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Odontocete occurrence in relation to changes in oceanography at a remote equatorial Pacific seamount

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ABSTRACT

Seamounts are considered hot spots of biodiversity and can aggregate pelagic predators and their prey. Passive acoustic monitoring was conducted over 3 mo in 2012 to document the occurrence of odontocetes near a seamount chain in the central equatorial Pacific in relation to oceanographic changes over time. Beaked whale echolocation signals were most frequently encountered. The main beaked whale signal was an unknown type, BW38, which resembled signals produced by Blainville's beaked

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whales. It had high occurrence during high sea surface temperature and low sea surface salinity. Cuvier’s beaked whales were the second most detected. They had an opposite pattern and were encountered more often when sea surface temperature was low and net primary productivity was high. Risso’s dolphins and short-finned pilot whales had high acoustic densities, and echolocated predominantly at night. Risso’s dolphins occurred more often during low sea surface height deviation. False killer whales were less frequently detected and mostly occurred during the day. Sperm whale detections were fewer than expected and associated with high chlorophyll *a*. Short duration Kogiidae encounters occurred on average every third day. These types of long-term site studies are an informative tool to comparatively assess species composition, relative abundance, and relationship to oceanographic changes.

Key words: odontocetes, long-term monitoring, passive acoustics, seamount, hotspot, ecology, oceanography, beaked whale, dolphin.

Oceanographic and bathymetric features structure the apparently homogenous pelagic ocean into varied ecosystems. Seamounts are considered hot spots of biodiversity in pelagic environments and are known aggregation sites of many large predators and their prey (*e.g.*, Haury *et al.* 2000; Worm *et al.* 2003; Amorim *et al.* 2009; Morato *et al.* 2009, 2010). And while they attract some marine mammal species, this is not the case for all species (Morato *et al.* 2008). For this study, we were interested in the odontocete occurrence near a chain of seamounts in the central equatorial Pacific in relation to oceanographic changes over time.

The subtropical gyres north and south of the equator are oligotrophic waters with low net primary productivity

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(Behrenfeld *et al.* 2006, Polovina *et al.* 2008). In contrast, the equatorial Pacific, roughly from the Galapagos Islands to the International Date Line, shows cooler waters and regions of upwelling (Wyrtki 1981), which supports growth of phytoplankton and consequently other organisms within the food web (*e.g.,* Young *et al.* 2015). The Line Islands are a prominent chain of atolls, reefs, and islands stretching from northwest to southeast (approximately 6°N, 162°W to 11°S, 151°W) across the equator. A perpendicular chain of deep seamounts (Fig. 1) stretches west of the Line Islands for over 200 nmi just north of the equator. The bathymetry has very few other dominant features within the larger vicinity of our study area.

Beaked whales, much like sperm whales, are pelagic, deep diving foragers with a habitat preference for underwater features such as shelf breaks, canyons, and seamounts, likely due to presumed increased prey abundance near these features (Jaquet and Whitehead 1996, MacLeod and D’Amico 2006). Very few data exist on the current status, species composition, or abundance of sperm whales, beaked whales, and other odontocete species in the central equatorial Pacific (Carretta *et al.* 2015). Historically, old whaling records indicate that some areas along the equatorial Pacific yielded successful sperm whale catches (Bannister and Mitchell 1980) and, more broadly, that sperm whales tended to be more abundant in areas with high concentrations of chlorophyll (Jaquet *et al.* 1996). Most surveys conducted since 1997 by the National Oceanographic and Atmospheric Administration (NOAA), National Marine Fisheries Service (NMFS) have focused their efforts on the eastern tropical Pacific and around the Hawaiian Islands. Three surveys (2005, 2011, 2012) extended to the central Pacific, including

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Palmyra Atoll and Kingman Reef to the north of our study site, yet still outside the region of equatorial upwelling (Forney *et al.* 2015). Odontocete models for our study area from Forney *et al.* (2015) show high relative densities of rough-toothed dolphins (*Steno bredanensis*), bottlenose dolphins (*Tursiops truncatus*), short-finned pilot whales (*Globicephala macrorhynchus*), and sperm whales (*Physeter macrocephalus*), and medium relative densities for pantropical-spotted dolphins (*Stenella attenuata*), spinner dolphins (*Stenella longirostris*), striped dolphins (*Stenella coeruleoalba*), and false killer whales (*Pseudorca crassidens*).

Acoustic long-term monitoring has become a useful approach over the past decades to collect information on relative and absolute abundance, species composition, distribution, and diel or seasonal patterns of acoustic presence (Mellinger *et al.* 2004; Širović *et al.* 2004, 2009; Soldevilla *et al.* 2010, 2011; Kerosky *et al.* 2012; Marques *et al.* 2013). This is particularly true for species that are rare or elusive (Munger *et al.* 2008, Marques *et al.* 2011, Baumann-Pickering *et al.* 2014). Odontocetes are known to produce echolocation clicks during navigation and foraging (Au 1993), some of which can be classified to species level based on spectral and temporal characteristics.

Beaked whales have species-specific frequency modulated (FM) echolocation pulses (Baumann-Pickering *et al.* 2013*a*). Currently, 10 FM pulse types in the North Pacific are classifiable (Baumann-Pickering *et al.* 2013*a*). Six of these are from known species: Baird’s (*Berardius bairdii)* (Dawson *et al.* 1998, Baumann-Pickering *et al.* 2013*c*), Blainville’s (*Mesoplodon densirostris)* (Johnson *et al.* 2006), Cuvier’s (*Ziphius cavirostris)* (Zimmer *et al.* 2005), Deraniyagala’s (*M. hotaula)*

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(Baumann-Pickering *et al.* 2010*b*), Longman's (*Indopacetus pacificus)* (Rankin *et al.* 2011), and Stejneger's beaked whales (*M. stejnegeri)* (Baumann-Pickering *et al.* 2013*b*). FM pulses from Deraniyagala's beaked whales, a recently rediscovered species (Dalebout *et al.* 2014), were recorded in the Northern Line Islands at Palmyra Atoll and Kingman Reef (Baumann-Pickering *et al.* 2010*b*, 2014). Additionally, four FM pulse types of unknown origin have been defined and named BW40, BW43, BW70, based on their respective peak frequencies (Baumann-Pickering *et al.* 2013*a*), as well as the signal type BWC, which was described from the waters around Cross Seamount, south of Hawaii (Johnston *et al.* 2008, McDonald *et al.* 2009, Baumann-Pickering *et al.* 2013*a*).

Delphinid species that are expected in central equatorial Pacific waters and have identifiable species-specific echolocation clicks in other geographic regions include Risso's dolphins (*Grampus griseus*) (Soldevilla *et al.* 2008), short-finned pilot whales (Baumann-Pickering *et al.* 2015), false killer whales (Baumann-Pickering *et al.* 2015), and killer whales (*Orcinus orca*) (Au *et al.* 2004). Sperm whales, as well as the Kogiidae as a group (dwarf, *Kogia sima*, and pygmy, *K. breviceps*, sperm whales), are identifiable to species and family level, respectively, in this area. Sperm whales produce strong, regularly paced echolocation clicks with interclick intervals of 0.5–1 s, spectral content primarily below 20 kHz, and multipulse structure (*e.g.,* Goold and Jones 1995; Møhl *et al.* 2000; Madsen *et al.* 2002; Miller *et al.* 2004, 2013; Thode 2005; Nosal and Frazer 2007). Kogiidae emit narrowband high frequency echolocation clicks with the majority of energy around 130 kHz and some energy reaching below 100 kHz (Marten 2000, Madsen *et al.* 2005). For this study, an assumption was made that the

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identifiable features of the clicks of these species defined in other regions, although possibly demonstrating slight geographic differences, were stable enough also to be correctly classified here.

Species that are currently difficult to classify based on echolocation clicks and are expected to occur near the recording site include spinner dolphins (Baumann-Pickering *et al.* 2010*a*), bottlenose dolphins (Roch *et al.* 2011), spotted dolphins and striped dolphins (Frasier 2015), Fraser’s dolphins (*Lagenodelphis hosei*) (Watkins *et al.* 1994), rough-toothed dolphins (Rankin *et al.* 2015), and melon-headed whales (*Peponocephala electra*) (Baumann-Pickering *et al.* 2010*a*).

We gathered autonomous, long-term acoustic data at an unnamed seamount in the central equatorial Pacific, in proximity to the Northern Line Islands, with which we investigated occurrence patterns and species composition of odontocetes in relation to remotely sensed oceanographic changes over the study period.

MATERIALS AND METHODS

Acoustic Recordings

A high-frequency acoustic recording package (HARP) (Wiggins and Hildebrand 2007) was deployed at an unnamed seamount near the equator (0º26.6′N, 164º8.1′W; Fig.1). It was bottom-moored at 1,300 m depth, the highest point of the seamount, and recorded from 6 March until 17 June 2012. The HARP was set to a sampling frequency of 200 kHz with 16-bit quantization, resulting in an effective bandwidth from 10 Hz up to 100 kHz. This recording bandwidth captured all odontocete acoustic signals expected in the area, although with a limited spatial range for the highest frequency echolocators such as Kogiidae

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due to their peak frequency lying beyond the frequency range of the system. The recorder was equipped with an omni-directional sensor (ITC-1042, International Transducer Corporation, Santa Barbara, CA), which had an approximately flat (±2 dB) hydrophone sensitivity from 10 Hz to 100 kHz of −200 dB re V/µPa. The sensor was connected to a custom-built preamplifier board and bandpass filter (Wiggins and Hildebrand 2007). The calibrated system response was corrected for during analysis.

Acoustic Data Analysis

All acoustic data were manually screened by SBP for odontocete echolocation signals with the MATLAB-based (Mathworks, Natick, MA) custom software program *Triton* (Wiggins and Hildebrand 2007), using long-term spectral averages (LTSAs) displaying one hour of recording at a time. No bad or poor quality data occurred. The LTSAs were created using a 5 s time average (500 spectra, 10 ms Hann-windowed frames) with 100 Hz frequency resolution. When echolocation signals were notable in the LTSA, the sequence was inspected more closely. The start and end times of each acoustic encounter were logged and a decision on which species produced these signals was made. SBP initially labeled these acoustic encounters as having been produced by either one of the species whose echolocation signals are known, or as unidentifiable. Classification of false killer whales, short-finned pilot whales, and Risso’s dolphins were based on descriptions of their echolocation clicks from around Hawaii for the first two species (Baumann-Pickering *et al.* 2015), and from Southern California for the latter (Soldevilla *et al.* 2008). It is known that geographic variability exists for clicks of Risso’s dolphins (Soldevilla *et al.* 2014). Given these differences, there is some level of uncertainty associated with

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these manual classifications.

Independently, an automated multistep beaked whale detector was run on the data set. All echolocation signals were initially identified with a click detector (Soldevilla *et al.* 2008, Roch *et al.* 2011). The individual click detections were digitally filtered with a 10-pole Butterworth band-pass filter, with a pass-band between 5 kHz and 95 kHz. Filtering was done on 800 sample points centered on the echolocation signal. Spectra of each detected signal were calculated using 2.56 ms (512 samples) of Hann-windowed data centered on the signal. Click parameters including peak frequency, center frequency, and bandwidth were calculated according to definitions from Au (1993). Duration was derived based on the detector output. Sweep rate was computed with spectrograms over 1.2 ms of data centered on the signal (0.3 ms Hann windows, 98% overlap). Sweeps were traced by selecting the frequency bins with maximum spectrum level for each frame. The −8 dB level from the maximum spectrum level of the traced sweep defined the beginning and ending of a sweep. This criterion was chosen empirically to balance the trade-off between increasing the sample size of signals with a high enough received level while keeping a relevant portion of the FM pulse intact. A bivariate linear regression was calculated through the sweep, resulting in a sweep rate. An expert system classified 75 s of data containing at least seven detections as having beaked whale clicks given these conditions: (1) echolocation signals had peak and center frequencies above 32 and 25 kHz, respectively, a duration of more than 355 μs, and a sweep rate of more than 23 kHz/ms; and (2) if more than 13% of all initially detected echolocation signals over 75 s remained after applying these criteria, the segment was classified as

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containing beaked whale FM pulses. This method has been used to detect acoustic encounters with North Pacific FM pulse types with a stable, approximately 5%, missed detection rate as determined through analyst verified ground truth data at sites across the North Pacific (Baumann-Pickering *et al.* 2013*a*, 2014). Baird's and Longman's beaked whales were not classifiable with this method. Baird's beaked whales are not expected in the area and are manually notable. Longman's beaked whales were candidates to be encountered in the study area, but if present, were logged within the group "unidentified odontocete." A third classification step, based on computer assisted manual decisions by trained analysts (JST, SBP), labeled the automatically detected segments to FM pulse type level and rejected false detections (method in Baumann-Pickering *et al.* 2013*a*). Adjacent segments of 75 s were joined into a single acoustic encounter.

Oceanographic Variables and Statistical Analysis

Oceanographic variables were retrieved through mediator services provided in Tethys, a workbench and database for passive acoustic metadata (Roch *et al.* 2013), using MATLAB routines that allowed download of satellite data from ERDDAP (Environmental Research Division's Data Access Program, NOAA, Southwest Fisheries Science Center; available at http://coastwatch.pfeg.noaa.gov/erddap/index.html).

Science quality, 1 d composite, daytime sea surface temperature (SST, spatial resolution 2.5 nmi) and chlorophyll *a* (CHL, 1.5 nmi) were Level 3, Standard Mapped Image (SMI) data that were collected by the National Aeronautics and Space Administration's (NASA) Aqua Spacecraft by the Moderate Resolution Imaging Spectroradiometer (MODIS). Net primary productivity (NPP) were experimental data computed by NOAA

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CoastWatch using sea surface temperature, chlorophyll *a*, and incident visible surface irradiance collected with Aqua MODIS (spatial resolution 2.5 nmi). Using the Behrenfeld and Falkowski (1997) method, a daily composite of vertically integrated net primary productivity was obtained. Sea surface height deviation (SSHD, science quality) was taken from the AVISO (Archiving, Validation and Interpretation of Satellite Oceanographic data) program with 15 nmi spatial resolution. The AVISO sea surface height program merges data from multiple satellites, such as Jason-1, TOPEX/Poseidon, European Remote Sensing (ERS) Satellites 1 and 2, the GEOSAT Follow-On (GFO), and others. Sea surface height is calculated as the height relative to the geoid, *i.e.*, a simplified earth surface with the ocean at rest. Sea surface height deviation quantifies the anomaly from the long-term mean dynamic height. Sea surface salinity (SSS) data with spatial resolution of 30 nmi were used from Aquarius, version 4, which was a collaborative mission of NASA and Argentina's space agency, Comisión Nacional de Actividades Espaciales (CONAE).

Graphs from satellite data on sea surface height deviation and net primary productivity were generated on the ERDDAP site between 10ºN to 10ºS and 174ºW to 154ºW to provide oceanographic context for the broader region.

Satellite data for a 20 km × 20 km square centered on the HARP location were queried for all variables. At least 33% of a data bin for SST, PPR, CHL, and 2% of a data bin for SSHD and SSS with course resolution, had to overlap with the square to be included into a daily mean value over the extraction area. This resulted in 23 spatial bins for SST and PPR (78% of total area overlapping), 62 bins for CHL (83% overlap), 4 bins for SSHD

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(13% overlap), and 1 bin for SSS (3% overlap). Data were binned in 8 d increments and a mean value was computed, while not accounting for days with missing entries. One 8 d bin of sea surface height deviation did not have data and a value was computed by linear interpolation between the bins before and after.

The numbers of minutes with acoustic detections during the same 8 d bins were calculated for all species, signal types, or groups for comparison with oceanographic variables. Statistical relationships were examined using R Project for Statistical Computing software (R Foundation for Statistical Computing, Vienna; available at http://www.R-project.org). Bivariate linear regressions were computed between the acoustic detections of each species, signal type or group and each oceanographic parameter. Generalized linear models (GLM) were calculated with all oceanographic variables as predictor variables and the acoustic detections per species, signal type or group as dependent variable. An automated forward, backward, and forward and backward selection process was used in R (*step* function) to select the best model. Model results are only presented for those dependent variables that had significant predictors.

RESULTS

Odontocete acoustic encounters containing echolocation signals occurred every day of the recording and were noted on average 6.5 h/d (681 h cumulative recording time of 2,478 recording hours over 104 d, Table 1). Four different beaked whale FM pulse types and five other odontocete echolocation signal types were classifiable.

The equator seamount study area had an average of 16 beaked whale acoustic encounters (1.2 h cumulative recording time) per

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day. A previously undescribed signal type, BW38 (named after its peak frequency), that was similar to FM pulse types produced by Blainville's beaked whale, but was consistently shifted about 5 kHz to higher frequencies (Fig. 2, Table 2), dominated the detections (Fig. 3) with 1,090 acoustic encounters and 89 cumulative hours of recordings.

A subset of 100 acoustic encounters, containing 49,714 FM pulses, recorded between 4 May and 10 May 2012, was used to calculate signal parameters of the BW38 FM pulse type. The BW38 type inter-pulse interval (IPI), a stable parameter and highly relevant to beaked whale acoustic discrimination, was nearly identical to known Blainville's beaked whale IPI (~280 ms) and shorter than the Cuvier's beaked whale IPI (~340 ms, Table 2). Despite some variability in peak and center frequencies, the frequency span over which the energy was distributed was highly stable (Table 2, Fig. 3B). There was a smaller spectral peak around 27 kHz, but the main energy started at around 30 kHz and did not extend considerably above 80 kHz.

Cuvier's beaked whale FM pulses were the second most detected beaked whale signal type (Fig. 3), with 539 acoustic encounters and 37 h of cumulative recording time. There was a possible opposing pattern of presence, with more acoustic encounters of Cuvier's beaked whales during weeks when acoustic encounters of BW38 FM pulse type were fewer. The BWC signal type, likely produced by a beaked whale but with unknown species affiliation, was detected over 25 acoustic encounters, a sum of 55 min of recordings. There were six acoustic encounters of Blainville's beaked whales, with a sum of 10 min of recordings. There was no diel pattern of occurrence for beaked whale signal types, except for BWC, which was detected exclusively at night.

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Risso’s dolphins (Fig. 4) and short-finned pilot whales (Fig. 4) were the most often acoustically encountered delphinid species. They occurred for 121 and 126 h of recordings over 70 and 54 acoustic encounters, respectively (Table 1). Both of these species were detected predominantly at night. False killer whales were regularly encountered at the recording site (Fig. 4), and most of their 28 acoustic detections (40 h of recording) occurred during the day. Acoustic encounters of unidentified odontocetes occurred 98 times (116 h of recording), and may be comprised of spinner, bottlenose, spotted, striped, Fraser’s, or rough-toothed dolphins, or of melon-headed whales or Longman’s beaked whales. Very few acoustic encounters with sperm whales were identified (3 h of recordings over nine acoustic encounters, Fig. 5). Acoustic encounters of pygmy and dwarf sperm whale click types (35 acoustic encounters) occurred throughout the recording period, on average every third day (Fig. 5).

The oceanography in the larger region around the equator seamount changed on a time scale of one to several weeks (Fig. 6). During March, an upwelling event occurred in the region with negative sea surface height deviation (SSHD), low sea surface temperature (SST), high sea surface salinity (SSS), and high net primary productivity (NPP, Fig. 6). April was dominated by downwelling with positive SSHD, higher SST, low SSS, and low NPP. Mid-May experienced a brief dip in SST accompanied by increased SSS and a peak in chlorophyll *a* (CHL). This was followed by a time of nearly neutral SSHD, increased CHL with increasing SST and low NPP.

Bivariate linear regression showed a positive trend in the relationship of SST and a negative trend of SSS with the BW38

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signal type (Table 3, Fig. 7B). GLM results indicated that BW38 signal type acoustic detections can be predicted with SST, NPP, and SSS (Table 4). There was a highly significant positive and a significant negative relationship of NPP and SST, respectively, with acoustic detections of Cuvier's beaked whales (Table 3, Fig. 7A). The GLM with the highest predictive capabilities had NPP as the only predictor variable (Table 4). The positive linear regression of SSHD and acoustic encounters of Risso's dolphins was significant (Table 3, Fig. 7C). The selected GLM had additionally NPP, SSH, CHL, and SSS as predictive variables. There was a significant positive relationship between sperm whales and CHL and a trend with SST. The best GLM selected SSHD, SSH, CHL, and SSS as predictor variables for sperm whale acoustic encounters.

DISCUSSION

A new signal type named BW38, likely produced by a beaked whale species, dominated the acoustic encounters. The signals largely resembled FM pulses produced Blainville's beaked whale in their spectral shape, but were consistently shifted about 5 kHz to higher frequencies (Fig. 2). The BW38 type inter-pulse interval (IPI), a stable parameter and highly relevant to beaked whale acoustic discrimination, was nearly identical to known Blainville's beaked whale IPI (~280 ms) and shorter than the Cuvier's beaked whale IPI (~340 ms, Table 2). The discovery of signal type BW38 brings up questions in regards to its origin, particularly due to its similarity to the Blainville's beaked whale FM pulse type. Previous comparisons of beaked whale FM pulses across regions and oceans indicated stability in the spectral properties of the species-specific signals (Baumann-Pickering *et al.* 2013*a*, 2014). Although BW38 is treated as a new

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signal type here, it is uncertain whether this is a signal originating from a yet to be determined species or if Blainville's beaked whales have changed their signal spectrum in this region based on prey and foraging behavior, age and sex distribution, or population level differences.

The acoustic presence of beaked whales at the equator seamount site, dominated by the BW38 signal type, and followed by Cuvier's beaked whales, was one of the highest of all the sites monitored acoustically in the North Pacific to date. In comparison, the highest recorded acoustic presence is known from Deraniyagala's beaked whales, which were detected every day of the recording period at the nearby Kingman Reef, Northern Line Islands (Baumann-Pickering *et al.* 2014). The BW38 signal type was recorded on 97% of recording days, while Cuvier's beaked whales were detected on 81% of recording days at the equator seamount site (Table 1). This indicates that the area is highly suitable habitat for deep-diving cetaceans. The beaked whale diel acoustic behavior remained as expected, with continuous foraging for all species (Baird *et al.* 2006) except for the unknown species producing the BWC signals that are detected almost exclusively at night across all sites where this signal type has been observed (Johnston *et al.* 2008, McDonald *et al.* 2009, Baumann-Pickering *et al.* 2014). The expectation of encountering FM pulses from Deraniyagala's beaked whales was not supported. This species has been acoustically detected at two sites in the Northern Line Islands, Palmyra Atoll and Kingman Reef, and the site of this instrument could potentially have been a nearby suitable habitat within its presumed distribution.

Risso's dolphins, together with short-finned pilot whales, were delphinid species most often acoustically encountered.

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Results on Risso’s dolphins may be in discrepancy with the lack of visual sightings from NOAA NMFS surveys in areas north of the equator seamount site (Carretta *et al.* 2015). It could be that the acoustic record overestimated the presence of this species due to (1) incorrect acoustic classification based on a species signal description from another geographic area, or (2) a small number of individuals were detected repeatedly at the equator seamount site over the recording period. Alternatively, presence of this species within central equatorial Pacific waters was possibly not captured in existing line-transect surveys that occurred largely north of the equatorial upwelling region. On the other hand, the high acoustic relative densities of short-finned pilot whales and medium acoustic relative densities of false killer whales were in agreement with predictive models based on NOAA NMFS line-transect surveys for the central North Pacific (Forney *et al.* 2015).

Despite the region appearing to be suitable habitat for deep-diving beaked whales, and predictive models suggesting higher densities of sperm whales in the broader study area (Forney *et al.* 2015), sperm whales were detected on only a few occasions (Table 1, Fig. 5). Sperm whales, with their intense echolocation clicks in the human audible range (*e.g.,* Møhl *et al.* 2003), have a relatively large acoustic detection range (>15 km radius). Hence, their low acoustic presence during the recording period did not meet our expectations of detecting a larger number of sperm whale acoustic encounters in these waters. There seems to be a seasonality in their occurrence based on old whaling data, which indicates higher numbers of sperm whales in the monitored region in autumn and possibly winter (Bannister and Mitchell 1980). The HARP may have been

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deployed during a period with lower abundance of sperm whales, and longer monitoring would be needed to assess this further.

Acoustic discrimination of pygmy and dwarf sperm whale signals is still under examination, and thus their acoustic detections are pooled into a single group (Kogiidae). They produce narrowband, high frequency (NBHF) clicks, with peak frequency around 130 kHz (Madsen *et al.* 2005), and only the lower amplitude, lower frequency component of these echolocation clicks (80–100 kHz, *i.e.*, less than the recorder Nyquist frequency) were detectable for this study (Marten 2000). Other species known to produce NBHF clicks are porpoises (*e.g.,* Akamatsu *et al.* 1998, Au *et al.* 1999, Bassett *et al.* 2009), several species of the genera *Lagenorhynchus* and *Cephalorhynchus* (Kyhn *et al.* 2009, 2010), and Franciscana dolphins (*Pontoporia blainvillei*) (Melcon *et al.* 2012), none of which are known to occur in the central equatorial Pacific. Given that only low amplitude portions of the clicks were detected, along with attenuation and absorption being very high for these frequencies, the detection range for Kogiidae signals was likely <1 km from the recorder. Hence, the average acoustic encounter duration was short, with 5.6 ± 2.8 min when the animals were within detection range of the instrument. There were acoustic detections of Kogiidae on average every third day. This means that either the animal density was relatively high or that the same individuals used the waters around the equator seamount site regularly.

Most habitat modeling efforts go well beyond the linear regressions performed here, because multiple variables interact and relationships may not be linear. The available acoustic data for this study were restricted to one site over approximately

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three months. This did not appear to be suitable for a full model development; however, the observed relationships between oceanography and odontocete presence are a first indicator.

In this study, it was shown that detections of the BW38 FM pulse type were positively correlated with SST, while Cuvier’s beaked whale detections were negatively correlated. Because the BW38 signal type dominated the recording, it was detected most often during the downwelling event associated with higher temperatures, while Cuvier’s beaked whale acoustic detections increased during the upwelling in March with high NPP, and also during the brief drop in temperature from mid to late May.

Acoustic encounters of Risso’s dolphins, similar to the BW38 FM pulse type, were positively correlated with SST and occurred more often during the period of downwelling. Predictive modeling for Risso’s dolphin acoustic detections in the Southern California Bight showed a positive relationship with SST and negative relationship with SST covariance together with a 4-week time lag (Soldevilla *et al.* 2011). Soldevilla *et al.* (2011) suggest that the time lag may be an indicator of food web succession, in which physical oceanographic changes initiate phytoplankton bloom and ultimately lead to dolphin predation on higher trophic level organisms.

Hazen and Johnston (2010) conducted measurements of active acoustic backscatter, several abiotic oceanographic variables, and visual observations of cetaceans along a transect from 10°S to 20°N at 170°W, approximately 10°W of the equator seamount site. They observed acoustic backscatter strength of potential odontocete prey items to be highly correlated with both CHL and low SSHD, with highest acoustic densities occurring near the equator. More odontocete sightings were noted when acoustic

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backscatter was high. Additionally, pilot whale sightings were associated with higher SST and lower SSHD compared to false killer whales. In our study, we did not find statistically significant relationships of either species with any oceanographic variables, which may not be unexpected as Hazen and Johnston (2010) sampled over a much wider range of ocean conditions. However, acoustic encounters of short-finned pilot whales were highest during the downwelling period with higher SST and concurrent higher SSHD (Fig. 4, 6). Acoustic presence of false killer whales was highest during the upwelling period with low SST, low SSHD, and high NPP.

There were only a few acoustic encounters with sperm whales in this study and a considerable number of zero count weeks that were not taken into consideration during modeling; hence, the positive relationship with CHL and the GLM result (SSHD + SSH + CHL + SSS), while statistically significant, may be somewhat anecdotal. However, sperm whale historic catches occurred more often in areas with higher CHL (Jaquet *et al.* 1996), and in more recent years near the study area, sperm whale presence was associated with increased secondary productivity (Jaquet and Whitehead 1996).

Long-term passive acoustic monitoring at this remote central equatorial seamount site has provided relative abundance of odontocetes adding to the few short-term visual and acoustic surveys in this remote area. A longer time series and additional recording sites is required to provide more detailed geographic differences in species composition, abundance, and distribution in relation to oceanographic changes over time.

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Akamatsu, T., D. Wang, K. Nakamura and K. Wang. 1998. Echolocation range of captive and free-ranging baiji (*Lipotes vexillifer*), finless porpoise (*Neophocaena phocaenoides*), and bottlenose dolphin (*Tursiops truncatus*). Journal of the Acoustical Society of America 104:2511–2516.

Amorim, P., M. Figueiredo, M. Machete, T. Morato, A. Martins and R. Serrão Santos. 2009. Spatial variability of seabird distribution associated with environmental factors: A case study of marine important bird areas in the Azores. ICES Journal of Marine Science: Journal du Conseil 66:29–40.

Au, W. W. L. 1993. The sonar of dolphins. Springer, New York, NY.

Au, W. W. L., R. A. Kastelein, T. Rippe and N. M. Schooneman. 1999. Transmission beam pattern and echolocation signals of a harbor porpoise (*Phocoena phocoena*). Journal of the Acoustical Society of America 106:3699–3705.

Au, W. W. L., J. K. B. Ford, J. K. Horne and K. A. Newman Allman. 2004. Echolocation signals of free-ranging killer whales (*Orcinus orca*) and modeling of foraging for chinook salmon (*Oncorhynchus tshawytscha*). Journal of the Acoustical Society of America 115:901–909.

Baird, R. W., D. L. Webster, D. J. Mcsweeney, A. D. Ligon, G. S.

This article is protected by copyright. All rights reserved

Schorr and J. Barlow. 2006. Diving behaviour of Cuvier's (*Ziphius cavirostris*) and Blainville’s (*Mesoplodon densirostris*) beaked whales in Hawai’i. Canadian Journal of Zoology 84:1120–1128.

Bannister, J., and E. Mitchell. 1980. North Pacific sperm whale stock identity: Distributional evidence from Maury and Townsend charts. Report of the International Whaling Commission (Special Issue 2):219–230.

Bassett, H. R., S. Baumann, G. S. Campbell, S. M. Wiggins and J. A. Hildebrand. 2009. Dall’s porpoise (*Phocoenoides dalli*) echolocation click spectral structure. Journal of the Acoustical Society of America 125:2677–2677.

Baumann-Pickering, S., S. M. Wiggins, J. A. Hildebrand, M. A. Roch and H.-U. Schnitzler. 2010*a*. Discriminating features of echolocation clicks of melon-headed whales (*Peponocephala electra*), bottlenose dolphins (*Tursiops truncatus*), and Gray’s spinner dolphins (*Stenella longirostris longirostris*). Journal of the Acoustical Society of America 128:2212–2224.

Baumann-Pickering, S., S. M. Wiggins, E. H. Roth, M. A. Roch, H. U. Schnitzler and J. A. Hildebrand. 2010*b*. Echolocation signals of a beaked whale at Palmyra Atoll. Journal of the Acoustical Society of America 127:3790–3799.

Baumann-Pickering, S., M. A. McDonald, A. E. Simonis*, et al.* 2013*a*. Species-specific beaked whale echolocation signals. Journal of the Acoustical Society of America 134:2293–2301.

Baumann-Pickering, S., A. E. Simonis, S. M. Wiggins, R. L. Brownell, Jr. and J. A. Hildebrand. 2013*b*. Aleutian Islands beaked whale echolocation signals. Marine Mammal Science 29:221–227.

Author Manuscript

This article is protected by copyright. All rights reserved

Baumann-Pickering, S., T. M. Yack, J. Barlow, S. M. Wiggins and J. A. Hildebrand. 2013*c*. Baird’s beaked whale echolocation signals. Journal of the Acoustical Society of America 133:4321–4331.

Baumann-Pickering, S., A. E. Simonis, M. A. Roch*, et al.* 2014. Spatio-temporal patterns of beaked whale echolocation signals in the North Pacific. PLOS ONE 9:e86072.

Baumann-Pickering, S., A. E. Simonis, E. M. Oleson, R. W. Baird, M. A. Roch and S. M. Wiggins. 2015. False killer whale and short-finned pilot whale acoustic identification. Endangered Species Research 28:97–108.

Behrenfeld, M. J., and P. G. Falkowski. 1997. Photosynthetic rates derived from satellite-based chlorophyll concentration. Limnology and Oceanography 42:1–20.

Behrenfeld, M. J., R. T. O’Malley, D. A. Siegel, *et al*. 2006. Climate-driven trends in contemporary ocean productivity. Nature 444:752–755.

Carretta, J. V., E. M. Oleson, D. W. Weller, *et al*. 2015. U.S. Pacific Marine Mammal Stock Assessments: 2014. U.S. Department of Commerce, NOAA Technical Memorandum, NOAA-TMNMFS-SWFSC-549. 414 pp.

Dalebout, M. L., C. Scott Baker, D. Steel, *et al.* 2014. Resurrection of *Mesoplodon hotaula* Deraniyagala 1963: A new species of beaked whale in the tropical Indo-Pacific. Marine Mammal Science 30:1081–1108.

Dawson, S., J. Barlow and D. Ljungblad. 1998. Sounds recorded from Baird’s beaked whale, *Berardius bairdii*. Marine Mammal Science 14:335–344.

Forney, K., E. Becker, D. Foley, J. Barlow and E. Oleson. 2015. Habitat-based models of cetacean density and distribution

Author Manuscript

This article is protected by copyright. All rights reserved

in the central North Pacific. Endangered Species Research 27:1–20.

Frasier, K. 2015. Density estimation of delphinids using passive acoustics: A case study in the Gulf of Mexico. Ph.D. thesis, University of California San Diego, La Jolla, CA 287 pp.

Goold, J. C., and S. E. Jones. 1995. Time and frequency domain characteristics of sperm whale clicks. Journal of the Acoustical Society of America 98:1279–1291.

Haury, L., C. Fey, C. Newland and A. Genin. 2000. Zooplankton distribution around four eastern North Pacific seamounts. Progress in Oceanography 45:69–105.

Hazen, E. L., and D. W. Johnston. 2010. Meridional patterns in the deep scattering layers and top predator distribution in the central equatorial Pacific. Fisheries Oceanography 19:427–433.

Jaquet, N., and H. Whitehead. 1996. Scale-dependent correlation of sperm whale distribution with environmental features and productivity in the South Pacific. Marine Ecology Progress Series 135:1–9.

Jaquet, N., H. Whitehead and M. Lewis. 1996. Coherence between 19th century sperm whale distributions and satellite-derived pigments in the tropical Pacific. Marine Ecology Progress Series 145:1–10.

Johnson, M., P. T. Madsen, W. M. X. Zimmer, N. Aguilar De Soto and P. Tyack. 2006. Foraging Blainville’s beaked whales (*Mesoplodon densirostris*) produce distinct click types matched to different phases of echolocation. Journal of Experimental Biology 209:5038–5050.

Johnston, D. W., M. McDonald, J. Polovina, R. Domokos, S.

Author Manuscript

This article is protected by copyright. All rights reserved

Author Manuscript

Wiggins and J. Hildebrand. 2008. Temporal patterns in the acoustic signals of beaked whales at Cross Seamount. Biology Letters 4:208–211.

Kerosky, S. M., A. Širović, L. K. Roche, S. Baumann-Pickering, S. M. Wiggins and J. A. Hildebrand. 2012. Bryde’s whale seasonal range expansion and increasing presence in the Southern California Bight from 2000–2010. Deep Sea Research Part I: Oceanographic Research Papers 65:125–132.

Kyhn, L. A., J. Tougaard, F. Jensen, *et al.* 2009. Feeding at a high pitch: Source parameters of narrow band, high-frequency clicks from echolocating off-shore hourglass dolphins and coastal Hector’s dolphins. Journal of the Acoustical Society of America 125:1783–1791.

Kyhn, L. A., F. H. Jensen, K. Beedholm, J. Tougaard, M. Hansen and P. T. Madsen. 2010. Echolocation in sympatric Peale’s dolphins (*Lagenorhynchus australis*) and Commerson’s dolphins (*Cephalorhynchus commersonii*) producing narrow-band high-frequency clicks. Journal of Experimental Biology 213:1940–1949.

MacLeod, C. D., and A. D’amico. 2006. A review of beaked whale behaviour and ecology in relation to assessing and mitigating impacts of anthropogenic noise. Journal of Cetacean Research Management 7:211–221.

Madsen, P. T., M. Wahlberg and B. Møhl. 2002. Male sperm whale (*Physeter macrocephalus*) acoustics in a high-latitude habitat: Implications for echolocation and communication. Behavioral Ecology and Sociobiology 53:31–41.

Madsen, P. T., D. A. Carder, K. Bedholm and S. H. Ridgway. 2005. Porpoise clicks from a sperm whale nose - Convergent evolution of 130 kHz pulses in toothed whale sonars?

This article is protected by copyright. All rights reserved

Author Manuscript

Bioacoustics 15:195–206.

Marques, T. A., L. Munger, L. Thomas, S. Wiggins and J. A. Hildebrand. 2011. Estimating North Pacific right whale *Eubalaena japonica* density using passive acoustic cue counting. Endangered Species Research 13:163–172.

Marques, T. A., L. Thomas, S. W. Martin, *et al.* 2013. Estimating animal population density using passive acoustics. Biological Reviews 88:287–339.

Marten, K. 2000. Ultrasonic analysis of pygmy sperm whale (*Kogia breviceps*) and Hubbs' beaked whale (*Mesoplodon carlhubbsi*) clicks. Aquatic Mammals 26:45–48.

McDonald, M. A., J. A. Hildebrand, S. M. Wiggins, D. W. Johnston and J. J. Polovina. 2009. An acoustic survey of beaked whales at Cross Seamount near Hawaii. Journal of the Acoustical Society of America 125:624–627.

Melcon, M. L., M. Failla and M. A. Iniguez. 2012. Echolocation behavior of franciscana dolphins (*Pontoporia blainvillei*) in the wild. Journal of the Acoustical Society of America 131:EL448–EL453.

Mellinger, D. K., K. M. Stafford and C. G. Fox. 2004. Seasonal Occurrence of sperm whale (*Physeter macrocephalus*) sounds in the Gulf of Alaska, 1999–2001. Marine Mammal Science 20:48–62.

Miller, P. J. O., M. P. Johnson and P. L. Tyack. 2004. Sperm whale behaviour indicates the use of echolocation click buzzes 'creaks' in prey capture. Proceedings of the Royal Society B: Biological Sciences 271:2239–2247.

Miller, B., S. Dawson and R. Vennell. 2013. Underwater behavior of sperm whales off Kaikoura, New Zealand, as revealed by a three-dimensional hydrophone array. The Journal of the

This article is protected by copyright. All rights reserved

Author Manuscript

Acoustical Society of America 134:2690–2700.

Møhl, B., M. Wahlberg, P. T. Madsen, L. A. Miller and A. Surlykke. 2000. Sperm whale clicks: Directionality and source level revisited. Journal of the Acoustical Society of America 107:638–648.

Møhl, B., M. Wahlberg, P. T. Madsen, A. Heerfordt and A. Lund. 2003. The monopulsed nature of sperm whale clicks. Journal of the Acoustical Society of America 114:1143–1154.

Morato, T., D. A. Varkey, C. Damaso, *et al.* 2008. Evidence of a seamount effect on aggregating visitors. Marine Ecology Progress Series 357:23–32.

Morato, T., C. Bulman and T. J. Pitcher. 2009. Modelled effects of primary and secondary production enhancement by seamounts on local fish stocks. Deep Sea Research Part II: Topical Studies in Oceanography 56:2713–2719.

Morato, T., S. D. Hoyle, V. Allain and S. J. Nicol. 2010. Seamounts are hotspots of pelagic biodiversity in the open ocean. Proceedings of the National Academy of Sciences of the United States of America 107:9707–9711.

Munger, L. M., S. M. Wiggins, S. E. Moore and J. A. Hildebrand. 2008. North Pacific right whale (*Eubalaena japonica*) seasonal and diel calling patterns from long-term acoustic recordings in the southeastern Bering Sea, 2000–2006. Marine Mammal Science 24:795–814.

Nosal, E.-M. and L. N. Frazer. 2007. Sperm whale three-dimensional track, swim orientation, beam pattern, and click levels observed on bottom-mounted hydrophones. Journal of the Acoustical Society of America 122:1969–1978.

Polovina, J. J., E. A. Howell and M. Abecassis. 2008. Ocean’s least productive waters are expanding. Geophysical Research

This article is protected by copyright. All rights reserved

Author Manuscript

Letters 35:L03618.

Rankin, S., S. Baumann-Pickering, T. Yack and J. Barlow. 2011. Description of sounds recorded from Longman's beaked whale, *Indopacetus pacificus*. Journal of the Acoustical Society of America 130:EL339–EL344.

Rankin, S., J. N. Oswald, A. E. Simonis and J. Barlow. 2015. Vocalizations of the rough-toothed dolphin, *Steno bredanensis*, in the Pacific Ocean. Marine Mammal Science 31:1538–1548.

Roch, M. A., H. Klinck, S. Baumann-Pickering, D. K. Mellinger, S. Qui, M. S. Soldevilla and J. A. Hildebrand. 2011. Classification of echolocation clicks from odontocetes in the Southern California Bight. Journal of the Acoustical Society of America 129:467–475.

Roch, M. A., S. Baumann-Pickering, H. Batchelor, *et al.* 2013. Tethys: A workbench and database for passive acoustic metadata. Oceans - San Diego 2013. IEEE *Xplore* Digital Library.

Širović, A., J. A. Hildebrand, S. M. Wiggins, M. A. McDonald, S. E. Moore and D. Thiele. 2004. Seasonality of blue and fin whale calls and the influence of sea ice in the Western Antarctic Peninsula. Deep-Sea Research II 51:2327–2344.

Širović, A., J. A. Hildebrand, S. M. Wiggins and D. Thiele. 2009. Blue and fin whale acoustic presence around Antarctica during 2003 and 2004. Marine Mammal Science 25:125–136.

Soldevilla, M. S., E. E. Henderson, G. S. Campbell, S. M. Wiggins, J. A. Hildebrand and M. A. Roch. 2008. Classification of Risso's and Pacific white-sided dolphins using spectral properties of echolocation clicks. Journal

This article is protected by copyright. All rights reserved

of the Acoustical Society of America 124:609–624.

Soldevilla, M. S., S. M. Wiggins and J. A. Hildebrand. 2010. Spatio-temporal comparison of Pacific white-sided dolphin echolocation click types. Aquatic Biology 9:49–62.

Soldevilla, M. S., S. M. Wiggins, J. A. Hildebrand, E. M. Oleson and M. C. Ferguson. 2011. Risso's and Pacific white-sided dolphin habitat modeling from passive acoustic monitoring. Marine Ecology Progress Series 423:247.

Soldevilla, M., L. Garrison, S. Baumann-Pickering, *et al.* 2014. Do spectral features of Risso's dolphin echolocation clicks vary geographically? The Journal of the Acoustical Society of America 135:2240–2241.

Thode, A. 2005. Three-dimensional passive acoustic tracking of sperm whales (*Physeter macrocephalus)* in ray-refracting environments. Journal of the Acoustical Society of America 118:3575–3584.

Watkins, W. A., M. A. Daher, K. Fristrup and G. Notarbartolo Di Sciara. 1994. Fishing and acoustic behavior of Fraser's dolphin (*Lagenodelphis hosei*) near Dominica, southeast Caribbean. Caribbean Journal of Science 30:76–82.

Wiggins, S. M., and J. A. Hildebrand. 2007. High-frequency Acoustic Recording Package (HARP) for broad-band, long-term marine mammal monitoring. International Symposium on Underwater Technology 2007 and International Workshop on Scientific Use of Submarine Cables & Related Technologies, IEEE:551–557.

Worm, B., H. K. Lotze and R. A. Myers. 2003. Predator diversity hotspots in the blue ocean. Proceedings of the National Academy of Sciences of the United States of America 100:9884–9888.

Author Manuscript

This article is protected by copyright. All rights reserved

Wyrtki, K. 1981. An estimate of equatorial upwelling in the Pacific. Journal of Physical Oceanography 11:1205–1214.

Young, J. W., B. P. V. Hunt, T. R. Cook, *et al.* 2015. The trophodynamics of marine top predators: Current knowledge, recent advances and challenges. Deep Sea Research Part II: Topical Studies in Oceanography 113:170–187.

Zimmer, W. M. X., M. P. Johnson, P. T. Madsen and P. L. Tyack. 2005. Echolocation clicks of free-ranging Cuvier’s beaked whales (*Ziphius cavirostris*). Journal of the Acoustical Society of America 117:3919–3927.

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Figure 1. Location of HARP (square: top left) in central equatorial Pacific. Bathymetric detail (HARP as red circle at 1,300 m depth) at an unnamed seamount chain near the equator in the vicinity of the Northern Line Islands, nearly due south of Kingman Reef and Palmyra Atoll. Few bathymetric features exist further south and west of the HARP location.

Figure 2. Characteristics of the beaked whale frequency-modulated (FM) pulse type of unknown origin, named BW38, based on peak frequency. (A) Mean spectra of BW38 FM pulse type (bold black line) in comparison to mean spectra of FM pulses produced by Blainville’s beaked whales (Md) and Deraniyagala’s beaked whales (Mh) (Baumann-Pickering *et al.* 2013*a*). (B) Concatenated spectrogram of all BW38 FM pulses sorted by peak frequency.

Figure 3. Acoustic encounters of BW38 FM pulse type (unknown origin, left) and Cuvier’s beaked whales (right). Long-term spectral average examples (top) and diel and weekly occurrence (bottom).

Figure 4. Acoustic encounters of Risso’s dolphins (top

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left), short-finned pilot whales (top right), false killer whales (bottom left), and unidentified odontocetes (bottom right). Long-term spectral average examples (top) and diel and weekly occurrence (bottom) are shown for each species or group.

Figure 5. Acoustic encounters of sperm whales (left) and Kogiidae (pygmy and dwarf sperm whales, right). Long-term spectral average examples (top) and diel and weekly occurrence (bottom).

Figure 6. Oceanographic changes in the broader area surrounding the study site during the recording period of the HARP using 8 d composite remotely sensed data. (A) Sea surface height deviation and (B) net primary productivity of carbon over 10ºN to 10ºS and 174ºW to 154ºW. (C) Progression of 8 d composite values for sea surface height deviation, mean chlorophyll *a* concentration, sea surface temperature, net primary productivity of carbon, and sea surface salinity over time taken from a 20 km × 20 km area (black square in A and B, not to scale) centered on the HARP location.

Figure 7. Linear regression (line) of oceanographic variables and weekly hours of acoustic detections of species or signal type (points) with 95% confidence intervals (shading).

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Table 1. Overview of acoustic encounters per species or signal type over 104 recording days or 2,478 recording hours.

Species or signal type	Days with detections	Hours with detections	Number of encounters	Encounter duration: mean ± SD (min)
All odontocete detections	104	612	1,954	18 ± 49
BW38 beaked whale type	101	89	1,090	5 ± 6
Cuvier's beaked whales	84	37	539	4 ± 5
BWC beaked whale type	9	1	25	2 ± 1
Blainville's beaked whales	3	<1	6	2 ± 1
Risso's dolphins	46	121	70	105 ± 78
Short-finned pilot whales	41	126	54	140 ± 12
False killer whales	23	40	28	86 ± 102
Unidentified	61	191	98	81 ± 88

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odontocetes				
Sperm whales	7	3	9	22 ± 14
Pygmy & dwarf sperm whales	27	3	35	6 ± 3

Table 2. Echolocation click parameter median and (10th, 90th) percentile values for the equator frequency-modulated pulse type BW38 (bold) in comparison to values from Blainville’s, Cuvier’s, and Deraniyagala’s beaked whales, and an unassociated-species signal type BWC (Baumann-Pickering *et al.* 2013*a*).

	Peak frequency (kHz)	Center frequency (kHz)	−10dB bandwidth (kHz)	Duration (µs)	Interpulse interval (ms)
Blainville’s	34.4 (31.3, 44.1)	37.3 (32.3, 44.0)	11.7 (5.5, 23.0)	581 (299, 950)	280 (111, 427)
BW38	**38.7 (34.0, 47.7)**	**41.3 (36.4, 48.8)**	**18 (7.8, 31.3)**	**533 (322, 905)**	**284 (96, 384)**
Cuvier’s	40.2 (20.3, 49.2)	35.9 (28.7, 42.5)	10.9 (5.1, 21.9)	585 (306, 976)	337 (94, 491)
Deraniyagala’s	47.3 (28.9, 69.1)	46.8 (33.5, 57.1)	19.5 (9.0, 36.7)	475 (305, 720)	194 (70, 429)
BWC	46.9 (28.9, 73.8)	47.4 (30.3, 65.4)	26.2 (5.9, 48.4)	779 (270, 1210)	127 (66, 338)

Table 3. Results of bivariate linear regression between each oceangraphic variable

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measured over 8 d bins and hours of odontocete echolocation detections over the corresponding time period. Oceanographic variables: SST, sea surface temperature; NPP, net primary productivity; SSHD, sea surface height deviation; CHL, chlorophyll *a*; SSS, sea surface salinity. Odontocete species: BW38, BWC: beaked whale FM pulse types of unknown origin; Zc: Cuvier’s beaked whale; Md: Blainville’s beaked whale; Gg: Risso’s dolphin; Gm: short-finned pilot whale; Pc: false killer whale; Pm: sperm whale; Kspp: Kogiidae (pygmy and dwarf sperm whale).

		BW38	Zc	BWC	Md	Gg	Gm	Pc	Pm	Kspp
SST	adj. r^2	0.20	0.24	−0.05	0.03	−0.04	0.06	−0.08	0.17	−0.08
	$F_{1,11}$	3.94	4.73	0.47	1.35	0.55	1.74	0.08	3.42	0.12
	P	0.073[a]	0.052[b]	0.508	0.269	0.472	0.214	0.787	0.092[a]	0.736
NPP	adj. r^2	0.09	0.67	−0.09	−0.09	0.12	0.01	−0.03	0.09	−0.04
	$F_{1,11}$	2.25	25.71	<0.01	<0.01	2.65	1.07	0.68	2.23	0.55
	P	0.162	<0.001[d]	0.946	0.993	0.132	0.324	0.427	0.164	0.476
SSHD	adj. r^2	0.04	0.06	0.03	−0.07	0.50	0.14	−0.08	−0.06	0.07
	$F_{1,11}$	1.49	1.78	1.35	0.17	12.82	2.94	0.14	0.27	1.94
	P	0.248	0.209	0.269	0.685	0.004[c]	0.114	0.714	0.615	0.192
CHL	adj. r^2	0.04	−0.02	−0.08	−0.09	0.06	−0.09	−0.05	0.30	−0.05
	$F_{1,11}$	1.44	0.82	0.15	0.02	1.73	<0.01	0.46	6.03	0.42
	P	0.256	0.385	0.710	0.893	0.216	0.954	0.513	0.032[b]	0.530
SSS	adj. r^2	0.21	0.07	−0.06	−0.03	−0.05	−0.06	<−0.01	−0.06	−0.07

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$F_{1,11}$	4.21	1.89	0.26	0.65	0.41	0.29	0.91	0.23	0.19
P	0.065^{a}	0.196	0.617	0.437	0.535	0.600	0.360	0.642	0.672

[a] $P < 0.1$

[b] $P < 0.05$

[c] $P < 0.01$

[d] $P < 0.001$

Table 4. Selected generalized linear model (GLM) results between oceangraphic variables measured over 8 d bins and hours of odontocete echolocation detections over the corresponding time period (DOF, degrees of freedom; AIC, Akaike information criterion). Oceanographic variables: SST, sea surface temperature; NPP, net primary productivity; SSH, sea surface height; SSHD, sea surface height deviation; CHL, chlorophyll *a*; SSS, sea surface salinity. Odontocete species: BW38, beaked whale FM pulse types of unknown origin; Zc, Cuvier’s beaked whale; Gg, Risso’s dolphin.

Species		BW38	Zc	Gg	Pm
GLM		SST + NPP + SSS	NPP	NPP + SSHD + SSH + CHL + SSS	SSHD + SSH + CHL + SSS
Null deviance, DOF		48.5, 12	28.8, 12	500.8, 12	2.14, 12
Residual deviance, DOF		7.9, 9	8.6, 11	85.4, 7	0.7, 8
AIC		40.5	37.6	75.4	10.7
SST	SE, t, P	0.72, −1.94, 0.085^{a}	—	—	—

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NPP	*SE*, *t*, *P*	0.01, −4.42, 0.002[c]	0.01, 5.07, 0.0004[d]	0.04, −2.07, 0.077[a]	—
SSH	SE, *t*, *P*	—	—	246.87, −3.21, 0.015[b]	18.13, 1.99, 0.082[a]
SSHD	SE, *t*, *P*	—	—	192.43, 3.68, 0.008[c]	15.26, −2.00, 0.080[a]
CHL	SE, *t*, *P*	—	—	41.12, −2.10, 0.073[a]	2.68, 3.27, 0.011[b]
SSS	SE, *t*, *P*	4.80, −5.58, 0.0003[d]	—	17.02, −1.43, 0.195	1.12, 1.95, 0.088[a]

[a] $P < 0.1$

[b] $P < 0.05$

[c] $P < 0.01$

[d] $P < 0.001$

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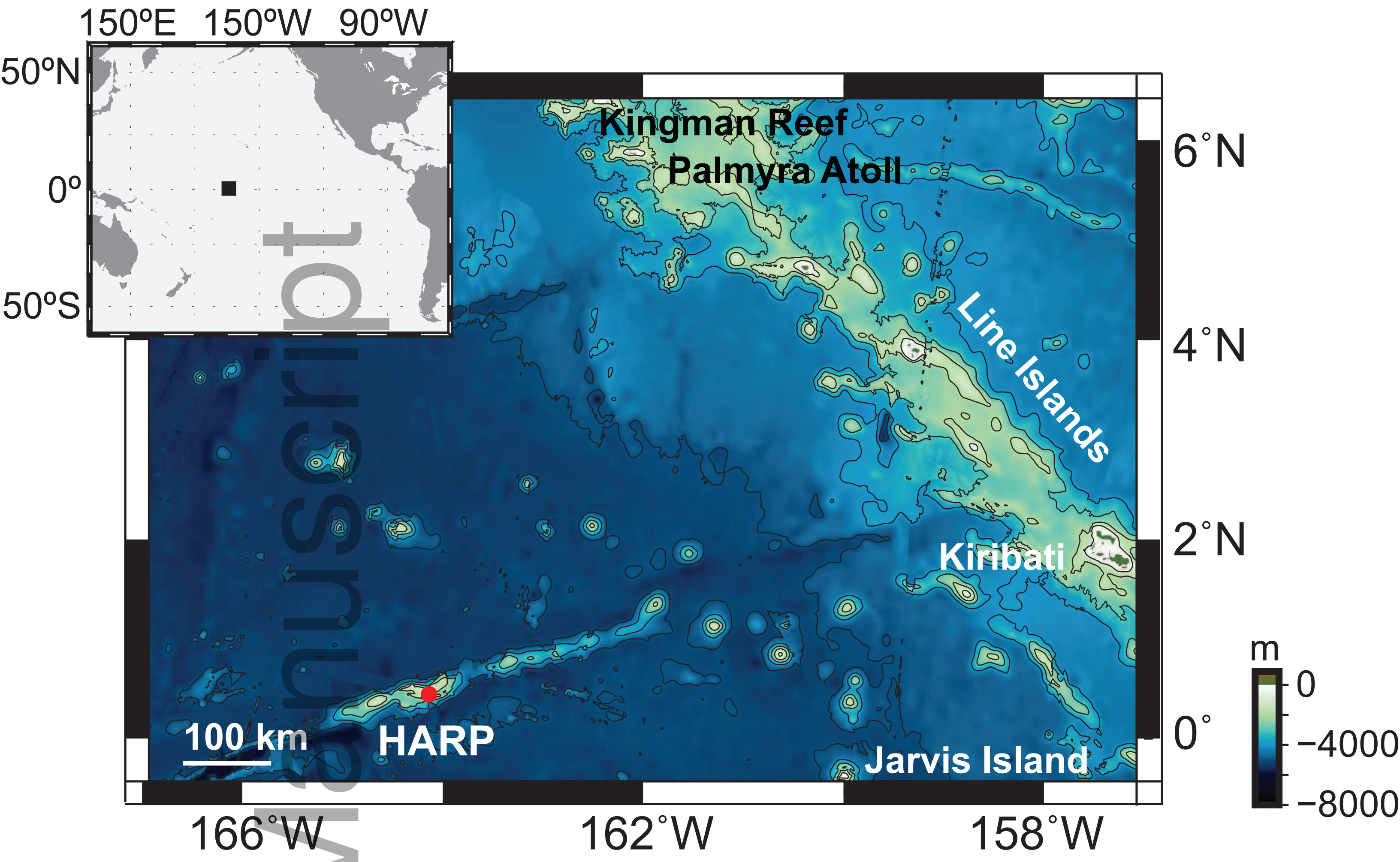

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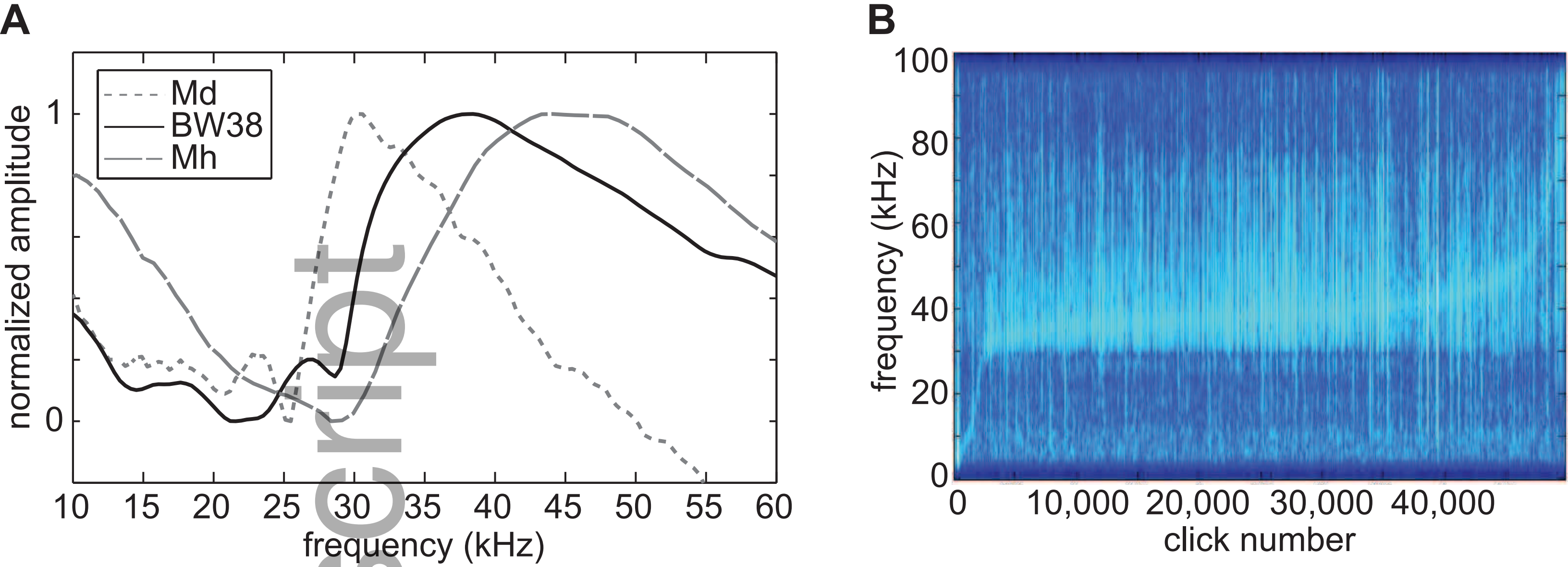

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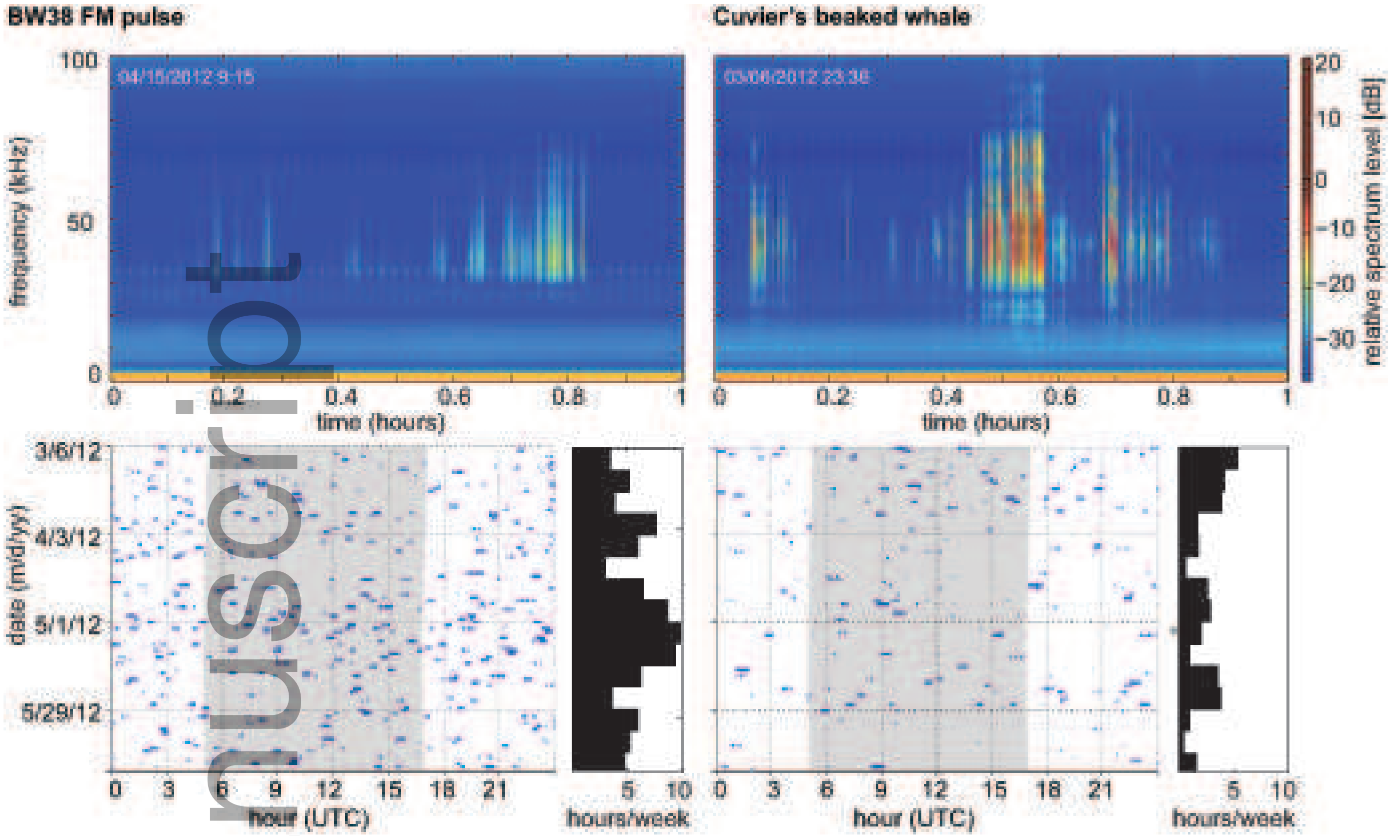

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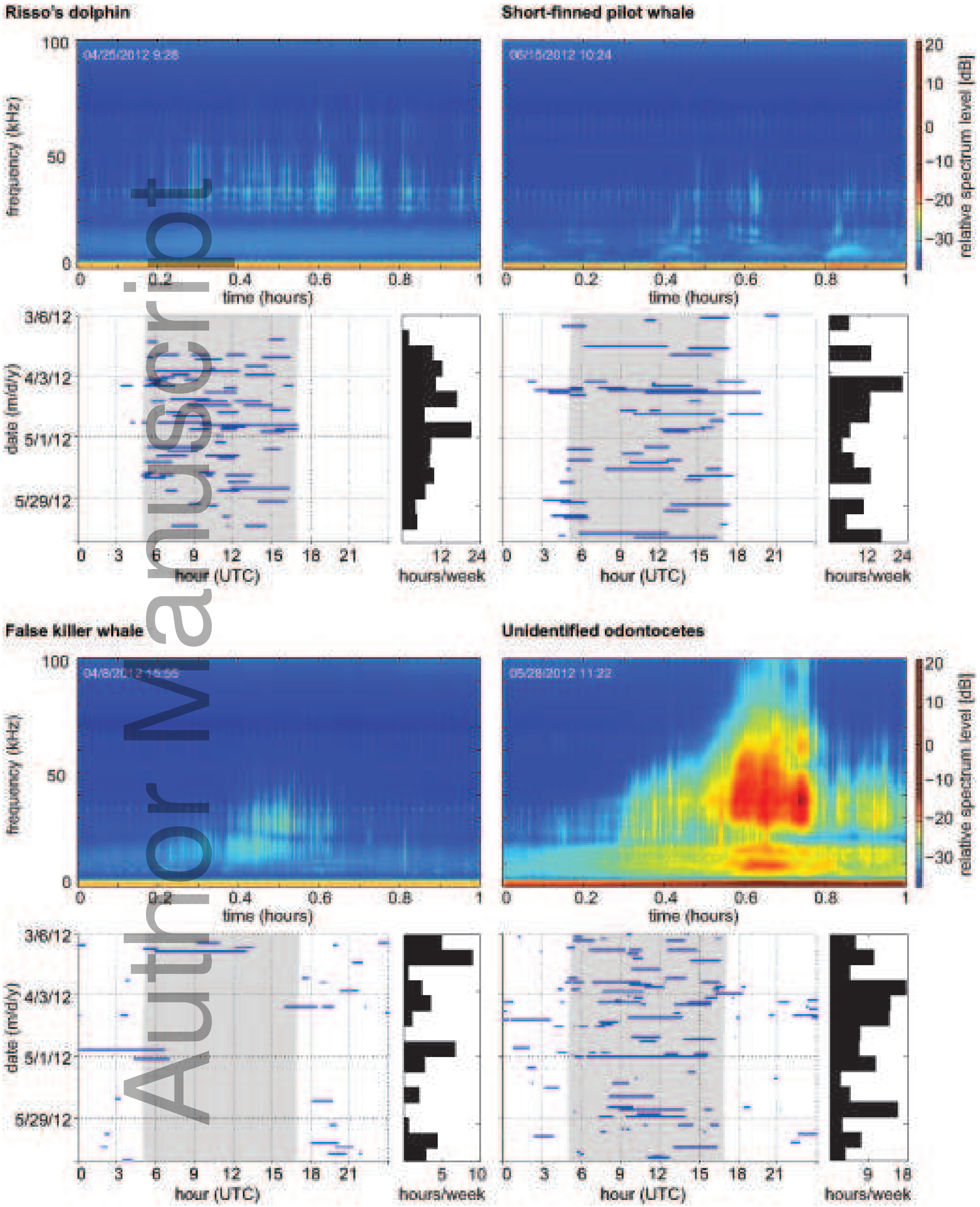

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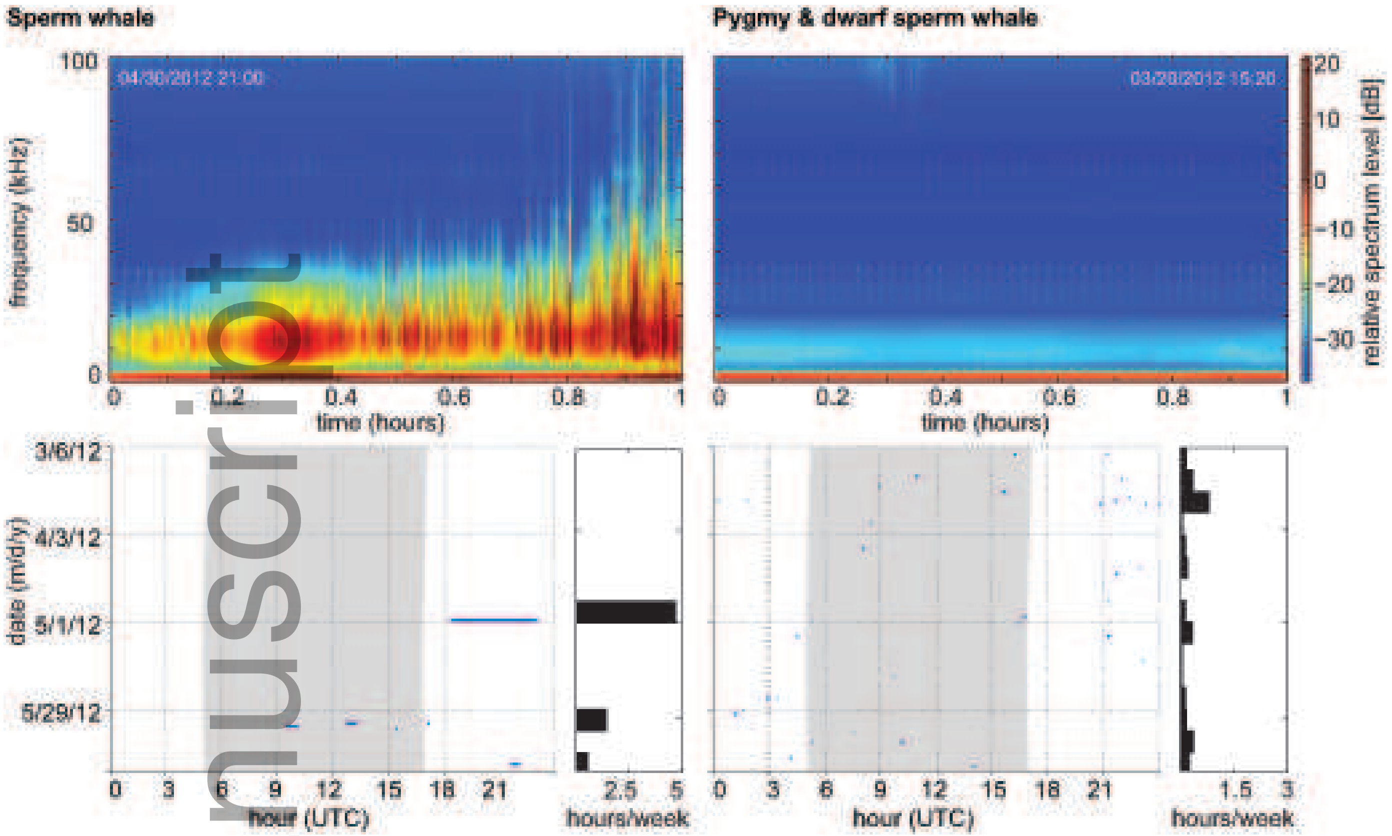

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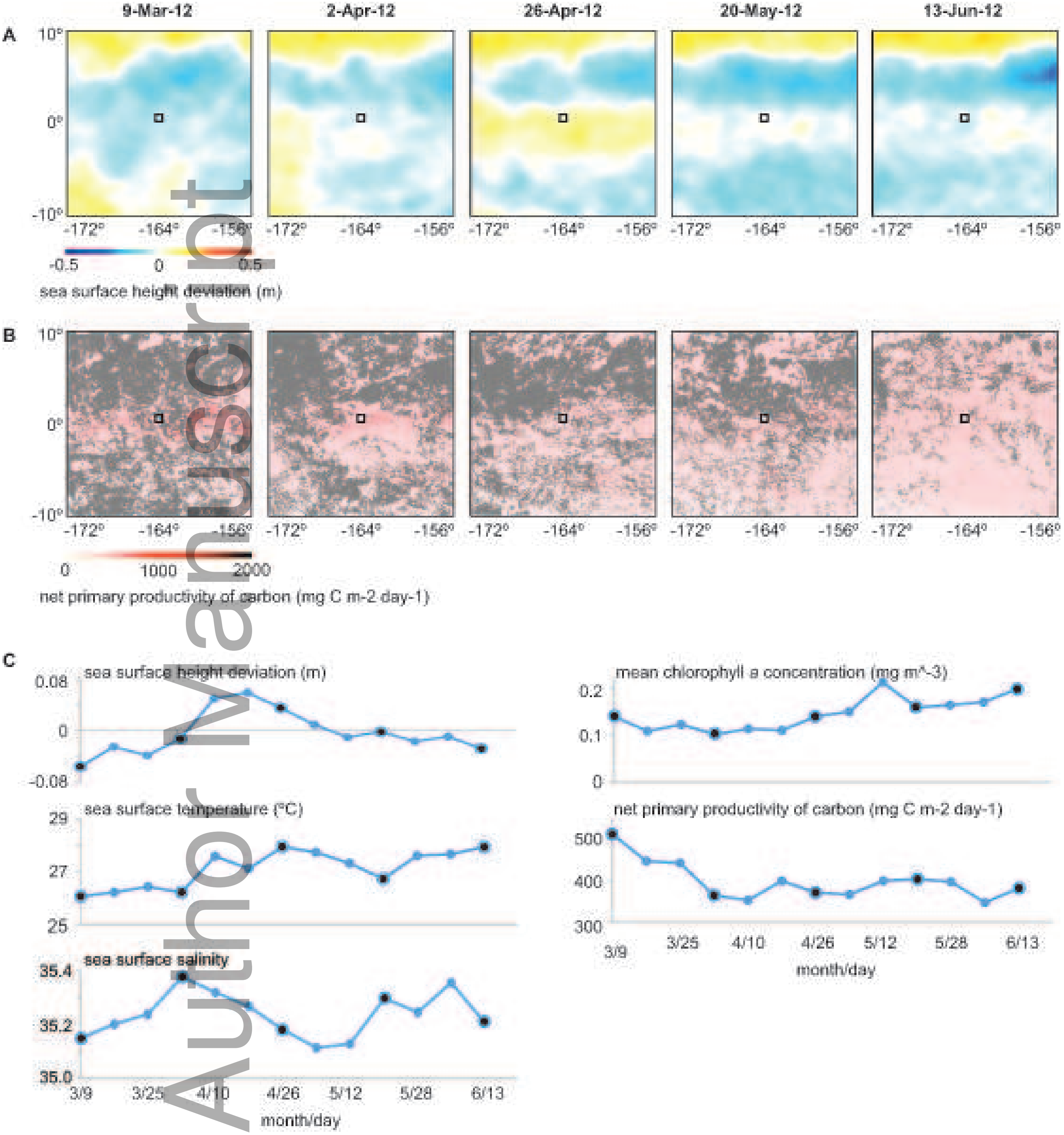

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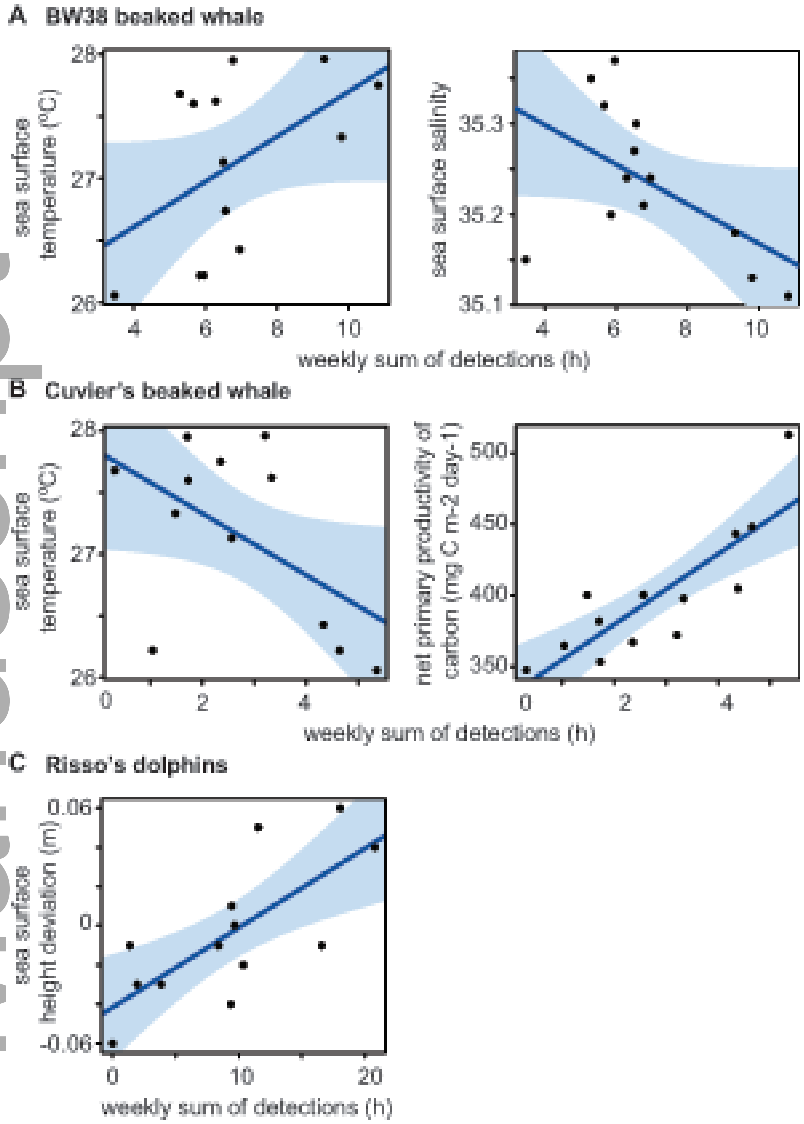

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