Review History

RSOS-191104.R0 (Original submission)

Review form: Reviewer 1

Is the manuscript scientifically sound in its present form?  
Yes

Are the interpretations and conclusions justified by the results?  
Yes

Is the language acceptable?  
Yes

Do you have any ethical concerns with this paper?  
No

Have you any concerns about statistical analyses in this paper?  
No
Recommendation?
Accept with minor revision (please list in comments)

Comments to the Author(s)
Please see attached (Appendix A).

Review form: Reviewer 2

Is the manuscript scientifically sound in its present form?
No

Are the interpretations and conclusions justified by the results?
No

Is the language acceptable?
Yes

Do you have any ethical concerns with this paper?
No

Have you any concerns about statistical analyses in this paper?
No

Recommendation?
Reject

Comments to the Author(s)
The authors describe humpback whale behavior at a salmon hatchery with a focus on flipper movements. Humpback flippers are interesting structures that can produce significant hydrodynamic forces for a wide range of functions from social signaling to effecting both foraging and non-foraging maneuvers. The manuscript is well written but the data is very hard to understand and interpret as it is currently displayed and described in the manuscript. Some of the methods described for taking photo/video of whale behavior is incomplete, such as filming frequency, and the photos shown in figures 3, 4, 6, 8 do not show time stamps or time intervals. No video is provided for review. The schematics added in figure 2 and figure 7 do not add much given the lack of actual data presentation. Time scale of flipper movements should at least be a minimum for description of behavior given the focus of the manuscript. If drone data had RTK that should be used in coordination with altimeter data for kinematic analysis, if possible.

The title should reflect that the observed behavior is not natural. This study is an interesting experiment of how humpback whales exploit an artificial food source, but it is unclear how broadly relevant the present results are to our understanding of how whales use flippers in natural contexts on natural prey and in natural distributions/abundances.

The first paragraph of the discussion describes new technology used in this study. What technology are the authors referring to exactly? The last paragraph on page 8 states that tag deployed on whale dorsal surfaces only record movements of whole whale. There are papers recently published I suggest the authors refer to going back to 2017 and 2016 that describe the use of cameras within tags that show movements of jaws and appendages relative to the body.
Decision letter (RSOS-191104.R0)

28-Aug-2019

Dear Ms Kosma

On behalf of the Editors, I am pleased to inform you that your Manuscript RSOS-191104 entitled "Pectoral herding: an innovative tactic for humpback whale foraging" has been accepted for publication in Royal Society Open Science subject to minor revision in accordance with the referee suggestions. Please find the referees' comments at the end of this email.

The reviewers and handling editors have recommended publication, but also suggest some minor revisions to your manuscript. Therefore, I invite you to respond to the comments and revise your manuscript.

• Ethics statement
If your study uses humans or animals please include details of the ethical approval received, including the name of the committee that granted approval. For human studies please also detail whether informed consent was obtained. For field studies on animals please include details of all permissions, licences and/or approvals granted to carry out the fieldwork.

• Data accessibility
It is a condition of publication that all supporting data are made available either as supplementary information or preferably in a suitable permanent repository. The data accessibility section should state where the article's supporting data can be accessed. This section should also include details, where possible of where to access other relevant research materials such as statistical tools, protocols, software etc can be accessed. If the data has been deposited in an external repository this section should list the database, accession number and link to the DOI for all data from the article that has been made publicly available. Data sets that have been deposited in an external repository and have a DOI should also be appropriately cited in the manuscript and included in the reference list.

If you wish to submit your supporting data or code to Dryad (http://datadryad.org/), or modify your current submission to dryad, please use the following link: http://datadryad.org/submit?journalID=RSOS&manu=RSOS-191104

• Competing interests
Please declare any financial or non-financial competing interests, or state that you have no competing interests.

• Authors’ contributions
All submissions, other than those with a single author, must include an Authors’ Contributions section which individually lists the specific contribution of each author. The list of Authors should meet all of the following criteria; 1) substantial contributions to conception and design, or acquisition of data, or analysis and interpretation of data; 2) drafting the article or revising it critically for important intellectual content; and 3) final approval of the version to be published.

All contributors who do not meet all of these criteria should be included in the acknowledgements.

We suggest the following format:
AB carried out the molecular lab work, participated in data analysis, carried out sequence alignments, participated in the design of the study and drafted the manuscript; CD carried out the statistical analyses; EF collected field data; GH conceived of the study, designed the study, coordinated the study and helped draft the manuscript. All authors gave final approval for publication.

• Acknowledgements
Please acknowledge anyone who contributed to the study but did not meet the authorship criteria.

• Funding statement
Please list the source of funding for each author.

Please ensure you have prepared your revision in accordance with the guidance at https://royalsociety.org/journals/authors/author-guidelines/ -- please note that we cannot publish your manuscript without the end statements. We have included a screenshot example of the end statements for reference. If you feel that a given heading is not relevant to your paper, please nevertheless include the heading and explicitly state that it is not relevant to your work.

Because the schedule for publication is very tight, it is a condition of publication that you submit the revised version of your manuscript before 06-Sep-2019. Please note that the revision deadline will expire at 00.00am on this date. If you do not think you will be able to meet this date please let me know immediately.

To revise your manuscript, log into https://mc.manuscriptcentral.com/rsos and enter your Author Centre, where you will find your manuscript title listed under "Manuscripts with Decisions". Under "Actions," click on "Create a Revision." You will be unable to make your revisions on the originally submitted version of the manuscript. Instead, revise your manuscript and upload a new version through your Author Centre.

When submitting your revised manuscript, you will be able to respond to the comments made by the referees and upload a file "Response to Referees" in "Section 6 - File Upload". You can use this to document any changes you make to the original manuscript. In order to expedite the processing of the revised manuscript, please be as specific as possible in your response to the referees. We strongly recommend uploading two versions of your revised manuscript:

1) Identifying all the changes that have been made (for instance, in coloured highlight, in bold text, or tracked changes);
2) A 'clean' version of the new manuscript that incorporates the changes made, but does not highlight them.

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2) A separate electronic file of each figure (EPS or print-quality PDF preferred (either format should be produced directly from original creation package), or original software format);
3) Included a 100 word media summary of your paper when requested at submission. Please ensure you have entered correct contact details (email, institution and telephone) in your user account;
4) Included the raw data to support the claims made in your paper. You can either include your data as electronic supplementary material or upload to a repository and include the relevant doi...
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5) All supplementary materials accompanying an accepted article will be treated as in their final form. Note that the Royal Society will neither edit nor typeset supplementary material and it will be hosted as provided. Please ensure that the supplementary material includes the paper details where possible (authors, article title, journal name).

Supplementary files will be published alongside the paper on the journal website and posted on the online figshare repository (https://rs.figshare.com/). The heading and legend provided for each supplementary file during the submission process will be used to create the figshare page, so please ensure these are accurate and informative so that your files can be found in searches. Files on figshare will be made available approximately one week before the accompanying article so that the supplementary material can be attributed a unique DOI.

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Once again, thank you for submitting your manuscript to Royal Society Open Science and I look forward to receiving your revision. If you have any questions at all, please do not hesitate to get in touch.

Kind regards,
Andrew Dunn
Royal Society Open Science Editorial Office
Royal Society Open Science
openscience@royalsociety.org

on behalf of Dr Denise Greig (Associate Editor) and Kevin Padian (Subject Editor)
openscience@royalsociety.org

Associate Editor Comments to Author (Dr Denise Greig):
Associate Editor: 1
Comments to the Author:
Thank you for this interesting submission. I enjoyed the graphics and the video. I agree with suggesting from both reviewers that you may want to describe the speed of some of the movements documented in the figures. I just had two minor comments on the text:
Page 5, line 8...I would say "newly documented" rather than "novel" because we do not know if it is new to the whales.
Page 5, line 55...I would split the sentence starting with "In 2016, we observed..." into two sentences or add a colon.
Reviewer comments to Author:
Reviewer: 1

Comments to the Author(s)
Please see attached

Reviewer: 2

Comments to the Author(s)
The authors describe humpback whale behavior at a salmon hatchery with a focus on flipper movements. Humpback flippers are interesting structures that can produce significant hydrodynamic forces for a wide range of functions from social signaling to effecting both foraging and non-foraging maneuvers. The manuscript is well written but the data is very hard to understand and interpret as it is currently displayed and described in the manuscript. Some of the methods described for taking photo/video of whale behavior is incomplete, such as filming frequency, and the photos shown in figures 3, 4, 6, 8 do not show time stamps or time intervals. No video is provided for review. The schematics added in figure 2 and figure 7 do not add much given the lack of actual data presentation. Time scale of flipper movements should at least be a minimum for description of behavior given the focus of the manuscript. If drone data had RTK that should be used in coordination with altimeter data for kinematic analysis, if possible.

The title should reflect that the observed behavior is not natural. This study is an interesting experiment of how humpback whales exploit an artificial food source, but it is unclear how broadly relevant the present results are to our understanding of how whales use flippers in natural contexts on natural prey and in natural distributions/abundances.

The first paragraph of the discussion describes new technology used in this study. What technology are the authors referring to exactly? The last paragraph on page 8 states that tag deployed on whale dorsal surfaces only record movements of whole whale. There are papers recently published I suggest the authors refer to going back to 2017 and 2016 that describe the use of cameras within tags that show movements of jaws and appendages relative to the body.

Author’s Response to Decision Letter for (RSOS-191104.R0)

See Appendix B.

Decision letter (RSOS-191104.R1)

23-Sep-2019

Dear Ms Kosma,

I am pleased to inform you that your manuscript entitled "Pectoral herding: an innovative tactic for humpback whale foraging" is now accepted for publication in Royal Society Open Science.

You can expect to receive a proof of your article in the near future. Please contact the editorial office (openscience_proofs@royalsociety.org and openscience@royalsociety.org) to let us know if
you are likely to be away from e-mail contact — if you are going to be away, please nominate a co-author (if available) to manage the proofing process, and ensure they are copied into your email to the journal.

Due to rapid publication and an extremely tight schedule, if comments are not received, your paper may experience a delay in publication.

Royal Society Open Science operates under a continuous publication model (http://bit.ly/cpFAQ). Your article will be published straight into the next open issue and this will be the final version of the paper. As such, it can be cited immediately by other researchers. As the issue version of your paper will be the only version to be published I would advise you to check your proofs thoroughly as changes cannot be made once the paper is published.

On behalf of the Editors of Royal Society Open Science, we look forward to your continued contributions to the Journal.

Kind regards,
Andrew Dunn
Royal Society Open Science Editorial Office
Royal Society Open Science
openscience@royalsociety.org

on behalf of Dr Denise Greig (Associate Editor) and Kevin Padian (Subject Editor)
openscience@royalsociety.org

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Appendix A

Review of Pectoral herding: an innovative tactic for humpback whale foraging

This study provides the first direct evidence for the ‘pectoral herding’ behavior of humpback whales. Bubble netting humpbacks wave their flippers in a non-hydrodynamically efficient way to scare schools of juvenile fish into their open mouths. Although this behavior has been previously hypothesized, it has not been otherwise confirmed. This study demonstrates video evidence of the flipper motion, how the prey responds to the flipper motion, and how it differs from other documented flipper uses. This paper is well written and very comprehensive. The authors sort through the different hypotheses for humpback flipper movements and convincingly demonstrate evidence for pectoral herding. Furthermore, the authors are careful to acknowledge the weaknesses of this study (n=2 individuals). I recommend this study for publication in RSOS and have only minor comments.

Observations:

These appear to be pretty slow lunges. Likewise, the flipper movements of whale B seem pretty slow compared to the thrust-generating flaps found in [25]. Particularly in your discussion pertaining to vertical herding I think the speed of the lunges and the flippers further supports your point of this not being a hydrodynamically active stroke. Since you’re not measuring the speeds you can only say so much, but it may be worth mentioning the slower speeds involved.

The complex flipper movement of whale A is really interesting, and so is the head tilt towards the moving flipper. Furthermore, this whale is practically not moving forward at all. It would be really interesting to know what the back flipper is doing.

Please do ensure that the important videos are attached in the supplementary material or a repository (currently they are available on dropbox), since they are very important to this paper. Not all the videos need to be presented, just the ones that you show in the figures.

Minor comments:

The introduction could use some additional copy editing. A few examples: 1) a comma after ‘sizable’, 2) the “;” after “prey with lunge feeding” should probably be a “:”. There are a few more instances as well. In this respect, the rest of the paper is pretty good.

Pg7 “Our current understanding about lunge feeding revolves around the theory that whales must either actively increase lift with their pectorals and/or use them to stabilize their body during a lunge.” I think this sentence is a bit misleading. During lunge feeding, it has been shown that humpback flippers can be used to generate additional thrust and it has been hypothesized (although it is almost certain) that they can be used for stability and maneuvering. Additionally, they could also play a hydrodynamically passive role during some lunging events and either be held in a neutral position or their motion could be a reaction to the accelerative and decelerative forces of the body. I think ‘must either’ is too simplistic and I would rephrase the sentence.

Pg8 “It is well known that humpback whales aggregate their prey with a bubble-net.” I think this paragraph is confusing. Has it actually been shown that “bubble-nets are rendered more inefficient if the prey does not naturally aggregate into dense patches”? Isn’t this the point of the bubble netting? I get the gist, but I would rephrase the first few sentences of the paragraph.
“However, our study reveals a flaw with the current tagging technology. Our findings illustrate that prey aggregation and capture are not limited to movements of the head, caudal peduncle, and tail flukes, but current tagging protocol deploys the tag on the back of the whale, recording only movements of the whole whale.” A slight caution with this sentence: camera tags do allow for examination of the flippers and have been around for several years (see The role of flippers, flukes, and body flexibility in blue whale maneuvering performance).

Figure 4 would benefit from highlighting the left flipper to show that the head roll is in the motion of the flipper.
Pectoral herding: an innovative tactic for humpback whale foraging

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Abstract

Humpback whales (Megaptera novaeangliae) have exceptionally long pectorals (i.e., flippers) that aid in shallow water navigation, rapid acceleration, and increased manoeuvrability. The use of pectorals to herd or manipulate prey has been hypothesized since the 1930s. We combined new technology and a unique viewing platform to document the additional use of pectorals to aggregate prey during foraging events. Here, we provide a description of “pectoral herding” and explore the conditions that may promote this innovative foraging behaviour. Specifically, we analysed aerial videos and photographic sequences to assess the function of pectorals during feeding events near salmon hatchery release sites in Southeast Alaska (2016 to 2018). We observed the use of solo bubble-nets to initially corral prey, followed by calculated movements to establish a secondary boundary with the pectorals – further condensing prey and increasing foraging efficiency. We found three ways in which humpback whales use pectorals to herd prey: 1) create a physical barrier to prevent evasion, 2) cause water motion to guide prey toward the mouth, and 3) position the ventral side to reflect light and alter prey movement. Our findings suggest that behavioural plasticity may aid foraging in changing environments and shifts in prey availability. Further study would clarify if “pectoral herding” is used as a principal foraging tool by the broader humpback whale population and the conditions that promote its use.

Background

The metabolic demand of a large body size forces baleen whales to require sizable dense prey patches. Large body sizes of baleen whales generate high metabolic demands that require the consumption of sizable, dense patches of prey [1-3]. However, filter feeding on these patches is energetically demanding for these animals and requires inventive effective methods for prey aggregation [2]. In rorquals, behavioural plasticity and foraging innovations are common among rorquals [4,5]. Humpback whales (Megaptera novaeangliae) provide an excellent example of how individual advances changes in behaviour can lead to diverse foraging tactics that maximize feeding efficiency [6-9]. They are known for a wide variety of foraging strategies including: lunge feeding [6,10], bubble-net feeding [6,11-14], flick feeding [6], cooperative feeding [15], lobtail feeding [7] and other idiosyncratic tactics [12,16-18].

Humpback whales are one of the world’s largest filter-feeders and regularly use lunge feeding to capture prey; an This particular technique is energetically costly [19] and sequential two-step process requires a two-step process. The whale first uses a high-velocity lunge to engulf large volumes of prey-laden water. The whale then closes its mouth and the baleen acts as a sieve to filter prey [14,20]. First, during a high-velocity lunge the whale engulfs a large volume of prey-laden water and second the prey is filtered from the water with specialized feeding anatomy [14,20]. The lunge can occur at depth [2,10,20-22] or on the surface [7,23,24]. In and in both locations situations lunge feeding requires acceleration to high speeds [2,26] because the animal must overcome considerable drag from an open mouth [20,22]. To counteract drag and increase speed, humpback whales open their mouths gradually, in synchrony with strong fluke strokes.
Humpback whales have a distinctive body morphology that allows for the successful and efficient capture of prey [28,29]. Notably, they have the longest pectorals (i.e., flippers) of any cetacean, measuring from one-quarter to one-third of their body length [30,31]. The pectorals of other cetaceans typically, whereas other cetaceans' pectorals do not exceed one-seventh the length of their bodies [32]. These exceptionally long appendages of humpback whales allow for effective navigation in shallower waters [32,33], quick rapid acceleration, and increased greater manoeuvrability and increased stability [6,34,35], whereby increasing capture abilities of small prey such as euphausiids, herring (Clupea spp.), capelin (Mallotus villosus), and sand lance (Ammodytes spp.) [36,32,37,38]. However, larger pectorals do have a hydrodynamic disadvantage and if not used effectively during foraging they can be detrimental to prey capture if not positioned effectively, however, larger pectorals may present a hydrodynamic disadvantage by increasing drag [39].

As the buccal cavity expands during a lunge, a hydrodynamically optimal position for the pectorals is for one or both to extend with the leading edge held at low angles of attack (α) [40]. Positioning the pectorals in this manner minimizes drag and provides the greatest amount of lift. The perpendicular position of extended pectorals also stabilizes the whale's body during a lunge [40]. During a rorqual lunge, the optimal pectoral position is one or both pectorals extended during ventral pouch expansion and the pectorals' leading edges held at low angles of attack (α ~ 0°) [40]. Positioning the pectorals in this manner is hydrodynamically efficient, corresponding to the greatest amount of lift and least amount of drag. The extended perpendicular position of the pectorals can also stabilize the body during a lunge [40]. Additionally, it has been hypothesized that rapid pectoral movement just prior to a lunge generates an upward pitching motion that counteracts the torque caused by rapidly engulfing water [35,40]. Segre et al. [25] defined four conditions for pectoral movement that would generate lift and increase propulsive thrust during an engulfment event: 1) both pectorals must move symmetrically, 2) pectorals are angled into the path of the stroke, 3) the stroke is oriented perpendicular to the whale's body, and 4) the stroke is aligned with the direction of travel [25]. Lift is generated as pectorals are rotated at an angle to the water flow (angle of attack or α). However, this angle must be small relative to the direction of travel [41]. Above a critical α, the pectoral will impede lift, making the movement detrimental to acceleration. Miklosovic [42] found that peak hydrodynamic efficiency of a humpback whale pectoral is around α = 7.5°. Above this, drag increases and lift decreases, with complete stall occurring at α ~ 17.5°. For symmetrical pectorals, lift is created as one pectoral is canted at an angle to the water flow (angle of attack or α), however, lift is only generated in an efficient manner when the pectorals are orientated at a small angle into their path of travel [41], if the pectoral is cantled at too high of an α, drag will increase. For a whale's pectoral to be an effective biological hydrofoil, it must produce substantial lift while minimizing drag [31]. Above a critical α, the pectoral will impede lift to a point of stall, making the movement detrimental to acceleration. Miklosovic [42] illustrated that the peak hydrodynamic efficiency of a humpback whale pectoral is around α ~ 7.5° and above this drag will increase and lift will decrease (with complete stall occurring at α ~ 17.5°). These studies illustrate that there are strict hydrodynamic criteria for using pectorals efficiently during lunge-feeding.
In addition to providing lift, decreasing drag, and promoting acceleration, pectorals may be used to corral or concentrate prey during lunge-feeding events. Humpback whales have multiple foraging strategies to aggregate prey, but concentration of prey may be increased by herding techniques [32,43]. Howell [44] was the first to suggest that humpback whales use their pectorals to direct schools of fish into their mouths. Brodie [39] elaborated on this theory by describing the use of white coloration on the pectoral's ventral surface to “flash” fish and herd prey toward the whale’s mouth. He stated, “if there are hydrodynamic disadvantages to such large flippers there must be selective compensation, one possibility being their role in concentrating prey” [39]. Both authors, however, reported reservations about their findings because they lacked the perspective necessary to document such behaviours [39]. Our objective was to use new technology (e.g., unoccupied aerial vehicles, small mobile video cameras) to document and describe the distinctive role of humpback whale pectorals in herding and aggregating prey. We focused our efforts on whales feeding near salmon hatchery release sites [45] in Southeast Alaska (2016 to 2018). Hatchery structures allowed for close approaches with minimal behavioural disruption. Our results enhance our understanding of the complex and innovative foraging tactics that may be critical to humpback whale survival as population dynamics and environmental conditions continue to change [46,47].

**Methods**

**Study Location and Timing**

This study was conducted in Chatham Strait, along the eastern shore of Baranof Island in Southeast Alaska (Fig. 1). We conducted systematic surveys from Warm Springs Bay north to Kelp Bay, with an emphasis on salmon hatchery release sites in Takatz Bay and Kasnyku Bay in 2016 (mid-May through the end of June) and 2017 (mid-April through end of July). We put forth a more directed effort to document foraging strategies by humpback whales in Kasnyku Bay in 2018 (May). All effort was timed to overlap with releases of juvenile salmon from Hidden Falls Hatchery (managed by the Northern Southeast Regional Aquaculture Association).

**Data collection**

We collected humpback whale sightings and behavioural observations as part of a three-year study (2016 to 2018) of humpback whale predation at Hidden Falls Hatchery and surrounding areas. We took identification photographs of each whale using digital SLR cameras with lenses ranging in focal lengths from 70mm to 300mm. Humpback whales were individually identified based on the pigmentation and trailing edges of their flukes and/or the shape and marks of their dorsal fins [48] and cross-referenced with the Southeast Alaska Humpback Whale Catalog [49]. This catalogue included all whale sightings through 2012 and additional observations from later time periods (Straley & Gabriele unpubl.). We made an effort to capture video and photographic sequences with a Nikon D7000 camera whenever whales were observed feeding at the surface. In 2017, we also used a GoPro Hero5 Black video camera affixed to the end of a 3.5-meter pole to provide an aerial perspective while standing on walkway platforms attached to hatchery net pens. These platforms provided a unique and close-up perspective without disturbing whale behaviour that enabled camera views directly above or within bubble-nets created by the feeding whales. In 2018, we used an unoccupied aerial vehicle (UAV; DJI Mavic Pro with 4k video at 24fps) to capture footage of whales surface lunge feeding near the facility. In addition to visual prey identification, we used a cast net and herring jig to sample prey in foraging areas. We removed juvenile salmon otoliths to differentiate hatchery-reared and wild origin fish according to methods described by Volk et al. [50].

**Data Analysis**
We used Adobe Premiere Pro to analyse video footage and Adobe Lightroom to assess photographic sequences. Kinematic assessments of whale foraging behaviour were made, with particular focus on the use of pectorals. We recorded pectoral positions, movements, and prey locations (when possible) using real-time and frame-by-frame processing. Whale foraging movements were then 3D modelled using Blender, with post-processing in Adobe Photoshop to accurately illustrate foraging behaviours seen in footage and photographs.

Lunge durations were calculated from videos, when possible. All footage and photographic sequences were viewed and categorized based on surface foraging behaviour. Bubble-net feeding was denoted by the formation of a ring of bubbles followed by a lunge through the centre. All documented feeding events utilized a bubble-net. A surface lunge was recorded as one of two commonly observed types: a vertical lunge, when the animal lunged upwards [24] and a lateral lunge, when the animal rotated approximately 90 degrees while lunging [24]. Pectoral herding was a newly documented feeding strategy, defined by directed movements of the pectorals to condense prey before a lunge. We identified three ways in which humpback whales used pectorals to herd prey: 1) create a physical barrier to prevent evasion by prey, 2) cause water motion to direct prey movement, and 3) position the white coloration on the ventral side to reflect light, causing prey to move in the opposite direction [12,39]. A feeding event was defined as beginning with that start of a solo bubble-net and ending when the whale closed its mouth after a surface lunge. Multiple feeding events from one whale on the same prey, in the same general location, were defined as a foraging session. We calculated lunge duration when possible.

Results

We captured videos and photographic sequences of two humpback whales independently engaged in previously undocumented foraging techniques. Both whales (“Whale A” and “Whale B”) initiated feeding events with a solo bubble-net. Before lunging, these whales used their pectorals to manipulate and further condense prey. We defined this technique as “pectoral herding”, with two methods of execution: “horizontal pectoral herding” and “vertical pectoral herding”. More detailed information of Whale A and Whale B encounters are provided in supplemental materials (S1,S2). We captured footage of one additional whale using horizontal pectoral herding, though a limited number of observations precluded this whale from further analyses.

Horizontal Pectoral Herding

We encountered Whale A (#2360 in Southeast Alaska Humpback Whale Catalog) on 27 days from 2016 to 2018. We observed solo bubble-netting during 15 feeding sessions (135 feeding events). Each solo bubble-net involved what we describe as horizontal pectoral herding prior to the lunge. Video footage depicting horizontal pectoral herding is provided in supplemental material (S3). During horizontal pectoral herding, Whale A initiated the feeding event by deploying an upward-spiral bubble-net to corral prey (Figs. 2 and 3; Stage A). At the closure of the bubble-net, Whale A rotated its head parallel to the surface of the water and toward the centre of the net. The whale then moved its left pectoral in and out of the water in a forward, sinusoidal motion along the initial edge of the bubble-net barrier (Figs. 2 and 3; Stage B). Whale A continued this pectoral movement while gradually opening its mouth and allowing the upper jaw to rise above the water line, while the lower jaw remained subsurface. The whale continued to open its mouth wider until it reached the opposite side of the bubble-net (Figs. 2 and 3; Stage C). Whale A’s head rotated in the direction of the left pectoral 51.9% of all documented feeding events. In these cases, the lower jaw was tilted at an angle that exposed prey to the largest circumference of the buccal cavity (Fig. 4). For all other feeding events, the degree of head tilt was unknown or Whale A maintained a stationary head position, bringing its lower jaw up out of the water to meet the upper jaw. Whale A never rotated its head away from the herding pectoral. Mean lunge duration, defined as the start of pectoral movement to the close of the mouth, was 8 ± 1 s (calculated from 32
of 36 videos). Not all videos could be used to calculate lunge duration because they did not document the entire process.

We observed Whale A using horizontal pectoral herding in four locations that spanned approximately 21 km of coastline. This included Warm Springs Bay, Takatz Bay (2016 hatchery release site), Kasnyku Bay (2016 and 2017 hatchery release site), and Kelp Bay. In 2016, we observed Whale A lunge feeding in Warm Springs Bay, Takatz Bay, and Kelp Bay. Although prey sampling was sparse and inconsistent, we observed juvenile salmon at all of these locations. In May of 2016 and 2017, we collected juvenile hatchery salmon from Warm Springs Bay (within 12 to 44 days of feeding sessions) and visually identified juvenile salmon during all Warm Springs Bay foraging events. Feeding sessions in Takatz Bay coincided with a salmon release event and continued onto the day following. Juvenile salmon were only visually identified in Takatz Bay, but all feeding sessions were in the vicinity of hatchery salmon releases. In 2017, Whale A was observed horizontal pectoral herding in Kasnyku Bay and Kelp Bay. The feeding sessions in Kasnyku Bay were associated with salmon releases (within 7 days of a release). Prey sampling and otolith marks from fish collected within 1 to 3 days of feeding sessions confirmed juvenile hatchery salmon in the area. We collected juvenile salmon (hatchery and wild) within 8 days of feeding sessions in Kelp Bay. Pacific herring (Clupea pallasii) were also sampled in Kelp Bay during 9 different feeding sessions. We were unable to differentiate whether prey being consumed in Kelp Bay were juvenile salmon or herring. Of all feeding sessions involving horizontal pectoral herding, 94.1% were identified as having targeted juvenile (hatchery-released chum and coho, wild pink (Oncorhynchus gorbuscha)) salmon.

**Vertical Pectoral Herding**

We documented Whale B (#2227 in Southeast Alaska Whale Catalog) solo bubble-net feeding at Hidden Falls Hatchery on 16 May 2017. During the 2.4 hr observation period, we recorded 13 solo bubble-net feeding events, all of which were in the vicinity of newly released hatchery-reared juvenile coho salmon (Fig. 5). We observed two well-documented types of kinematic feeding behaviours for Whale B: vertical lunge and lateral lunge. We also documented vertical pectoral herding, which has not been previously documented in the scientific literature. Video footage depicting all three lunge types is provided in supplemental material (54).

Vertical pectoral herding was used in 30.8% of all feeding events. We identified vertical pectoral herding when Whale B moved its pectorals from a neutral state (as in vertical lunge and lateral lunge) to a protraction-abduction posture (Fig. 6). After establishing this posture, the whale simultaneously moved both pectorals forward and into a V-shaped position on either side of its mouth, with pectorals curved ventrally (Fig. 7). A vertical lunge was used during 23.1% of all feeding events. When employing this technique, the whale’s pectorals first abducted with the tips curved up. Prior to closing its mouth, the pectorals adducted to a vertical lunge position, tight against the side of the body. Finally, the pectorals retracted and angled posteriorly as the whale lunged to the surface (Fig. 7). The distinguishing feature between vertical lunge and pectoral herding was a slight upward dorsal oriented curve to the pectorals and less visibility of the pectorals as they were abducted with a swept-back configuration. A lateral lunge was used in 46.2% of the feeding events (Fig. 6). When using this technique, the whale pivoted on its left pectoral and rolled approximately 90 degrees while lunging. The left pectoral was exposed and occasionally broke the surface of the water as the whale used it to manoeuvre.

When documenting Whale B’s feeding events, we observed notable differences in light conditions. Both vertical lunge (3 of 3) and lateral lunge (5 of 6) occurred in shaded waters. All vertical pectoral herding events (4 of 4) occurred in sunlit water, which was easily identified from photographs due to a sun-induced green tint of the water (Fig. 6). Whale B employed different tactics in the same location only when light conditions varied. In general, Whale B appeared to use vertical pectoral herding in sunlit areas but switched to vertical
lunge or lateral lunge when the same area became shaded. The single lateral lunge event in sunlight waters was located near a surface obstacle in the centre the bubble-net. Possible avoidance behaviour was documented as the whale lunged near the buoy. Prey movement in the direction opposite of vertical pectoral positioning was visible in 2 of 13 engulfment events (Fig. B). In “before” snapshots (i.e., images taken prior to vertical pectoral positioning), we observed a dense aggregation of prey between the mouth and pectoral. In “after” snapshots (i.e., images taken once pectorals were placed in V-shaped position) we observed less dense prey patches in the area between the mouth and pectoral. We also identified a greater relative density of prey that had moved toward the whale’s mouth. We could not calculate lunge duration for Whale B because the whale started to lunge in water too deep to visually see the whole process using aerial footage. The variation in light conditions also prevented the identification of consistent cues for the start of a lunge.

Discussion

It is well known that humpback whale pectorals aid in acceleration and maneuverability during feeding events [28,29]. Our study recognizes an alternative use of pectorals during foraging. Here, we have provided the first empirical evidence for a longstanding hypothesis that humpback whales use their pectorals to herd and aggregate prey [39,43,44]. Our study combined the use of new technology and a unique viewing opportunity at Hidden Falls Hatchery to provide the vantage points necessary for such documentation. Although the concept that humpback whales use their pectorals to manipulate prey is not new, the use of pectorals in conjunction with a bubble-net (as a secondary barrier) had never been documented. Using direct video footage and photographic sequences, we described this foraging technique as “pectoral herding”, with two methods of execution: horizontal pectoral herding and vertical pectoral herding. We observed two humpback whales using bubble-nets as a primary barrier to corral prey, proceeded by deliberate movements of the pectorals to establish a secondary barrier before the lunge. These observations suggest that pectorals are used to further condense prey inside the bubble-net, thereby increasing feeding efficiency for each event. From our results, we found three ways in which humpback whales use pectorals to herd prey: 1) create a physical barrier to prevent evasion by prey, 2) cause water motion to direct prey movement, and 3) position the white coloration on the ventral side to reflect light, causing prey to move in the opposite direction [12,39]. These three methods of pectoral herding are not mutually exclusive and can be used in conjunction with one another.

Horizontal Pectoral Herding

The documented solo bubble-nets began and ended in the same general location. Thus, there is greater elapsed time for bubbles created near the beginning portion of the net, compared to the end. The greater dissipation of bubbles and possibility that fish are scared toward the beginning portion of the net (as a result of whale activity near the bubble-net closure site) suggests a potential weakness in the primary barrier. We hypothesize that Whale A uses horizontal pectoral herding to strengthen the beginning portion of the solo bubble-net and establish a secondary barrier to further condense prey, thereby increasing the amount of prey consumed during each lunge. Because the energetically costly movement of the left pectoral likely hinders the acceleration of the whale toward the prey patch, we assert that an alternative use must be at play. We found that lunge durations of Whale A averaged 8 seconds, whereas Werth et. al. [51] documented mean engulfment rates from a solo humpback whale lunge to be closer to 2 seconds. This difference in engulfment rates with and without horizontal pectoral herding supports our hypothesis that any additional movement must substantially aid in prey capture. We conclude that Whale A used its pectorals in two of the three ways to herd prey: 1) create a physical barrier to prevent evasion by prey and 2) cause water motion to direct prey movement. In addition, pectoral movements could create eddies and/or drag that increases the whale’s capacity to alter prey movement. We note that our descriptions of horizontal pectoral herding rely upon...
observations from a single whale. However, we documented the use of this particular foraging technique by one additional whale, suggesting potential for cultural transmission of this foraging behavior.

In over half of the documented events, Whale A rotated its head in the direction of the left pectoral before closing its mouth (during all other fully documented events, the head remained centred and never rotated in the opposite direction). This suggests that the left pectoral was herding prey and that the whale turned its mouth into the path of swimming prey, further increasing the amount of fish consumed per lunge. The lower jaw turned at an angle that exposed prey to the largest circumference of the buccal cavity, which likely prevented escape between the lower jaw and the surface of the water. The rostrum was also above the surface of the water to avoid blocking prey from entering the buccal cavity when the whale turned its head. When the whale’s head remained centre, the lower jaw surfaced to meet the upper jaw. During these events, the whale may have sensed that its buccal cavity was full of fish, making head rotation counterproductive [52].

**Vertical Pectoral Herding**

Our current understanding about lunge feeding revolves around the theory that whales use their pectorals to actively increase lift and/or stabilize their body during a lunge. The pectoral position used by Whale B suggests that the whale violated two out of the four criteria proposed for a hydrodynamic stroke [25]. First, the pectorals were not oriented at an efficient angle into the path of the stroke ($\alpha > 17.5^\circ$). The stroke was also not oriented perpendicular to the body, which would inhibit stability during the lunge. Therefore, we claim that the pectoral movements of Whale B were not intended to increase hydrodynamic efficiency, stability, or lift. Whale B’s forward speed was likely hindered by a high angle of attack and V-shaped position of the pectorals around the mouth. During three of the four pectoral herding events, the rostrum and left pectoral broke the surface of the water at approximately the same time (within one second of each other). There is no hydrodynamic reason for the pectorals to be in line with or above the position of the mouth during a lunge. By eliminating the use of pectorals for stabilization and thrust, we deduced that Whale B’s pectorals were used to create a secondary barrier along the edges of the mouth during a lunge, manipulating prey movement toward the mouth and increasing foraging efficiency.

Light conditions and prey reactions also suggest that Whale B used its pectorals to herd prey. There were three main locations around the net pens that had recurring feeding events. During Whale B’s feeding session, the eastern side of the net pens transitioned from sunlit waters to shade. In all three of these locations, Whale B used vertical pectoral herding when lunging in the sun. During the only sunlight feeding event without vertical pectoral herding, we hypothesize that Whale B was manoeuvring around a buoy and that the whale would have used vertical pectoral herding if the obstacle were not present. When waters transitioned from sunlight to shade in these three main locations, the whale used vertical or lateral lunges instead of vertical pectoral herding. This provides support for the hypothesis that behaviour shifts were based on light conditions rather than locational differences. Brodie [39] suggested that the ventral side of the pectorals can be used to “flash” fish and cause them to move in the direction of the dark mouth, which functions as a deceptive refuge. When prey movement was visible in sunlit waters, we observed prey moving in the direction of the mouth, apparently in response to the position of the pectorals. This is convincing evidence that pectorals alter prey behaviour. The lack of vertical pectoral herding in shaded water suggests that the physical presence of the pectorals alone is not effective enough to cause fish to move toward the mouth. The combination of light reflection and a physical barrier likely provides a foraging benefit to justify the hydrodynamic detriment caused by vertical pectoral herding. Thus, it is probable that Whale B used pectorals in two of the three ways to herd prey: 1) create a physical barrier to prevent evasion by prey and 3) position the white coloration on the ventral side to reflect light and cause prey to move in the opposite direction [12,39].
Prey and behavioural plasticity

Schooling fish cluster in response to predators or other startling disturbances [53-57], and humpback whales have been known to take advantage of this behaviour [27]. Sharpe et al. [15] experimented with an artificial pectoral and found that herring respond to a rotating pectoral by fleeing in the opposite direction. It has also been suggested that humpback whales manipulate prey by slapping their pectoral fins or flukes on the surface of the water [7,27]. Whale A’s pectoral movement makes a startling disturbance that could alter the direction of prey within the bubble-net barrier. We were unable to see prey in videos of Whale A foraging. However, the continued use of horizontal pectoral herding, in combination with its hydrodynamic disadvantages, is strong evidence for an increase in foraging efficiency. Additionally, a study on hatchery-reared juvenile salmon [58] showed that fish avoid lights and seek out dark refugia when lights were activated and/or flashing. Because juvenile salmon were the target prey during Whale B’s feeding events, we believe that light reflected off the ventral surface of the pectorals served as a stimulus to scare fish in the direction of the dark “refuge” of the whale’s mouth. We were able to directly observe prey movement toward the mouth in response to Whale B’s pectoral placement in some of the videos. Pectoral movement and flashing may directly stun or disorient prey [7].

It is well known that humpback whales use bubble-nets to aggregate prey [12,27]; however, bubble-nets may not be as efficient as rendered more inefficient when prey do not naturally aggregate into dense patches. This is because schooling fish would aggregate within a single area of the bubble-net, enabling the consumption of most contained fish in a single lunge. Non-schooling fish may very well distribute themselves throughout the bubble-net, resulting in fewer fish consumed per lunge. Acoustic prey surveys at our study site showed that groups of juvenile coho (Oncorhynchus kisutch) and chum (Oncorhynchus keta) salmon were small, patchy, and short-lived compared to those formed by herring and krill [59]. Whales tend to moderate their behaviour to efficiently exploit different prey types and respond to dynamic prey conditions [14,60]. It is possible that the two whales we observed have independently altered their foraging strategies to accommodate non-schooling fish and more effectively incorporate hatchery-released juvenile salmon into their diets. Because aerial documentation of solo bubble-netting whales has been limited, we cannot conclude whether or not pectoral herding is restricted to these whales and the unique prey resource of hatchery-reared juvenile salmon. Pectorals are an efficient secondary barrier and may be used by other whales lunging on different prey. For Whales A and B, 93.9% of pectoral herding events exclusively targeted juvenile salmon. The remaining events may have also targeted herring as prey. Additionally, a bubble-net may be substantially larger than the size of a whale’s open mouth, restricting engulfment to only a portion of the prey enclosed within the net. A secondary barrier further condenses prey, conceivably enhancing the energy gained per lunge.

McMillan et al. [18] documented humpback whales using a feeding strategy called “trap-feeding”. The authors inferred that whales use pectorals to manipulate prey by flicking fish into their mouth. The available footage of the pectoral movement in this study relies on a lateral perspective with poor visibility below the water’s surface and no view of prey. This makes it difficult to connect pectoral movements to a specific behaviour or make inferences about prey responses. Additionally, lateral footage makes it difficult to differentiate between the use of pectorals as a stabilizing force during a lunge and pectoral movements to manipulate prey. In general, most whale observations are obtained from land or boat, yielding lateral views that limit the perspective and skew our perception of individual behaviours. With innovative technology (e.g., unoccupied aerial vehicles, small video cameras), we can now gain the perspectives necessary for more accurate interpretations of marine mammal foraging tactics. Our observations, which relied on an aerial perspective, provide insight into the position of humpback whales in relation to prey (above and below the water) as well as a more detailed depiction of the whale’s movements and position during feeding events. Based on lateral-
aerial comparisons of pectoral herding by humpback whales, we believe that conventional boat or land-based footage should be supplemented by aerial imagery in order to gain insight and avoid misinterpretations about marine mammal behaviour.

Despite the advantages of using advanced technology, our study is limited by small sample sizes and a lack of quantitative kinematics. Our findings depended on functional interpretations of movements made by two whales with only above-surface documentation. A more inclusive survey of solo feeding humpback whales (encompassing broader spatial scales and additional whales) would provide greater insight into how these animals are taking advantage of their lengthy appendages during foraging. Furthermore, future investigations should pair aerial footage of feeding whales with prey distribution data, and synchronous motion suction cup tags (i.e., DTAGs) to better quantify kinematic behaviours and prey dynamics, both above and below the surface [61]. Notably, however, our study suggests a flaw with current tagging technology. Although tags are often deployed on the backs of whales to record movements (pitch, yaw, and roll) of the entire whale, we found that prey aggregation and capture is not limited to movements of the head, caudal peduncle, and tail flukes. Thus, tag sensors that also quantitatively recorded these movements of the pectorals would allow for a clearer understanding of how these appendages are kinematically being used. Finally, more accurate lunge durations (e.g., starting when the whale’s mouth opened) would help us compare acceleration rates between lungen with and without pectoral herding, furthering our understanding about the hydrodynamic impacts caused by pectoral movements.

In summary, our results provide empirical evidence of the use of pectorals to herd prey. They also illustrate considerable variation among individual humpback whale foraging strategies. With our documentation of pectoral herding, we have provided support for plasticity in foraging behaviour of cetaceans. These animals are highly innovative, with individual whales successfully using different tactics to approach the same prey and in the same situation [27]. Maintaining a suite of foraging strategies likely aids humpback whales in a changing environment, where food availability fluctuates, and competition may impact population dynamics. Further investigation would enhance our understanding about whether humpback whales use pectoral herding as a principal foraging technique as well as the conditions that promote its use.

Ethics statement:
This research was conducted under National Marine Fisheries Service (NMFS) permits 14122 and 18529, University of Alaska Institutional Animal Care and Use Committee (IACUC) permit 907314-3, and State of Alaska Department of Fish and Game permit CF-18-049.

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Author’s contributions:
M.M.K., A.J.W., A.R.S., and J.M.S. contributed to the experimental conception and design; M.M.K. was primarily responsible for data collection; M.M.K. was primarily responsible for analysing and interpreting data with contributions from A.J.W., A.R.S., and J.M.S.; M.M.K. drafted the article. All authors revised the article and provided final approval for the version to be published.

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