Cetacean occurrence offshore of Washington from long-term passive acoustic monitoring

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Abstract
A variety of cetacean species inhabit the productive waters offshore of Washington State, USA. Although the general presence of many of these species has been documented in this region, our understanding of fine-scale habitat use is limited. Here, passive acoustic monitoring was used to investigate the spatial and temporal distributions of ten cetacean species at three locations offshore of Washington. Between 2004 and 2013, a total of 2845 days of recordings were collected from sites on the continental shelf and slope, and in a submarine canyon. Acoustic presence was higher for all species at sites farther offshore. Detections were highest during the fall and winter for blue (Balaenoptera musculus), fin (B. physalus), and humpback whales (Megaptera novaeangliae), likely related to reproductive behavior, while minke whales (B. acutorostrata) were only detected on two days. Odontocetes showed temporal separation, with sperm whale (Physeter macrocephalus) detections highest in spring, Risso’s (Grampus griseus) and Pacific white-sided dolphins (Lagenorhynchus obliquidens) highest in summer, and Stejneger’s beaked whales (Mesoplodon stejnegeri), Cuvier’s beaked whales (Ziphius cavirostris), and the BW37V signal type highest in winter or spring. There was interannual variation in detections for most mysticete species, which may be linked to oceanographic conditions: blue and fin whale detections increased during 2007 and 2008, and fin and humpback whale detections increased in 2011. These results inform our understanding of cetacean behavior and habitat use in this region and may aid in the development of conservation strategies suited to the dynamic conditions that drive cetacean distribution.

Introduction

The continental shelf and nearby offshore waters of Washington State make up a highly dynamic and diverse pelagic ecosystem. In this area, the southward-flowing California Current undergoes large seasonal fluctuations that contribute to upwelling, which is strongest in spring and summer (Huyer et al. 1979) and brings nutrient-rich waters to the surface, enhancing productivity and subsequently supporting higher trophic levels.

Many species of cetaceans are drawn to these nutrient-rich waters. Blue (Balaenoptera musculus), fin (B. physalus), humpback (Megaptera novaeangliae), and minke whale (B. acutorostrata), as well as Risso’s (Grampus griseus) and Pacific white-sided dolphins (Lagenorhynchus obliquidens) are some of the species found along the continental shelf and slope (Green et al. 1992, Calambokidis and Barlow 2004, Barlow and Forney 2007, Forney 2007, Bailey et al. 2009, Oleson et al. 2009, Schorr et al. 2010, Calambokidis et al. 2015). Deep-water habitats are used by sperm (Physeter...
*macrocephalus* and beaked whales (Green et al. 1992, Barlow and Forney 2007). Sightings are typically higher from spring to fall (Green et al. 1992, Watkins et al. 2000, Stafford et al. 2001, Calambokidis et al. 2015) when many of these species can take advantage of productive high-latitude waters to forage.

Most of the large whale species found in this region, such as blue, fin, humpback, and sperm whales, were heavily targeted by historical whaling (Gregg et al. 2000, Monnahan et al. 2014, Rocha et al. 2014) and are currently considered endangered (Carretta et al. 2020). For humpback whales, abundance in the North Pacific has been increasing (Calambokidis and Barlow 2004, Calambokidis et al. 2004, Forney 2007, Barlow et al. 2011), however, out of the three distinct population segments that can be found offshore of Washington, one is currently listed as endangered and another is threatened (Barlow et al. 2011, Bettridge et al. 2015, NOAA 2016).

Other species, such as minke whales and Risso’s and Pacific white-sided dolphins, are not currently considered threatened, but they have not been well studied either (Carretta et al. 2019). Even less is known about the beaked whale species found in the region, such as Cuvier’s (*Ziphius cavirostris*), Stejneger’s (*Mesoplodon stejnegeri*), and Hubbs’ (*Mesoplodon carlhubbsi*) beaked whales. Moore and Barlow (2013, 2017) found that the abundance of Cuvier’s beaked whales was declining in the California Current Ecosystem, but that *Mesoplodon* abundance had increased. However, the increase in *Mesoplodon* abundance may have been impacted by increased temperatures (Moore and Barlow 2017) and, since identifying *Mesoplodon* sightings to species level is rare, it is difficult to make any sort of population assessment for Stejneger’s or Hubbs’ beaked whales in the region (Carretta et al. 2019).

The U.S. west coast has been the site of repeated visual marine mammal surveys (Barlow and Forney 2007). While these studies provide a general understanding of cetacean distribution, the addition of acoustic surveys can provide further insight into cetacean habitat use (Barlow and Taylor 2005, Rankin et al. 2008, Hanson et al. 2013, Vu 2015, Keating et al. 2016, Simonis et al. 2020). There can also be differences between when sightings peak and when acoustic detections peak. For example, visual sightings of fin whales, as well as catches during historic whaling, were highest during summer (Green et al. 1992, Mizroch et al. 2009), but calling peaked during winter (Moore et al. 1998, Watkins et al. 2000, Soule and Wilcock 2013), highlighting the importance of conducting both visual and acoustic surveys to fully assess the spatial and temporal distribution and habitat use of marine mammal species.

Cetaceans frequently use sound for communication, foraging, and navigation, making them prime candidates to study using passive acoustics (Mellinger et al. 2007). Mysticetes produce distinct, low-frequency signals ranging from short sweeps to long, frequency modulated (FM) calls that allow for reliable identification of species-specific call types. Offshore of Washington, two of the call types commonly produced by blue whales are B calls and D calls. B calls are low-frequency (20 Hz), long-duration (20 s) calls that are often regularly repeated and are possibly associated with reproduction (McDonald et al. 2006, Oleson et al. 2007a). D calls are down sweeps that last several seconds and are considered a social call (McDonald et al. 2001, Oleson et al. 2007a, Lewis et al. 2018). Fin whales produce short (approximately 1 s duration), low-frequency calls known as 20 Hz calls (Watkins 1981), which are sometimes produced in long, patterned sequences that show geographic variation (Širović et al. 2009, 2017, Castellote et al. 2012, Oleson et al. 2014, Heilbe et al. 2020). Humpback whales produce a variety of calls, ranging from 100 to 3000 Hz, which can be classified as song and non-song vocalizations (Payne and McVay 1971, Thompson et al. 1986, Dunlop et al. 2007, Stimpert et al. 2011, Fournet et al. 2015). Song has been recorded only from males (Winn and Winn 1978, Tyack 1981, Baker and Herman 1984, Herman et al. 2013, Herman 2017) on both breeding and feeding grounds (Mattila et al. 1987, McSweeney et al. 1989, Gabriele and Frankel 2002, Clark and Clapham 2004, Vu et al. 2012). Predominant non-song call types in the North Pacific include growls and whups—low-frequency (peak frequency < 150 Hz), short (1 s or less), and quiet calls, particularly relative to song (Wild and Gabriele 2014, Fournet et al. 2015, 2018). In the North Pacific, minke whales produce a fairly stereotyped call that consists of a brief pulse followed by a long, frequency and amplitude modulated component called a boing (Thompson and Frield 1982, Rankin and Barlow 2005, Delarue et al. 2013). These calls vary between different regions, but generally have a peak frequency of approximately 1400 Hz, an overall duration of 2–4 s, and a pulse repetition rate of either 92 or 115 s⁻¹ (Rankin and Barlow 2005).

Odontocete species use echolocation clicks to forage, and since their clicks are typically species-specific, they can be used for species identification. The echolocation clicks produced by sperm whales generally contain energy from 2 to 20 kHz, with the majority of energy between 10 and 15 kHz (Møhl et al. 2003). Risso’s and Pacific white-sided dolphins produce broadband echolocation clicks that can be discriminated by their unique frequency banding patterns (Madsen et al. 2004, Soldevilla et al. 2008, 2017). Beaked whale echolocation signals are unique in their polycyclic structure and FM pulse upswipe. The peak frequency, spectral peaks, and inter-pulse interval of these signals vary among species and can be used for species discrimination (Johnson et al. 2004, Zimmer et al. 2005, Baumann–Pickering et al. 2013a, 2013b, Griffiths et al. 2018).
In this study, we used species-specific cetacean call types to analyze long-term passive acoustic recordings from three locations offshore of Washington State and examine the spatial and temporal distribution of four mysticete and six odontocete species. Long-term, year-round monitoring is essential for understanding how species’ distributions may be impacted by changing population levels and oceanographic conditions. With a better understanding of habitat preferences and seasonal presence, it may be possible to more effectively manage and conserve these species.

Methods

Data collection

High-frequency acoustic recording packages (HARPs) were deployed across three sites off the coast of Washington (Fig. 1) on 16 occasions, in an effort to survey the acoustic presence of cetaceans within the U.S. Navy’s Northwest Training Range Complex. All HARPs were deployed on the seafloor and had a calibrated hydrophone suspended 10–30 m above the instrument (Wiggins and Hildebrand 2007). Of the 16 HARP deployments, most sampled continuously at 80 or 200 kHz, but seven deployments had duty-cycled recordings (Table S1). The three deployment locations were selected to span a variety of habitats: site Shelf was located offshore of Cape Elizabeth, on the continental shelf at 100–150 m and within the boundary of the Olympic Coast National Marine Sanctuary, site Slope was located on the continental slope at about 600–900 m, site Canyon was a deep offshore location in Quinault Canyon at almost 1400 m (Fig. 1, Table S1). These sites were monitored intermittently from July 2004 to August 2013 (Table S1, Fig. 2).

Terminology

A variety of methods were used to identify cetacean calls in this dataset. Hereafter, the term “detection” will only be used when generally referring to identified calls and will be further qualified when used to refer to calls identified using a specific methodology (Kowarski and Moors-Murphy 2020). Calls that were identified by human analysts will be referred to as “manual detections,” while calls that were identified by a computer algorithm will be referred to as “automatic detections.” For cases where calls were automatically detected and then each detection was verified by a human analyst, results will be referred to as “manually validated detections.”

Fig. 1 Map showing the locations of deployment sites from 2004 to 2013. Grayscale shows depth in meters and thin gray lines mark 50 m bathymetry contours. The star, circle, and diamond represent sites Shelf, Slope, and Canyon, respectively. The broken line represents the Olympic Coast National Marine Sanctuary boundary. The gray box in the inset map of the west coast of the USA indicates the location of the study site. Map generated using Maptool, a product of seaturtle.org.

Fig. 2 The total number of years with recording effort (gray bars) during each week at each site. The weekly bins shown are the same as used in the data analysis and indicate how many years of data were averaged for a given week. Shelf had data 2004–2013, Slope had data 2004–2008, and Canyon had data 2011–2013.
Call detection

Decimated datasets were produced to allow for more effective scanning of long-term spectral averages (LTSAs) and spectrograms. For analysis of blue and fin whale calls, data were decimated to a 2 kHz sampling frequency and for analysis of humpback and minke whale calls, data were decimated to a 10 kHz sampling frequency. Full bandwidth recordings were used for analyzing all other call types. Data were analyzed manually, using Triton, a custom MATLAB program designed to allow for visual scans of LTSAs (Wiggins and Hildebrand 2007), or automatically, using appropriate detection algorithms. Further details on call detection are provided below for each species.

Blue whale B and D calls were detected manually for most deployments, using LTSAs with 5 s time average and 1 Hz frequency resolution. Analysts scanned LTSAs for the hourly presence of these calls and used 60 s spectrograms (1500 point fast Fourier transform (FFT) length, 90% overlap) displayed from 0 to 200 Hz to confirm call presence. However, for data recorded from 2011 to 2013, blue whale B calls were detected automatically, using spectrogram correlation (Mellinger and Clark 2000, Širović et al. 2015). The parameters used to run this detector varied by deployment (Table S2, Table S3) since detector performance is impacted by seasonal and interannual shifts in B call frequency and abundance (McDonald et al. 2009, Širović 2016). Based on analysis from three deployment periods, the missed detection rate was <12% and the false detection rate was <10%. The transition to using this detector was made to increase the efficiency of analyzing a large dataset, but it meant that both manual and automatic detection methods were used for this call type (Table S1). Although caution should be exercised when making comparisons within and between sites in cases where these different methods were used, B call detections from both methods were converted to hourly presence so that detections were comparable. The number of hours with call presence each day were summed and averaged over weekly and monthly bins.

The presence of fin whale 20 Hz calls was detected automatically using an energy detector that calculated the difference in acoustic energy between the signal (22 Hz) and background levels (average energy between 10 and 34 Hz) in an LTSA (Širović et al. 2004, 2015, Nieuwkerk et al. 2012). The ratio produced is reported as a daily average and is referred to as a ‘fin whale acoustic index’. This daily average was then averaged over weekly and monthly bins.

Humpback whale calls were detected manually for deployments at Shelf from August 2006 to June 2009 and were detected using an automatic detector for all other deployments (Table S1). As with blue whale B calls, the transition to an automatic detector was meant to increase the efficiency of analysis. During manual analysis, a trained analyst scanned 1 h LTSAs that were created using a 5 s time average and 10 Hz frequency resolution and displayed from 0 to 5 kHz. Signals of interest were viewed in a 30 s spectrogram (1000 point FFT length, 65% overlap) displayed from 0 to 2 kHz to confirm the source of the call. For automatic detection, a detector based on a generalized power law was used, which has a false detection rate under 5% (Helble et al. 2012). This detector can detect the wide range of humpback whale vocalizations (including both song and non-song call types) across different regions and noise conditions while keeping missed and false detection rates below 5% (Helble et al. 2012, Rekdahl et al. 2017, Henderson et al. 2018, Zeh et al. 2020). All automatic detections were subsequently verified by a trained analyst using spectrograms that ranged 0.35–3 s in duration and 0–2000 Hz in frequency (spectrogram windows were modified when necessary for call verification), and any false detections were removed. There was no effort to classify song and non-song calls with either method. Calls were grouped into encounters, where each encounter was separated by at least 30 min of recording that did not contain any calls of interest. For deployments with duty-cycled recordings, if the duty-cycle off period was less than 30 min, and calls continued after the recording gap, then the encounter was determined to span the gap. A lack of calls after the recording gap, or a 30 min duty-cycle off period, meant the encounter would end with the last call before the recording gap, as there was no way to determine if calls continued during these times. Although detection methods varied at Shelf (Table S1), this same encounter metric was used to report both manual and automatic detections of humpback whales, and the total minutes of encounters were summed each day and averaged over weekly and monthly bins.

Minke whale boings were detected using the same generalized power-law detector used for humpback whale calls (Helble et al. 2012) but were verified using spectrograms that ranged 1–6 s in duration and 800–1800 Hz in frequency. This detection method allowed for the manually validated detection of individual minke whale boings that were summed for each day and averaged over weekly and monthly bins.

All remaining call types were analyzed using full bandwidth recordings and are reported as encounters, where the methods for delineating encounters were the same as described previously for humpback whale calls. Hourly LTSAs, created using a 5 s time average and 100 Hz frequency resolution, were manually scanned from 0 to 100 kHz for the presence of sperm whale, Risso’s dolphin, and Pacific white-sided dolphin clicks. When clicks were identified in an LTSAs, a 5 s spectrogram (1000 point FFT length, 0% overlap) was examined, if necessary, to confirm click type presence.
Cuvier’s and Stejneger’s beaked whale FM pulses, as well as the BW37V signal type (presumed to be produced by Hubbs’ beaked whale, Griffiths et al. 2018), were detected automatically by running a Teager-Kaiser energy detector to identify all echolocation signals (Soldévilla et al. 2008, Roch et al. 2011) and then using an expert system to discriminate between delphinid clicks and beaked whale FM pulses (Roch et al. 2011, Baumann-Pickering et al. 2013a). Discrimination was based on detections within a 75 s segment and only segments with more than seven detections were used in further analysis. Echolocation signals were removed if they had a peak and center frequency below 32 and 25 kHz, respectively, a duration less than 355 µs, and a sweep rate of less than 23 kHz ms⁻¹. If more than 13% of all initially detected echolocation signals remained after applying these criteria, the segment was classified to have beaked whale FM pulses. This threshold was chosen to obtain the best balance between missed and false detections. The automatically detected segments were then analyzed by a trained analyst to remove false detections and label as species-specific pulse types (Baumann-Pickering et al. 2013a). The rate of missed detections was approximately 5% (Baumann-Pickering et al. 2013a, 2014). There was no detection effort at Shelf or Slope, as Shelf was too shallow for the typical habitat of these beaked whale species and the sampling frequency was too low for four out of the five deployments at Slope (Table S1).

**Propagation modeling**

Detection areas should be taken into account when comparing detections of low-frequency baleen whale calls across recording sites (Helble et al. 2013). We used the methodology described by Širović et al. (2015) to determine the detection areas for the three sites in our study, but with adjusted parameters for our study area and call types. To summarize, transmission loss (TL) was modeled using the Effects of Sound on the Marine Environment (ESME) 2012 Workbench framework (D. Mountain, Boston University, http://esme.bu.edu) and sound propagation was modeled using a Range-dependent Acoustic Model (RAM) simulator (Širović et al. 2015) for all call types except minke whale boings, a call at a higher frequency, for which it was more appropriate to use a BELLHOP model (Porter 2011, Wang et al. 2014).

We ran propagation models for four different frequencies (20, 45, 350, and 1500 Hz) that corresponded to the frequencies of dominant portions of different baleen whale call types (Table S4). Models were calculated along 16 radials that were centered at each recording location and were 200 km long for blue and fin whale frequencies, 100 km long for humpback whale calls, and 50 km long for minke whale boings. Parameters needed for range estimation were specific to each call type (Table S4). We used average background sound levels from August for each site (ambient sound levels had < 5 dB variation throughout the year) and assumed a 2 dB signal-to-noise ratio detectability level for each call type (Širović et al. 2015).

Detection areas (Table S5) were then used to normalize the reported fin whale 20 Hz call and minke whale boing detections by dividing call metrics by the calculated detection area in 1000 km². Although cross-site comparisons would be improved by detection area normalization for all low-frequency call types, all other call types were reported as hourly presence or total minutes of calling, and it was not meaningful to normalize these detections. However, detection areas were still reported for all low-frequency call types for comparison within this study and with other passive acoustic studies.

**Data analyses**

To compare variation in seasonal presence, the relative daily acoustic presence of a given species was calculated for the site where the overall detections of that species were generally the highest. This analysis was based on the total number of days with detections for a given call type, to facilitate reporting of detections using different metrics. For fin whale 20 Hz calls that were automatically detected, we set a threshold to determine the number of days with acoustic presence, as the fin whale acoustic index does not intrinsically provide binary presence/absence data (even if 20 Hz calls are absent, the signal-to-noise ratio for the bands used is typically > 0). Therefore, only days with an acoustic index of one or greater (maximum index values typically range from 15 to 20) were counted towards the total number of days with fin whale 20 Hz call presence. Relative daily presence was calculated for an individual species or call type as the percent of days with acoustic presence during each season from one full year of data. Because recording effort varied at each site, data from the following time periods were used for each site 1 May 2007–30 April 2008 at Slope, 1 February 2011–30 September 2011 and 1 October 2012–1 January 2013 at Canyon. Seasons were defined as winter: December–February, spring: March–May, summer: June–August, fall: September–November. The resulting relative daily presence of species did not account for the different detection ranges across sites and call types.

To further examine spatial and temporal patterns, call detection metrics were grouped into weekly bins to examine seasonal patterns, and into monthly bins to examine interannual patterns at each site. For detections reported in hourly bins, presence was reported as average daily hours per week or per month, for seasonal and interannual plots, respectively. For detections reported as encounters, presence was reported as the average daily...
minutes of detections, again, per week or per month. For minke whale boing detections, the total number of calls was normalized by the detection area for each site (Table S5), resulting in average daily detections per week (or per month) per 1000 km² for seasonal (or interannual) plots. For the fin whale acoustic index, normalization accounted for transmission loss (TL) as well as detection area (Table S5), as described by Širović et al. (2015). Therefore, the fin whale acoustic index is reported as the average daily index per week (or per month) per 1000 km²/TL for seasonal (or interannual) plots. Diel plots (detections versus time of day) were also created to examine any changes in calling between day and night for each call type, except for the fin whale acoustic index.

Since recording effort varied across years and among sites, the average weekly detections reported in the seasonal plots were normalized by recording effort. Figure 2 shows the total number of years with effort for each week at each site. For interannual plots, the effort is noted on a second y-axis (right-hand side) to show the percent of effort for a given month. Generalized additive models (GAMs) were also used to examine the seasonal and interannual variation of daily detections for each species at each site. Models were created with a Tweedie distribution and a log link function using the mgcv package (Wood 2011) in R (R Core Team 2020). The response variable in each model was the total number of hours with call presence or total minutes of detections (dependent on species) per day. Predictor variables for the model were Julian day and year. Julian day was modeled with a smooth function that was estimated by a cyclic cubic regression spline with up to four degrees of freedom and year was modeled as a factor. Models were not developed for minke whale boings, as they were only detected on two days. Additionally, models did not account for autocorrelation in the predictor variable. Call totals on adjacent days are likely not independent from one another, particularly for baleen whale species (Širović et al. 2004). Because we were not examining the effect of environmental variables in our models and were only investigating the relationship between Julian day and year, we did not feel that increasing our bin size was warranted. By not accounting for autocorrelation in our models, we may have fit a more complicated model than is justified and our confidence intervals may be underestimated. However, because the models were restricted to four degrees of freedom, the seasonal models are quite simple. Although this restriction may prevent models from successfully capturing finer-scale seasonal patterns for some species, overall, the models show that only some sites had interannual variability, and seasonal patterns were generally consistent across sites.

Results

Detections were higher at sites farther offshore for all species, and seasonal changes in calling were observed for all species that were commonly detected (Fig. 3). Blue whale B calls, fin whale 20 Hz calls, and humpback whale calls were more prevalent during the fall and winter, while blue whale D calls were more prevalent during the spring and fall (Fig. 3). Detections of sperm whales, Risso’s dolphins, and Pacific white-sided dolphins were highest during the summer, while beaked whale detections were highest during the winter or spring, depending on species (Fig. 3). Spatial and temporal patterns in calling are described in more detail below for each species.

Blue and fin whales

Blue whale calls were detected at all three sites, with B calls more prevalent than D calls overall. B call detections were highest at Slope and lowest at Canyon, and were highest during the fall and winter at all sites (Fig. 4, Table S6). D call manual detections had an inconsistent seasonal pattern: at Shelf there was a significant peak in manual detections in late summer and fall, Slope had intermittent peaks throughout the year, and at Canyon, calls were significantly higher in winter and early spring (Fig. 4, Table S6). However, at all sites, D call manual detections were low during the spring and early summer (Fig. 4). There was no clear diel pattern for either blue whale call type. There was some interannual variation in the number of detections: at Shelf, B call detections were high during 2006, 2007, and 2008, but decreased in 2009, at Slope, calls were high during 2006 and 2007, at Canyon, they were high in 2013 (Figs. 4b and 5, Table S6). For D calls, manual detections were high in 2009 at Shelf and in 2013 at Canyon (Figs. 4b and 5, Table S6).

The fin whale acoustic index was highest at Canyon and showed a seasonal peak in the fall and winter at all sites (Fig. 4, Table S6). Since the energy detector used for 20 Hz calls provides an average daily index of calling, we were unable to examine diel patterns for this call type. There was no clear interannual trend in the 20 Hz index, but the average daily fin whale acoustic index appeared high at Shelf in 2011, although this was not significant in the GAM (Fig. 5, Table S6). Instead, the models showed that the acoustic index was significantly lower during 2006 at Shelf, but higher during 2007 and 2008 at Shelf and Slope, as well as during 2012 at Shelf and Canyon, and still during 2013 at Canyon (Fig. 4b, Table S6).

Humpback and minke whales

Humpback whale detections were highest at Canyon and lowest at Slope, although calls increased during the fall and winter at all three sites (Fig. 6a). At Shelf, detections began...
increasing during the summer and were highest during the fall and winter, with a drop in November (Fig. 6a). At Slope, detections occurred from September to December and were rare the rest of the year (Fig. 6a). At Canyon, detections were rare during spring and summer but were high throughout the fall and winter (Fig. 6a). The models captured these slight variations in the seasonal presence of humpback whale calls at each site because, while all sites show a significant peak in detections during the fall and winter, the peak at Shelf occurs earliest in the year and the peak at Canyon occurs latest (Fig. 6b, Table S6). There was no clear diel pattern to humpback whale detections. Interannually, detections increased during 2011 at Shelf (Fig. 5) and the model showed that calls were significantly higher in 2011, as well as during 2012 and 2013 (Fig. 6b, Table S6). At slope, Minke whale boings were detected only at Canyon (Fig. 6a). There was one manually validated detection on April 26, 2013. Other manually validated detections occurred on November 15, 2012 within a 3 h period (~0300–0600 h). Since calls mainly occurred on one day, further examination of diel, seasonal, or interannual trends for this species was not possible.

**Sperm whales, Risso’s dolphins, and Pacific white-sided dolphins**

Sperm whale clicks were manually detected year-round at all three sites but were highest at Slope (Fig. 7a). At
both Shelf and Slope, manual detections peaked from late spring to early summer (Fig. 7, Table S6), while at Canyon, occasional peaks occurred throughout the year (Fig. 7a). There was no diel pattern for sperm whale clicks. Also, there was no clear interannual pattern in manual detections, although the number of clicks did appear to fluctuate over the years of the study: manual detections were low during 2006, 2007, and 2008 at Slope, during

![Fig. 4](image-url)
Risso’s dolphin clicks were manually detected at all three sites and were highest at Canyon (Fig. 7a). Clicks were most common during the summer and early fall at all sites, although this seasonal pattern was most prominent at Canyon (Fig. 7, Table S6). Risso’s dolphin clicks occurred almost exclusively at night, particularly at Canyon (Fig. 9). There was no clear interannual pattern in Risso’s dolphin clicks, but the models indicated a decrease in detections during 2008 at Slope and an increase at Canyon during 2012 and 2013 (Figs. 7b and 8, Table S6).

Pacific white-sided dolphin manual detections were highest at Slope and lowest at Shelf. Clicks occurred seasonally, from summer to early winter, at all three sites (Fig. 7a). This seasonal pattern was only significant at Slope and Canyon (Fig. 7b, Table S6). Pacific white-sided dolphin clicks occurred more often at night, particularly at Slope and Canyon (Fig. 9). There was no clear interannual pattern in Pacific white-sided dolphin click manual detections: at Shelf, clicks were low from 2006 to 2008, at Slope, clicks were also low during 2006 and 2008, at Canyon, clicks were low during 2013 (Figs. 7b and 8, Table S6).

**Beaked whales**

While Stejneger’s, Cuvier’s, and presumable Hubbs’ (BW37V) beaked whale clicks all occurred at Canyon, Stejneger’s beaked whale clicks were detected most frequently (Fig. 10a). Manually validated detections of Stejneger’s and Cuvier’s beaked whale clicks showed similar seasonal patterns: few clicks from July to September, an increase during fall and winter, and a decrease throughout the spring (Fig. 10). Likely Hubbs’ beaked whale (BW37V) clicks
were detected in winter, starting in December, but occurred primarily during the spring (Fig. 10a). There was no discernable diel or interannual pattern for any beaked whale species (Fig. 8).

Discussion

Cetacean detections were generally more common at the two sites farther offshore (sites Slope and Canyon), and only blue and humpback whales had a substantial number of detections on the continental shelf (site Shelf). The continental slope (site Slope) showed the most blue whale B calls, as well as the highest levels of clicks from sperm whales and Pacific white-sided dolphins, while detections of fin, humpback, and minke whales, and Risso’s dolphins were highest around the submarine canyon (site Canyon). In addition to these spatial patterns, we observed seasonal changes in calling for all species except minke whales, for which calls did not occur frequently enough to establish temporal patterns. These seasonal patterns were most consistent across sites for blue whale B calls, the fin whale 20 Hz acoustic index, and humpback whale calls. We also found increased nighttime calling in Risso’s and Pacific white-sided dolphins. In general, many of these spatial and temporal patterns have been observed previously (Green et al. 1992, Watkins et al. 2000, Barlow and Forney 2007, Oleson et al. 2009, Soldevilla et al. 2010b) and therefore support earlier findings about the distributions of these species offshore of Washington and demonstrate the stability of these patterns over long time periods. Additionally, the high degree of calling found at offshore locations highlights the importance of conducting cetacean surveys in deep pelagic habitats that are clearly of great significance to these species.

When interpreting results from passive acoustic studies, it is important to acknowledge that the methodology is inherently biased towards animals that are vocalizing. A lack of acoustic detections does not mean that animals were not present in the area; they could have been engaged in non-vocal behaviors or producing calls that were not used for species identification in this study. It is also possible the inclusion of duty-cycled data resulted in an underestimate of acoustic presence during the early years of the study; therefore, it is necessary to consider methodological differences when comparing acoustic presence across years. Additionally, although we are confident that we recorded Stejneger’s beaked whales in our recordings (Baumann-Pickering et al. 2013b), there have been
no acoustic detections of Stejneger’s beaked whales with concurrent visual confirmation. This is also true for the BW37V click type, which is hypothesized to be produced by Hubbs’ beaked whale (Griffiths et al. 2018), but for which there have been no concurrent visual confirmations to date. Therefore, our results for these species should be interpreted with caution.

**Fig. 7**

(a) Mean weekly presence of sperm whale (Pm, light gray bars), Risso’s dolphin (Gg, white bars), and Pacific white-sided dolphin (Lo, dark gray bars) clicks at three locations offshore of Washington. Data were averaged across years with recording effort from 2004 to 2013, red error bars represent standard error. The number of years with recording effort for each week is shown in Fig. 2. Note different y axis scale was used between sites for sperm whale and Risso’s dolphin clicks. B Corresponding generalized additive models (GAMs) with significant ($p < 0.01$) results for the sperm whale, Risso’s dolphin, and Pacific white-sided dolphin clicks at each site. Total daily minutes of call presence are modeled as a function of Julian day (left) and year (right). The shaded band (left) and horizontal bars (right) represent two standard error bounds. Asterisks represent years that are significantly different from the first year (see Table S6 for $p$ values). Y-axis scales vary to show model fit. Gray boxes indicate GAMs that were not statistically significant.

**Blue and fin whales**

Sightings of blue whales offshore of Washington, although relatively rare, typically occur along the continental slope (Calambokidis and Barlow 2004, Barlow and Forney 2007, Bailey et al. 2009), while fin whale sightings are most common at or beyond the shelf break (Green et al. 1992, Oleson
et al. 2009, Schorr et al. 2010). Similarly, we found that blue whale call detections were highest at Slope and Shelf, while the fin whale acoustic index was highest at Canyon (Fig. 4). Submarine canyons are often areas of higher krill abundance (Santora et al. 2018) and may provide foraging opportunities for fin whales (Burnham et al. 2021), possibly explaining evidence of increased fin whale presence around these bathymetric features (Schorr et al. 2010, Aulich et al. 2019).

Blue whale B calls and the fin whale acoustic index were highest during the fall and winter (Fig. 4), as has been observed previously offshore of Washington (Moore et al. 1998, Watkins et al. 2000, Stafford et al. 2001, Soule and Wilcock 2013, Koot 2015, Weirathmueller et al. 2017), and in other areas of the eastern North Pacific (Watkins et al. 2000, Barlow and Forney 2007, Oleson et al. 2007b, 2014, Širović et al. 2013, 2015, Rice et al. 2021). Both call types are widely assumed to be associated with reproductive behavior (Watkins 1981, Watkins et al. 1987, McDonald et al. 2001, Croll et al. 2002, Oleson et al. 2007a, 2007b, Lewis et al. 2018), while blue whale D calls, which we manually detected much more sporadically (Fig. 4), are generally associated with other social behaviors and foraging (McDonald et al. 2001, Oleson et al. 2007a, 2007b, Lewis et al. 2018). In other regions, it is typical for D calls to show a seasonal increase, often during spring and summer (Oleson et al. 2007b, Rice et al. 2021), when blue whales are feeding in more productive high-latitude waters. The waters offshore of Washington are not considered a primary feeding area for blue whales (Calambokidis et al. 2015), thus the lack of D calls we manually detected during summer may be explained by limited blue whale presence during this season. Instead, blue whales may feed in areas to the south, offshore of California (Oleson et al. 2007b, Calambokidis et al. 2015), and farther north, in the Gulf of Alaska, where D calls were manually detected throughout the spring and summer (Rice et al. 2021). The majority of the D calls in this study occurred either in the early spring or late summer, at the margins of the seasonal increase in B calls (Fig. 4), supporting the suggestion that blue whales are primarily seasonal visitors to the region.

Since blue and fin whales both consume krill offshore of Washington (Flinn et al. 2002), the lack of fin whale calls during summer might be taken to indicate movement out of the region to forage in a different area as well. However, we did not monitor for the presence of 40 Hz calls in this study, which may be more common during foraging (Watkins 1981, Širović et al. 2013) and were the primary fin whale call type recorded during spring off Vancouver Island, British Columbia (Burnham et al. 2021). In other North Pacific regions, fin whale year-round presence has been documented by the detection of both 20 Hz and 40 Hz calls (Širović et al. 2013, Rice et al. 2021). Therefore, because we did not attempt to
detect 40 Hz calls in this data, and because visual surveys and historic catch data show increased fin whale presence offshore of Washington during the summer (Green et al. 1992, Mizroch et al. 2009), it seems likely that at least some fin whales are utilizing this region year-round, for foraging in the summer and breeding during the winter, even though the acoustic detections reported here only highlight this latter behavior.
There were noticeable interannual variations for both blue and fin whales, primarily during 2007/2008 and 2011/2012, which correspond with a transition into a cool phase of the Pacific decadal oscillation (PDO) and a switch in the El Niño southern oscillation (ENSO), respectively (Bjorkstedt et al. 2011). At Slope in 2007, the winter peak in blue whale B calls was higher than in previous years, while at Shelf, the highest peak in D call manual detections occurred in the late summer and fall of 2008 (Fig. 5). While this increase in B calls at Slope during 2007 was significant in our model, the increase of D calls in 2008 was not (Fig. 4b, Table S6). For fin whales, there were also significant increases in the acoustic index during 2007 and 2008 at Shelf and Slope (Fig. 4b, Table S6). Since productivity is typically higher during cool phases, these increases in calls could be a result of increased prey availability (Peterson et al. 2017, Lilly and Ohman 2018). Historical catches of blue whales were higher offshore of British Columbia during cool phases (Calambokidis et al. 2009), supporting a hypothesis that their presence is likely higher in the region during these periods of higher productivity. While this cool phase continued until 2013, there was an abrupt shift from an El Niño in 2010 to a La Niña in 2011 (Bjorkstedt et al. 2011). At Shelf, we observed an increase in fin whale calls during the fall and winter of 2011/2012, compared to previous years (Fig. 5). Again, the increased productivity that follows a return to cooler water temperatures may have led to an increase in the presence or a behavioral shift that resulted in higher calling during this year. Forage fish, which compose part of the fin whale diet offshore of Washington (Flinn et al. 2002), showed increased productivity in 2011 (Peterson et al. 2019), providing a possible explanation for the increase in calls. Offshore of California, marine mammal distributions were also affected by ENSO events, with potential movement out of impacted regions (Keiper et al. 2005). However, for both blue and fin whales, our models show a significant increase in calls during 2013 at Canyon; therefore, it is possible that the presence of these species was increasing in the region during the later years of this study, explaining the apparent increase in 2011 and 2012. It is unclear whether the interannual changes in calling observed offshore of Washington are a direct result of a regional increase in productivity or a more indirect result of distributional shifts spurred by oceanographic conditions in other regions.

Humpback whales

Humpback whale detections were highest at Canyon and Shelf (Fig. 6), which is generally consistent with visual surveys offshore of Washington, where humpback whales are primarily sighted over the continental shelf (Barlow and Forney 2007, Oleson et al. 2009), sometimes concentrated around canyons (Green et al. 1992). It is unclear why detections would be comparatively lower along the continental slope, although this was also observed in the Gulf of Alaska (Rice et al. 2021). Differences in detection area likely do not explain this spatial pattern, as the detection areas for Slope and Canyon are similar (Table S5).

Humpback whale detections were higher during the later years of the study at Shelf (2011–2013, Fig. 6b), and were also detected over a longer period. Until 2008, calls typically occurred from September through December (Fig. 5).
Starting in 2011, detections started during the summer and continued through January (Fig. 5). This change coincides with the abrupt ENSO shift that occurred in 2010/2011 (Bjorkstedt et al. 2011). As with fin whales, increased productivity could have resulted in increased or prolonged presence of humpback whales offshore of Washington during these years, explaining the higher number of detections and the longer calling season that we observed. However, abundance estimates and increased sightings in the inner waters of Washington during these years point towards an increasing humpback population in the region (Calambokidis et al. 2017; Calambokidis and Barlow 2020). Therefore, it is possible that these changes may reflect an increasing trend in humpback presence offshore of Washington as opposed to a transitory response to an ENSO shift.

While acoustic detections occurred almost exclusively during winter (Fig. 6), humpback whale sightings are highest offshore of Washington during the summer (Green et al. 1992, Oleson et al. 2009, Calambokidis et al. 2015) when many humpback whales forage in the region (Calambokidis et al. 2015). From these visual observations, we know that the low number of detections during spring and summer is not due to the absence of humpback whales. While there is evidence that humpback whales move inshore (Gregg et al. 2000, Oleson et al. 2009), and out of our detection range, to feed in more coastal waters during the summer (Calambokidis et al. 2015), the primary reason for this seasonal variation in calling is likely related to a shift from foraging behavior during the summer to reproductive behavior during the winter. During the winter breeding season, male humpback whales produce song (Winn and Winn 1978, Tyack 1981, Baker and Herman 1984, Herman et al. 2013, Herman 2017). Because a song consists of long, repetitive series of vocalizations (Payne and McVay 1971, Dunlop et al. 2007), it is possible for detections to be higher even in the presence of fewer animals. Our humpback whale detections are likely biased towards song because non-song calls are often short, quiet calls with a very low fundamental frequency (Stimpert et al. 2011, Wild and Gabrielle 2014, Fournet et al. 2015) that may have been missed by our detection algorithm or during manual scanning. The detection area for song is also larger than for non-song calls (Table S5) and the metric we used to describe humpback whale calling (daily minutes of calling) likely highlighted this seasonal difference in acoustic behavior more than a metric such as presence/absence would have. Efficient discrimination of humpback song and non-song calls would require the aid of an automatic classifier, which was beyond the scope of this study. However, we hypothesize that we mostly detected humpback whale song in our data based on the strong seasonal pattern we observed, which matches the seasonal occurrence of song in other regions of the North Pacific (Norris et al. 1999, Au et al. 2000, Watkins et al. 2000, Stafford et al. 2007). If the calls we detected were confirmed as song, it would add to the growing list of high-latitude locations where song has been recorded (McSweeney et al. 1989, Gabrielle and Frankel 2002, Clark and Clapham 2004, Stafford et al. 2007, Stimpert et al. 2012, Vu et al. 2012, Garland et al. 2013, Kowarski et al. 2018).

**Minke whales**

Offshore of Washington, sightings of minke whales typically occur along the continental shelf (Forney 2007, Oleson et al. 2009) and there is evidence of individuals showing site fidelity to nearshore foraging areas during summer (Hoelzel et al. 1989, Dorsey et al. 1990, Towers et al. 2013). The low number of boings we detected may be due to the presence of minke whales closer to shore, outside of our detection range, or to a reduction in vocalizations to avoid detection by transient killer whales (*Orcinus Orca*), which are a known predator of minke whales (Ford et al. 2005) and were acoustically detected at these same recording locations (Rice et al. 2017). However, as minke whales produce additional vocalizations in this region, it is possible we are not capturing their full occurrence by using just one call type. Offshore of British Columbia, for example, downsweeps and pulse chains were the main call types recorded from minke whales during the summer (Nikolich and Towers 2020).

In the North Pacific, boings have primarily been detected during the winter at low latitudes (Thompson and Friedl 1982, Rankin and Barlow 2005), indicating that minke whales may transition from lower latitude breeding grounds in the winter to higher latitude feeding grounds for the summer, as occurs in the Atlantic (Risch et al. 2014, Vikingsson and Heide-Jorgensen 2015). To date, the only other detections of minke whale boings at higher latitudes occurred during the summer and fall in the Chukchi Sea (Delarue et al. 2013). If minke whales are moving north in the spring and back south in the fall, it is possible that our sparse manually validated detections, which occurred during these transition seasons (Fig. 6), were from individuals undertaking such a migration, either to a region farther north of Washington or to farther inshore waters.

**Odontocete spatio-temporal patterns**

Detections were higher at offshore sites for all odontocete species (Figs. 7 and 10), as found in previous studies (Green et al. 1992, 1993, Barlow and Forney 2007, Oleson et al. 2009). However, between the three odontocete families analyzed, there was limited overlap in peak click detections: sperm whales were detected most in the early summer, delphinid species in the summer and fall, and beaked whales in the winter and spring (Figs. 3, 7, and 10). Since we detected echolocation clicks for these species, our detections are...
likely a better proxy of foraging than of overall species presence offshore of Washington. Therefore, these seasonal and spatial trends are potentially related to the presence of prey.

The spatial and temporal patterns of odontocete click detections that we describe highlight the importance of conducting comparable studies over large spatial scales. Studies ranging along the west coast of North America have led to hypotheses about the movements of different populations, and since acoustics are increasingly being used to discriminate between populations, it may be feasible to verify these hypotheses and better inform conservation strategies using these methods.

**Sperm whales**

Although sperm whales are known to forage at high latitudes during the summer (Madsen et al. 2002, Whitehead 2003), manually detected clicks were lower during this season offshore of Washington compared to other regions in the North Pacific (Mellinger et al. 2004, Diogou et al. 2019, Rice et al. 2021). This, coupled with the low number of visual sightings from surveys of the region (Green et al. 1992, Barlow and Forney 2007), suggests that the waters offshore of Washington likely do not represent a primary foraging area for sperm whales and the region generally appears to be utilized less by sperm whales than other regions of the eastern North Pacific. Additionally, offshore of British Columbia, there is evidence that male and female sperm whales seasonally vary their prey consumption (Flinn et al. 2002), as well as their distance from shore (Gregr et al. 2000, Flinn et al. 2002). Acoustic analyses of sperm whales may therefore need to account for these demographic differences to accurately reveal spatial and temporal distribution patterns.

**Risso’s and Pacific white-sided dolphins**

Risso’s and Pacific white-sided dolphin clicks occurred more often at night (Fig. 9). This pattern has been reported previously for these species (Soldevilla et al. 2010b, 2010a) and is likely associated with the diel vertical migration of mesopelagic prey, as observed in other delphinid species (Benoit-Bird and Au 2003; Benoit-Bird et al. 2004). Because both Risso’s and Pacific white-sided dolphins primarily prey on squid offshore of Washington (Norris and Prescott 1961; Stroud et al. 1981; Kenney and Winn 1986), we might expect some degree of habitat partitioning to reduce competition for resources. However, although we saw a possible preference for different habitats, we did not see a clear spatial or temporal separation of these species: manual detections were highest for both species during summer, Pacific white-sided dolphin manual detections were highest at Slope, and, although Risso’s dolphin manual detections were highest at Canyon, Pacific white-sided dolphin clicks were, in fact, more prevalent at this site (Fig. 7). Since these species seem to overlap while feeding offshore of Washington, they may be preying upon different species. Pacific white-sided dolphins prey on fish in addition to squid in other regions (Norris and Prescott 1961) and are reported to do so opportunistically offshore of Washington (Stroud et al. 1981).

The presence of this nocturnal pattern in Pacific white-sided dolphin clicks, as well as the increase in manual detections during summer (Fig. 7), also supports hypotheses about the behavior and movements of different subpopulations of Pacific white-sided dolphins in the North Pacific. Offshore of California, two populations of Pacific white-sided dolphins can presumably be acoustically discriminated (Walker et al. 1986, Soldevilla et al. 2008, 2010b, Henderson et al. 2011), and the California/Oregon/Washington subpopulation is believed to move between California in the winter and Oregon/Washington in the summer (Walker et al. 1986, Green et al. 1992, Forney and Barlow 1998). This population produces clicks more often at night (Soldevilla et al. 2010b), which may indicate that the detections we report are from this northward-southward moving subpopulation. However, there is also evidence that Pacific white-sided dolphins may undergo inshore-offshore movement throughout the year (Green et al. 1992, Soldevilla et al. 2010b, Kanes 2018). A better delineation of subpopulations for Risso’s and Pacific white-sided dolphins in the North Pacific, which may be possible using acoustic discrimination (Soldevilla et al. 2010b), would likely further our understanding of the more fine-scale movements of these species.

**Beaked whales**

Although beaked whales exhibited temporal separation from other odontocete species, manually validated detections of all beaked whale species occurred primarily in the winter and spring (Fig. 10). In the Gulf of Alaska, Stejneger’s and Cuvier’s beaked whales showed spatial separation, with Stejneger’s clicks highest along the continental slope while Cuvier’s clicks were highest at an offshore seamount and were almost absent at the slope (Rice et al. 2021). Additionally, during visual surveys offshore of Washington, Cuvier’s beaked whales were typically sighted farther offshore than Stejneger’s beaked whales (Barlow and Forney 2007, Moore and Barlow 2013) and acoustic detections of Cuvier’s beaked whales offshore of Oregon were higher than detections of Stejneger’s beaked whales (Simonis et al. 2020). Since we did not have a site farther offshore than Canyon, we may not have successfully captured the distribution of Cuvier’s beaked whales offshore of Washington, possibly explaining the low level of Cuvier’s beaked whale manually validated detections. This may also be true for the possible Hubbs’ beaked whale (BW37V) click type since it was detected in even lower numbers offshore of Washington and
previous detections of this click type along the U.S. west coast occurred in deeper water than site Canyon (Griffiths et al. 2018; Simonis et al. 2020, Table S1).

The lack of manually validated beaked whale detections during the summer months is interesting, as the year-round distribution of beaked whales is still not well understood. For Cuvier’s beaked whales, a similar seasonal pattern was found in the Gulf of Alaska (Rice et al. 2021) and offshore of Southern California (Baumann-Pickering et al. 2014), with manually validated detections decreasing in the late summer. Meanwhile, in the Gulf of Alaska, Stejneger’s beaked whales were recorded year-round and clicks peaked in the fall (Rice et al. 2021). Whether the lack of clicks offshore of Washington during summer is due to a change in behavior or to these species moving to a different area to forage is currently unknown. Since beaked whales inhabit pelagic waters and are difficult to visually observe, acoustic surveys can greatly increase our knowledge of these cryptic species. However, there is a need for more extensive acoustic surveys in offshore waters, as knowledge of the more fine-scale distribution of beaked whale species is still quite limited. This is especially warranted since beaked whale abundance has fluctuated in the last few decades (Moore and Barlow 2013, 2017) and the current status of these populations is unknown (Carretta et al. 2019).

Conclusion

In this study, we used passive acoustic monitoring to examine the spatial and temporal distributions of ten cetacean species off the coast of Washington. Seasonal patterns were evident for all species except minke whales, for which manually validated detections were rare. For mysticetes, increased detections during the fall and winter are likely related to reproduction-associated calling, whereas, for odontocetes, seasonal changes in click detections are likely related to the presence of prey. Risso’s and Pacific white-sided dolphins were also the only species for which a diel pattern was found, as clicks occurred more often at night.

On a small scale, we were able to investigate how acoustic presence varied between the continental shelf, slope, and a submarine canyon, and found that the two sites farther offshore had higher acoustic presence. In other regions, submarine canyons are important foraging habitats for many cetacean species (Moors-Murphy 2014, Fernandez-Arcaya et al. 2017) and all species examined in this study had acoustic presence at site Canyon. This highlights the significance of adequately surveying such habitats, as well as other offshore regions, so that conservation strategies accurately reflect current cetacean distributions.

On a large scale, many of the seasonal patterns we detected, such as for blue and sperm whales, as well as Risso’s and Pacific white-sided dolphins, seem to corroborate findings in other regions and support hypotheses about the movements of these populations. Additionally, we found interannual changes in detections for most of the large whale species we examined, which corresponded with changes in oceanographic conditions. While it is important to understand the habitat use and behavior of cetaceans offshore of Washington, it is also necessary to understand how these same populations utilize other regions, as well as the factors that may impact their distribution.

Although many of our findings support those of previous research in the region, there is a need for continued visual and acoustic surveys in areas utilized by marine mammals to better understand changes and impacts caused by sources such as climate change and anthropogenic sounds. It is the use of these surveys, in combination, over large temporal and spatial scales that will be able to inform successful conservation strategies.

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Author contributions AŠ, EMO, SMW, JAH, and SBP contributed to the study conception, design, and management. AR, AJD, EMO, JST, and LMV performed data analysis. AŠ and SBP contributed to code development and modeling for data analysis. AR generated all tables and figures. The first draft of the manuscript was written by AR and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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Availability of data and materials Metadata analyzed during this study are available via the Tethys database from the corresponding author on reasonable request.
Declarations

Conflicts of interest The authors declare that they have no conflict of interest.

Ethical approval This research was conducted in the Olympic Coast National Marine Sanctuary under permits OCNMS-2006–003-(A1, A2, A3) and OCNMS-2010–010-(A1).

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