Geographic and seasonal variation of blue whale calls in the North Pacific

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ABSTRACT

The call characteristics and distribution of blue whales in the North Pacific were examined by use of acoustic surveys. Two distinct vocalisation types have been previously attributed to blue whales from limited regions in the North Pacific (*cf.* Thompson and Friedl, 1982; Rivers, 1997). Hydrophone data from sixteen sites in the North Pacific were examined for these blue whale vocalisations. There were distinct geographic and seasonal differences between the occurrence of the two vocalisation types. The hydrophones that were more westerly recorded the 'northwestern' Pacific vocalisation, those in the eastern Pacific recorded the 'northeastern' Pacific vocalisation and those in the central Pacific recorded both types. Northeastern vocalisations were recorded from July-December in the northeast Pacific and February-May in the eastern tropical Pacific. Northwestern vocalisations were recorded most often from July-December, and were essentially absent from March-May in the northwestern Pacific. These results suggest that the different vocalisation types may represent at least two distinct groups of blue whales in the North Pacific.

KEYWORDS: BLUE WHALES; DISTRIBUTION; ACOUSTIC SURVEY; NORTH PACIFIC; VOCALISATION

INTRODUCTION

The blue whale (*Balaenoptera musculus* spp.) is a cosmopolitan species that occurs in all the world's oceans. Although now protected, because of historical whaling pressure it is considered endangered throughout its range (Yochem and Leatherwood, 1985). From 1868-1967, an estimated 365,870 blue whales were killed worldwide. Just less than 9,000 were killed in the North Pacific Ocean, with most of these taken either off Baja California, Mexico or south of the Aleutians and west towards the Kamchatka peninsula (Nishiwaki, 1966; Rice, 1974; Brueggeman *et al.*, 1985). In the northeastern Pacific, the current best estimate for the blue whale population is 1,940 (CV = 0.15; Forney *et al.*, 2000), and the number of animals found along the coast of central California appears to be increasing (Calambokidis *et al.*, 1990; Barlow, 1994). There are no current population estimates for the northwestern Pacific.

Many baleen whales produce loud, low-frequency signals that are probably used for communication (Reysenbach de Haan, 1966; Evans, 1967; Winn and Perkins, 1976; Thompson *et al.*, 1979). Whale vocalisations can indicate the presence and movements of a species within an area (*cf.* Watkins and Moore, 1982; Clark and Ellison, 1988; 1989; Clark and Fristrup, 1997; Stafford *et al.*, 1999b), and characteristics of vocal behaviour have been used to distinguish populations of humpback, fin, sperm and killer whales among others (Winn *et al.*, 1981; Ford and Fisher, 1982; Thompson *et al.*, 1992; Weilgart and Whitehead, 1997). It has been suggested that this may also be the case for blue whales (Thompson *et al.*, 1996). Blue whale vocalisations recorded in the Atlantic, off southern Chile and in the Indian Ocean are all distinctly different from one another and from vocalisations described for the North Pacific (Cummings and Thompson, 1971; Edds, 1982; Alling *et al.*, 1991; Clark and Fristrup, 1997).

Blue whale sounds recorded in the northeastern Atlantic are similar to those recorded in the northwestern Atlantic (Charif and Clark, 2000) which suggests that blue whales in the North Atlantic share at least one vocalisation type. This basin-wide similarity in the Atlantic does not appear to be the case for the Pacific. Two different vocalisation types attributed to blue whales in the North Pacific have been reported: the first has been reported from numerous locations in the northeastern Pacific (Cummings and Thompson, 1994; McDonald *et al.*, 1995; Thompson *et al.*, 1996; Clark and Fristrup, 1997; Rivers, 1997; Stafford *et al.*, 1998; 1999a) and the second, much less well documented, from central-latitude hydrophones near Kaneohe, Hawaii and Midway Island (Northrup *et al.*, 1971; Thompson and Friedl, 1982). As yet, acoustic methods cannot provide a quantitative estimate of population size but could provide information on both geographic variation and seasonal occurrence of whales. This paper is an attempt to address these last two topics using blue whale vocalisations in the North Pacific.

The recent availability of long-term passive acoustic data from a number of regions and sources in the North Pacific makes it possible to monitor a large part of this region for whale vocalisations. Two recent publications used some of the same acoustic data sources as presented here, although the data were from different years, to examine large whale occurrence in the North Pacific. Curtis *et al.* (1999) used omni-directional hydrophone data from the North Pacific (1994-1995) to examine sources of ambient noise in the ocean and did not distinguish between the vocalisations of blue and fin whales, assigning all 17Hz sounds as whale vocalisations. Watkins *et al.* (2000) subsampled beam-formed data from 1996-1997 and specifically addressed the seasonality and geographic variation of blue, fin and humpback whales in the North Pacific but did not distinguish between the two distinct vocalisation types discussed in this paper. This paper reports on the differences in seasonal and spatial occurrence of two different types of blue whale vocalisations. Determination of when and where the two different vocalisation types are recorded can provide key insight into the geographic variation of blue whale vocalisations.

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METHODS

Study area

For the purposes of this study, the North Pacific Ocean was divided into three very general regions: the western Pacific, eastern Pacific and the central Pacific (Figs 1 and 2). The northwestern Pacific region includes the subarctic Pacific, from the Aleutians west to the Kamchatka peninsula and south to the subarctic transition zone and encompasses much of the region of the western subarctic gyre, hereafter WSAG (Springer *et al.*, 1999). This region is characterised by complex surface circulation in which oceanic fronts, eddies and upwelling fronts occur. These types of frontal regions were considered reliable whaling grounds for all species of commercially targeted baleen whales (Uda and Dairokuno, 1957; Nasu, 1966).

The northeastern Pacific region includes the upwelling zone along the west coast of North America and the highly productive eastern tropical Pacific (ETP) north of the equator. The coastal upwelling domain (Ware and McFarlane, 1989) is dominated largely by the California current system whose northern-southern boundaries occur on average at about 50-25°N latitude.

The central North Pacific region was considered to be anything within the central subtropical gyre. This central gyre has anti-cyclonic circulation resulting in convergence and downwelling of surface waters and, relative to the western and eastern regions, is not considered to be a region of high productivity.

Data collection

Acoustic data from omni-directional hydrophones in the North Pacific were examined for blue whale vocalisations. The acoustic data examined were from sixteen hydrophones,

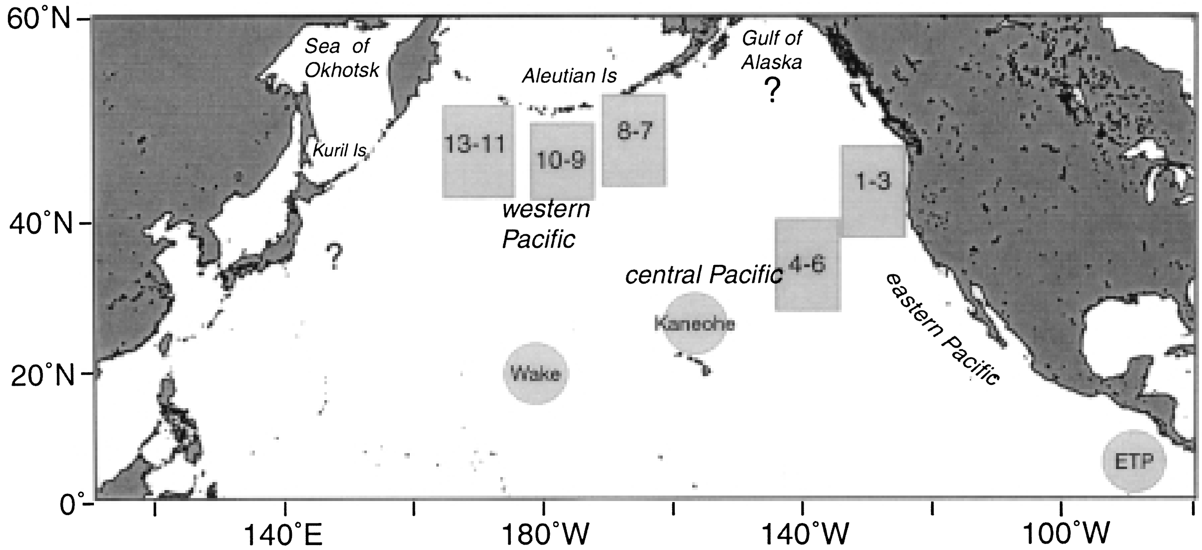

Fig. 1. Location of hydrophones selected from arrays in the North Pacific Ocean. Numbered hydrophones are from various arrays, including US military arrays. The hydrophone labelled ETP is located at 8°N95°W and is from an array of six hydrophones moored by NOAA/PMEL in the eastern tropical Pacific (see Stafford *et al.*, 1999b). ? = areas without hydrophone coverage.

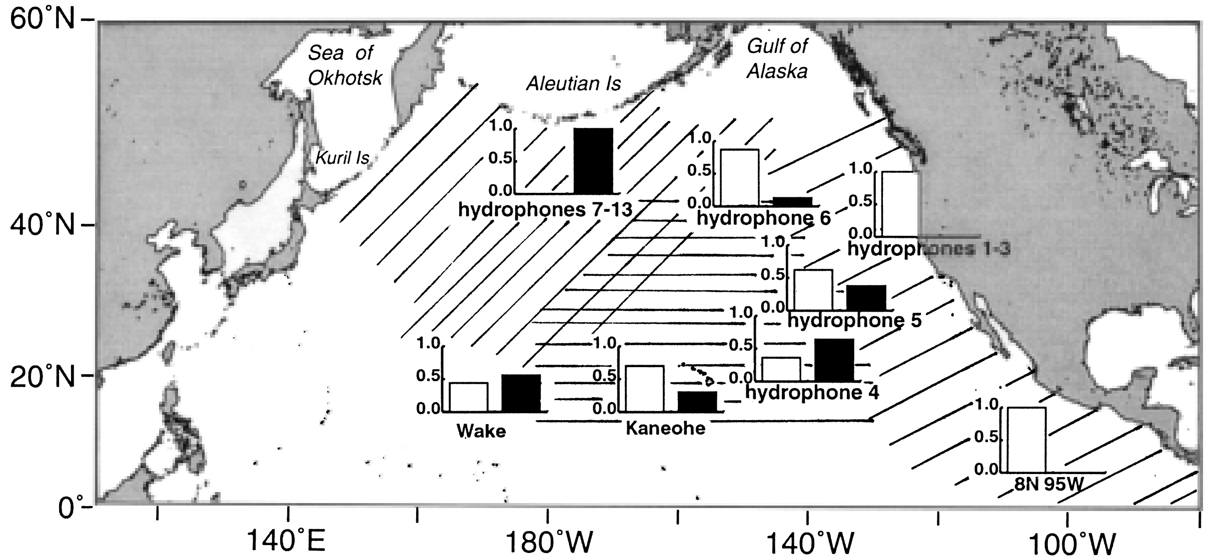

Fig. 2. Proportion of the northeastern (white bars) and northwestern (black bars) vocalisations at each hydrophone. Hydrophones 7-13 had identical proportions as did hydrophones 1-3 so only one graph is shown for each of these two groups. See Fig. 1 for general position of hydrophones. Proportions were determined by number of hours of one kind of vocalisation over the total number of hours of either vocalisation, i.e. the proportion of NWP calls would be = NWP calls/(NWP calls + NEP calls). Shaded areas show general regions in the North Pacific as described in the text (i.e. central Pacific) and do not represent acoustic coverage of these areas. /// western Pacific region; ≡ central Pacific region; / / / eastern Pacific region.

Table 1

Periods sampled, total hours of available data and hours of data in which either northeast or northwest Pacific calls were recorded in the eastern, central and western Pacific. Percentage of hours with calls is given in parentheses below the number of hours. Although northwestern calls were recorded during one or two hours from hydrophones 1 and 3 respectively, the percentage of total hours is much less than 1 (<0.001) therefore the occurrence of this call type in these regions was effectively 0. SR = sample rate in Hertz, LP = low-pass filter cut-off. Hydrophone locations are shown in Figure 1.

	Eastern Pacific				Central Pacific					Western Pacific						
Hydrophone no.	1	2	3	8N95W	4	5	6	Wake	Kaneohe	7	8	9	10	11	12	13
SR/LP (Hz)	Nov. 1995-Nov. 1996 128/60			May 1996-May 1997 100/40	Nov. 1995-Nov. 1996 128/60			Apr. 1992-Dec. 1992 100/25	Aug. 1992-Apr. 1993 100/30	Nov. 1995-Nov. 1996 128/60						
Total hours available	6,894	6,901	6,616	8,735	7,279	7,307	7,156	4,187	5,025	7,224	7,277	7,208	6,995	7,099	7,255	7,267
Hrs with NE calls	371	458	612	4,188	511	376	1,051	54	617	0	0	0	0	0	0	0
(%)	(5.4)	(6.6)	(9.2)	(50)	(7)	(5.1)	(14.7)	(1.2)	(12.3)							
Hrs with NW calls	1	0	2	0	907	227	163	69	261	1,984	2,854	4,273	3,897	3,755	4,186	3,205
(%)	(0)		(0)		(12.5)	(3.1)	(2.3)	(1.6)	(5.2)	(27.5)	(39.2)	(59.3)	(55.7)	(52.9)	(57.7)	(44.1)

including hydrophones from US Navy SOund SUrveillance System (SOSUS) arrays (Fig. 1). Single hydrophones were located off Kaneohe, Hawaii and Wake Island. One hydrophone was located in the eastern tropical Pacific and was deployed by the National Oceanic and Atmospheric Administration's (NOAA) Pacific Marine Environmental Laboratory (PMEL). While the exact locations of the US Navy arrays are currently protected, the location of the PMEL hydrophone is not. One year of data was examined from the US Navy and PMEL hydrophones, and just under eight months of data were examined from the Wake and Kaneohe hydrophones. Sample rates, cut off frequencies, dates of data examined and total number of hours of data available are given in Table 1.

The acoustic data were analysed for the presence of sounds typically associated with North Pacific blue whales. As noted in the Introduction, the sounds attributed to blue whales in the North Pacific differ in their characteristics (e.g. frequency, duration, modulation) depending on whether they were recorded in the northeastern or northwestern Pacific. From this point forward the two acoustic types will be referred to as the northeastern and northwestern Pacific vocalisations. A preliminary repertoire of four sounds has been described for the northeastern Pacific vocalisation type (Thompson *et al.*, 1996; Rivers, 1997; Stafford *et al.*, 1998). The most widespread vocalisation consists of two parts with fundamental frequencies < 20Hz; the two parts are separated in time by up to 25s and are often referred to as parts A and B. The only northwestern Pacific vocalisation type previously described is a 2-part moan with fundamental frequencies > 20Hz and has been recorded in the central and western Pacific (Northrup *et al.*, 1971; Thompson and Friedl, 1982).

Concurrent datasets covering the entire North Pacific Ocean were not available, so the datasets examined here covered different time periods (Table 1) and were occasionally of poor quality (i.e. the Wake Island dataset which had high levels of ambient noise and large gaps in data availability). Every hour of available data was examined for blue whale vocalisations. If data were missing, or if background noise due to shipping or seismic events was so loud as to make it impossible to detect any other signals, the hour in question was not included in the analysis. Presence (+) or absence (0) of the two vocalisation types (northeastern and northwestern Pacific) was noted for each hour of data for each hydrophone examined based on visual inspection of spectrograms (5.12s Fast Fourier Transform (FFT), 50% overlap, Hanning window) following Thompson and Friedl (1982)[1]. A vocalisation type was considered present irrespective of the number of times it occurred within that hour. A monthly proportion score was determined by dividing the number of hours during which a vocalisation type was seen in a month by the total number of hours of data available for that month (i.e. if a blue whale vocalisation was scored as present during 100h during July, and 600h were available for that month, the score for that month was 100/600 = 0.167). Seasonality for each region was determined by plotting these monthly proportions. Occurrences of vocalisations from different individual whales were not noted as in Watkins *et al.* (2000).

Acoustic characteristics of representative northwestern and northeastern types were measured for a limited number of sounds with high signal to noise ratio. Measurements of beginning frequency, ending frequency and duration were digitised from a graphic workstation. Intervocalisation intervals (the time from the end of one sound to the beginning of the following sound) were also measured. The assumption was made that a series of sequential sounds were produced by a single animal. If no sounds were detected for over 6h, then a series of sounds after this time gap was attributed to a different animal. Therefore, although the sample size for an individual animal might include tens of sounds, the sample sizes reported here are the minimum number of individuals. Averages and standard deviations for each of the time and frequency values were obtained for vocalisations from presumed individual whales. These data were then averaged over all presumed individual whales. These measured sounds were used as the basis for comparing differences between regions and seasons.

RESULTS

Over 110,000h of data were examined from sixteen different hydrophones in the North Pacific Ocean. Northeastern Pacific blue whale vocalisations were detected during 8,238h from nine hydrophones. Northwestern Pacific blue whale vocalisations were detected during 25,784h from

[1] Differences in the occurrence of northeastern Pacific blue whale calls between this study and Stafford *et al.* (1999a) are due to several factors: Stafford *et al.* (1999a) combined hydrophones 1, 2 and 3 in their presentation of call occurrence for the northeastern Pacific; they also used data from formed beams recognising that beamforming provides significant gain in signal-to-noise ratio and thus allows detection of more calls. Stafford *et al.* (1999a) reported occurrence in terms of the average number of days/month (vs. hrs/month reported here). This meant that a day in which there were blue whale calls during only two hours had the same weight as a day in which there were calls during 22h.

fourteen hydrophones (Table 1). There were distinct geographic differences in the occurrence of each vocalisation type as shown by a comparison of the proportions of total detections of the two vocalisation types for each hydrophone site (Fig. 2). The hydrophones that were more westerly recorded the northwestern Pacific vocalisation, those in the northeastern Pacific recorded the northeastern Pacific vocalisation and those in the central North Pacific recorded both types (but at much lower levels).

In order to quantify the differences between the two vocalisation types, over 3,000 sounds from patterned sequences from a minimum of 54 blue whales were analysed. The northwestern Pacific vocalisation is shorter overall and higher in frequency than the northeastern Pacific vocalisation. The northwestern vocalisations are mainly frequency-modulated moans whereas northeastern Pacific vocalisations include an amplitude-modulated sound followed by a frequency-modulated moan.

Description of sound types

Northeastern Pacific vocalisations

Over 1,700 northeastern Pacific type vocalisations from a minimum of 19 animals were measured for total duration and frequency. The predominant type of blue whale sound recorded in the northeastern Pacific consisted of a repeating pattern of two sounds (Fig. 3a). The first part is amplitude modulated and referred to as part A, while the second part is a frequency modulated downsweep and referred to as part B. In general, the pattern in the northeastern Pacific consisted of repeated series of AB vocalisations, but often A sounds were followed by a series of B sounds (Fig. 4a). Sometimes a third sound (‘C’) at 11Hz occurs between A and B sounds (Clark and Fristrup, 1997; Stafford *et al.*, 1999a). A fourth sound (‘D’) was first described by Thompson *et al.* (1996). These sounds were short pulses which swept from about 98Hz to 25Hz and lasted about 1s (Thompson *et al.*, 1996). These D sounds were not detected on the data presented here although the lower frequency range of these sounds is within the range of some of the data examined.

On average, for the data presented here, the A vocalisation lasted 18.2s (±2.5, $n = 16$) and had its lowest components at 15.3Hz (±0.4, $n = 16$). The B vocalisation swept from 18Hz (±0.3, $n = 19$) to 16.1Hz (±0.2, $n = 19$) over 17.5s (±1.5, $n = 19$). The mean time between the A and B vocalisations was 25.6s (±6.2, $n = 18$). When an A vocalisation was followed by more than one B vocalisation, the mean time between B vocalisations was 30.6s (±0.7, $n = 5$). The mean time from the end of a B vocalisation to the beginning of the following A in a series was 58.2s (±6.5, $n = 6$). C vocalisations swept up from 11.0Hz (±0.4, $n = 4$) to 11.7Hz (±0.4, $n = 4$) over 8.7s (±1.9, $n = 4$). Detection of any of these vocalisations was considered as detection of a northeastern Pacific blue whale vocalisation.

Northwestern Pacific vocalisations

Over 1,300 northwestern Pacific type vocalisations from a minimum 35 blue whales were measured for total duration and frequency. Four distinct low-frequency sounds were associated with northwestern Pacific blue whales.

The first (I) was a long, two- to three-part sound often with a break between parts (Fig. 3b). This vocalisation lasted 22.7s on average (±1.1, $n = 16$). In general it consisted of a tone at 20.2Hz (±0.2, $n = 35$) lasting 6.2s (±0.8, $n = 35$), then a jump down in frequency to 18.4Hz (±0.4, $n = 35$) over 2.5s (±0.9, $n = 35$), followed by another slightly upswept tone 4.6s (±0.9, $n = 35$) in duration at 18.7Hz (±0.6, $n = 35$). There may or may not be a slight gap between this first section and either an up-down sweep from 18.2Hz (±0.2, $n = 15$) to 19.3Hz (±0.2, $n = 15$) over 3.1s (±0.5, $n = 15$) back down to 18.4Hz (±0.2, $n = 15$) over 7.0s (±0.9, $n = 15$) or a jump up in frequency (no upsweep) to 19.1Hz (±0.5, $n = 20$) followed by a 6.9s (±1.4, $n = 20$) downsweep to 18.6Hz (±0.4, $n = 20$).

The second type of sound (II) resembled the first, consisting of only the first two parts of the vocalisation described above and lasting on average 16.9s (±1.8, $n = 24$). The first part was a 6.6s (±0.8, $n = 24$) tone at 20.2Hz (±0.2, $n = 24$) followed by a downsweep to 18.8Hz (±0.8, $n = 24$) lasting 2.3s (±1.1, $n = 24$) and ending with an 8.0s (±2.2, $n = 24$) slight sweep to 18.5Hz (±0.6, $n = 24$).

The third (III) and fourth (IV) sounds were usually seen together. The third vocalisation was similar to the first two but much shorter: it lasted 11.1s (±2.2, $n = 8$) and began as a 6.9s (±2.0, $n = 8$) tone at 20.2Hz (±0.2, $n = 8$) that then swept down to 18.1Hz (±0.4, $n = 8$) over the next 4.1s (±1.23, $n = 8$). This vocalisation was usually followed 5.7s (±2.3, $n = 3$) later by the fourth type of vocalisation. This was a long, downsweep from 55.8Hz (±3.6, $n = 3$) to 32.1Hz (±1.5, $n = 3$) over 7.8s (±1.2, $n = 3$) and was markedly different

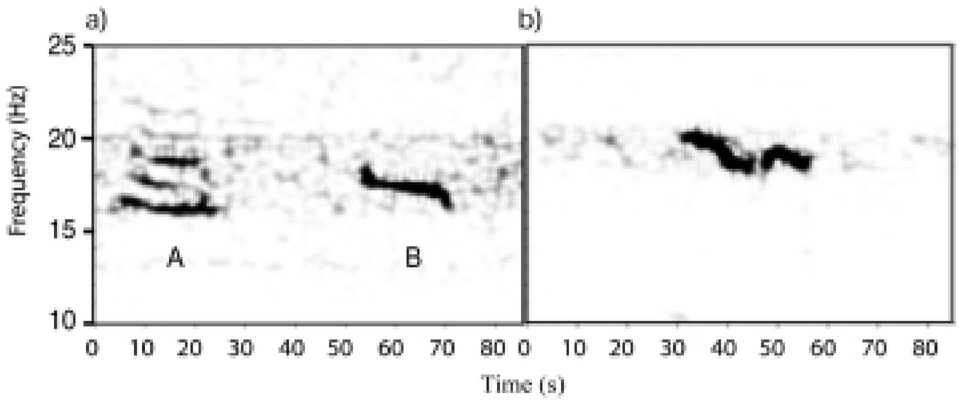

Fig. 3. Spectrograms of exemplar vocalisations recorded from the northeastern and northwestern Pacific (FFT 5.12s, 97% overlap, Hanning window). (a) AB pair from the northeastern Pacific. The A vocalisation is amplitude modulated and the B vocalisation is frequency-modulated. (b) Northwestern Pacific vocalisation. This sound is a two-part frequency modulated moan. The northwestern Pacific vocalisation is higher in frequency and longer than either the A or B sounds of the northeastern Pacific vocalisation.

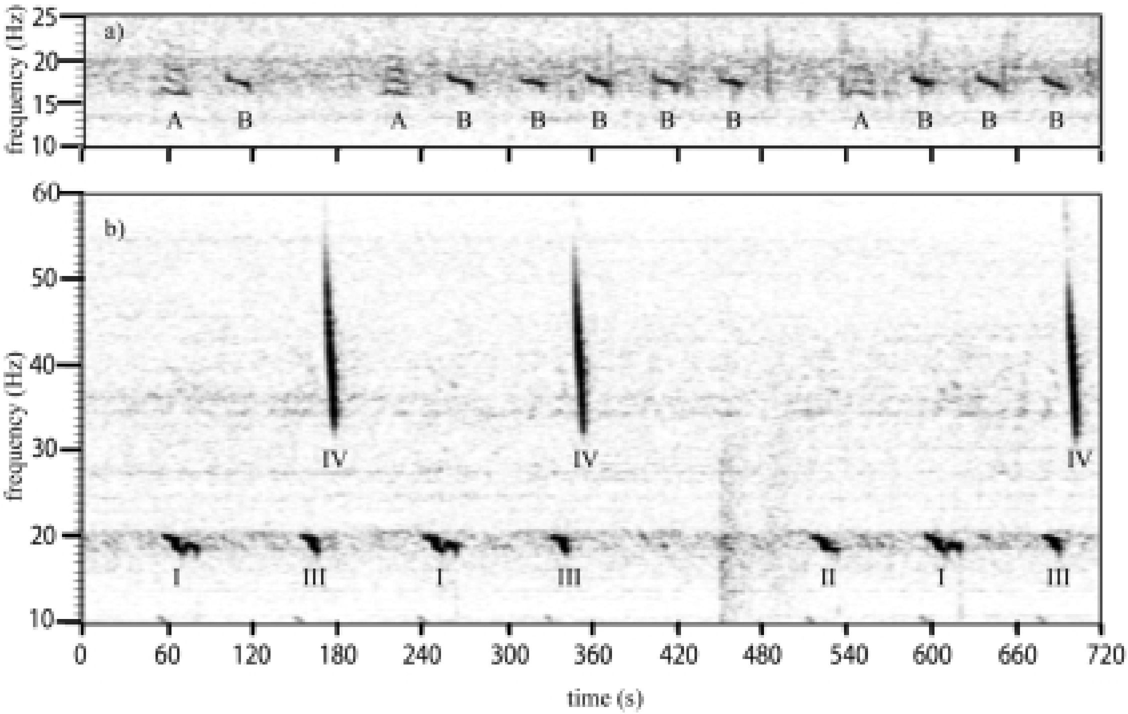

Fig. 4. Spectrograms and time series of patterned sequences of northeastern Pacific and northwestern Pacific blue whale vocalisations (FFT 5.12s, 87.5% overlap, Hanning window). (a) Northeastern Pacific blue whale vocalisations. Typically these sounds appear as repeating A-B pairs, but occasionally the A sound is followed by multiple B sounds as shown above. (b) Sequence of northwestern blue whale vocalisations that shows the four different sounds ascribed to this blue whale vocalisation type.

from any of the other sounds. As it was never seen without being preceded by the third vocalisation, it seems clear that the two are produced as a pair. The mean time between successive vocalisations was 56.9s (±8.0, $n = 21$). Fig. 4b shows a series of patterned northwestern Pacific vocalisations which includes examples of each of the sounds described above. Detection of any of these vocalisations was considered as detection of a northwestern Pacific blue whale vocalisation.

Distribution and seasonality of vocalisations

Northeastern Pacific vocalisations

The northeastern Pacific vocalisation was recorded on hydrophones located in the northeastern Pacific, the ETP and to a much lesser extent at Kaneohe and Wake (Table 1). There were no northeastern vocalisations detected on hydrophones in the central (hydrophones 7 and 8) and western (hydrophones 9 and 10) Aleutians or the northwestern Pacific (hydrophones 11-13). Northeastern Pacific blue whale vocalisations were detected from July to December in the northeastern Pacific (hydrophones 1, 2 and 3). No vocalisations were detected on any of these three hydrophones from February to June (Figs 5a-c). They were detected throughout the year in the ETP but most often from February to May (Fig. 5d). Northeastern Pacific vocalisations were recorded in the central Pacific primarily on hydrophone 6, which is the furthest north and east of the central hydrophones. Except in November, northeastern Pacific vocalisations were recorded at very low levels (< 0.10) on the central Pacific hydrophones (Figs 6a-c). Northeastern vocalisations were detected infrequently on the Wake Island hydrophone, rarely during August-October (< 0.013) and then sporadically in November and December (Fig. 6d). These vocalisations were detected at the Kaneohe site most often in August-September (< 0.05) and rarely from October-March (< 0.02). Kaneohe vocalisation patterns for March-July are unknown because data were not available for this site during these months (Fig. 6e).

Northwestern Pacific vocalisations

Northwestern Pacific vocalisations were recorded on 14 of the 16 monitored hydrophones, but only rarely on hydrophones 1-3 (< 0.001) and the Wake Island hydrophone (< 0.016, Table 1). There was a clear seasonal signature in vocalisation reception in the central (hydrophones 7 and 8) and western Aleutians (hydrophones 9 and 10) and the northwestern Pacific (hydrophones 11-13): the proportion of northwestern vocalisations increased from June-August, remained at high levels until the end of October, decreased to very low levels by February. They were essentially absent from March to May (Figs 7a-g). The occurrence of vocalisations at the more eastern central Aleutians site (hydrophone 7, Fig. 7a) was lower than for the western Aleutians and the northwestern Pacific. Vocalisations on the easternmost hydrophones in the Aleutians (7 and 8) increased later in the summer and decreased earlier in the winter than at hydrophones 9-13, with few to no vocalisations from January-May (Figs 7a,b).

Occurrence of the northwestern Pacific vocalisations on the hydrophones in the offshore northeastern Pacific (4,5,6) was quite low throughout the year, with the exception of the southernmost hydrophone (4) in which a seasonal pattern of vocalisation reception was evident (Figs 6a-c). Vocalisations were detected over 25% of the time between August and

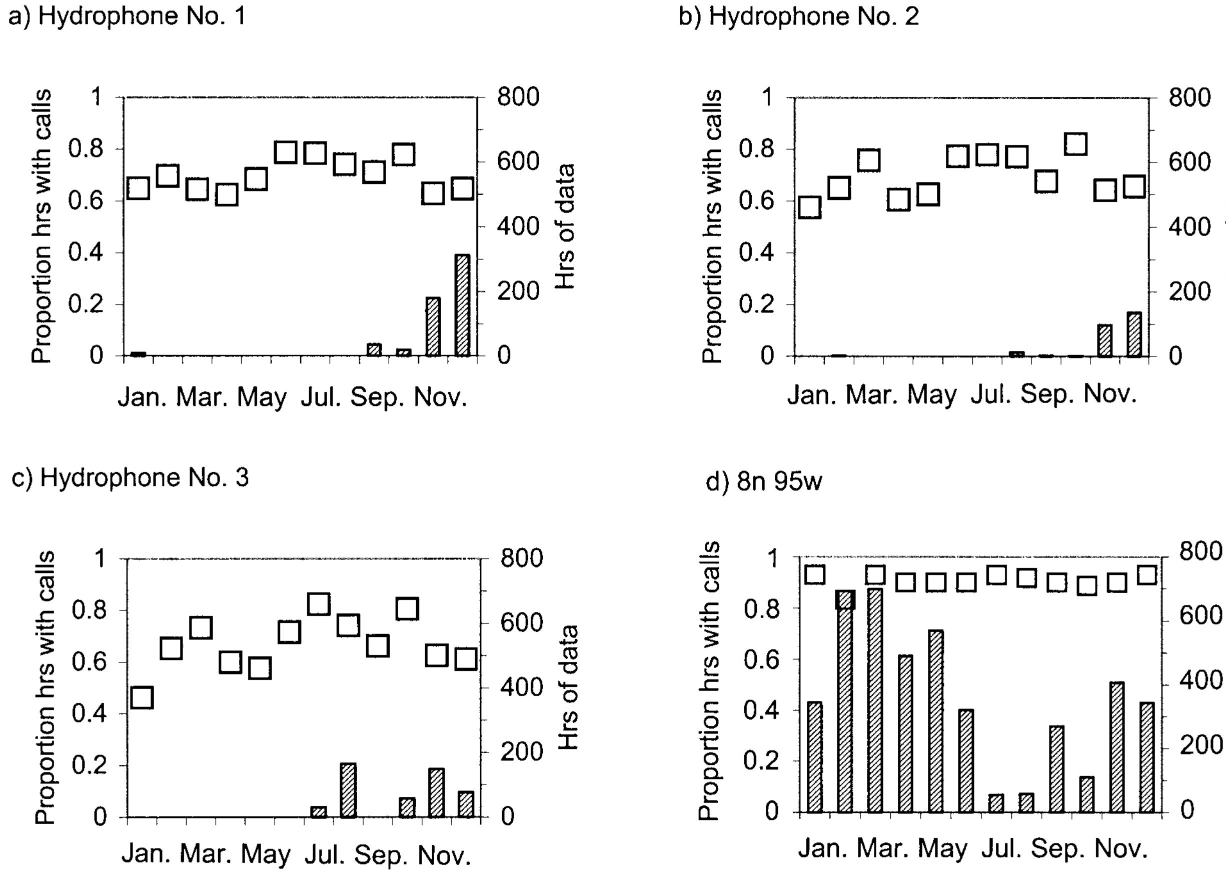

Fig. 5. Seasonal occurrence of blue whale calls recorded on hydrophones and number of hours examined by month in the eastern Pacific. Histograms represent the proportion of hours available by month during which blue whale sounds were detected (left ordinate). Hatched bars represent northeastern Pacific sounds. The open squares show the sample size of the number of hours of data examined per month (right ordinate). Approximate locations of the hydrophones are shown in Fig. 1.

November and sounds were reduced or absent from December-July. All of the central region hydrophones showed low levels of calling early in the year. The lack of a full year of data for the Kaneohe and Wake regions makes it difficult to discern any seasonal pattern for this area. However, western vocalisations were recorded at Kaneohe primarily in the month of January and at Wake from April through July at low levels (Figs 6d,e).

DISCUSSION

Blue whale vocalisations recorded at numerous sites in the North Pacific show geographic and seasonal variation. There are two very distinct blue whale vocalisation types recorded in the North Pacific. The first, the northeastern Pacific vocalisation, is typically recorded as a patterned sequence of A-B sounds. In the eastern North Pacific, this is the predominant vocalisation type recorded. The second type, or northwestern Pacific vocalisation, is typically a long, low-frequency moan that is also produced as a sequence of sounds. This is the only blue whale vocalisation type that has been recorded to date in the western Pacific. Both vocalisation types are recorded in the central Pacific.

Although the two vocalisation types have different geographic distributions, they show similar seasonality in the North Pacific. Both vocalisation types are recorded most often in the summer and autumn and least often in the early winter and spring on the northern latitude hydrophones, suggesting a simultaneous, separate, migration from higher to lower latitudes during the late autumn. The northeastern Pacific vocalisation is recorded throughout the year but during the winter months it is recorded primarily in the ETP. Migration of blue whales between the northeastern Pacific and the ETP has been documented via photo-identification (Calambokidis *et al.*, 1998; Chandler *et al.*, 1999) and satellite telemetry (Mate *et al.*, 1999) studies and supported by acoustic data (Stafford *et al.*, 1999a).

It is not known whether the northwestern Pacific blue whales vocalise throughout the year. There are no acoustic data available for these animals in the southern regions of the northwestern Pacific; and it is unclear where these blue whales may be found during the months when their vocalisations are not recorded on the northwestern hydrophones. With the exception of a single report from data recorded off Midway Island (Northrup *et al.*, 1971), there are no recordings of blue whale vocalisations from the North Pacific published in the literature from any region south of the northwestern Pacific region defined here. Northrup *et al.* (1971) discuss the winter occurrence of long 20Hz signals recorded in the central Pacific. Vocalisations they describe from Midway Island are similar to the northwestern Pacific vocalisations discussed here but are somewhat higher in frequency (25-23Hz) and longer by several seconds (25s duration). This difference in frequency could represent a sub-division of western vocalisations but more data are needed to confirm this. Blue whales were occasionally taken by whaling vessels off Taiwan (Tomilin, 1957), and this may represent the southwestern-most record for this species in the North Pacific. It is clearly necessary to obtain any available

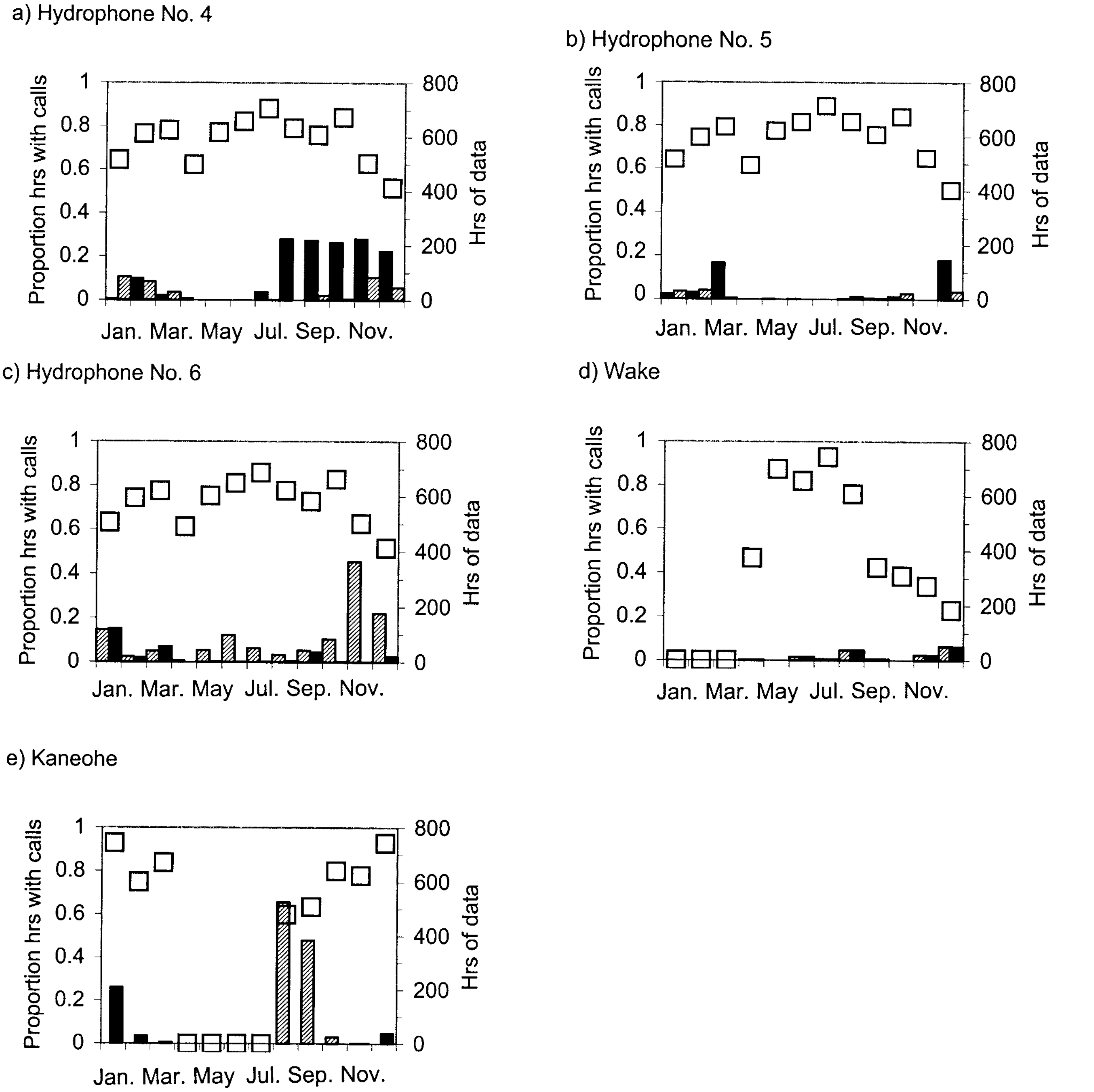

Fig. 6. Seasonal occurrence of blue whale calls recorded on hydrophones and number of hours examined by month in the central Pacific. Histograms represent the proportion of hours available by month during which blue whale sounds were detected (left ordinate). Hatched bars represent northeastern Pacific sounds while dark bars represent northwestern sounds. The open squares show the sample size of the number of hours of data examined per month (right ordinate). Approximate locations of the hydrophones are shown in Fig. 1.

recordings from regions in the southwestern North Pacific and examine them for blue whale vocalisations to help establish the winter range of these animals.

The seasonality and geographic locations of recorded vocalisations matches the whaling record fairly well. Gilpatrick *et al.* (1997) provide an excellent synopsis of whaling effort in the North Pacific. Whales were observed year-round off Japan, Korea and California (Tomilin, 1957) but otherwise blue whales were considered to migrate in a generally seasonal north-south direction. Whalers spent little time in the far North Pacific during winter months (probably for practical reasons regarding weather and day length) although the acoustic data presented here and elsewhere (Curtis *et al.*, 1999; Watkins *et al.*, 2000) indicate that blue whales are in these waters at this time of year. It may be that some North Pacific blue whales remain at high latitudes in the North Pacific throughout the winter. The extent of diatom infestation on some Antarctic blue whales killed early in the whaling season suggested to Hart (1935) that some of these animals may have over-wintered at high latitudes.

Overall blue whale vocalisation occurrence was higher in the western Pacific than the eastern Pacific (Watkins *et al.*, 2000; this study). It has been well documented that blue whale distribution closely matches that of their prey (Nemoto, 1955; 1970; Berzin and Rovnin, 1966; Springer *et al.*, 1999), and it would therefore be expected that more whales will be found in areas of higher productivity. If it is hypothesised that greater occurrence of sounds implies greater numbers of blue whales, then the western subarctic gyre region may represent an important seasonal concentration of blue whales. Greater vocalisation

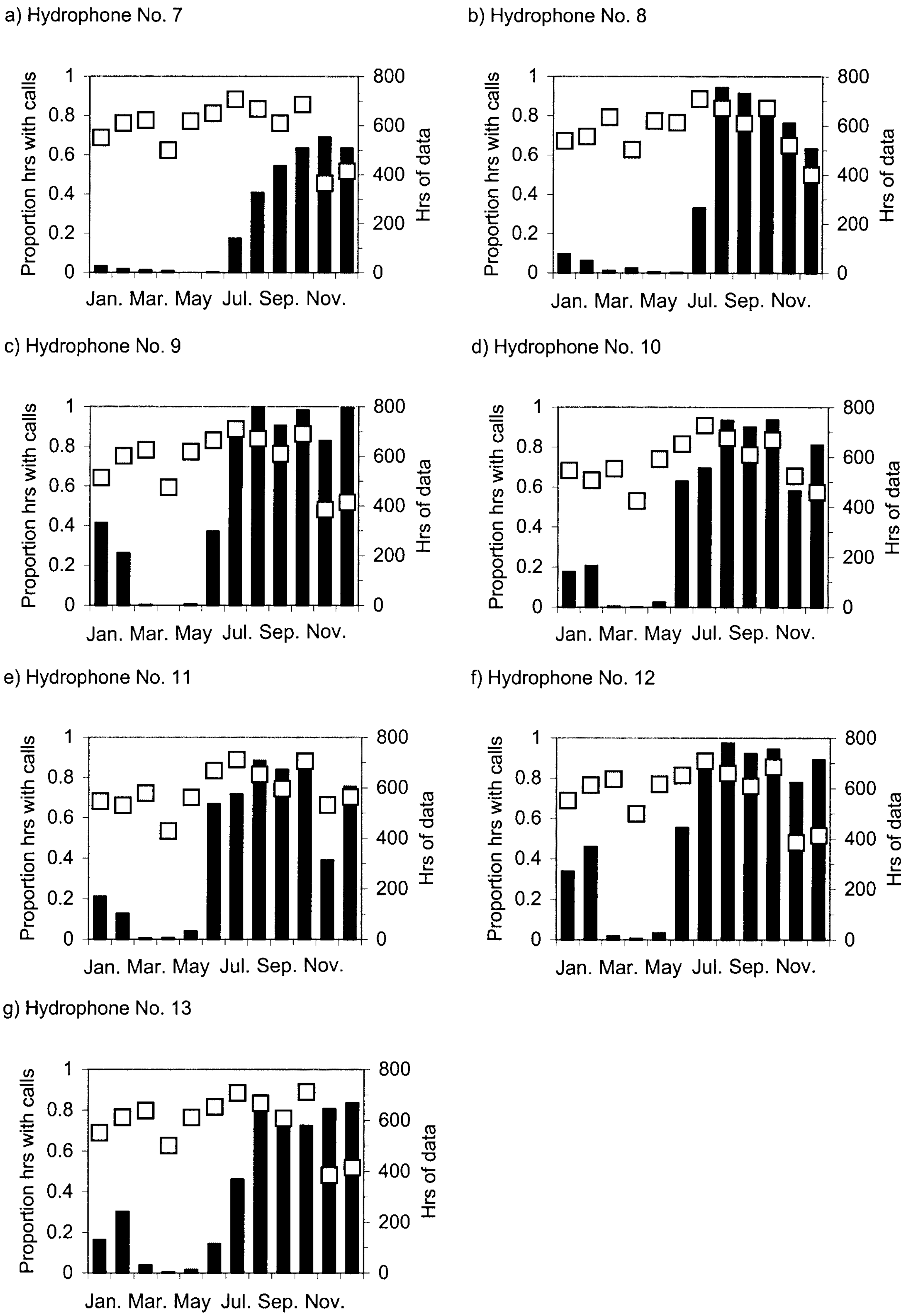

Fig. 7. Seasonal occurrence of blue whale calls recorded on hydrophones and number of hours examined by month in the western Pacific. Histograms represent the proportion of hours available by month during which blue whale sounds were detected (left ordinate). Dark bars represent northwestern sounds. No northeastern Pacific blue whale sounds were detected on these hydrophones. The open squares show the sample size of the number of hours of data examined per month (right ordinate). Approximate locations of the hydrophones are shown in Fig. 1.

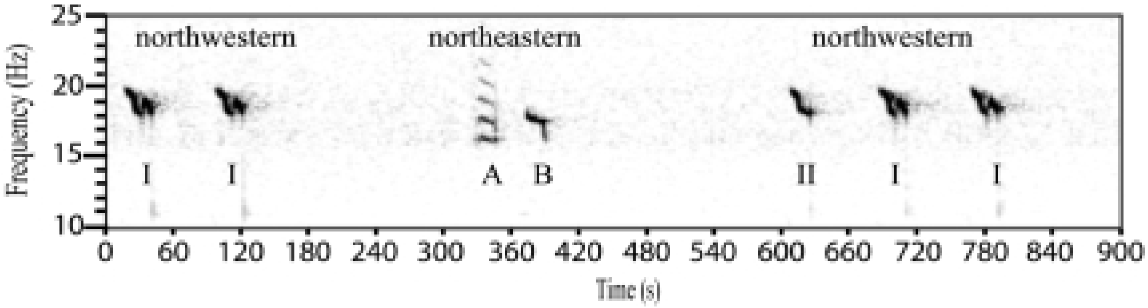

Fig. 8. Spectrogram showing an example of geographic overlap of northwestern and northeastern Pacific blue whale vocalisations (FFT 5.12s, 87.5% overlap, Hanning window).

occurrence for the northwestern Pacific vocalisation may be due to the high productivity of the western subarctic Pacific relative to the eastern or central subarctic Pacific. Both zooplankton and phytoplankton biomass in this region as well as fisheries landings are much higher in the western subarctic than the eastern subarctic (Sugimoto and Tadokoro, 1997; Mackas and Tsuda, 1999; Springer *et al.*, 1999; Taniguchi, 1999). In an analysis of marine bird and mammal surveys, Springer *et al.* (1999) noted that the western subarctic Pacific supported greater numbers of euphausiid-eating oceanic birds and that in general, resident bird and mammal species were more abundant in summer in the western subarctic Pacific than the eastern subarctic Pacific. The WSAG has been found to be more productive than the eastern subarctic gyre because it is formed from multiple current systems including the convergence of the warm Kuroshio with the colder Oyashio current (Sugimoto and Tadokoro, 1997; Mackas and Tsuda, 1999; Springer *et al.*, 1999; Taniguchi, 1999). This combination of water types with different physical and chemical properties supported higher plankton (including Euphausiids) and nekton biomass than the eastern gyre.

It should not be implied, however, that there are more whales overall in the northwestern Pacific than in the northeastern Pacific. Blue whales have been shown to occur along the west coast of the United States and Canada during the feeding season with particularly large concentrations of individuals found in the Santa Barbara Channel Islands region (Barlow, 1995; Fiedler *et al.*, 1998). The California current domain is a highly productive area and at times may be more productive than the eastern subarctic domain (Brodeur *et al.*, 1996). We would therefore expect more blue whales to be found off of California, for instance, than Oregon, Washington or Vancouver Island, Canada. Curtis *et al.* (1999) detected the harmonics of blue whale vocalisations in data recorded off of southern California and interpreted this as indication of a strong blue whale presence there. This study did not have access to acoustic data from the southern California region and it was therefore not possible to compare the relative abundances of northeastern and northwestern type Pacific blue whale vocalisations.

Although fewer data were available for the central Pacific region than the eastern or western, vocalisation occurrence was markedly much lower for this region. The hydrophones in the central Pacific region were the only hydrophones on which both northeastern and northwestern Pacific vocalisations were recorded with any regularity. Nevertheless, no clear pattern emerged from these data to indicate that both types of vocalisations show similar seasonal patterns in vocalisation reception at the same sites. However, on rare occasions, both vocalisation types have been recorded on the same hydrophone at the same time (Fig. 8). The late summer/early autumn recording of vocalisations at Kaneohe and Wake may represent the passage of migrating animals through these areas.

There were two peaks in the 1992-3 Kaneohe data set that can be attributed to the two different vocalisation types (Fig. 6e). Blue whale acoustic data from this same area discussed in Thompson and Friedl (1982) were also described as bi-modal (one peak from July-September and another from November-January) but only one vocalisation type was described, the one similar to the northwestern Pacific vocalisation. The Kaneohe data presented here did not include data for May-July. Thompson and Friedl (1982) did not record any ‘20-Hz long pulses’ in June and noted that these vocalisations were infrequent in May but were more frequent in July. If the present data set is similar to theirs, there may not have been many vocalisations missed in May or June but whale vocalisations in July would be absent from the present dataset. If the two peaks seen in the data presented here are consistent over time, then July would be a month when northeastern Pacific blue whale vocalisations might be expected, not northwestern Pacific vocalisations. The authors of a recent study of fin whale sounds from the same Kaneohe data as presented here did not note the distinction between the two blue whale call types shown here (McDonald and Fox, 1999).

It is difficult to draw any conclusions from the data recorded near Wake Island. Overall, there were few vocalisations recorded and those that were detected were of poor quality. Nevertheless, the detection of both northeastern Pacific and northwestern Pacific vocalisations on bottom-mounted hydrophones at Wake does illustrate that this region may be occasionally used by either northwestern Pacific or northeastern Pacific blue whales. Better quality, longer-term data from this region are needed.

None of the three recent large-scale North Pacific acoustic studies (Curtis *et al.*, 1999; Watkins *et al.*, 2000; this study) used identical methodologies. Thus it is very difficult to combine the information from these studies to present a longer-term picture. Curtis *et al.* (1999) and this study used data from omni-directional hydrophones whereas Watkins *et al.* (2000) used formed beams. Curtis *et al.* (1999) did not distinguish between blue and fin whale sounds, so the regional and seasonal occurrence of blue whale vocalisations cannot be directly compared with the current study. Watkins *et al.* (2000) counted the number of occurrences of blue whale vocalisations rather than present a proportion of vocalisation by month (as was done in this study). Nevertheless, the seasonality and relative occurrence of blue whale vocalisations for different regions in Watkins *et al.* (2000) is in good agreement with the results presented here indicating some interannual consistency in calling. In addition to gross seasonal similarities, all three studies found greater vocalisation occurrence in the west than in the east, similar seasonal trends for the eastern and western Pacific, and detection of blue whale vocalisations (or 17Hz vocalisations in the case of Curtis *et al.*, 1999) well into the winter months at northern latitudes.

While oceanographic factors clearly influence the distribution of some baleen whales (e.g. Nemoto, 1955; 1970; Uda and Nasu, 1956; Uda and Dairokuno, 1957; Nasu, 1963; 1966; 1974; Springer *et al.*, 1999), a consideration that cannot be ignored in an acoustic study such as the one presented here is the effect of oceanography on the propagation of sound (Moore *et al.*, 1998). The northwestern hydrophones are located in the subarctic North Pacific where the axis of the deep sound channel is closer to the surface than it is at more southerly latitudes. Therefore it cannot be ruled out that whale vocalisations are recorded more often in the northwestern Pacific than in the central or northeastern Pacific because the source may be closer to or within the sound channel at these latitudes and the sounds are therefore better able to propagate through deep water than sounds made in the surface layer above the sound channel.

The clear differences in blue whale vocalisation characteristics, combined with the geographic differences in the proportion of the vocalisation types recorded, suggest that there are at least two groups of blue whales in the North Pacific. This east Pacific-west Pacific division of North Pacific blue whales, suggested here by acoustic data, and the overlap of these two groups in the central Pacific was hypothesised decades earlier by several authors (Tomilin, 1957; Berzin and Rovnin, 1966; Rice, 1974). The functional nature of these two groups is uncertain. It is possible that the vocalisations recorded are a breeding display of male blue whales, as has been reported for fin whales (Watkins *et al.*, 1987) and that these two groups of whales represent two different breeding classes of males, or spatially segregated groups of males. However, there is little data on the sex of vocalising blue whales and, at least in the eastern Pacific, these vocalisations are recorded year-round and not just during the presumed breeding season (i.e. winter; Yochem and Leatherwood, 1985). A more parsimonious explanation for the geographic variation in vocalisation types is that these two groups of blues whales may be two separate populations. This supports the findings of Gilpatrick *et al.* (1997) that blue whales killed in the northeastern Pacific were morphologically distinct from those killed in the central or western North Pacific and are therefore a separate population. For other species, differences in vocalisation characteristics have been used to distinguish distinct populations of baleen whales including humpback (Winn *et al.*, 1981; Payne and Guinee, 1983; Helweg *et al.*, 1990) fin (Thompson *et al.*, 1992) and sperm whales (Weilgart and Whitehead, 1997).

The acoustic data do not distinguish a 'central' division of blue whales, distinct from either eastern or western, as has been proposed by several authors based on whaling data (Nishiwaki, 1966; Ivashin and Rovnin, 1967; Best, 1993; Forney and Brownell, 1996). Rather, all the vocalisations recorded along the Aleutians and westward were northwestern Pacific vocalisations. This lack of an acoustic distinction between the central Aleutians (hydrophones 7 and 8) and western Aleutians/western Pacific (hydrophones 9-13) and the lack of significance in size differences between western and central blue whales in the North Pacific (Gilpatrick *et al.*, 1997) suggest that these animals may be part of the same population. In addition, vocalisations recorded on hydrophones in the central Pacific (a hypothesised wintering grounds for a 'central' stock of blue whales) were either northeastern or northwestern Pacific vocalisations. Further acoustic, behavioural and genetic data are needed to confirm or refute this two-population hypothesis or suggest other explanations for the geographic variation in vocalisations.

Acoustic data from regions currently not monitored in the North Pacific, such as Japan and the Gulf of Alaska (Fig. 1), are necessary to address questions such as the southern extent of the northwestern Pacific vocalisation type and what vocalisation types might be recorded in the Gulf of Alaska. There have been no recent sightings of blue whales off southern Japan and Korea and it has been suggested that these animals may have been a unique population that was extirpated by whaling (Gilpatrick *et al.*, 1997; NMFS, 1998). Obtaining acoustic data from this region could provide evidence regarding the presence/absence of blue whales there. If vocalisations were recorded off southern Japan and Korea, the seasonality of vocalisations and vocalisation type might provide further insight into the existence of such a unique population or provide support for a southward movement of the animals that make the northwestern Pacific vocalisation.

The Gulf of Alaska was well known by whalers as a reliable place to find blue whales (Reeves *et al.*, 1985). The whaling season for the Gulf of Alaska/Aleutian chain region was May-October (Brueggeman *et al.*, 1985) with animals most abundant from June-August (Stewart *et al.*, 1987). Nevertheless, recent shipboard and aerial surveys in these areas found no blue whales in either location (Rice and Wolman, 1982; Stewart *et al.*, 1987). Acoustic data from the Aleutians indicates that the animals previously hunted by whalers probably belonged to the northwestern Pacific population. Assigning the Gulf of Alaska animals to either the eastern or western population is more problematic. There are two reports of mark-recovery from blue whales in the North Pacific (Ivashin and Rovnin, 1967). One animal was marked near Vancouver Island and killed about a year later, 1,600km to the northwest near the southern tip of Kodiak Island. A second mark (recorded as shot into a sperm whale but recovered from a blue whale) was implanted southeast of the Sea of Okhotsk and recovered in the Gulf of Alaska. These tag recoveries seem to indicate that animals from both regions might have used the Gulf of Alaska. The animals off Vancouver Island, Canada are known to make the northeastern Pacific vocalisation (Stafford *et al.*, 1998; 1999a) while those near the Sea of Okhotsk make the northwestern Pacific vocalisation. These previous findings suggest that both vocalisation types would be recorded during an acoustic survey of the Gulf of Alaska.

It is still unknown why blue whales vocalise and what proportion of the population vocalises at any one time. Knowledge of the behavioural context of sound production in blue whales is necessary to understand the role acoustic communication has in their life histories and whether or not vocalisation differences are a reliable indication of population differences. Other data needed include photo-identification to identify individuals, biopsies to determine genetic differences and migratory tracks of individual whales from satellite telemetry. Acoustic studies can play an important role in the conservation of endangered species by providing information about geographic and seasonal distributions over large regions of the ocean that were considered unmonitorable. Combined with *in situ* data, passive acoustic observation will continue to be a powerful tool for remotely monitoring vocalising cetaceans over large temporal and geographic scales.

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