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Feeding calls produced by solitary humpback whales

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Humpback whales (*Megaptera novaeangliae*) are acoustically oriented baleen whales that are well known for complex vocal behaviors that are seasonally and geographically stratified. Their acoustic repertoire includes highly stereotyped songs that have been associated with breeding behaviors and a series of lesser-studied nonsong vocalizations, also known as "social sounds" that are produced throughout their migratory range and across behavioral contexts (Payne and McVay 1971, Silber 1986, Au *et al*. 2006, Dunlop *et al*. 2007, Zoidis *et al*. 2008, Fournet *et al*. 2015, Videsen *et al*. 2017). Nonsong vocalizations, which are defined as any phonation produced independently of song, are diverse and vary widely in their acoustic structure and use (Rekdahl *et al*. 2013, Wild and Gabriele 2014, Fournet *et al*. 2015). On migratory corridors, the use of nonsong vocalizations appears to be context-driven and may serve to facilitate intragroup or intergroup communication (Dunlop *et al*. 2008, Videsen *et al*. 2017), while on breeding grounds nonsong vocalizations have been documented in groups of aggressively competing males and in cow-calf pairs (Silber 1986, Zoidis *et al*. 2008, Videsen *et al*. 2017). Efforts to classify nonsong vocalizations have been made on North Atlantic and North Pacific foraging grounds (Thompson *et al*. 1986, Stimpert *et al*. 2011, Fournet *et al*. 2015); however, only one call has been placed into a definitive behavioral context (D'Vincent *et al*. 1985, Sharpe 2001).

The "feeding call" is a highly stereotyped tonal call with a peak frequency of approximately 500 Hz (Cerchio and Dahlheim 2001, D'Vincent *et al*. 1985). To date, it has only been documented among groups (>2 individuals) of Alaskan humpback whales engaged in synchronized foraging events while feeding on Pacific

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herring (*Clupea pallasii*). (Greenough 1981, Baker 1985, D'Vincent *et al*. 1985, Sharpe 2001). The association between feeding calls and group foraging events is well established and has been consistently documented in Southeast Alaska from 1979 to the present (Jurasz and Jurasz 1979, D'Vincent *et al*. 1985, Neilson *et al*. 2015). Although the foraging style associated with feeding call varies, *i.e*., the use of bubble nets and surface lunges *vs*. subsurface lunges without bubble nets (Jurasz and Jurasz 1979, Baker 1985, Sharpe 2001, Doyle *et al*. 2008), the acoustic properties of the call itself are similar throughout Southeast Alaska (D'Vincent *et al*. 1985, Cerchio and Dahlheim 2001, Sharpe 2001, Fournet *et al*. 2015). Functionally, feeding calls have been hypothesized to (1) coordinate individuals during herring foraging events, (2) recruit animals into group foraging events, and (3) manipulate prey (Jurasz and Jurasz 1979, Baker 1985, D'Vincent *et al*. 1985, Cerchio and Dahlheim 2001, Sharpe 2001, Doyle *et al*. 2008). These possible functions may not be mutually exclusive. Investigating the social and behavioral context associated with feeding call production is essential for assessing these hypotheses. In this paper, we provide evidence for *solitary* animals producing feeding calls while foraging, and propose that in this context feeding calls serve a prey manipulation function.

Data were provided by five independent research projects, collected from 1995 to 2017 and supplemented with data from a directed shore-based study in 2012 (Table 1). Data collection protocols for the independent research projects were systematic according to the goals of each project and are described elsewhere for each study (Straley *et al*. 1993, Sharpe 2001, Fournet 2014, Neilson *et al*. 2015, Gabriele *et al*. 2016). Directed observations were collected in 2012 in Frederick Sound as part of a systematic effort to investigate the relationship between nonsong vocal behavior and social context in humpback whales on their foraging grounds.

Data from independent researchers were included only when observers (1) were actively engaged in systematic data collection in pursuit of a research goal; (2) made specific reference in field notes to the whale being alone (hundreds of meter away from the nearest whale) while producing a feeding call; (3) had experience documenting feeding calls in the field; and (4) could aurally distinguish the call above the surface of the water, through the hull of the observation vessel and/or recorded a feeding call with a signal-to-noise ratio (SNR) of at least 15 dB (Table 2). Hydrophone recordings of feeding calls were examined aurally and visually in Raven Pro 1.5 (Cornell Laboratory of Ornithology) and compared to published spectrograms of feeding calls from the literature. Individuals photographed in this study were compared to the NPS/UAS collaborative Southeast Alaska Humpback Whale Catalog (Straley and Gabriele 1997) for identification and sex determination.

Directed visual and acoustic observations were simultaneously and systematically collected from June to August 2012 in the vicinity of the Five Finger Lighthouse Island (57.270278°N, 133.631389°W; Fig. 1). Timed visual surveys were made from the 18.3 m lighthouse tower using a Leica T110 theodolite to capture spatial, behavioral, and group size data for humpback whales in the survey area, as well as to document vessel presence and activity. Whales traveling within three body lengths of each other and exhibiting coordinated surfacing behavior were said to be members of a single group (Baker and Herman 1989, Dunlop *et al*. 2008, Ramp *et al*. 2010). Each whale or group of whales within visual range of the lighthouse (up to 17.5 nm) was counted only once per survey. Survey teams consisted of two observers, a theodolite operator and a data operator. Surveys lasted 30 min, were separated by 5 min of rest, and were repeated in 3 h blocks between sunrise and sunset, weather permitting. Observers changed roles after each 30-minute survey to

Table 1. Description of data collection locations, protocols, years, and acoustic equipment for observations collected as part of independent regional humpback whale monitoring projects throughout Southeast Alaska.

	Glacier Bay National Park	Alaska Whale Foundation	University of Alaska Southeast	Oregon State University	Alaska Whale Foundation/Pitzer College
Study objective	Abundance in Glacier Bay and Icy Strait; residence times, spatial and temporal distribution, reproductive parameters and feeding behavior	Coordinated foraging in Southeast Alaska; relationship fidelity, task specialization, individual vocal variation	Population dynamics and foraging behavior in Southeast Alaska	Nonsong classification, calling behavior and social behavior (group size, dispersion, abundance)	Nonsong behavior (call repertoire, call diversity) and environmental features
Location	Icy Strait	Chatham Strait	Iyoukeen Cove	Frederick Sound, Five Finger Lighthouse	Frederick Sound, Five Finger Lighthouse
Hydrophone	HTI-96-MIN	Reson TC4030	HTI-99	Cetacean Research Technology, C-55	Cetacean Research Technology SQ26-08
Freq resp/ sample rate/ sample res	2 Hz–30 kHz, 48 kHz, 16-bit	20 Hz–25 kHz, 44.1 kHz, 16- bit	2 Hz–125 kHz, 96 kHz, 24-bit	10 Hz–10 kHz, 44.1 kHz, 16-bit	20 Hz–25 kHz, 44.1 kHz, 16-bit
Hydrophone sensitivity	−165 dB	−164 dB	−164 dB	−165 dB	−169 dB
Years	1995, 2009, 2017	2000	2009	2012	2015
Method	Photo ID, behavioral observations, prey collection/identification, opportunistic passive acoustic sampling	Photo ID, behavioral observations, video recording, prey collection/ identification, passive acoustic sampling	Photo ID, behavioral sequencing, opportunistic passive acoustic sampling	Passive acoustic sampling, shore-based focal follows, shore-based scan point sampling.	Passive acoustic sampling, shore-based whale counts, real-time sound streaming, opportunistic shore-based video

Table 2. Summary of independent observations of solitary animals producing feeding calls aggregated from throughout Southeast Alaska between 1995 and 2017.

	16 August 1995	12 August 2000	17 August 2002	22 May 2009	13 August 2009	12 August 2012	22 July 2015	14 September 2017
	Pleasant Island, Icy Strait	Danger Point, Chatham Strait	False Point, Chatham Strait	Mud Bay, Icy Strait	Iyoukeen Cove, Chatham Strait	Five Finger Lighthouse, Frederick Sound	Five Finger Lighthouse, Frederick Sound	Pleasant Island, Icy Strait
Lone whale	Y	Y	Y	Y	Y	Y	Y	Y
Heard in air/through hull	Y	Y	Y	Y	N	Y	—	N
Recorded, SNR $\geq$15 dB	N	Y	Y	N	N	Y	Y	Y
Surface lunge	Y	Y	Y	N	Y	N	Y	Y
Bubbles	Y	Y	Y	N	Y	Y	Y	Y
Prey observed	Y	Y	Y	Y	N	N	Y	Y
Sex	U	F	U	M	U	U	F	U
ID	879	2070	318	875	—	—	1159	879

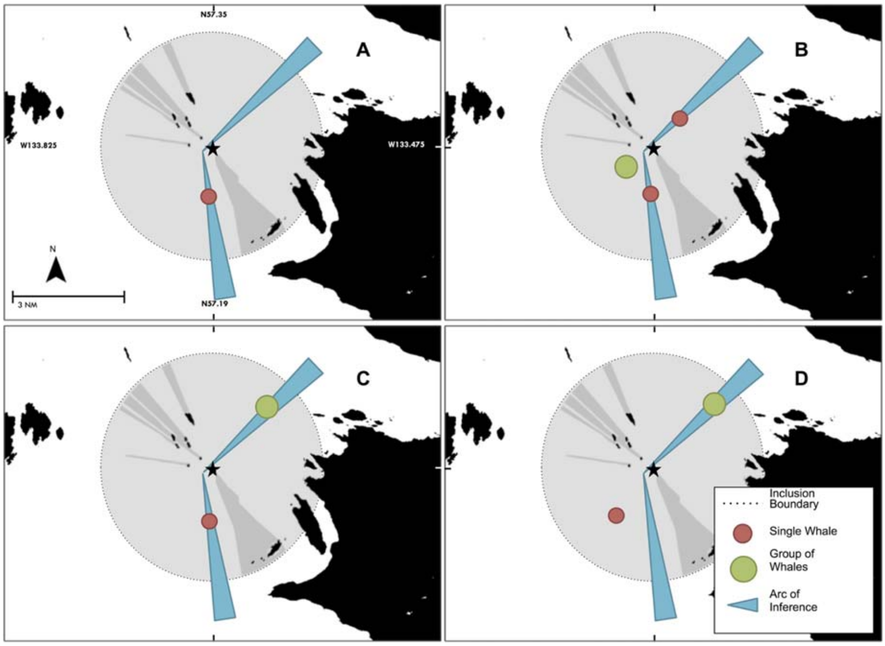

Figure 1. Five Finger Lighthouse survey area including the 6.5 km inclusion boundary; blind spots indicated in dark gray. Lighthouse is marked with a star. Surveys containing whales beyond the 6.5 km boundary were excluded. Potential localization outcomes using the phone-pair bearing localization method (clockwise from top): (A) one singleton within the bearing range, highly likely call produced by a singleton; (B) multiple singletons within bearing range, highly likely call produced by a singleton; (C) singleton and group of whales within bearing range, inconclusive if call produced by a singleton; (D) group of whales only within bearing range, use of the call by a singleton unsupported.

minimize eye strain. The schedule was designed to cover all times of day (dawn through dusk) equally throughout the summer months. As such, the period of time between blocks varied from 5 min to 3 h depending on weather and sampling schedule. Observer teams were changed after every block. Whales that were very near shore or blocked by nearby islands were in "blind spots" not visible to the visual observers in the lighthouse tower (Fig. 1).

To accompany the visual surveys, simultaneous acoustic recordings near the Five Finger Lighthouse were collected by one vessel-based observer using two omnidirectional dip hydrophones separated by 4 m, weighted, and deployed to a depth of 25 m for recording (Table 1). The observer listened to acoustic output in real time; when a vocalization was aurally detected, the observer would record the time, GPS location and compass heading of the vessel, and hydrophone array. At the start of each 30-minute visual survey, the vessel was positioned to ensure that the observer had maximum visibility of blind spots not visible by shore-based observers. Vessel-based observers were familiarized with the survey area, with an emphasis on blind spots, and would visually scan blind spots throughout the 30-minute observation period with binoculars and/or the naked eye and promptly notified the visual observers of any whales in those areas. Because of the tidal activity in the area the vessel would drift either north or south throughout the deployment, which allowed for maximal blind spot visibility during each survey. The blind spot on the southwest side of the lighthouse island was in view of the vessel observer at almost all times; if at any time that blind spot was out of view of the vessel observer, a shore-based observer would be stationed on the south end of the island to monitor for whale activity in that region.

Surveys were included in analysis only if (1) a feeding call with a SNR of 15 dB or higher was recorded during the survey period, (2) all sighted whales were within 6.5 km of the lighthouse (Fig. 1), and (3) visibility was qualitatively considered "good" or "excellent." For each survey fitting the inclusion criteria, the total number of sighted whales was counted, a pod composition (single animal, cow-calf pair, or group of whales) was assigned to each group, and an overall survey composition (all singles, singles and cow-calf pair, or mixed group and singles) was assigned to each survey. Provided the duration of time between surveys did not exceed 5 min, this process was then applied to the two subsequent surveys to assess whether survey composition changed after the detection of a feeding call.

Acoustic recordings associated with directed data collection were manually reviewed and feeding call samples were extracted using Raven Pro 1.5. Two measures were incorporated into acoustic analysis to ensure that these feeding calls originated from whales within visual range: An approximate detection range was calculated for each call and feeding calls were localized to generate a bearing between the vessel and the caller. The following model was used to estimate the range of detection for each feeding call in the survey area:

$$\mathrm{SNR} = \mathrm{SL} - \mathrm{TL} - \mathrm{AN}$$

where SNR equals the measured signal-to-noise ratio (signal excess) of a given feeding call, SL are the source levels of recorded feeding calls liberally estimated at 170 $\mathrm{dB_{RMS}}$ re 1 μPa at 1 m (Dunlop *et al.* 2013; Fournet *et al.* 2016, 2017), TL is the known transmission loss for the region calculated as a 15 log range dependency (Malme *et al.* 1982) and AN is *in situ* ambient noise level ($\mathrm{dB_{RMS}}$ re 1 μPa at 1 m) in the 200–600 Hz range recorded in the 2 s immediately preceding the call of interest (inband power feature, Raven Pro 1.5). Median source levels for humpback whale nonsong vocalizations on migratory corridors have been measured as 158 $\mathrm{dB_{RMS}}$ re 1 μPa at 1 m (Dunlop *et al.* 2013), and in Southeast Alaska average source levels for nonsong vocalizations have been measured as 142 $\mathrm{dB_{rms}}$ re 1 μPa at 1 m (135–160 dB; Fournet *et al.* 2016, 2017).

For the 2012 paired-hydrophone data, bearings to whale vocalizations were estimated based on the phone-pair bearing option using Ishmael v. 1.x (Mellinger 2001). Using this method, the time difference of the signal arrival for the pair of phones determines a hyperbola on which the calling animal lies. When the phones are close together, this hyperbola manifests as a pair of bearings joined at the hydrophone array and radiating outward toward the caller. Phone-pair bearings are quite precise below 20 km (Frankel *et al.* 1995); however, due to the vessel being adrift the associated compass heading were inexact. A 5° "arc of inference" was assumed on each bearing ray to account for changes in caller location underwater and the error associated with compass headings (Fig. 1). For each call, the location of the deployment vessel, the locations of all whales visually identified during the concurrent scan, and the arc of inference were plotted in ArcGIS10 (Environmental Systems Resource Institute 2012) to assess whether the call had the potential to originate from each whale or group of whales. If only a single animal fell within the arc of inference, then the production of the call by a singleton was considered highly likely. If multiple animals traveling as singletons fell within the arc of inference then the use of the call by a singleton was also considered highly likely. If both singletons and groups containing multiple individuals fell within the arc of inference than the use of the call by a singleton was considered inconclusive. If the arc of inference contained only animals traveling in groups, or did not contain any whales then the use of the call by singletons was considered unsupported (Fig. 1).

Eight opportunistic observations of solitary humpback whales in Southeast Alaska ranging from 1995 to 2017 fit the inclusion criteria for contributed observations (Table 2). In Icy Strait, three observations of solitary animals producing feeding calls were collected by GBNP as part of the 1995, 2009, and 2017 humpback whale monitoring efforts (Gabriele *et al*. 2016). On 16 August 1995, in a 41-minute observation starting at 1425 AKDT, an observer (CMG), familiar with the acoustic structure of feeding calls and with previous experience recording them in the field, documented a single humpback whale (SEAK-ID #879, sex unknown) near Pleasant Island in Icy Strait (58.313889°N, 135.642778°W) repeatedly blowing bubbles in a circular pattern and vertically lunging through the surface of the water. Patchy prey were identified using the vessel's depth sounder and an audibly distinguishable feeding call was detected resonating through the hull of the vessel. The call stopped just prior to a final burst of bubbles and a terminal surface lunge. This repeated several times over a 12-minute observation session with the single animal blowing bubbles, vocalizing, and lunging through patchy prey. Not all lunges were made at the surface of the water. No acoustic recordings were made due to technical difficulties.

On 22 May 2009, a solitary male humpback whale (SEAK ID #875,) was observed moving east to west over an apparent layer of prey near Mud Bay also in Icy Strait (58.26950°N, 135.89183°W); prey were again identified using the vessel depth sounder. During the 19-minute encounter, three feeding calls were audible through the hull of the boat between 1030 and 1036 AKDT. There was no evidence of surface lunges during this encounter. No working acoustic recording system was available onboard during this observation.

On 14 September 2017, SEAK #879 was resighted alone in Icy Strait in the vicinity of Pleasant Island (58.314006°N, 135.635401°W) between 1123 and 1143 AKDT. The individual was blowing bubbles in a circular pattern, producing feeding calls, and vertically lunging at the water's surface preying on small schooling fish. The fish are presumed to be young herring based on photographs from this observation and photographs of a large group of bubble-net feeding whales in the area the previous weeks. During the 20-minute encounter, three feeding calls were noted, and one 16 s feeding call with a SNR of 30 dB was recorded. Another humpback whale, also traveling alone, was sighted approximately 1.8 km away during the encounter.

Three observations of solitary humpback whales were collected in Chatham Strait in 2000, 2002 (by FS), and 2009 (by JMS). On 12 August 2000 at 0940 AKST an observer began a 1:29 focal follow of a single animal (SEAK # 2070, a female) in the vicinity of Danger Point, near Angoon, Alaska (57.516324°N, 134.601420°W). Several loud vocalizations were detected through the hydrophone and one vocalization with a SNR of 21 dB was recorded. On one occasion, a

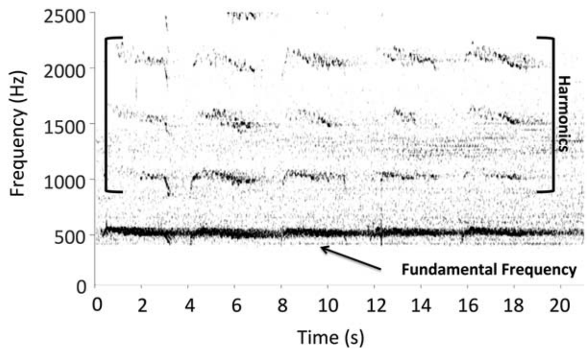

Figure 2. Spectrogram of 19.7 s feeding call recorded in 2012.

vocalization was loud enough to be heard without the aid of the hydrophone. In eight instances, the animal was observed lunging through a ring of bubbles at the water's surface following the termination of a feeding call audible through the hydrophone. Loud feeding calls were detected as the animal was seen in pursuit of a large school of fish, identified in the field as Pacific herring. The observer confirmed the presence of the school with the fish-finder for the duration of the encounter. The focal follow was terminated when a second humpback whale came in to visual range; the second animal was not documented joining the focal animal.

On 17 August 2002 at 1530 AKST, a solitary humpback whale (SEAK #318, sex unknown) was documented near False Bay in Chatham Strait (57.951251°N, 134.929619°W) repeatedly producing feeding calls concurrent with bubble production and surface lunging; during the encounter a 3 s feeding call with a SNR of 22 dB was recorded. The vocalization terminated just prior to the animal breaking the surface of the water. This animal was observed in both previous and subsequent days engaged in group foraging on herring in Chatham Strait.

On 13 August 2009, a solitary animal was documented producing feeding calls in Iyoukeen Cove, Chatham Strait (57.90853°N, 134.92970°W) at 0730 AKDT. The single animal was documented repeatedly blowing bubbles and lunging vertically out of the water's surface following the termination of a feeding call audible through a hydrophone. Three feeding calls with SNR values ranging from 24 to 32 dB and durations ranging from 16 to 29 s were recorded concurrent with visual observations. The animal was alone in the region for approximately 2 h before a group of animals entered the area and began cooperatively foraging on herring; the lone individual did not join the group at this time. The observer noted that groups of humpback whales had been bubble net feeding on herring the region on adjacent days.

Two observations of solitary individuals producing feeding calls were documented in Frederick Sound in the Five Finger Lighthouse region in 2012 and 2015. One observation was made in concert with the directed observations described in this study. On 12 August 2012 at 1246 ASKT, an observer (MF) documented a feeding call audible through the hull of a 3-m zodiac near the Five Finger Lighthouse (57.27144°N, 133.63724°W). The observer documented that a string of bubbles broke the surface of the water simultaneous with the detection of the feeding call, and within 5 s of the termination of the feeding call a humpback whale surfaced approximately 50 m away from the vessel. A 19.7 s feeding call with a SNR of 18 dB was recorded during the encounter (Fig. 2). Shore-based observers engaged in theodolite-based sampling noted three other whales dispersed throughout the survey area at the time. According to the theodolite measurements, the next nearest animal was 2.3 km away from the vessel. All of the animals observed in the region at this time were traveling alone. Three medium-sized vessels were transiting within 8 km of the zodiac at the time of the recording; these vessels were audibly detectable on the recording, accounting for the reduced SNR value.

Video footage recorded on 22 July 2015 (by FMS) showed a single humpback whale located approximately 20 m from the Five Finger Island and approximately 185 m from a moored hydrophone (57.271944°W, 133.63444°N) producing a clockwise bubble curtain and subsequently lunging at the water's surface a steep rocky beach. Concurrent acoustic recordings that were broadcast to observers *via* outdoor speakers during the encounter confirmed a feeding call with a SNR of 20.7 dB that occurred simultaneously with the eruption of the bubble curtain and ceased just prior to the surface lunge. Researchers noted a large school of small fish, which were photographically confirmed as Pacific herring. The school stayed in the vicinity of the island for several days; samples taken on 23 July reconfirmed the prey as Pacific herring.

As a result of combined visual and acoustic data collection in 2012, a total of 127 feeding calls were recorded within 92.6 h of acoustic data with SNR values ranging from 5 to 30 dB (Fig. 3). Twenty-four feeding calls were detected in 11 surveys with SNR values ranging from 15 to 30 dB (Fig. 3). The number of whales sighted per survey ranged from 1 to 11 whales (Table 3); survey compositions were variable (Table 3). Thirteen of the 24 feeding calls documented across 5 d in 2012 were available for localization. Of these, eight calls were confidently linked to singletons, and five were inconclusive (one singleton within arc of inference, $n = 2$; multiple singletons within arc of inference, $n = 6$; small group and singleton within arc or inference, $n = 5$). At no time did the arc of inference include only whales traveling in groups. At no time did the arc of inference fail to include a whale. There were four instances of a survey composition change following a feeding call event (Table 4). In all four instances, neither a feeding call of any SNR nor group formation were observed during subsequent visual surveys.

Frederick Sound is heavily trafficked; multiple vessels were present at all times that feeding calls were detected in 2012. The median ambient noise measurement for 2-second samples collected preceding each feeding calls was 103.5 dB_{RMS} re 1 μPa at 1 m in the 200–600 Hz bandwidth (range = 98–109 dB; Fig. 3). Detection ranges varied from 0.4 to 6.3 km (Fig. 3). While these values are approximations based on a simplistic transmission loss model, these range estimates illustrate the unlikeliness of detecting a feeding call produced by a whale beyond the visual inclusion range of the directed survey efforts. Beyond this, a substantial number of calls exhibited well-structured harmonics, and showed few signs of excessive attenuation (*i.e.*, temporal blurring, loss of high frequency components; Fig. 2) indicating that these calls were produced at close range to hydrophone observers. This is particularly relevant given that any survey that contained a humpback whale sighting between 6.5 and 17.5 km was removed from analysis; collecting calls with SNR values in the observed range, and with fine scale acoustic features is highly unlikely if the calls were produced beyond the range of visual survey effort. The SNR values observed for feeding calls recorded as part of directed efforts in 2012 fall within the same range as the SNR values collected at close range by independent observers. Given the layout of the islands in this area, the height of the shore station, the

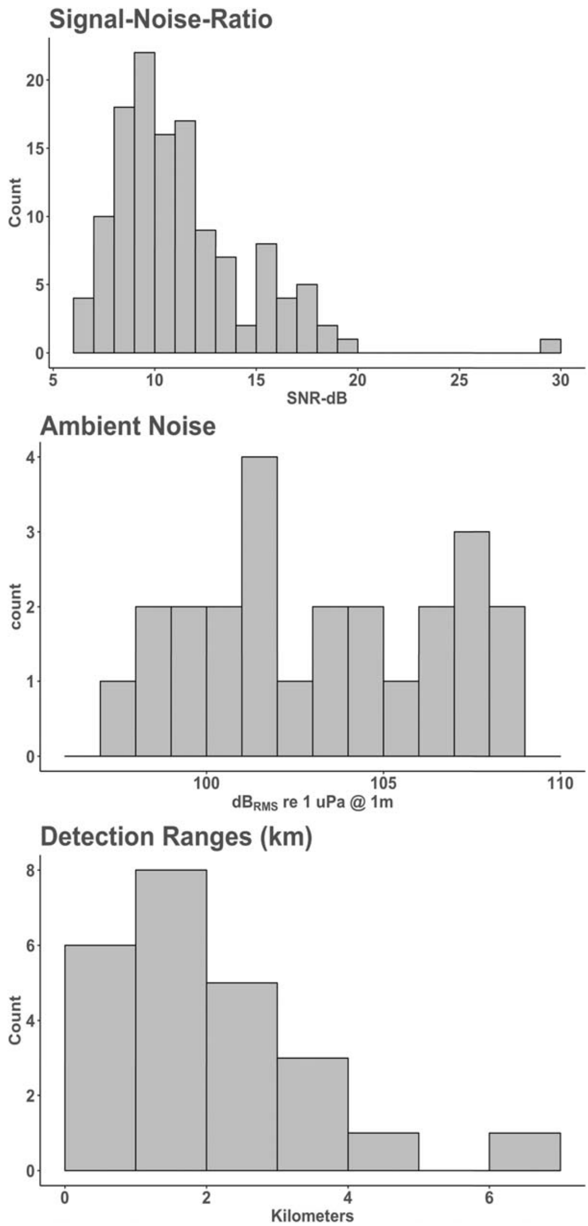

Figure 3. Histograms of: (top) signal-to-noise ratio values (dB), (middle) ambient noise values (dB_{RMS} re 1 μPa at 1 m in the 200–600 Hz range), and (bottom) feeding call detection ranges (km). All values were collected in association with simultaneous visual and acoustic observation efforts in Frederick Sound in 2012.

omission of any surveys that contained humpback whales beyond the 6.5 km boundary, and the redundancy of a vessel-based observer, the probability of all observers visually overlooking a group of foraging whales within the acoustic

Table 3. Composition of visual surveys including maximum and minimum number of whales sighted for each survey type.

Survey composition	# of surveys	# of days	# of calls	Maximum whales	Minimum whales
All singles	7	7	14	6	1
Mixed group and singles	3	3	7	11	4
Singles and cow-calf	1	1	3	6	6

detection range is low. Despite this, however, it remains possible that some of the observations recorded in this study came from individuals beyond the visual range of observers (individuals in blind spots, along shorelines, or beyond survey range).

By using a combination of methodologies employed throughout Southeast Alaska, we generated a data set that strongly supports our assertion that solitary individuals produce feeding calls. Although our sample size is small, these records are consistent, span 22 yr from 1995 to 2017, and include a broad geographic area in northern Southeast Alaska. Through the collaboration of four experienced independent research groups, and by comparing notes documenting the occurrence of the feeding call used by solitary feeding whales, our observations of solitary whales producing feeding calls are consistent with the hypothesis that whales may produce these calls to manipulate prey.

Several marine species utilize sound to manipulate the prey field. For example, snapping shrimp (*Alpheus heterochaelis*) rapidly snap shut an enlarged claw, producing a sound capable of stunning prey (Versluis *et al*. 2000), and common bottlenose dolphins (*Tursiops truncatus*) produce "bang" sounds to alter prey schooling behavior (*Tilapia* spp., Marten *et al*. 2001). Killer whales (*Orcinus orca*) use vocalizations in a similar frequency range to the humpback whale feeding call (200–600 Hz) to induce shoaling in Atlantic herring (*Clupea harengus*) (Simon *et al*. 2006). Prey manipulation is also a proposed function for the "Megapclick" vocalization, produced by North Atlantic humpback whales in association with nighttime foraging events (Stimpert *et al*. 2007). While prey manipulation has been speculated as a function of the feeding call by coordinated groups of humpback whales in Southeast Alaska (Jurasz and Jurasz 1979,

Table 4. Instances of survey composition changes following a feeding call event. Total number of whales counted in each survey in parenthesis. Feeding calls were detected during the "Original" survey. "Following" surveys began 5 min after the original survey; "Subsequent" surveys began 5 min after the "Following" surveys.

Date	Original survey	Following survey	Subsequent survey
8 July 2012	Mixed groups and singles (count = 4)	Single (count = 9)	Singles (count = 4)
15 July 2012	Single (count = 1)	No whale	No whale
7 August 2012	Mixed groups and singles (count = 11)	Mixed groups and singles (count = 7)	Singles (count = 4)
7 August 2012	Single and cow-calf (count = 6)	Single (count = 2)	Single (count = 2)

D'Vincent *et al.* 1985, Sharpe 2001) sufficient data to confirm this hypothesis has been lacking.

The only prey that have been definitively associated with humpback whale feeding call production in the Eastern North Pacific are herring. Hearing sensitivity in Pacific herring is highest in the 200–500 Hz range (Mann *et al.* 2005); the average peak frequency of the humpback whale feeding call overlaps this range, making it well-suited for herding these prey (Cerchio and Dahlheim 2001). Further, playback experiments of feeding calls to Pacific herring elicit defensive responses, including increased school density and fleeing behavior (Sharpe 2001). Generally, the foraging behaviors observed in this study are consistent with those reported for groups of whales engaged in coordinated foraging activities (*i.e.*, feeding call production, bubble production, surface lunging, association with Pacific herring; Jurasz and Jurasz 1979, D'Vincent *et al.* 1985, Sharpe 2001), with the notable difference that animals in this study were foraging alone. The use of feeding calls by lone foraging individuals is incongruent with the hypothesis that this call is exclusively linked to sociality or group formation. In the shore-based data set, none of the 24 instances where a feeding call was detected was followed by group formation or subsequent coordinated foraging events, despite consistent observer effort. Similarly, there was no report of individuals joining a calling singleton in any of the opportunistic reports, although in several instances other animals were documented in the region. This weakens the argument that feeding calls are always used as either group coordination signals or recruitment signals, but it should not be dismissed that the use of this call may facilitate social interactions in some contexts.

While the factors that encourage or initiate group formation are not well understood, this study suggests that spatial and temporal overlap of vocalizing individuals may not to be enough to motivate recruitment. It is typical for humpback whales on foraging grounds to feed independently or in small ephemeral groups of one to two individuals (Baker *et al.* 1985, Clapham 1996); large group formation is generally thought to be an exception to this rule. In Southeast Alaska, however, there are two assemblages of whales that form large coordinated foraging groups consisting of the same principal individuals over decades, both of which have been associated with feeding call production (Baker 1985, Sharpe 2001, Gabriele *et al.* 2016, Pierszalowski *et al.* 2016). Four individuals in this study, SEAK #318, #875, #879, and #2070 have been known to participate in coordinated group foraging concurrent with feeding call use. It is likely that the individual experience of a given whale drives, at least to a degree, its foraging behavior and response to feeding calls. We propose that whales who often participate in group foraging events may be predisposed to use feeding calls when other whales are unavailable, or when prey patch size is insufficient to incite group formation. Although individuals who engage in coordinated foraging exhibit fixed behavioral roles within a group, irrespective of group size (Mastick 2016), we speculate that these solitary whales may produce a feeding call when alone whether or not they typically play the "vocal" role during group feeding events.

In conclusion, documentation of feeding call use by solitary humpback whales throughout Southeast Alaska and over a 20-year time period expands the known behavioral context of feeding calls, sheds light into the acoustic ecology of this vocally adaptable species, and suggests that a primary function of this call is prey manipulation. Our observations further demonstrate that the use of feeding calls is not exclusively linked to group coordination, and may not be exclusively linked to recruitment. While this study cannot speak to the question of how often solitary whales exhibit this behavior, we assert that the phenomenon is geographically and temporally widespread on Southeast Alaskan foraging grounds.

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