Underwater components of humpback whale bubble-net feeding behaviour

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(Accepted: 24 March 2011)

Summary

Humpback whales (*Megaptera novaeangliae*) employ a unique and complex foraging behaviour — bubble-netting — that involves expelling air underwater to form a vertical cylinder-ring of bubbles around prey. We used digital suction cup tags (DTAGs) that concurrently measure pitch, roll, heading, depth and sound (96 kHz sampling rate), to provide the first depiction of the underwater behaviours in which humpback whales engage during bubble-net feeding. Body mechanics and swim paths were analysed using custom visualization software that animates the underwater track of the whale and quantifies tag sensor values. Bubble production was identified aurally and through spectrographic analysis of tag audio records. We identified two classes of behaviour (upward-spiral; 6 animals, 118 events and double-loop; 3 animals, 182 events) that whales used to create bubble nets. Specifically, we show the actual swim path of the whales (e.g., number of revolutions, turning rate, depth interval of spiral), when and where in the process bubbles were expelled and the pattern of bubble expulsion used by the animals. Relative to other baleanopterids, bubble-netting humpbacks demonstrate increased manoeuvrability probably aided by a unique hydrodynamicly enhanced body form. We identified an approximately 20 m depth or depth interval limit to the use of bubble nets and suggest that this limit is due to the physics of bubble dispersal to which humpback whales have behaviourally adapted. All animals were feeding with at

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DOI:10.1163/000579511X570893

least one untagged animal and we use our data to speculate that reciprocity or by-product mutualism best explain coordinated feeding behaviour in humpbacks.

Keywords: humpback whale, feeding, bubble net, kinematic, spiral-loop, double-loop.

1. Introduction

Humpback whales (*Megaptera novaeangliae*) are large baleen whales (8.5 m at 0.5 years to 14.3 m at 17 years of age; Stevick, 1999) that feed on a variety of relatively small prey species, each of which aggregate in dense concentrations. Common prey include krill (euphausiid spp.), and schooling fish such as herring (*Clupea* spp.), capelin (*Mallotus villosus*) and sand lance (*Ammodytes* spp.) (e.g., Matthews, 1937; Tomilin, 1967; Overholtz & Nicolas, 1979; Ichii & Kato, 1991). In the Gulf of Maine, humpback whales typically target small fish, primarily herring (*Clupea harengus*) and offshore American sand lance (*Ammodytes dubius*; Hain et al., 1982; Kenney et al., 1985; Payne et al., 1986, 1990). American sand lance, the preferred prey for whales in the southern Gulf of Maine and the only prey identified during our study, live in relatively shallow water, school in large aggregations and are relatively weak swimmers (Overholtz & Nichols, 1979; Hain et al., 1982; Weinrich et al., 1997). In particular, their tendency to school near the surface during daylight hours, often in ‘chimney-like’ vertical columns, enables efficient feeding by predatory humpback whales (Hain et al., 1982; Friedlaender et al., 2009; Hazen et al., 2009).

Like all balaenopterids, humpback whales feed by engulfing a large volume of water containing prey and separating food and water using sieve-like baleen plates (Slijper, 1962; Mackintosh, 1965). However, humpback whales have unique behavioural and morphological adaptations that distinguish them from other baleen whales.

Behaviourally, humpback whales capture prey by engaging in complex feeding manoeuvres that are often accompanied by the apparently directed use of air bubbles. The ability of bubble barriers to corral or herd fish has been reported by a number of authors (e.g., Smith, 1961; Blaxter & Batty, 1985; Sharpe & Dill, 1997). Bubble use by humpback whales has been observed in many of their feeding habitats and is reported to occur in a variety of configurations. These bubble-feeding behaviours appear to vary in nature among both individuals and regions; for example, bubble clouds (the production of a single or multiple bursts of seltzer-sized bubbles) are commonly observed from humpback whales in the Gulf of Maine, but never in Alaskan waters.

Of the various bubble configurations reported, the most complex appears to be the bubble net (Jurasz & Jurasz, 1978; Watkins & Schevill, 1979; Hain et al., 1982). Existing descriptions of this unique and complex behaviour are currently derived only from surface observations, predominately Jurasz & Jurasz (1979) and Hain et al. (1982). As described by Jurasz & Jurasz (1979), bubble nets are rings of distinctive bubbles that appear at the surface in a closed circle or figure '9'. In the Gulf of Maine, bubble nets have been further described by Hain et al. (1982) as a ring formed by a series of discrete bubble columns, blown at 3–5 m depth, by a whale that is rotated inward with the flippers in a vertical plane. The nets were described as incorporating 1.25–2 revolutions with smaller bubbles grading into larger bubbles as the net was closed. In both descriptions, whales fed in the centre of the completed bubble net at or near the surface.

Morphologically, as compared to other baleen whales, humpbacks whales are adapted for manoeuvrability. The species is unique in the greater length and higher aspect ratio of its flippers and the existence of a series of protuberances (tubercles) along the leading edge of the flippers (Fish & Battle, 1995; Fish, 2002; Miklosovic et al., 2004). These features have been hypothesized to aid manoeuvrability by increasing lift and decreasing drag, allowing animals to accomplish greater turning at lower speeds (Fish & Battle, 1995; Fish, 2002; Miklosovic et al., 2004). In addition, humpbacks have large flukes relative to their body size providing greater thrust for quick manoeuvres (Woodward et al., 2006). While other balaenopterid whales typically feed by swimming rapidly forward in a relatively straight line and lunging in a narrow plane to engulf prey (Ridgeway & Harrison, 1985; Goldbogen et al., 2006), the morphologic adaptations favouring manoeuvrability are thought to allow humpbacks to undertake the fine-scale movements needed to create bubble nets (Fish & Battle, 1995; Fish, 2002; Miklosovic et al., 2004; Woodward et al., 2006). However, the movements thought to be used by humpback whales to create bubble nets are based only on surface observations and no information exists regarding the actual kinematics of the sub-surface manoeuvres used during feeding events. Therefore, the degree to which and/or how humpback whales would need to manoeuvre when creating bubble nets is unknown.

In this paper, we use data from short-term (<24 h) deployments of synchronous motion, acoustic recording tags (Johnson & Tyack, 2003) to provide the first quantitative descriptions of the subsurface behaviours used by humpback whales engaged in bubble-net feeding. We provide both detailed kinematic descriptions and quantitative analyses of the behaviour patterns accompanying bubble-net feeding, including the onset, pattern and duration of bubble emission. Additionally, we examine the hypothesis that swim patterns and bubble production occur in a way that act to aggregate prey rather than simply surrounding it. We, therefore, provide novel information regarding behaviour unique to humpback whales; the creation of bubble nets to capture prey. In doing so, we provide data demonstrating the complex suite of behaviours needed to create nets, which would be facilitated by the increased manoeuvrability thought to result from the specialized morphological adaptations (flipper size and shape) unique to the species. In addition, we use our data to examine a possible vertical limit to bubble net creation and use (approximately 20 m) and speculate on the apparent coordinated nature of bubble net feeding in humpback whales.

2. Material and methods

2.1. Field methods

2.1.1. Study area and population

The study took place in the southern Gulf of Maine, primarily within the Stellwagen Bank National Marine Sanctuary (42°18′43″N, 70°18′53″W) in July 2006 and July 2007. In addition, one animal in our study was tagged in the Great South Channel (41°27′9″N, 69°18′12″W) in 2004; its tag was recovered near the Northeast Peak of Georges Bank (41°42′30″N, 68°22′3″W) several days after detachment. Because the records of surface feeding came late in the tag record, we assume that the feeding behaviour took place near the spot of recovery.

2.1.2. Tagging

We used digital acoustic recording, synchronous motion tags (DTAGs; Johnson & Tyack, 2003) to record the orientation, movements and acoustic behaviour of feeding whales. DTAGs are small, non-invasive, archival tags attached via suction cups that contain a pressure sensor (depth) and 3-axis magnetometer and accelerometers to determine heading, pitch and roll at a sampling rate of 50 Hz. The tags used two embedded hydrophones (Fs-64 and 96 kHz) to record acoustic information concurrent with the other sensors. Tags had a memory-limited data collection duration of approximately 20 h. The tags also contained a VHF transmitter allowing the tracking of whales independent of visual observation and to aid in the retrieval of tags. Once recovered, data were downloaded for analysis.

Tags were placed on humpback whales that were approachable, but not pre-selected. Attachment used a 7 m rigid-hulled inflatable boat (RHIB) with a 15 m, bow-mounted, cantilevered pole or a 4 m RHIB and 7 m hand held pole. Tagged whales were individually identified using naturally distinctive markings on their dorsal fin and tail flukes (Katona & Whitehead, 1981; Blackmer et al., 2000). This allowed us to know if an animal was tagged more than once, a situation that occurred twice during the study. Tags were placed as high on the back of the animal as possible to facilitate tracking the VHF signal emitted by the tags. Tags were set to release at a pre-defined time, which was determined by a series of factors including memory capacity, weather conditions and programmed release for other simultaneously deployed tags.

Responses of the whales to the tagging event varied from none to indications of short-term disturbance such as diving, trumpet blowing, or accelerating (Weinrich et al., 1991). The first 10 min of behavioural data (2–4 dives) from all tags were discarded because of this potential response period.

2.1.3. Focal animal follows

Tagged animals were followed at a distance of 100–400 m by the RHIBs or, if necessary, at greater distances by larger support vessels (either the 16 m R/V Auk or the 70 m R/V Nancy Foster). During daylight hours (approximately 0600–2000 h) and when weather permitted, surface behaviours were selected from an ethogram of >80 humpback whale behaviours and the times (to the second) at which they occurred were recorded (e.g., Weinrich, 1991; Weinrich et al., 1992). These data were synchronized using time and GPS positions to directly associate tag-derived data with their surface counterparts. Bubble-net feeding events were initially identified by observing a circle of bubbles on the surface followed by the whale's emerging though the ring with its mouth gaped. Because the swim track signature of these bubble-net behaviours in TrackPlot (see below) was so distinct from other portions of the whale swim tracks, we were able to identify additional bubble-net feeding events during analysis. This allowed us to use data from periods when inclement weather or other environmental conditions precluded focal follows.

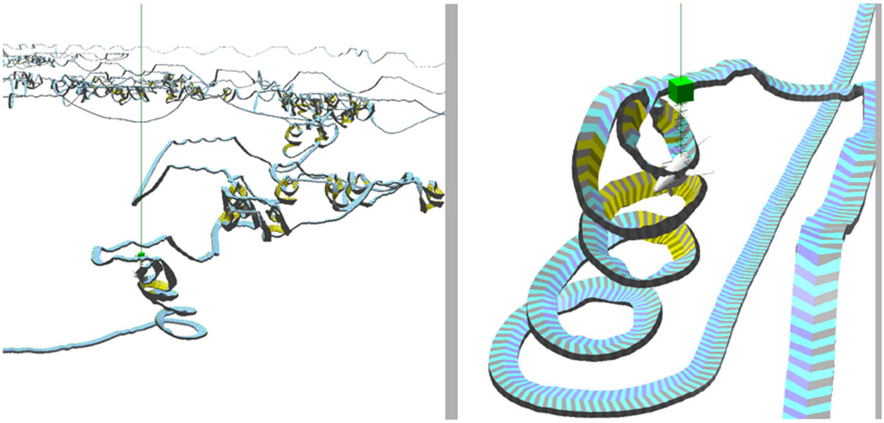
2.2. Data analysis

2.2.1. Visualization of tag data

The DTAG data provided a continuous record of the tagged animal's 'attitude' (azimuth, pitch and roll) and depth. We converted this to a pseudo-track (see Johnson & Tyack, 2003) by assuming that the animal was travelling at a constant speed of one meter per second. Although this speed assumption is likely not precisely accurate, the pseudo track provides a valuable tool for understanding different kinematic behaviour patterns (i.e., Friedlaender et al., 2009; Hazen et al., 2009), and has been shown to accurately depict the movement patterns (but not geographic location) of the tagged animals (Schmidt et al., 2010).

Data were visualized and analyzed using TrackPlot, a custom software application designed for the project (Ware et al., 2006). TrackPlot uses a ribbon to represent the 3D swim path (track) of the whale, with the ribbon's centre being the pseudotrack centre (Figure 1). In scale, the ribbon is four meters wide and is twisted around the along-track direction to show roll behaviour. A pattern of chevrons on the top surface of the ribbon provides travel direction, segments the ribbon into 1-s intervals and gives an additional orientation cue. Loops, turns and twists in the ribbon correspond to the same orientations in the DTAG and, therefore, the whale. TrackPlot also features rapid track traversal and an active zooming, rotational interface allowing us to rapidly visualize different sections of a pseudo-track at different scales and from different angles (Figure 1). This assured that we could obtain the best visualization of the data and investigate a behavioural event in the context of its pre and post behaviours.

TrackPlot also supports the generation of basic dive statistics, such as duration, maximum depth, rate of descent, rate of ascent and rate of turn (change in heading). Dive duration of a feeding behaviour was calculated from the tag record by manually selecting the point of tag submergence for a terminal dive and calculating the interval to the tag's subsequent return to the surface (depth reading of <1 m). Maximum depth for a dive/behaviour



(a) (b)

Figure 1. DTAG derived data were visualized and analysed using TrackPlot, a custom software application. TrackPlot creates a ribbon that represents the temporally accurate, 3D swim path of the tagged whale. Chevrons on the ribbon's top surface reveal travel direction and segment the ribbon into 1-s time intervals. Loops, turns and rolls in the ribbon correspond to the same orientations in the DTAG and, therefore, the whale. Panel (a) is a visualization of several hours of data, while (b) shows a zoomed-in and rotated portion of the initial dive in panel (a). TrackPlot features rapid track traversal and an active zooming, rotational interface that allows the users to move through the track and view behaviour from different angles. This figure is published in colour in the online edition, which can be accessed via http://www.brill.nl/beh

was determined by identifying the deepest record during a dive interval. Additionally, selecting any point in the track provided a read-out of the depth and time for that location. This feature was used to correlate timed surface behaviour observations with subsurface kinematic patterns. This feature was also used for determining the depth and time at which we first heard bubbles released by the whale and the duration of bubble emission (see below).

To investigate variation in turn rate (change in heading) and body orientation (roll angle) during the creation of a bubble net, we manually identified the beginning and end of a bubble-producing swim track (dive). TrackPlot would then integrate the turn rate or roll angle over that interval (e.g., total degrees turned/time interval). This information was saved to a file along with the turn angle, start depth, end depth, start time and end time. Time series averages (and their standard deviations) were calculated by first determining mean segment duration; the segment's durations were then normalized to match this mean. The mean turn rate and roll angle and their standard deviation was then computed for each time step in the normalized segment to determine if it changed throughout the course of the dive sequence. We hypothesized that if animals exhibited increasing rates of turn the spirals were becoming tighter and prey could be compacted in the upper portions of the bubble net. If rate of turn remained constant or decreased through the bubble net sequence we hypothesized that the animal did not spiral inwards and bubbles were likely used to corral rather than concentrate prey. Similarly, we hypothesized that if animals demonstrated increasing roll angle through the spiral sequence this would be indicative of a constricting spiral and the concentration of prey in the upper portions of the net.

2.2.2. Determination of bubble production

We identified bubble production by a whale by listening to the tagged animal's audio record for clearly defined bubbles and visualizing a spectrogram of the tag's acoustic record using *Raven*, a bio-acoustic analysis program (Charif et al., 2006). Bubbling behaviour produced a signature sound, which was further connected to whale bubbling behaviour by matching sounds recorded from humpback whales seen to simultaneously emit bubbles in clear Hawaiian waters (although this was not a feeding context). Hawaiian acoustic data were provided to us by Alison Stimpert, Biology Department, University of Hawaii, Honolulu HI, USA. We identified a continuous emission of bubbles as a 'stream' and pulsed expulsions as 'bursts'. No attempt was made to determine whether the placement of tags on the whales affected the recording of bubbling sounds. However, the placement of tags had relatively low variability, typically located along the dorsal surface near or anterior to the dorsal fin.

Since audio and sensor files are time-synchronized in the DTAG record, we were able to locate the depth at which bubble production was first recorded in each behavioural event. In some cases, the number of dives analysed for bubble production was less than the total number of dives recorded because the sound of passing ships interfered with bubble sounds. For one animal (192a_06) we used a random numbers generator to sub-sample 20 events for analysis from the 109 available in the record.

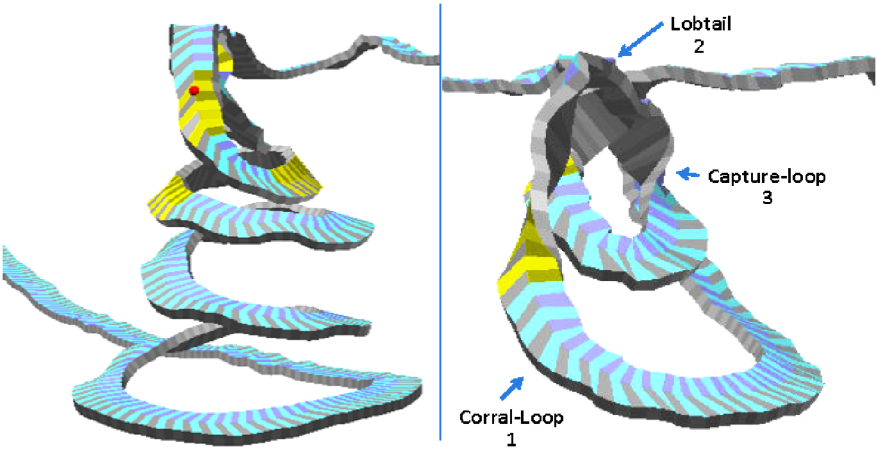
2.2.3. Relationship of bubble feeding to water depth

To understand the relationship between a whale's bubble-producing dive behaviour and the bottom depth over which it was feeding, we used ArcGIS

9.2 Geographic Information System software (ESRI, Redlands, CA, USA). We combined whale position data, using surface position fixes that combined Leica laser-range finder binoculars with the RHIB's GPS position during focal follows, with multibeam bathymetry (Valentine et al., 2001) to determine the approximate water depth over which animals were feeding. We used a linear regression model to test for a relationship between ocean depth and the maximum depth of the foraging dive where a humpback whale produced a bubble net.

3. Results

We recorded 300 tag-derived bubble-net feeding events from 9 individual humpback whales; of the 300 events, 180 were complemented by surface observations. We found two distinct kinematic techniques associated with animals observed feeding via bubble nets; 'upward-spirals' and 'double-loops' (Figure 2). Because the swim track signature of these bubble net behaviours



(a) (b)

Figure 2. TrackPlot visualizations of the two main kinematic behaviours used by humpback whales to create bubble-nets as an aid to capturing prey; (a) an upward-spiral net and (b) a double-loop net. Upward-spirals were produced as a single, continuous step, while the double-loop technique was produced using 3 separate steps: (1) the deep corral-loop, (2) a lobtail at the surface and (3) the capture-loop. At the end of each behaviour the whale appeared in the net with its mouth gaped. This figure is published in colour in the online edition, which can be accessed via http://www.brill.nl/beh

in TrackPlot was so distinct from other portions of the whale swim tracks, we used all tag-derived events for kinematic analysis. We also identified two additional behaviours of note, each recorded from a single animal: a combined spiral-net/double-loop technique (one of the 9 individuals) and a free-form technique where the animal, while surfacing in a bubble net with its mouth open (feeding), swam neither a swim path that could produce a bubble net nor expelled bubbles. Our analysis does not include numeric data on this tenth tagged animal as it neither expelled bubbles nor swam a curvilinear path that could be described. An example of its swim path is in Figure 8.

3.1. Upward-spiral bubble-net feeding

We analysed 118 upward-spiral bubble-net feeding events from six animals (Table 1; seven animals are contained in Table 1: animals 198d_07 and 199a_07 are the same animal tagged on different days). The kinematic behaviour consisted of a clockwise upward spiral (Figure 3), mean ± SD = 2.1 ± 0.3 revolutions (individualized mean range 1.5 ± 0.3 to 2.3 ± 0.4). The combined mean duration of the dive segment associated with spiralling was 70.6 ± 15.2 s (individualized mean range 38.7 ± 4.0 to 102.7 ± 21.2 s (Table 1)). The combined mean rate of turn during spirals was 11.1 ± 1.7°/s, (individualized mean range 7.9 ± 0.8 to 14.2 ± 1.2°/s (Table 1)).

Body orientation (roll angle) during the spiralling event varied among animals. Three animals tended to increase their body roll angle from the beginning to the end of the spiral; two animals showed an initial increase in body roll angle that then diminished through the spiral; and one animal, tagged on two different days, exhibited increased roll angle during the initial part of the spiral, followed by decreasing roll angle in the mid portion of the spiral and increasing roll angle again during the terminal portions of the spiral (Figure 4a–d). The rate of turn for four of the six animals showed an increased turning rate in the final portion of the spiral (Figure 4e). Taken in aggregate, there was a tendency for turning rate to increase through the spiral duration (Figure 4f). The combination of increasing turn-rate and change in body-roll angle tended to form a constricting spiral (Figure 5).

Upward-spiralling behaviour occurred in many parts of the water column (Table 1). The deepest point of initiation was 41.1 m and the deepest point of termination was 35.4 m. The shallowest point of initiation was 17.8 m and the shallowest termination was 4.4 m. The mean depth interval (initiation to

Table 1. Kinematics of upward-spiral bubble-net feeding behaviour in humpback whales feeding on schools of small fish (*Ammodytes dubius*). Data derived from synchronous motion, acoustic recording tags (DTAGs) attached to feeding whales.

Animal	Number of events	Start depth of spiral (m) (σ)	End depth of spiral (m) (σ)	Depth interval of spiral (m) (σ)	Spiral duration (m) (σ)	Number of revolutions	Spiral turn rate (°/s) (σ)
189b_04	4	34.9 (1.8)	28.3 (3.0)	6.6 (2.0)	38.7 (4.0)	1.37 (0.2)	7.9 (0.8)
195b_06	26	34.0 (4.7)	10.2 (1.4)	23.8 (5.2)	102.7 (21.2)	2.25 (0.4)	7.9 (0.8)
198c_07	7	23.8 (1.4)	6.7 (0.8)	17.1 (1.5)	50.5 (10.8)	1.48 (0.27)	10.7 (1.8)
198d_07*	10	20.0 (2.1)	5.3 (.83)	14.9 (2.1)	49.7 (8.1)	1.88 (0.2)	13.8 (1.25)
199a_07*	50	24.4 (1.53)	7.3 (2.0)	17.1 (3.0)	76.8 (18.0)	2.25 (0.35)	10.9 (1.97)
200b_07	3	19.6 (2.0)	12.0 (1.8)	7.7 (1.6)	62.2 (6.6)	1.97 (0.31)	11.41 (1.34)
202a_07	18	32.3 (3.4)	20.5 (4.6)	11.8 (4.1)	61.4 (14.4)	1.7 (0.3)	10.2 (1.3)

[*] Same animal tagged on different days.

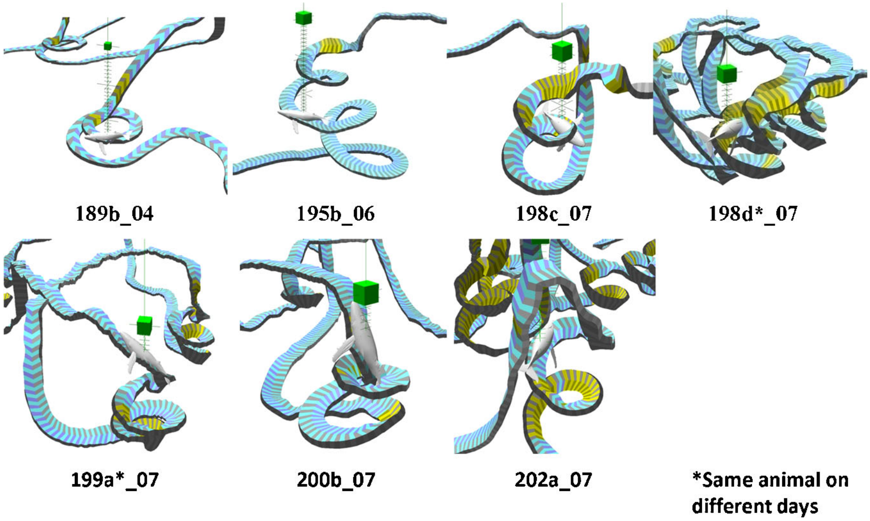
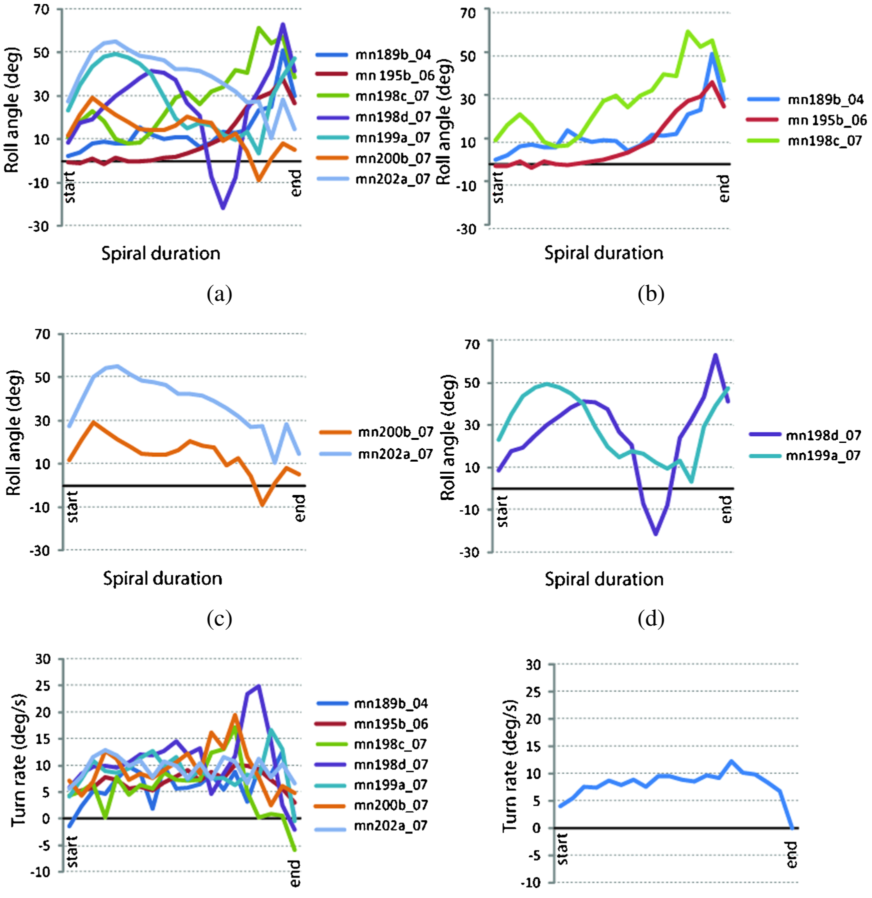


Figure 3. Sample TrackPlot visualizations of the swim path used by individual study animals to create upward-spiral bubble nets to capture prey. Data derived from synchronous motion, acoustic recording tags (DTAGs) attached to the whales. This figure is published in colour in the online edition, which can be accessed via http://www.brill.nl/beh

termination of spiralling) was 14.2 m (individual mean range 6.6–23.8 m). For two animals (mn189b_04 and mn202a_07) the entire spiral sequence occurred at depth, with termination deeper than 20 m. Concurrent surface behaviour data on mn202a_07 showed that this animal surfaced with its mouth closed and at distances >50 m from where the bubble net reached the surface.

We were able to acoustically identify 70 complete bubble production events during the creation of bubble nets using the upward-spiral method (Table 2). Bubble onset typically occurred at the deepest portion of the animal's dive, when the animal initiated its first turn (5 animals, 61 events). Bubble production consisted of a continuous, long duration (approximately 50–60 s) stream (4 animals, 30 events) or stream-to-burst sequence (2 animals, 31 events) that was emitted throughout the spiral (Table 2, Figure 6). Two animals, 198c_07 and 198d_07/199a_07, departed from this pattern. Animal 198c_07 produced short duration (approximately 4 second) bursts only at the top of the spiral. Animal 198d_07 produced streams-to-bursts only in the bottom section of its dive during one tag application, while producing streams throughout the spiral during its second tag application (199a_07).



(a) (b)

(c) (d)

(e) (f)

Figure 4. Animals changed their body roll angle and turn rate (change in heading) as they proceeded through the creation of an upward-spiral bubble net. Change in body roll angle varied by animal (a). Three animals increased their roll angle in the latter portions of the spiral (b), two animals showed initial increase roll angle in the early portions of the spiral (c) and one animal, tagged on two different days, exhibited a bimodal pattern of increased roll angle during the initial portions of the spiral, decreased roll angle in the mid-section and increased roll angle again in the upper portions near the terminus of the spiral (d). Rate of turn increased through the spiral duration for 4 of the 6 animals (e). In aggregate, there was a tendency for animals to increase their rate of turn as they proceeded through spiral formation (f). This figure is published in colour in the online edition, which can be accessed via http://www.brill.nl/beh

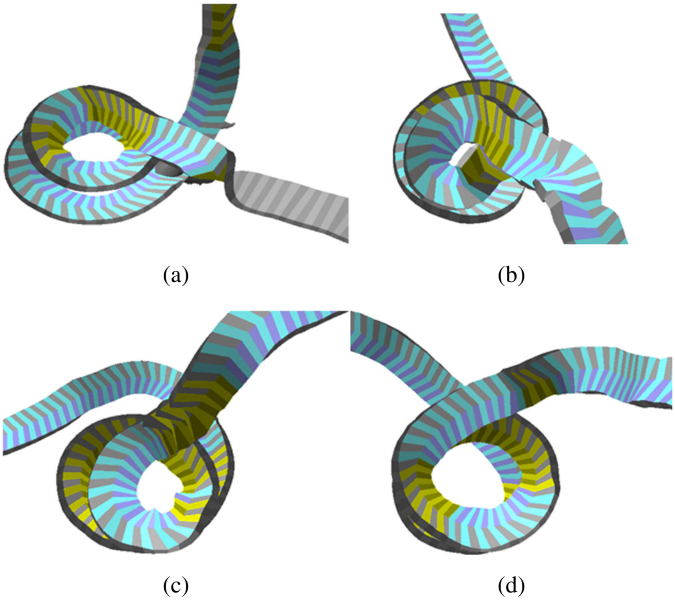


Figure 5. Sample TrackPlot visualizations of turn rate and body roll contributing to spiral formation. Constricting spirals formed by: (a) increasing turn rate and increased body roll through the spiral (mn198c_07), (b) increasing turn rate and bimodal body roll through the spiral (mn198d_07) and (c) increasing turn rate and decreased body roll through the spiral (mn202b_07). A non-constricting spiral (d) formed by relatively constant turn rate and bimodal body roll (mn199a_07). Body roll angle of $> 40°$ are shown in yellow. Data derived from synchronous motion, acoustic recording tags (DTAGs) attached to feeding humpback whales. This figure is published in colour in the online edition, which can be accessed via http://www.brill.nl/beh

3.2. Double-loop bubble-net feeding

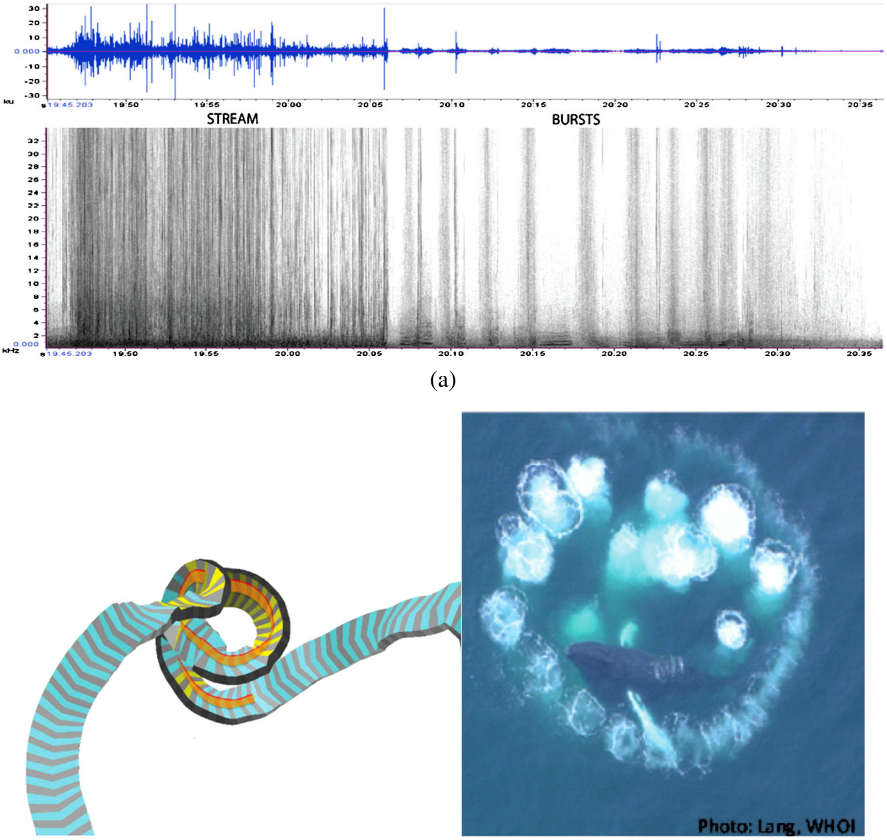
In 2006, we recorded a total of 182 double-loop bubble nets produced by three whales (animals 189b_06 and 192_06 are the same individual tagged on different days). Double-loop bubble-net feeding behaviour consisted of two individual dive loops separated by a surfacing that included one or more ‘lobtails’ (using the flukes to forcefully strike the water’s surface). The sequence’s initial loop was termed the ‘corral-loop’, while the second dive, which terminated in the lunging behaviour and the consumption of prey, was termed the ‘capture-loop’ (Figure 2). One animal was tagged on two different days (189b_06 and 192a_06) and exhibited similar behaviour on both days (Table 3, Figure 7).

Table 2. Bubble production by humpback whales during upward-spiral technique used for bubble-net feeding directed at schools of small fish (*Ammodytes dubius*).

Animal	Number of events analysed	Bubble style	Bubble location	Depth bubble onset (m) (σ)	Depth bubble termination (m) (σ)	Bubble duration (s) (σ)
189b_04	4	Stream	Throughout spiral	34.9 (1.8)	28.3 (3.0)	63.6 (6.72)
195b_06	24	Stream to burst	Throughout spiral	25.4 (4.93)	7.7 (2.29)	61.4 (19.43)
198c_07	9	Burst	Top of spiral	10.5 (1.3)	7.6 (1.6)	4.4 (1.7)
198d_07*	7	Stream to burst	Bottom of spiral	20.3 (1.41)	13.2 (1.29)	22.9 (1.98)
199a_07*	6	Stream	Throughout spiral	24.0 (0.72)	12.6 (1.56)	52.9 (3.94)
200b_07	3	Stream	Throughout spiral	18.9 (2.85)	12.5 (1.55)	55.7 (18.55)
202a_07	17	Stream	Throughout spiral	32.9 (5.87)	19.8 (10.45)	54 (29.06)

Data derived from synchronous motion, acoustic recording tags (DTAGs) attached to feeding whales. Bubble production was identified aurally and through spectrographic analysis using the acoustic software package Raven.

* Same animal tagged on different days.



(a)

(b) (c)

Figure 6. Raven generated spectrogram showing an example of stream-to-burst bubble production used to create a bubble net (a), TrackPlot visualization of the spiral swim path used to create the bubble net with portion of the track during which bubbles were expelled coloured orange, portion of the track in which body roll angle exceeded 40° coloured yellow and chevron indicating the direction of travel (b) and an aerial photograph of a humpback showing surface manifestation of stream-to-burst bubble net production (c). Data for (a) and (b) derived from synchronous motion, acoustic recording tags (DTAGs) attached to feeding humpback whale number198d_07. This figure is published in colour in the online edition, which can be accessed via http://www.brill.nl/beh

The mean maximum depth for all corral-loops was 21.6 ± 3.0 m (individualized mean range 20.6 ± 2.8 to 22.2 ± 3.1 m). The mean dive duration for the corral-loop was 62.4 ± SD 14.0 seconds (individualized mean range 54.9 ± 9.8 to 66.0 ± 13.5 s). The mean rate of turn for all corral-loops was 5.8 ± 1.3°/s (individualized mean range 5.5 ± 0.3 to 6.5 ± 1.17°/s (Table 3)).

Table 3. Kinematics of double-loop bubble-net feeding behaviour in humpback whales directed at schools of small fish (*Ammodytes dubius*).

Animal	Number of events	Corral loop depth (m) (σ)	Corral loop duration (s) (σ)	Corral loop turn rate (deg/s) (σ)	Capture-loop depth (m) (σ)	Capture-loop duration (s) (σ)	Capture-loop turn rate (°/s) (σ)
189b_06*	13	21.7 (3.5)	66.0 (13.5)	5.4 (1.1)	12.4 (1.2)	34.7 (3.5)	10.4 (1.0)
192a_06*	109	21.6 (2.9)	65.9 (16.0)	5.5 (1.3)	12.2 (1.1)	36.2 (4.0)	9.9 (1.1)
189c_06	33	22.2 (3.1)	54.9 (9.8)	6.5 (1.2)	13.6 (1.0)	34.2 (2.6)	10.5 (0.8)
196a_06	27	20.6 (2.8)	55.5 (9.8)	6.5 (1.1)	11.8 (1.1)	27.3 (2.1)	13.2 (1.0)

Data derived from synchronous motion, acoustic recording tags (DTAGs) attached to feeding humpback whales.

[*] Same animal tagged on different days.

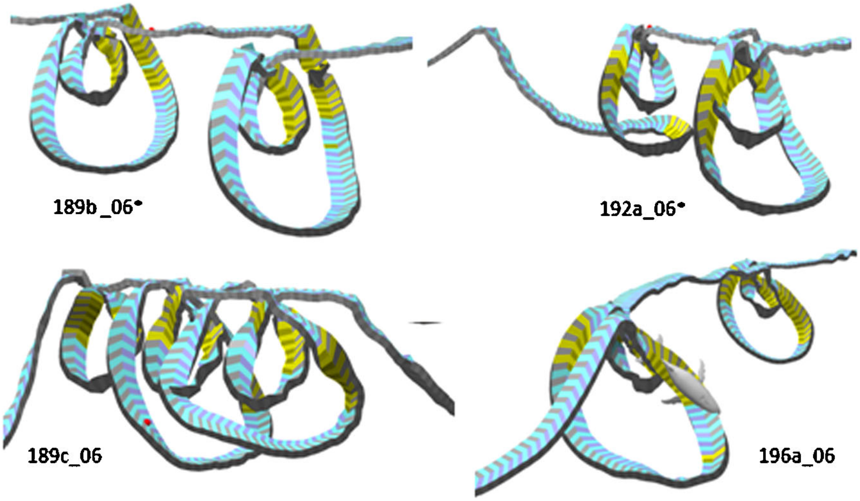


Figure 7. Sample TrackPlot visualizations of double-loop swim path used by individual study animals during the creation of a bubble net to capture prey. Animals 189b_06 and 192a_06 are the same animal that exhibited the same behaviour on different days. Data derived from synchronous motion, acoustic recording tags (DTAGs). This figure is published in colour in the online edition, which can be accessed via http://www.brill.nl/beh

The mean maximum depth for all capture-loops was 12.5 ± 1.0 m (individualized mean range 11.8 ± 1.1 to 13.6 ± 1.0 m). The mean dive duration for all capture-loops was 32.6 ± 3.5 s (individualized mean range 27.3 ± 2.1 to 36.2 ± 4.0 s). The mean rate of turn for all capture-loops was 10.6°/s (individualized mean range 9.9 ± 1.1 to 13.2 ± 1.0°/s; Table 3).

We chose 60 double-loop feeding events for which we had complete sound files (e.g., sound from passing boats or ships did not interrupt the acoustic record) to examine parameters of bubble production during double-loop feeding (Tables 4 and 5).

During the corral-loop, one animal, tagged on two different days (189b_06 and 192a_06), used a stream (189b_06) and burst or stream (192a_06) bubble expulsion emitted from the bottom of the loop through most of its ascent on all of its dives ($N = 10$ and $N = 20$, respectively), one animal (189c_06) used a burst expulsion during its descent, but expelled bubbles during a minority (7/19) of its corral-loop dives and one animal (196a_06) did not expel bubbles during its swimming of the corral-loop ($N = 11$).

During the capture-loop, one animal, tagged on two different days (189b_06 and 192a_06), expelled bursts of bubbles during its descent, but

Table 4. Bubble production by humpback whales during the corral-loop portion of double-loop bubble-net feeding directed at schools of small fish (*Ammodytes dubius*).

Animal	Number of events analysed/containing bubbles	Bubble style	Number of expulsions (N) (σ)	Bubble location	Depth of bubble onset (m) (σ)	Depth of bubble termination (m) (σ)	Bubble duration (s) (σ)
189b_06*	10/10	Stream	1.4 (0.97)	Bottom of loop–most of ascent	18.4 (2.80)	10.0 (3.33)	29.9 (5.52)
192a_06*	20/20	Stream ($N = 9$) Bursts ($N = 11$)	1.4 (0.84)	Bottom of loop–most of ascent	18.3 (3.75)	4.4 (3.33)	29.5 (8.07)
189c_06	19/7	Burst	4.7 (3.15)	Descent–bottom of loop	15.3 (3.72)	19.9 (2.34)	10.1 (3.97)
196a_06	11/0	NA	0	NA	NA	NA	NA

Data derived from synchronous motion, acoustic recording tags (DTAGs) attached to feeding humpback whales. Bubble production was identified aurally and through spectrographic analysis using the acoustic software package Raven.

[*] Same animal tagged on different days.

Table 5. Bubble production by humpback whales during the capture-loop portion of double-loop bubble-net feeding directed at schools of small fish (*Ammodytes dubius*).

Animal	Number of events analysed/containing bubbles	Bubble style	Number of expulsions (N) (σ)	Bubble location	Depth of bubble onset (m) (σ)	Depth of bubble termination (m) (σ)	Bubble duration (s) (σ)
189b_06*	10/3	Burst	2.5 (0.89)	Descent–bottom of loop	5.1 (1.21)	11.6 (0.67)	7.0 (2.03)
192a_06*	20/9	Burst	2.4 (0.92)	Descent–bottom of loop	7.2 (2.19)	9.1 (2.18)	10.9 (7.21)
189c_06	19/19	Burst	4.1 (0.97)	Bottom of loop	10.9 (1.81)	11.5 (1.53)	8.7 (2.64)
196a_06	11/11	Burst	2.7 (0.65)	Bottom of loop	10.6 (2.18)	10.4 (1.27)	5.4 (1.43)

Data derived from synchronous motion, acoustic recording tags (DTAGs) attached to feeding humpback whales. Bubble production was identified aurally and through spectrographic analysis using the acoustic software package Raven.

[*] Same animal tagged on different days.

used bubbles in only a minority of its capture-loop dives (3/10 and 9/20). Animals 189c_06 and 196a_06 expelled bursts at the bottom of all capture-loops ($N = 19$ and $N = 11$, respectively).

Combining the corral-loops and capture-loops into the double-loop sequence, animals tended to show a preference for expelling bubbles in one or the other. Animal 189b_06/192a_06 emitted bubbles during all of its corral-loops (10/10 and 20/20), but in a minority of its capture loops (3/10 and 9/20). Animals 189c_06 and 196a_06 expelled bubbles in a minority of their corral-loops (7/19 and 0/11, respectively), but in all of their capture-loops (19/19 and 11/11, respectively). Animals emitted streams or bursts in the corral-loop, but only bursts in the capture-loop.

3.3. Anomalous techniques

While most animals exhibited only a single bubble-feeding strategy, one whale combined the two techniques. Animal 192a_06 engaged primarily in double-loop feeding as described above, but on 11 occasions used an upward spiral to create the corral-loop. We also recorded one animal (192b_06) that, while surfacing in bubble nets with its mouth gaped, showed no indication of behaviours capable of forming a bubble net. In the 10 events we recorded from this animal, its more free-form swim track was variable, but relatively linear (not spiralled or looped) and no bubble expulsion could be identified from the acoustic record (Figure 8).

3.4. Dive-depth vs. bottom depth

We found no significant relationship between bottom depth and the maximum depth of a bubble-producing foraging dive ($R^2 = 0.13$, $F = 2.84$, $N = 104$, $p < 0.0001$).

4. Discussion

We combined tag-derived and time-synchronized audio and kinematic data, focal surface observations, and novel visualization software to provide the first detailed descriptions of the underwater behaviours employed by humpback whales as they created bubble nets as an aid to capturing prey. We identified two general classes of behaviour (upward-spiral and double-loop)

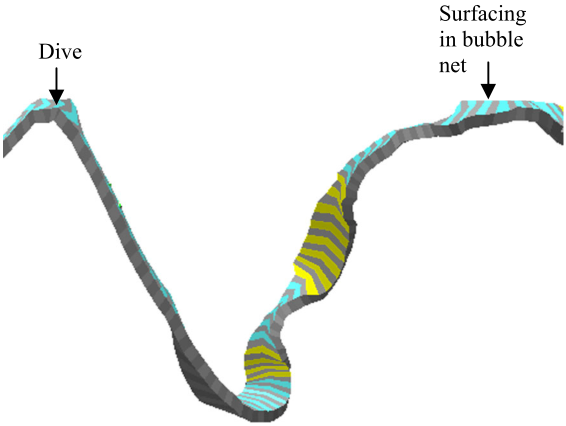


Figure 8. Sample TrackPlot visualization of the swim path used by animal 192b_06, which surfaced through the centre of 10 bubble nets with its mouth gaped (feeding), but swam neither a swim path that could create or mimic a net nor produced bubbles during the dive preceding surfacing in the net. This figure is published in colour in the online edition, which can be accessed via http://www.brill.nl/beh

that animals used to create bubble nets, each of which would require substantial manoeuvrability and be aided by the unique hydrodynamicly enhanced morphology of humpbacks.

Our data substantially expand upon existing descriptions, which are derived only from surface observations summarized by Ingebrigsten (1929), Jurasz & Jurasz (1979) and Hain et al. (1982). Specifically, we show the actual swim path of the animals (e.g., number of revolutions, turning rate, depth interval of spiral), when and where in the process bubbles were expelled and the pattern of bubble expulsion used by the animals. In the upward-spiral technique, the onset of bubble production was generally consistent, beginning at the deepest point of the dive and at or just before the initiation of a turn that then became the start of the spiral. Continuous expulsion of bubbles (presumably forming a bubble-stream curtain) was most common, but some individuals also formed nets from individual bursts of bubbles (presumably forming discrete columns) or a sequential gradation of the two techniques (stream to bursts). Individual animals tended to be consistent in their strategy, with most of the variation occurring among, not within, individuals. However, individuals did show variation, as demonstrated by animal 192a_06 that used a spiral-net to create a corral-loop in 11 of its 109 double-loop events.

While emitting bubbles during spiral-net formation, animals oriented their bodies in a variety of ways. Some exhibited increased roll angle in the initial stages of the spiral, others in the later stages; one whale, tagged on two separate days, showed a bimodal trend with increased roll angle during the initial and final portions. Some animals increased their turn rate towards the end of the spiral (four of six animals), which supports the conjecture that spiral-nets function to compact the whales' prey prior to capture. However, not all animals did so, which suggests that some animals use nets to contain, not concentrate, prey or that some prey patch conditions are conducive to containment and others to compaction. This supports our depiction of the highly plastic nature of humpback whale behaviour, with different animals accomplishing a similar task in varying ways or responding to different conditions with altered behaviours.

While spiral-net behaviour has been partially described from surface observations in previous studies of humpback whale feeding behaviour, double-loop behaviour used to create a bubble net has not been previously described. The typical behaviour pattern consists of a three-step process: (1) the corral-loop (the deeper first dive often containing an initial bubble event), (2) a brief surfacing with 1–3 lobtails (using the flukes to forcefully strike the water's surface) and (3) the capture-loop (the shallower second dive where additional bubbles can be released and when the actual feeding occurs). Since swim loops and bubbles occur prior to the lobtails, it is unlikely that the lobtail is used to mark a location for the net's creation, as was suggested by Weinrich et al. (1992).

The dive aspects of corral and capture-loop formation were consistent across animals and relative to one another. For all animals, the deepest portion of the corral-loop was approximately 21 m, the dive duration for the loop was approximately 60 s and the turn rate to form the loop was approximately 6°/s. For the capture-loop, the deepest portion was approximately 13 m (slightly less than the body length for an adult Gulf of Maine humpback whale (True, 1904; Stevick et al., 1999), the dive duration was approximately 33 s and the rate of turn to form the loop was approximately 11°/s. Hence, the capture-loop was a quick, shallow dive of approximately half the depth, dive duration, and twice the turning rate relative to the corral-loop. We remain unable to determine how the lobtail phase of this sequence aids the whale in prey capture. However, since the corral-loop consists of a single circle that would contain rather than concentrate prey, we speculate that the lobtail action might serve to mass the fish more tightly within the net, thereby increasing feeding efficiency of the whale(s). Clustering behaviour is a common response of fish to predators or other frightening stimuli (Pitcher & Parrish, 1993) and the percussive sound created when the whale's flukes strike the water's surface during a lobtail could elicit such a response in sand lance.

The consistent dive depth (approximately 13 m) and associated small standard deviations of the capture-loop across all animals is most likely a result of an animal diving to a distance equivalent to its body length before turning up and into the net. For spiral-net and corral-loops, dive depth of a bubble-producing dive was independent of water depth and most frequently started at 20–25 m with a vertical span of <20 m. Hazen et al. (2009) used dive data from our whales tagged in 2006 and concurrent SIMRAD EK-60 echosounder measures of prey fields to determine that maximum dive depth of bubble-feeding whales was independent of maximum prey field depth.

Sharpe (2001) used echosounder tracking of bubble-feeding humpbacks in Alaska to identify the same approximately 20 m limit to bubble use and conducted tank experiments to observe the rise of simulated bubble nets to the surface. He concluded that the differential rise speed of the different sized bubbles comprising a net resulted in substantial gaps emerging after a rise distance of approximately 20 m. That different sized bubbles move through viscous mediums at different speed is a common tenant of fluid mechanics (Hassan et al., 2008). Thus, the association of bubble releases within an approximately 20 m depth interval observed in two separate oceans might be related to the physics of bubble dispersion over depth, to which humpback whales have adapted their behaviour. As such, it could be a universal aspect of bubble-net feeding in humpbacks.

While for most animals bubble production and swim tracks matched what might be expected to unilaterally create a net, for some animals it did not. For instance, whale 198c_07 produced only single-burst bubble expulsions of short (approximately 4-second) duration towards the top of the spiral. Similar mismatches occurred during double-loop feeding; one whale (196a_06) swam, but did not produce any bubbles during the corral-loop. It did produce a number of short (approximately 5-second) bursts at the bottom of all capture-loops, but these would seem unlikely to form the net observed at the surface.

It is possible that these cases can be resolved by considering the behaviour of associates of the tagged whale. All of the tagged animals were feeding in groups that contained at least one associated animal and coordination among feeding humpback whales has been noted numerous times (Whitehead, 1983; Baker, 1985; D'Vincent et al., 1985; Weinrich, 1991; Weinrich & Kuhlberg, 1991), with cooperation (D'Vincent et al., 1985; Ramp et al., 2010) and role specialization (Sharpe, 2001) hypothesized. Hence, bubbles produced during only portions of a spiral might add to the bubbles produced by associates and increase the capture success of the net. It is also possible that swimming spirals without producing bubbles might synchronize movements of the group, or that the body might be used as a herding device (Brodie, 1977).

While cooperative feeding by humpbacks has been hypothesized, the evolution of cooperative strategies is most likely to occur under conditions where close kin relationships are maintained (Hamilton, 1964) and the social system of humpback whales (e.g., promiscuous breeding, short mother–calf bond, single birth offspring, wide dispersal of juveniles (Weinrich, 1991; Clapham, 1994, 2000) is unlikely to promote such relationships and strategies. In addition, any theoretical basis for humpback cooperation must also account for the many instances in which the behaviour of the tagged whale was capable of unilaterally creating the net, but our behavioural sequencing data showed that other animals also fed in the net. Additionally, cases such as animal 192b_06 that repeatedly surfaced in the centre of a net with its mouth gaped, but neither swam a path that would produce or mimic a net nor expelled bubbles must be included. While kin selected cooperation seems unlikely, reciprocity or by-product mutualism might be occurring, with potential cheaters acting as net robbers (Sachs et al., 2004).

Our findings demonstrate that the creation of bubble nets require humpback whales to perform complex body manoeuvres that are not used by other baleanopterids, which employ a more linear feeding method (e.g., Goldbogen et al., 2006). Such manoeuvrability would require adaptations favouring increased hydrodynamic performance, such as that provided by the humpback's unique flipper morphology (Fish, 1995; Fish & Battle, 2004). Whether or not the evolution of the humpback flipper was caused by the manoeuvrability required during complex feeding movements, their presence has certainly contributed to the development of unique behavioural traits (such as bubble-netting) that allow humpbacks to feed in a manner different from other balaenopterids. This might allow humpbacks to exploit prey patches with increased efficiency or to access highly mobile prey that would otherwise be unavailable.

Acknowledgements

We thank the officers and crew of the NOAA research vessels Nancy Foster and Auk for their capable assistance during field operations. We also thank the various members of our field team over the years, including Roland Arsenault, Pat Halpin, Elliot Hazen, Tom Hurst, Just Moller, Susan Parks, Cara Pecarcik, Allison Rosner, Kate Sardi, Jamison Smith, Alison Stimpert, Jennifer Tackaberry, Becky Woodward and Jeremy Winn. Funding was provided by the Stellwagen Bank National Marine Sanctuary, Office of National Marine Sanctuaries, and the National Oceanographic Partnership Program. Whale tag data were collected under permit Nos 775-185 (Northeast Fisheries Science Centre) and 605-1904 (Whale Centre of New England) issued by the United States National Marine Fisheries Service. We thank Jim Hain and Robert D. Kenney for providing the photos for the cover of this issue. The manuscript benefitted from the comments of Phil Clapham, Bruce Alexander Schulte and two anonymous reviewers.

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