoire—a long "song" that recurs in cycles lasting up to 30 minutes and perhaps longer.

History of Recordings

The first recordings of humpback whales that we know of were obtained in 1952 by Schreiber (7) from a U.S. Navy hydrophone installation on the underwater slope of Oahu, Hawaii. Although Schreiber did not identify the species, Schevill (2) subsequently recognized the sounds recorded by Schreiber as coming from humpbacks. Most of the sounds that we describe here were recorded by Frank Watlington of the Palisades Sofar Station at St. David's, Bermuda. Watlington recorded from a hydrophone installation, similar to Schreiber's, deep in the North Atlantic on the slope of Bermuda.

Humpback whales may winter near Bermuda as well as pass nearby during their spring migration to northern Atlantic waters (8). The fortunate location of the broad-band hydrophones used by Watlington made it possible for him to record humpback sounds during spring migrations from 1953 to 1964. The broad-band hydrophone from which all of the recordings analyzed here were made was in about 700 meters of water, about 3 kilometers southeast of the entrance to Castle

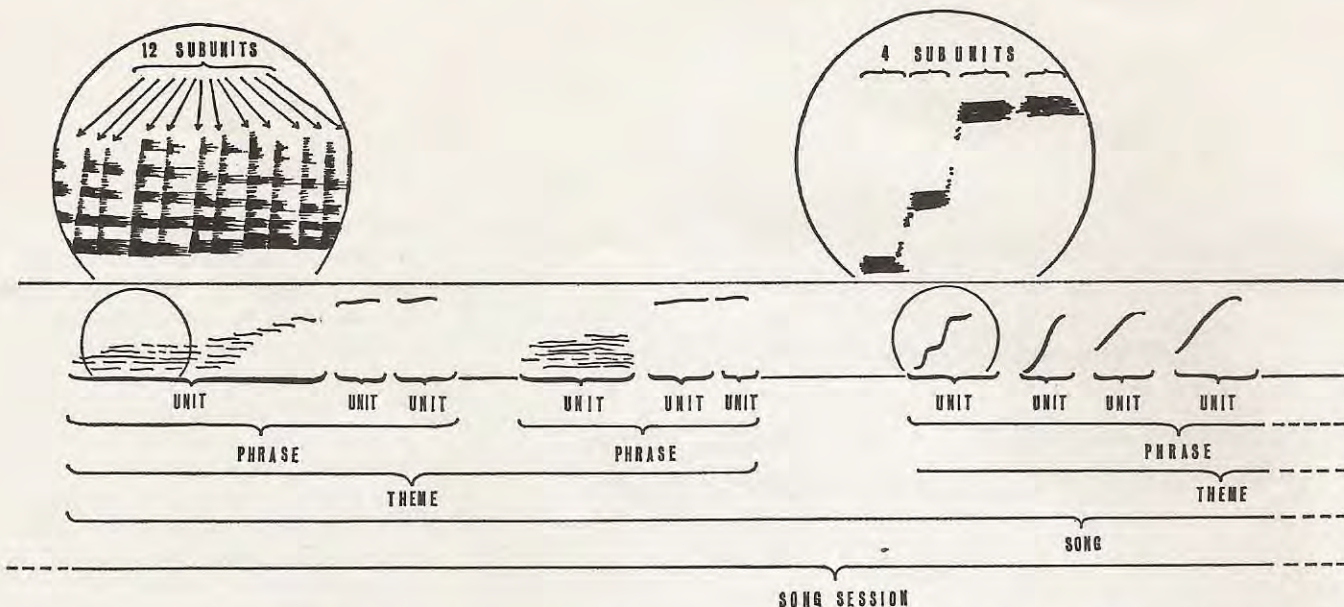


Fig. 1. Diagrammatic sample of whale spectrograms (also called sonagrams) indicating terminology used in describing songs. Frequency is given on the vertical axis, time on the horizontal axis. The circled areas are spectrograms that have been enlarged to show the substructure of sounds which, unless slowed down, are not readily detected by the human ear.

Harbour. Watlington's hydrophone-preamplifier combination was flat in response (± 3 decibels) from 500 hertz to 10 kilohertz, with an amplitude loss of 6 decibels per octave below 500 hertz. A cable from this hydrophone extended to Watlington's office, where the sounds were taped by a Magne-corder, type PT 6-AH, operating at 19.1 centimeters per second. Thus, when whales uttered sounds within range of the hydrophone, Watlington was able to make recordings free of the usual shipboard and cable noises, with the assurance that the whales were not being disturbed by the presence of an observer.

Evidence that Sounds Are Correctly Ascribed to Humpbacks

Schevill and Watkins (9), apparently referring to some of the same sounds from the same Watlington tapes that we have described here, have already pointed out that the sounds come from humpback whales. Additional evidence that this is true comes from observations by Watlington. By using binoculars, he was able, on several occasions, to observe whales blowing in the vicinity of the hydrophones during a recording of "whale sounds." On rare occasions, Watlington was able to verify that these whales were humpbacks by noting the prominent white flippers when the whales breached. However, such observations did not accompany

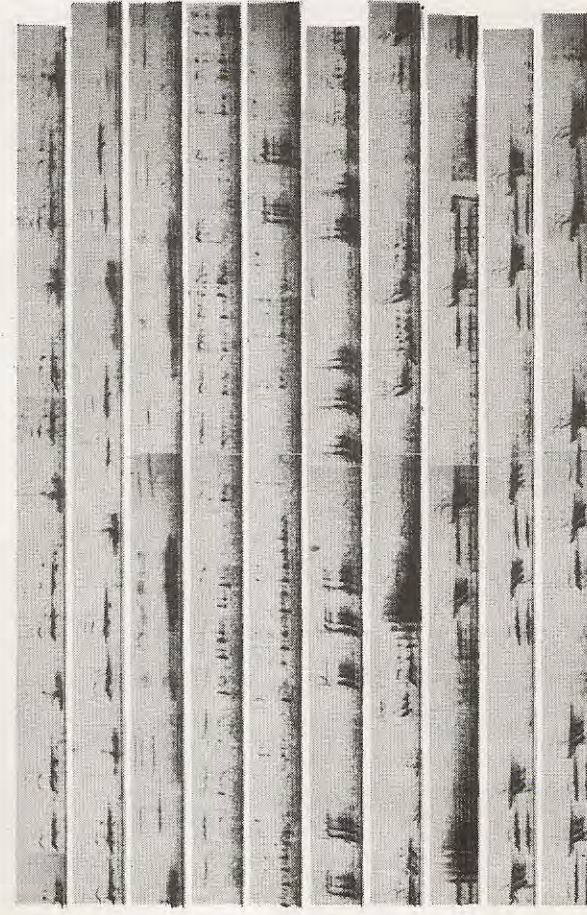
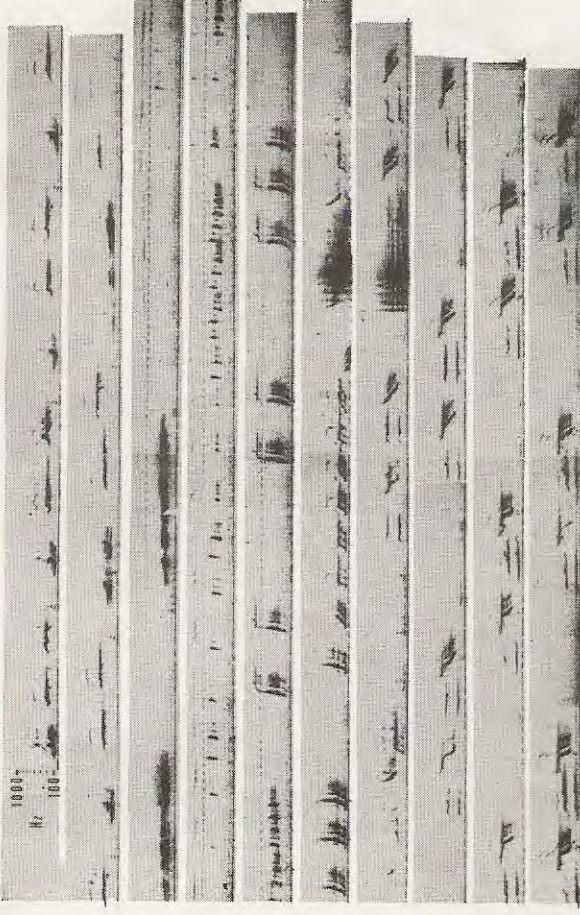
all of the recordings analyzed in detail here.

In addition to the tapes provided by Watlington, we have taken into consideration several hundred hours of recordings made by Payne, who has studied humpback sounds and behavior off Bermuda during the past five springs (1967 to 1971). Payne and Payne (10) have reviewed many of these tapes by noting the form of the sounds in a simple shorthand and, in some cases, by spectrographic analysis. All of our general conclusions about songs are based on considerations of both the Watlington and Payne recordings, but all spectrographic analyses shown here are from the Watlington recordings.

The evidence that Payne's recordings come from humpbacks is as follows: (i) when the sounds (such as those to be analyzed here) that were heard

were loud and whales were visible in the area, the whales proved in each instance to be humpbacks; (ii) interposition of a motorboat's wake between identifiable, nearby humpbacks and a hydrophone reduced the intensity of the sounds being recorded (the bubbles in the wake presumably acted as a partial screen); (iii) unfavorable orientation of a hydrophone array in relation to a visible group of humpbacks reduced the intensity of the sounds recorded (one occasion); (iv) pauses in an exceptionally loud series of sounds were correlated with blowing of a nearby humpback at the surface (several occasions) and with a breaching humpback (one occasion); and (v) while drifting in a boat on a very calm sea, Payne went near a pair of clearly identifiable humpbacks and heard one whale emit a complete sequence of sounds, of the sort described here,

Fig. 2. Here, as well as in Figs. 3 to 5, the right side shows a machine spectrographic analysis of two complete songs (labeled 1 and 2). Frequency and time scales are indicated. The left side is a tracing of the spectrograms on the right, emphasizing loud notes of the song and leaving out noise, echoes, distant whales, and all harmonics (except in the case of pulsive sounds, which depend on their harmonic structure for the effect they have on the human ear). The gap between spectrographs of songs 1 and 2 is designed to make the individual songs clear and is not indicative of any gap in time. This figure shows two songs of whale I, recorded 28 April 1964 by F. Watlington of the Palisades Sofar Station, St. David's, Bermuda. Note dynamite blasts occurring in pairs every 10 minutes. These two songs are part of a series of seven from this whale, and by comparison with earlier songs, lacking the dynamite blasts, we find that the blasts do not have any detectable effect on the whale's rendition of its song. We have other examples of whales singing, without change in the form of the song, right through loud underwater sounds generated by other research activities in the area. The dashed line at about 500 hertz represents propeller noise from a passing freighter. Echoes are prominent, making louder sounds appear three times on the original spectrograms.



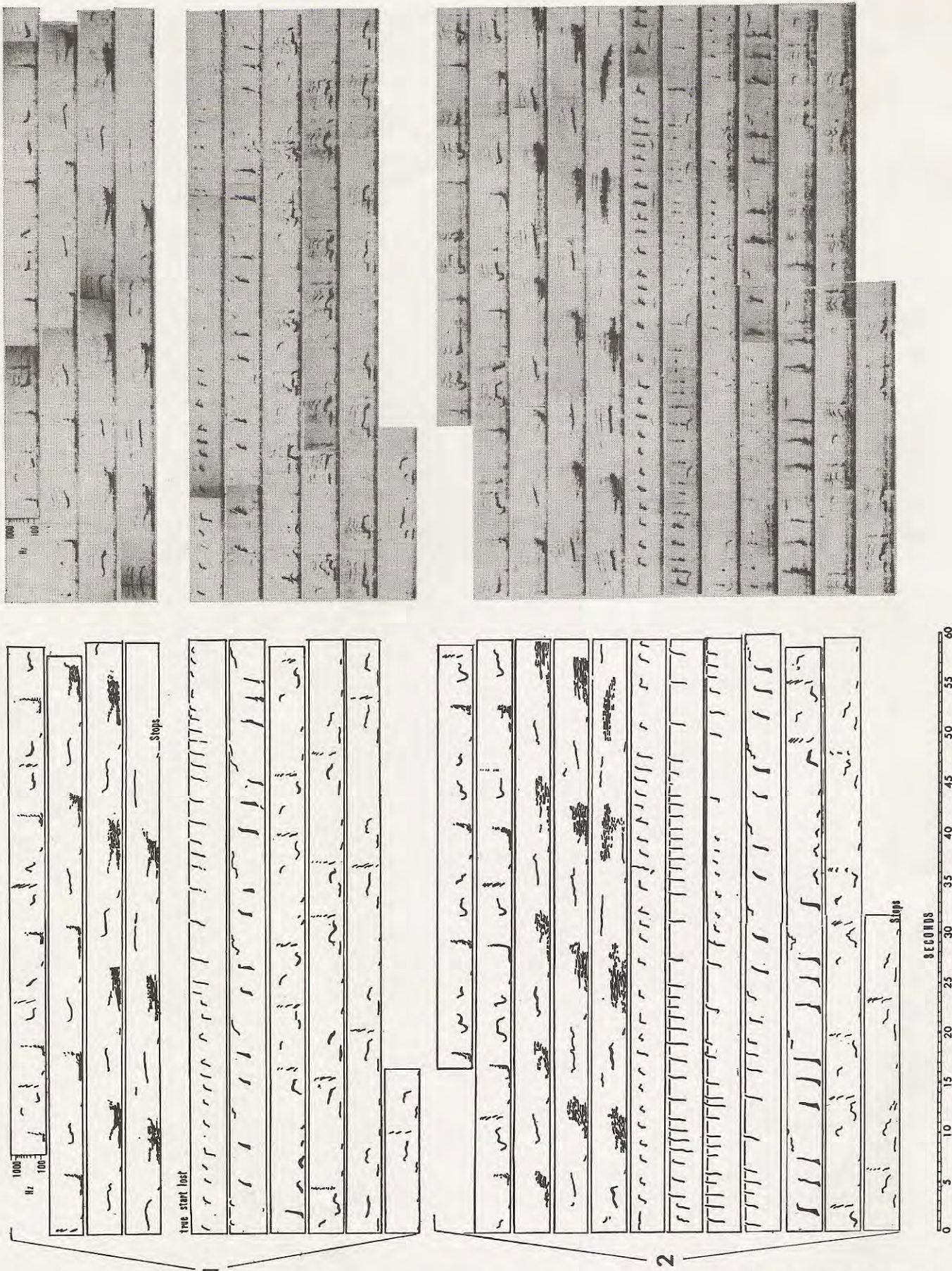


Fig. 3. Whale II, recorded by Watlington in spring, 1963. At the end of line 4 the whale stopped briefly, and a small bit (just after it started singing again, line 5) was not taped. Note, however, that the whale resumed singing in proper sequence of the song. Sounds of a second and more distant whale are prominent on the spectrographic record midway through song 2. At the end of the second song, whale II stopped singing—one of our few examples of the end of a song.

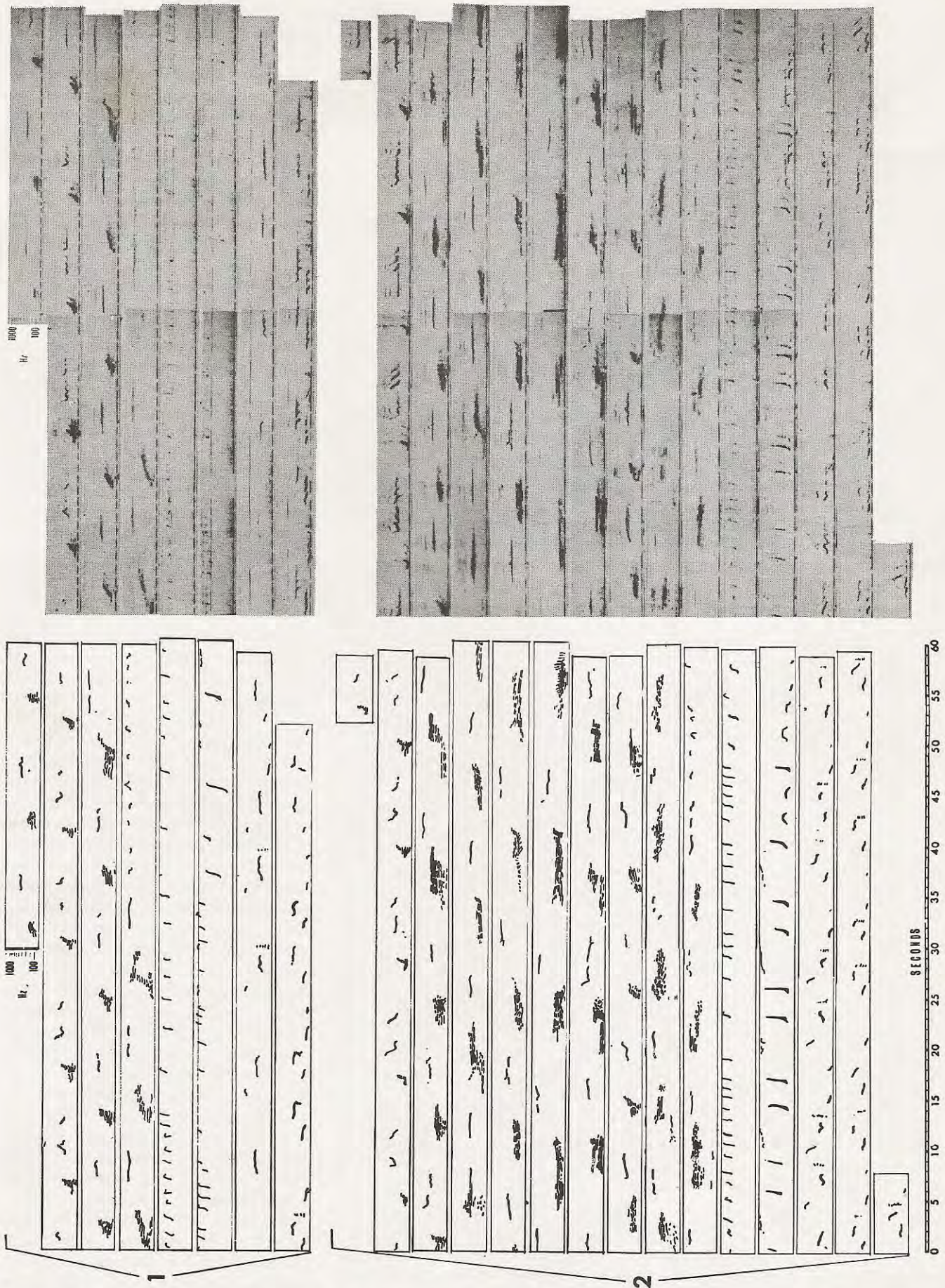


Fig. 4. Whale III, recorded by Watlington in May 1963. The first song is much shorter than the second, which begins with an unusually long first theme.

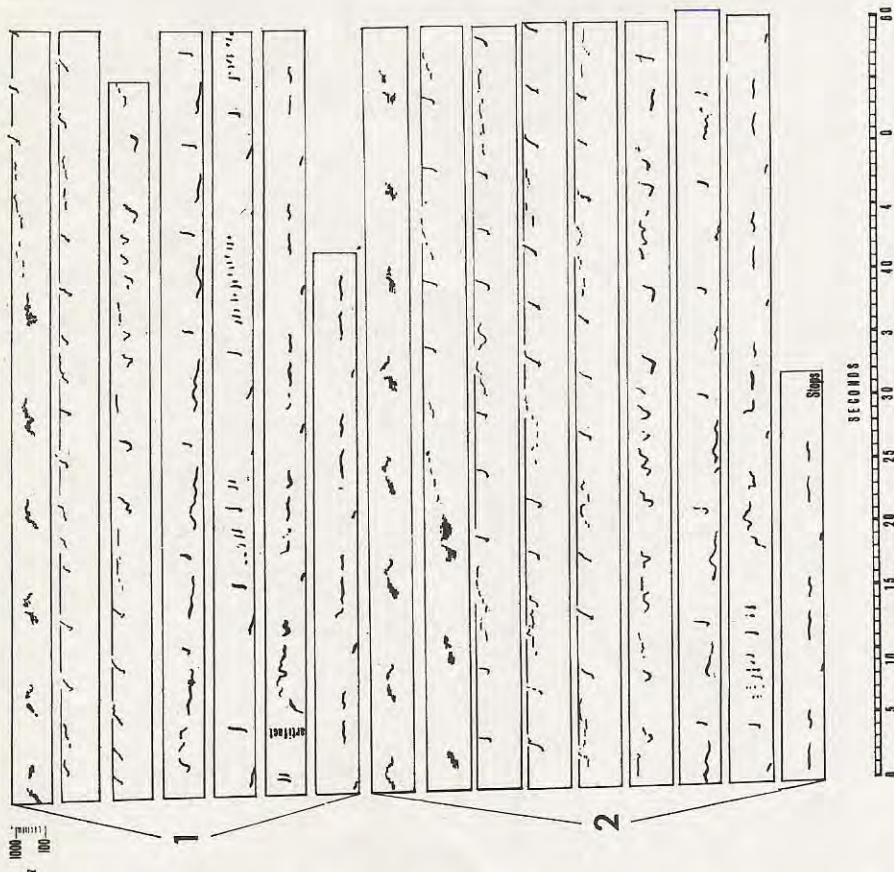
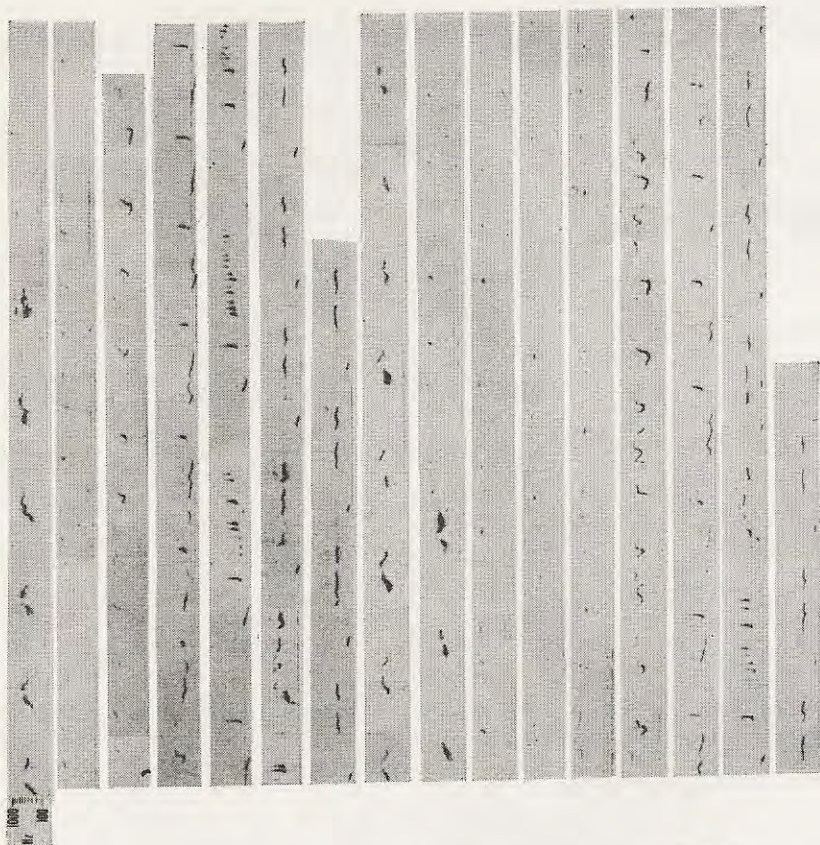


Fig. 5. Whale IV, recorded by Watlington 12 April 1961. This is an example of a different song type (type B) from the previous three examples. The poor signal-to-noise ratio of the recording caused the spectrograms for the highest frequency, lowest intensity signals to be quite faint. At the end of song 2, the whale stopped singing. This was actually the fourth and last consecutive song Watlington recorded from this whale on this occasion, and thus also indicates a true ending.

while the pair were submerged. He was using no hydrophone, the sounds coming directly through the bottom of the boat. Observations such as these have removed most of our doubts that what we have been analyzing are humpback sounds; yet the great variability of the sounds still leaves us with residual reservations about ascribing to one species (the humpback) *all* of the sounds we are analyzing here.

Analysis of Humpback Sounds

On first hearing humpback vocalizations, one has the impression of an almost endless variety of sounds. Spectrographic analysis shows, however, that all prolonged vocalizations occur in long, fixed sequences and are repeated with considerable accuracy every few minutes. Because one of the characteristics of bird songs is that they are fixed patterns of sounds that are repeated, we call the fixed patterns of humpback sounds "songs." The principal differences between bird and humpback songs are that bird songs usually last for a few seconds, while humpback songs last for minutes; and one song of a bird is usually separated from the next by a period of silence, whereas humpback songs are repeated without a significant pause or break in the rhythm of singing.

The term "song," as used in discussions of sounds made by animals, has received considerable attention. In one case, no fewer than nine pages of a comprehensive glossary by Broughton (see 11) are devoted to a detailed discussion of the many uses, misuses, and meanings of "song." Broughton finally arrives at three meanings, or categories of meanings, of the term "song," which he characterizes as *sensu latissimo*, *sensu stricto*, and *sensu strictissimo*. The median of these three (*sensu stricto*) is defined as "a series of notes, generally of more than one type, uttered in succession and so related as to form a recognizable sequence or pattern in time." By that definition (and by Broughton's other two as well), we feel justified in using the term "song" to describe repetitive sound patterns of humpback whales.

In describing the humpback whale song, we will adhere to the following designations. The shortest sound that is continuous to our ears when heard in "real time" will be called a "unit." (Some units when listened to at slower

speeds, or analyzed by machine, turn out to be a series of pulses or rapidly sequenced, discrete tones. In such cases, we will call each discrete pulse or tone a "subunit.") A series of units is called a "phrase." An unbroken sequence of similar phrases is a "theme," and several distinct themes combine to form a "song." Finally, a series of songs within which there is no pause longer than 1 minute is termed a "song session." Some sessions last for hours.

In summary: subunit < unit < phrase < theme < song < song session. A diagram is shown in Fig. 1.

The shortest complete humpback song we have yet timed lasts 7 minutes, and the longest more than 30 minutes. Since these two songs are quite different in form and were recorded in different years, they are probably from different whales. But even the same whale, repeating its own song, will show different cycle lengths during a song session. For example, two successive songs of whale III (Fig. 4) last 7 minutes and 12½ minutes, respectively. In spite of such variations in length, we call these vocalizations "songs" because they differ primarily in the number of times the phrases of a given theme are repeated. In our sample, the sequence of themes is invariable, and no new themes are introduced or familiar ones dropped during a song session. Except for the precise configuration of some units and the number of phrases in a theme, there is relatively little variation in successive renditions of any individual humpback's song. Yet, although we will not deal with it in detail here, we must not overlook this variation, for it is obviously an important feature of the songs.

Besides the variation among successive songs of one individual, there are often large differences among songs sung by different individuals. This raises the question of whether there is a single, species-specific song pattern, or whether each humpback sings its own pattern. All songs of humpback whales that we have heard consist of the following three main sections: (i) trains of rapidly repeated pulses that often alternate with sustained tones; (ii) many short, high-frequency units, most of which abruptly rise in frequency; and (iii) lower, more sustained notes that are monotonously repetitious in rhythm and frequency and contain many units that fall in frequency. We feel that these three sections constitute

a very general, species-specific song pattern.

Within this very general framework, the many variations sung by individuals seem to sort naturally into several distinct categories or song types, the number of which is still unclear. In all song sessions in our sample, each

whale adheres to its own song type throughout the session. We consider here two song types (designated as types A and B). As will become clear, these two song types have strong similarities, even though they depart in form markedly at one point.

We include three examples of type

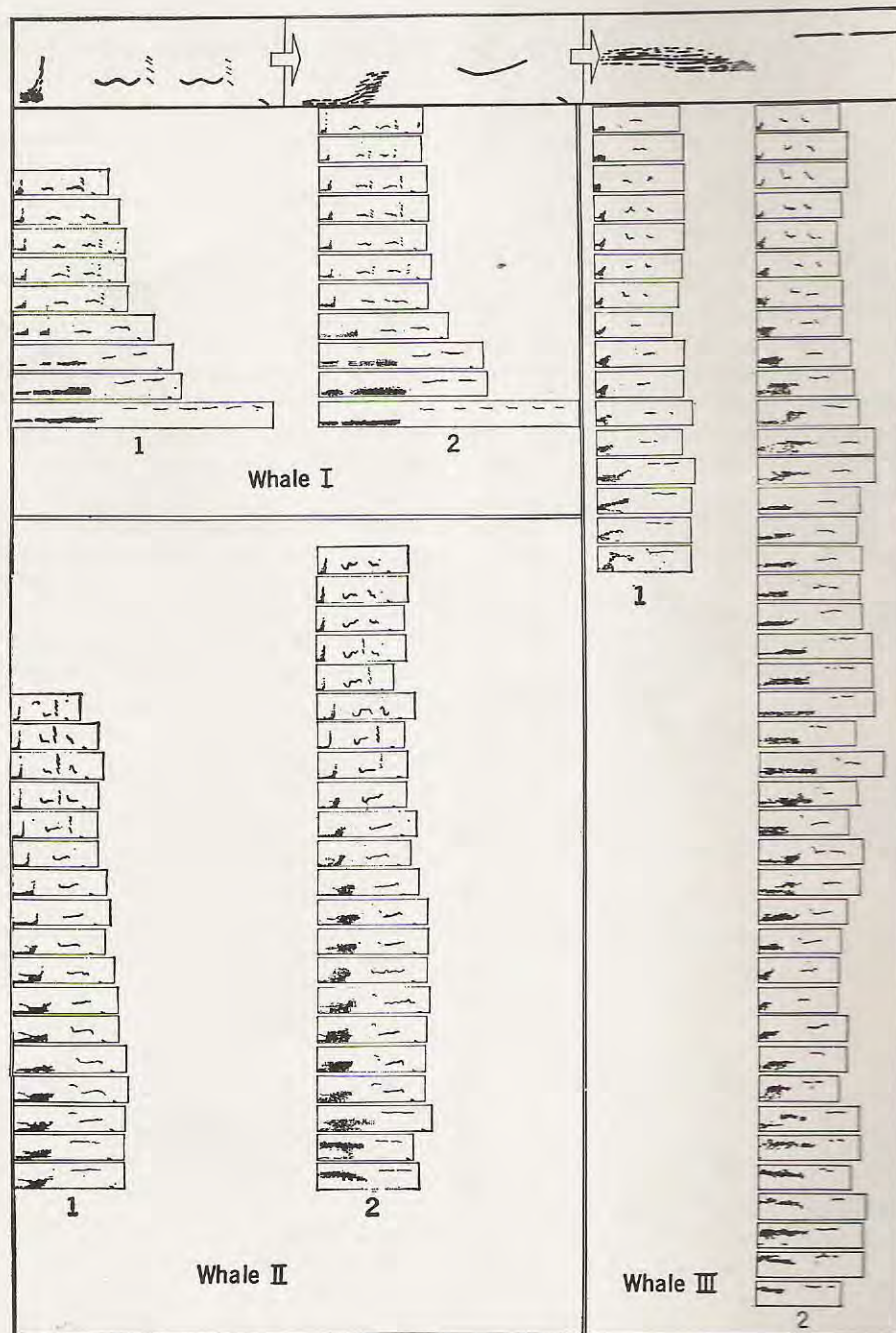


Fig. 6. Theme 1. In this figure, as in Figs. 7 to 9, the enlarged top view shows diagrammatically a typical example of the phrases of which the theme is composed. Beneath, at reduced scale, are tracings of all phrases in each of two songs of whales I, II, and III. No phrases or other sounds are omitted or changed in order, and no time is left out. Observe, by referring to the enlarged top view, the slow evolution of this phrase. Note that the short pulse train becomes longer and higher in frequency with each repetition. We have aligned each phrase so that each moment of onset of sound is brought out to the left edge of the column. The sequence of phrases within the theme reads from top to bottom. Note that in song 1 of whale III, theme 1 contains more than twice as many phrases as does theme 1 of song 2 of the same whale.

A (whales I to III, Figs. 2 to 4) and one of type B (whale IV, Fig. 5). The recording of whale IV was done in 1961 and is the only recording we have from that year. Hence, our treating whale IV's song as representative of a type is an assumption; the possibility remains that this whale was aberrant.

A clear example of song type A is shown in Fig. 2 (whale I). This figure shows sound spectrograms, at a greatly reduced scale, for a complete pair of songs. The pair of songs was lifted from the middle of a continuous song session that contained at least seven songs (there may have been more, but Watlington's tape ran out). The frequency scale in all spectrograms shown here is logarithmic, since that is roughly the way in which the human ear interprets frequency. Had we wished to define precisely the frequency components of each unit, we might have favored a linear frequency display, but our chief purpose was to facilitate comparisons between spectrograms and the sounds they depict. The spectrograms in Figs. 2 to 5 were made by the exceedingly tedious process of extracting successive 9.6-second segments of tape-recorded sounds and analyzing them on a Kay spectrograph (model 6061B), being careful that no time on

the tapes was omitted. The effective filter bandwidth was 60 hertz, and the highest "real time" frequency seen by the spectrograph under these circumstances, 2000 hertz.

Once the spectrograms were made, the hundreds required for each song were carefully matched, glued to large sheets of paper, and photographically reduced. Because the ocean is a noisy place (some of the tapes include wave noise, ship noise, dynamite blasts, and distant whales), and because loud sounds in the water are invariably followed by trains of echoes, we have isolated the whale sounds by tracing them on a separate sheet, thus omitting echoes and noise. Our tracings also exclude harmonics, since they are of little or no consequence in establishing sequences and are often spuriously generated by the spectrograph (12). The only sounds for which we have traced harmonics are brief, pulsive sounds that, to a human listener, are atonal (even when slowed down) and must therefore have a rich harmonic structure. The tracings, of course, fail to show variations in darkness of line—the only indication of intensity that spectrograph machines provide. However, darkness of line, even on the spectrograms shown here, can only be

relied on to reveal relative intensities within any particular 9.6-second sample, since the level of input to the spectrograph machine was often adjusted between successive samples in order to obtain the least distorted rendition. However, a thick line indicates ocean reverberations, in some cases, thus denoting a loud sound.

From inspection of the spectrograms, it is immediately obvious that phrases in most themes are repeated several times before the whale moves on to the next theme. As mentioned above, we find it true of all song types in our sample that, although the number of phrases in a theme is not constant, the sequence of themes is. (For example, the ordering of themes is A,B,C,D,E . . . and not A,B,D,C,E . . .). We have no samples in which a theme is not represented by at least one phrase in every song, although in rare cases a phrase may be uttered incompletely or in highly modified form (compare phrase 4 in the first and second songs of whale III, Fig. 8). Figures 6 to 9 compare themes in song type A as sung by what we assume to be different whales, since the songs were recorded at different times. In this analysis, all phrases within any given theme are shown for each of

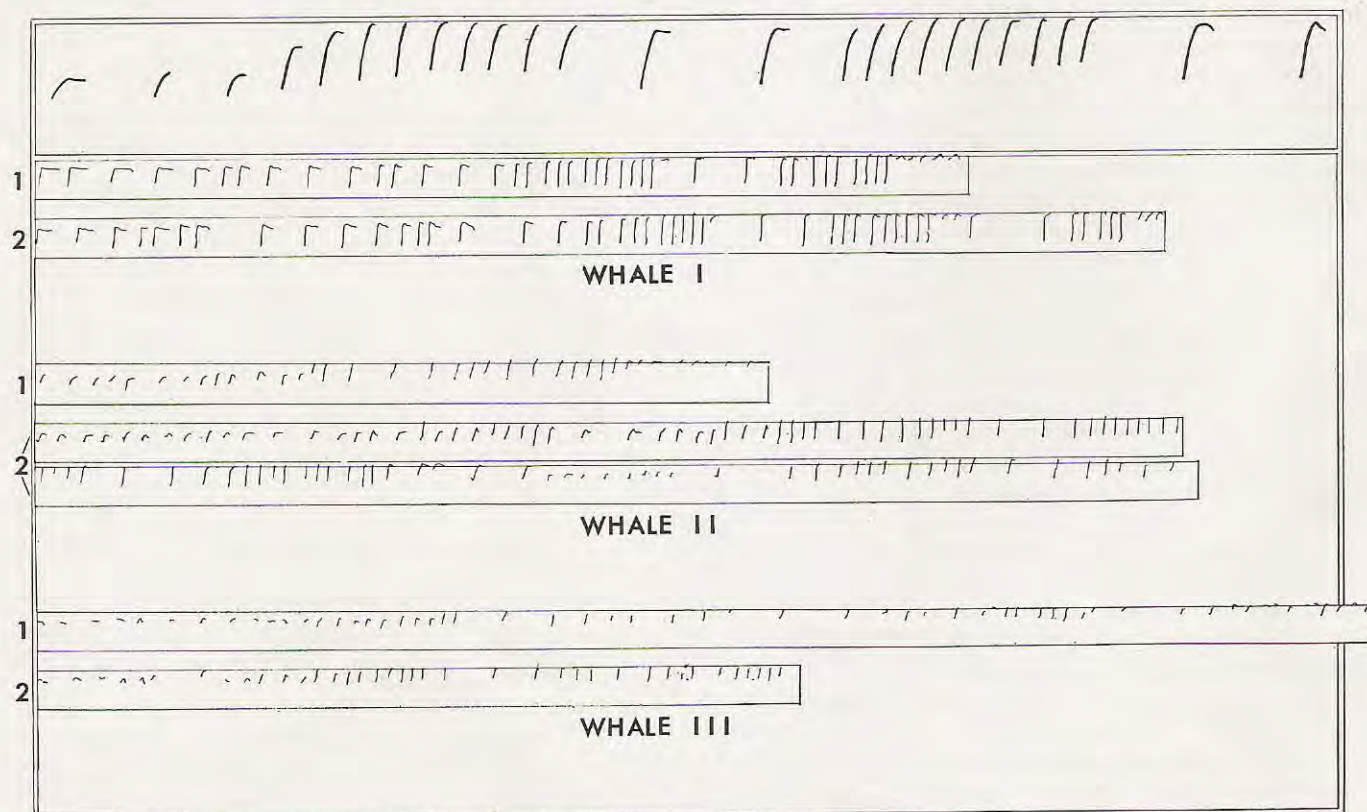


Fig. 7. Theme 2 consists of one long phrase. Note that, in the second song of whale II, this theme is three times as long as in song 1. The interunit spacing of this theme also varies considerably from song to song of the same whale.

two songs sung by each of three whales (I, II, and III). No sounds have been omitted, changed in order, or shifted in time (although we have cut our traced record into pieces, we present the pieces in their original sequence and have omitted none of them).

Before discussing song type A, we must make one final point. Some phrases in humpback songs are further complicated by being inexact replicas within a theme. That is, the phrases systematically change, or "evolve," with each successive repetition during a theme. The phrases in theme 1 of song A are a good example of this. The six themes of song type A are as follows.

Theme 1: Figure 6 shows that each phrase in this theme consists of three principal units—unit 1, a sound like a motor running [a pulse train in which the number of pulses (subunits) per second changes during the train], followed by units 2 and 3, a pair of sustained or wavering tones. (Sometimes each sustained tone is followed by a faint pulse, and sometimes the phrase ends with a very low grunt.) With each repetition of this phrase, unit 1 becomes longer, and, toward the end of the theme, each sustained tone tends to occur at a higher frequency than the previous one. (In song type B, the pulse trains are given without sustained tones between them or with just a brief tone tacked on to the end of the train of pulses—see whale IV.) Thus, in song type A,

theme 1 consists of a series of sequentially modified phrases changing in a predictable fashion.

Theme 2: We arbitrarily designate the onset of theme 2 as the moment when sustained tones give way to shorter tones, or rapidly ascending frequency sweeps. Theme 2 is one of the most variable in our sample. It may consist of a great variety of sounds, but all, or most, of them are ascending frequency sweeps or brief (less than 1 second) high-frequency squeaks or chirps. The theme has no obvious subsets that repeat predictably. Theme 2 is quicker in tempo and less rhythmic than the rest of the song, which is composed of more measured, drawn-out phrases.

Theme 3: The phrases in theme 3 have as their first unit a loud, ascending frequency sweep, which is emitted from one to three times and is followed by several fainter, high-frequency harmonic arpeggios. In some cases, the arpeggios become more elaborate with each repetition of this phrase, until, by the end of the theme, the component notes become more sustained. (See Fig. 10 for an expanded, scale view of arpeggios from the songs of whale II and whale IV.) The loud, ascending frequency sweep, marking the beginning of each phrase 3, usually occurs twice (only once in case of whale III) at the outset, but in the course of the theme changes to three repetitions and stays at three. When there is a transition from two to three,

it is as irreversible as the basic sequence of phrases in a song.

Theme 4: Theme 4 is one phrase long. It starts with a loud, ascending sweep that is similar to unit 1 in theme 3. Each successive unit in this theme rises and falls in frequency, but returns each time to a lower frequency than the preceding unit. (This gives the impression of a deepening series of roars or bellows.) The last units of theme 4 are low-frequency grunts (which may be descending pulse trains).

Theme 5: The phrases of this theme typically have six units. Unit 1 is a downward sweeping note; unit 2, a loud, low, rising or slightly warbling note (followed sometimes by one or more brief, descending, pulsive notes that are hard to detect in poor recordings). Units 3 and 4 are very like units 1 and 2. Units 5 and 6 are grunts. Since there are usually two such grunts, each phrase in theme 5 usually consists of six units. However, there may be three (rarely more) grunts, and sometimes one or even none. This whole phrase is usually repeated once; thus, theme 5 is usually two phrases long.

Theme 6: The components of this theme are unit 1, a loud, sustained tone; unit 2, a descending note (sometimes in the form of a slowly falling warble); unit 3, another sustained tone similar to unit 1; unit 4, a descending note similar to unit 2 (sometimes there are faint pulsive notes after units 2 or 4, or both); and a series of one to

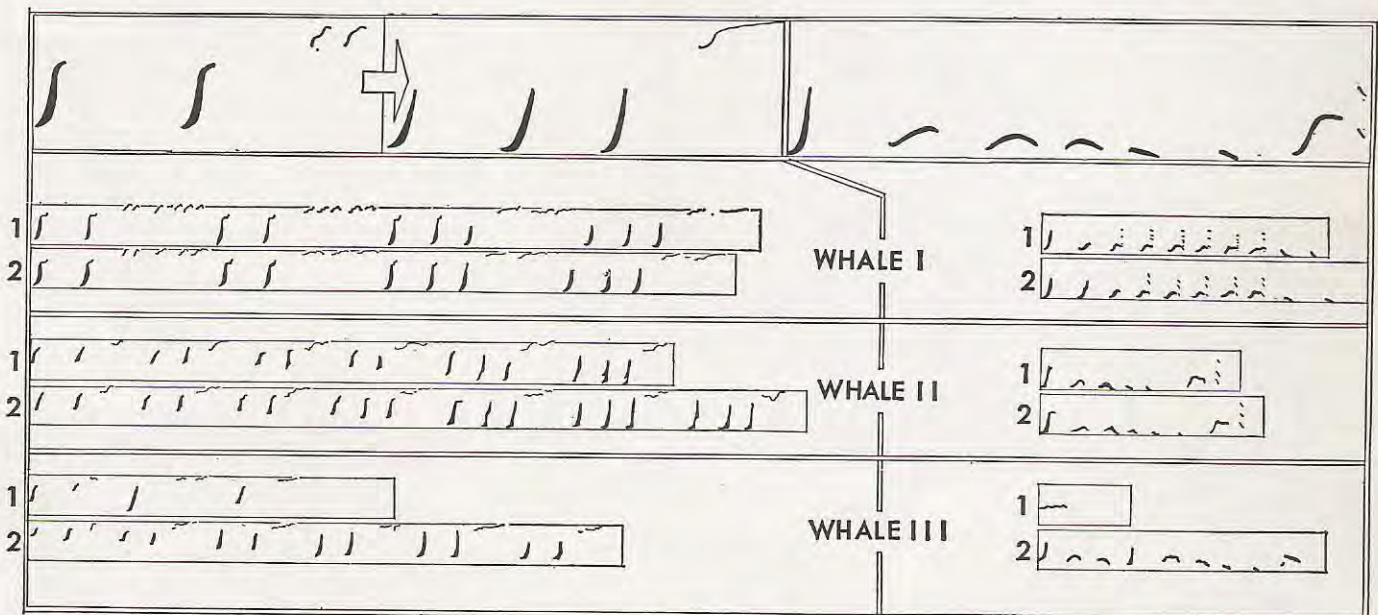


Fig. 8. (Left) Theme 3. Note the evolution of the phrases comprising this theme from two loud sweeps rising in frequency, followed by short, high, harmonic arpeggios, to three loud sweeps rising in frequency, followed by more sustained, rising notes; (right) theme 4 (only one phrase long) is the shortest theme in song type A.

four grunts (units 5, 6, and so on). This phrase is usually repeated quite exactly ten or more times. An interesting sound that is sometimes superimposed on the grunts may represent the audible component of a train of ultrasonic pulses, but this possibility must await recordings on equipment sensitive to ultrasound.

Song type B (as shown by whale IV) resembles type A in themes 1, 2, and 3, but by theme 4 the parallel is less clear. The series of descending

notes shown on line 4 of Fig. 5 is not comparable to anything in song type A, unless it could be thought of as a series of units similar to those in theme 4, but with the duration of the units, and the silences between them, being much greater. The subsequent very short and rapidly delivered notes are certainly unlike type A songs. At the end of its first and second songs, whale IV emits sustained notes that are followed by a low grunt. In a broad sense, this is quite similar to the basic

phrase of theme 6 in song type A. However, in type A the sustained notes differ markedly in pitch, whereas they are delivered at roughly constant pitch in song type B. In some ways, type B is intermediate between type A and the very different song type C. (We have various examples of type C from 1969, but they will not be discussed here.)

Since variability within a fixed general pattern is such a prominent feature of humpback songs, it may be worth taking a detailed look at some of the

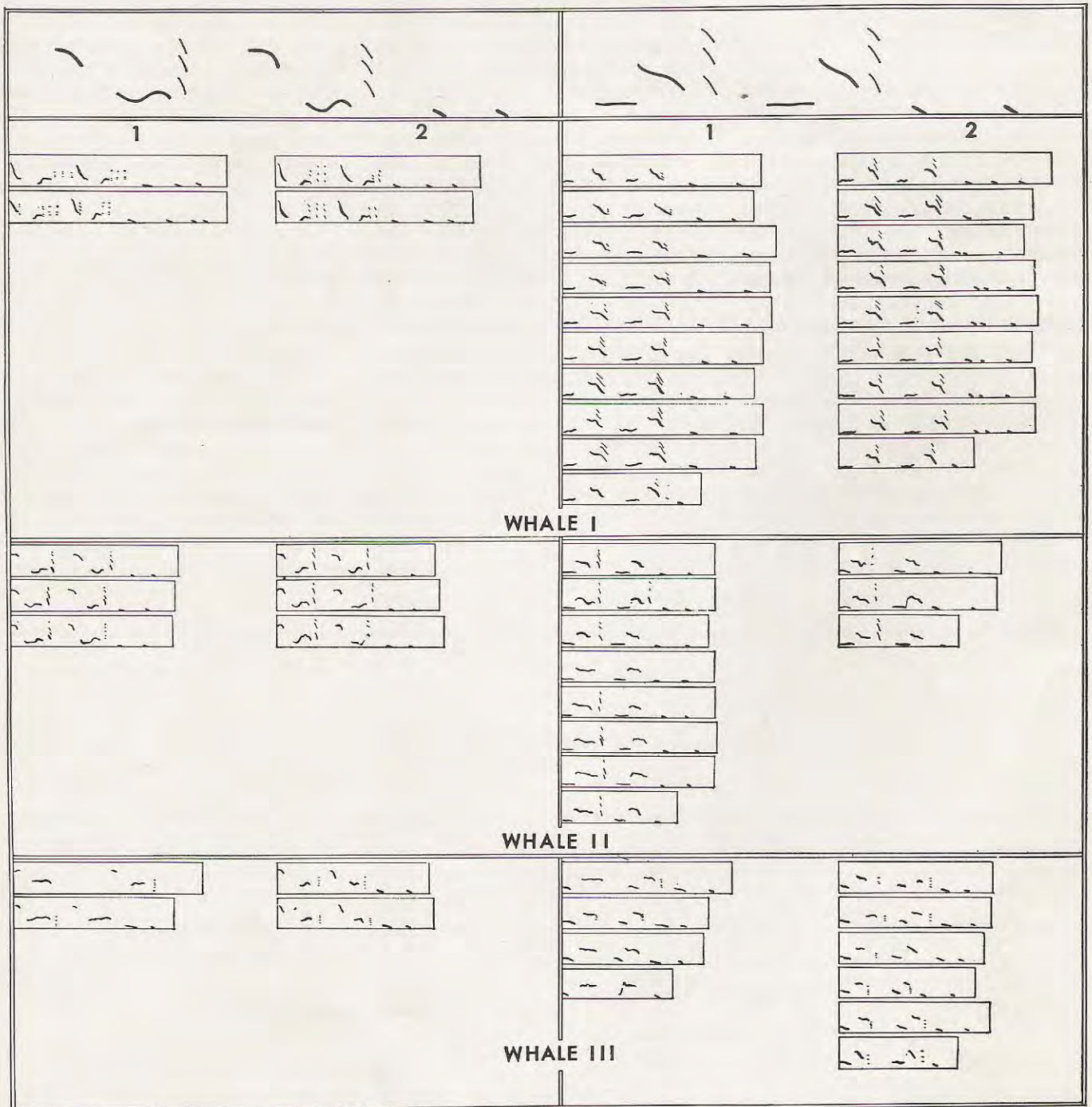


Fig. 9. Themes 5 (left) and 6 (right). The starting moments of the first unit in each phrase are aligned at the left margin of the column. Note the very regular duration and spacing of these sounds.

highest frequency units in the song—the arpeggios following the loud rising units in theme 3 (Fig. 10 shows such units from whales II and IV, song types A and B, respectively). The complexity of the arpeggios and their variation from song to song are obvious.

Beginnings of Songs

Following the last phrase of the final theme in either song type A or B, the whale starts the first sound in the next song (which we have labeled the first, and shortest, pulse train of theme 1) without any noticeable break in the rhythm of singing. The pause between any two phrases of the last theme is, if anything, longer than the pause between the last phrase of one song and the first phrase of the succeeding song. This fact should make it apparent that not only is our designation of phrase beginnings and ends arbitrary, but so is our choice of the start of a song. It is also possible that what we have designated a "song" may, in fact, be a long segment of a still longer song, but that possibility must await further analysis.

The criterion we have used here to determine a starting point is influenced by our large sample of recorded songs from the years 1969 and 1970. In these songs, the overwhelming majority of starts, stops, and blows occurs at a point corresponding roughly to the starting point we have chosen here. Watlington's tapes include very few records of whales beginning to sing and only slightly more of the ends of song sessions. (Usually the tape ran out, the noise level from passing ships rose to mask the whale sounds, or recording was stopped.) Thus the Watlington sample is really too small to warrant any conclusion on this point. It is clear, however, that, regardless of where a song may begin, the whale continues the sequence of themes in the same irreversible order (that is, 3, 4, 5, 6, 1, 2, 3, 4, 5 . . .).

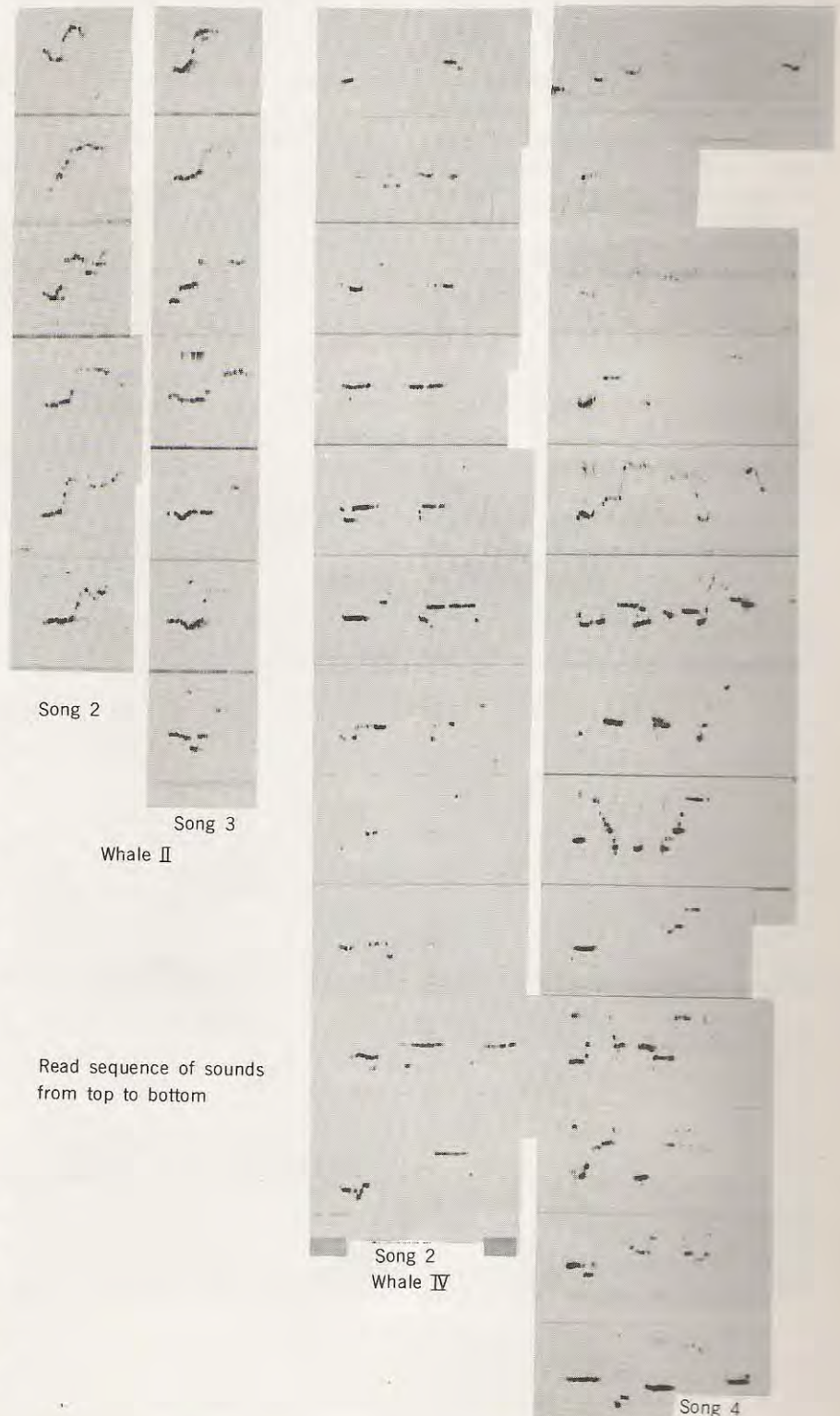
Fig. 10. Linear, wide-band spectrograms (upper frequency limit 2 kilohertz, effective filter bandwidth 200 hertz) show the complex and variable structure of the highest notes in phrase 3. Columns 1 and 2 are from songs 1 and 2 of whale II. Columns 3 and 4 are from songs 1 and 2 of whale IV. Read sequence of sounds from top to bottom. (The intermediate lower and louder frequency sweeps are omitted here.)

Evidence that One Whale Is Responsible for a Song

We have been assuming throughout this discussion that any given song or song session is the performance of one whale.

The evidence that a song is produced by one whale and not by two or more in alternation ("duetting") follows. In

long samples of sounds: (i) we never heard anything less than a song (if we had ever heard songs in which themes, phrases, or units were absent but in which there were pauses of appropriate length to accommodate the missing piece, we might suspect that two whales cooperate to produce a complete song); (ii) no units, or subunits (excluding what are obviously echoes),



have been found to overlap in time; (iii) in some recordings (not reported or diagramed here) we find two complete songs that differ in average volume (indicating two whales, one near and one distant), each progressing in its own rhythm and form with no obvious relationship to the other. An example of a distant whale singing may be seen in the spectrograms, not the tracings, of the second and third themes of the second song of whale II. Here the loudest sounds of a distant whale's phrase 6 are detectable. In addition, some of Payne's 1969-1970 tapes include several whales producing sounds at once. In some cases (presumably when the hydrophone was roughly halfway between two whales), two sound sources are at equal volume, but analysis reveals that both sources are rendering complete songs. Neither whale seems to depend on the other for any phrases or notes. In many cases,

one of the sources stops while the other continues repeating complete songs.

None of our observations absolutely excludes the possibility that songs are actually duets between whales swimming very close together. (Pairs or trios of humpbacks are frequently observed near Bermuda, and they are often in bodily contact when traveling together.) But if the whales are duetting, they are very precise in their alternation of sounds and unfailingly wait their turn to add their own notes.

Sex of the Performing Whale

On the question of whether songs come from males, females, or both, we have nothing yet to offer. It is possible that there will prove to be significant differences between the vocal apparatus of males and females. However, since we are not really sure that the larynx

produces these sounds (though it seems likely that it must be involved), we would not even know what part of a humpback corpse to examine if we had one (and we have never had one). Mature male humpback whales are smaller than mature females, but, because there is so much overlap in size, it is only on very favorable occasions at sea that one could hope to determine the sex of a given whale. In addition, it has been our experience that humpback whales stop singing when we get close enough to distinguish subtle differences in their morphology. [Levenson (6) reports the same difficulty, as does Schevill (2), although Schevill's remarks are restricted to *Odontocetes*.] It will take a very fortunate occasion indeed to see whether males, females, or both sexes produce the songs.

Other Species

The songs we have described are often sung very loudly (a detailed discussion of the theoretical consequences of this is in preparation); therefore, one need not be within viewing range of the source to record the songs. Although this makes recording easy, it raises the constant specter that we have tried too hard to find similarities between songs recorded on different occasions near Bermuda. It is also possible that we may, in fact, be lumping together vocalizations of more than one species.

As mentioned earlier, there is good evidence that finback whales produce their moans in set patterns, and Cummings and Philippi (13) have evidence of cyclic sounds from what they believe to be a right whale (*Eubalaena glacialis*). If their species determination is correct, it could mean that singing is a common form of Mysticete vocalization. For this reason, also, we advance the possibility that we may have combined the sounds of a stray right whale or some other species with true humpback sounds. The large number of humpback whales in the vicinity of Bermuda during April and May (the only months from which our analyzed records were taken) and the apparent lack of right whales in that area at the same time (with the exception of one pair that Payne observed 25 miles southwest of Bermuda on 13 April 1970) argue against this concern. Yet the possibility remains that some other species have been included with our data on humpbacks.

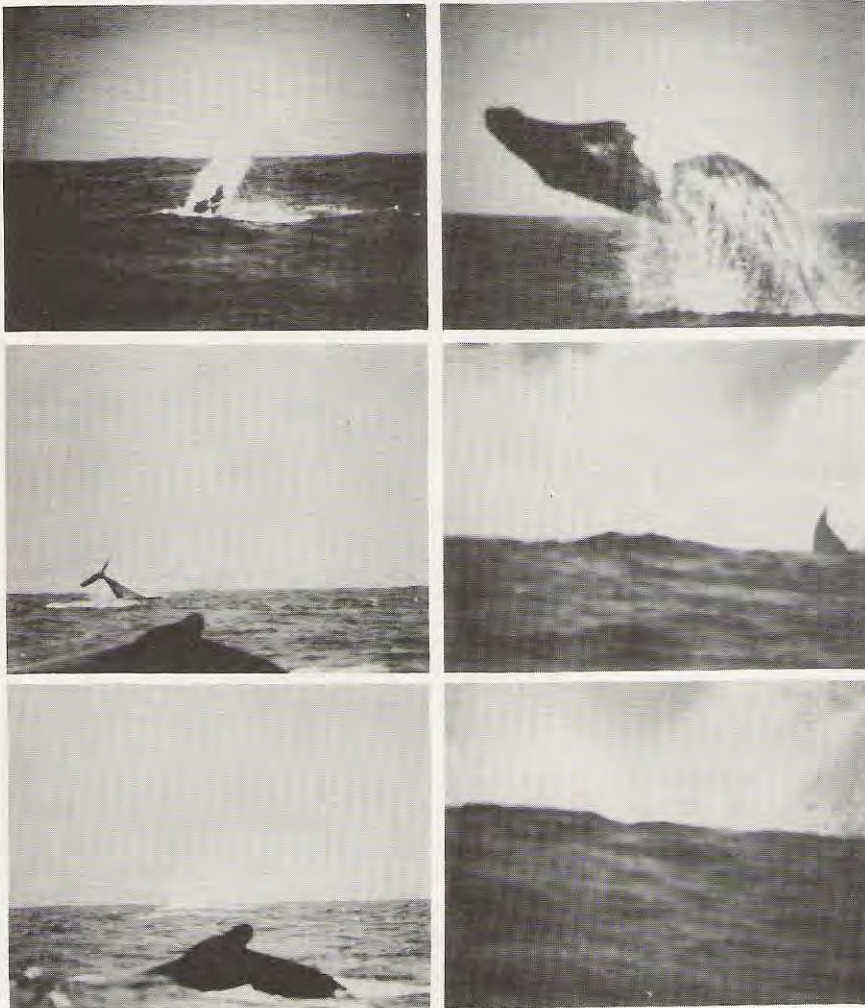


Fig. 11. Upper left, "finning"; remainder of left column, "lobtailing" (two pictures separated by one-half second—the dorsal fin of a nearby whale just starting to dive is prominent). Right column, three pictures (by R. M. Johnson) of a humpback "breaching," showing the impressive splash that follows. Frames are about one-half second apart.

Possible Significance of the Song

Schevill (2) notes: "The sonorous moans and screams associated with the migrations of *Megaptera* past Bermuda and Hawaii may be an audible manifestation of more fundamental vernal urges, for in New England waters and at other seasons we do not hear anything nearly so spectacular from this species." The implication here is that courtship is seasonal. However, there is good evidence, from measurements of embryos collected by whalers, that, even though most successful humpback matings occur during two peak seasons each year, some matings do occur throughout the year (14). Mating, of course, does not always immediately succeed courtship in all species. Even if some humpback pairs mate year-round, it is quite likely that courtship activities leading to pair formation are seasonal. In this case, the songs may be related to pair formation.

The playful behavior of humpbacks near Bermuda in April and May has suggested to some observers that they are courting. The whales slam their tails on the surface of the water (lob-tailing), wave and slap their fins on the water (finning), and frequently and repeatedly jump (breaching) (Fig. 11). However, since these activities are frequently observed at other latitudes and at other times of year (8, p. 288; 15), they do not seem to be particularly linked with singing. If we wish to consider such antics, as well as songs, part of courtship, then we might conclude that the songs are involved with seasonal pair formation, and the acrobatics with year-round mating. Of course, if pair formation occurs year-round, such theories have no meaning.

Winn (16) has heard and recorded humpback songs near Puerto Rico in February, so the songs are apparently

sung for at least 3 to 4 months. Thus, if songs are part of pair formation, we would expect it to be a lengthy process lasting from midwinter until well into spring.

In the North Atlantic, this time period (February to May) also corresponds to northward migration. Thus, one might imagine that the songs serve as a sort of flock call to hold a loose cluster of individuals together during their long migration. Until there is further evidence, we can only guess what function this remarkable series of vocalizations serves.

Summary

1) Humpback whales (*Megaptera novaeangliae*) produce a series of beautiful and varied sounds for a period of 7 to 30 minutes and then repeat the same series with considerable precision. We call such a performance "singing" and each repeated series of sounds a "song."

2) All prolonged sound patterns (recorded so far) of this species are in song form, and each individual adheres to its own song type.

3) There seem to be several song types around which whales construct their songs, but individual variations are pronounced (there is only a very rough species-specific song pattern).

4) Songs are repeated without any obvious pause between them; thus song sessions may continue for several hours.

5) The sequence of themes in successive songs by the same individual is the same. Although the number of phrases per theme varies, no theme is ever completely omitted in our sample.

6) Loud sounds in the ocean, for example dynamite blasts, do not seem to affect the whale's songs.

7) The sex of the performer of any

of the songs we have studied is unknown.

8) The function of the songs is unknown.

References and Notes

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14. Tomilin (8, p. 280) bases his claim (that mating occurs year-round) on 68 humpback fetuses collected during whaling operations in the North Pacific. By extrapolating from embryo lengths, he calculated conception dates and, thus, the number of humpbacks conceived in each month: January, 1; February, 9; March, 12; April, 14; May, 4; June, 3; July, 1; August, 1; September, 12; October, 8; November, 3; and December, 0. Although two periods of increased mating activity are apparent, they are not sharply defined. Yet, even from such a small sample, we see that successful matings have occurred in 11 out of 12 months.
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