





Feeding characteristics and prey profitability in five herring-feeding killer whales (*Orcinus orca*) in northern Norway

Aimee F. Matika¹ | Eve Jourdain²  | David E. Cade³  |
Richard Karoliussen² | Philip S. Hammond¹

¹Sea Mammal Research Unit, Scottish Oceans Institute, University of St Andrews, St Andrews, Scotland, UK

²Norwegian Orca Survey, Andenes, Norway

³Department of Biology, Hopkins Marine Station, Stanford University, Pacific Grove, California

Correspondence

Eve Jourdain, Norwegian Orca Survey, Breivikveien 10, 8480 Andenes, Norway.
Email: post@norwegianorcaurvey.no

Funding information

British Broadcasting Corporation; Sea World and Busch Gardens Conservation fund; Sea World and Parks

Abstract

This study used multisensory data tags with integrated 4K video to investigate feeding behavior and prey profitability in five adult male killer whales (*Orcinus orca*) at herring wintering grounds in Norway, in 2016 and 2017. Video recorded two killer whales engaged in carousel feeding, and two engaged in seiner feeding (i.e., feeding on herring discs around purse seiner vessels). The feeding behaviors identified from the video data allowed for determination of associated kinematic signatures, which were used to further identify and characterize carousel feeding and deep feeding dives over the entire logger duration. Prey consumption during on camera feeding bouts was also measured to calculate profitability of feeding bouts for the different behaviors. Average number of prey consumed per minute was 1.08 ± 0.43 for carousel feeding and 0.43 ± 0.07 for seiner feeding ($n = 122$ prey capture events). Using kinematic data, a total of 18 carousel feeding bouts and 206 deep feeding dives were identified. Whales spent at least 37%–65% of time over 24 hr feeding. Using field metabolic rate estimates from the literature and the energetic content of herring caught locally, killer whales required an estimated 285–578 herring/day to balance daily energy requirements.

KEYWORDS

energy budgets, energy intake, feeding behavior, metabolic rate, *Orcinus orca*, prey requirements

1 | INTRODUCTION

Found in all the world's oceans, killer whales (*Orcinus orca*) occupy the highest estimated trophic level of any marine mammal (Pauly et al., 1998). As apex predators occurring in large social groupings (Ford, 2018), they influence community structure within the marine environment (Estes et al., 2016; Springer et al., 2003; Williams et al., 2004). In northern Norway, killer whales rely on the Norwegian Spring Spawning stock of Atlantic herring (hereafter referred to as NSS herring, *Clupea harengus*) as a major food source (Christensen, 1982; Similä et al., 1996; Similä & Ugarte, 1993). Long term photo identification studies conducted between 1986 and 2003 at former herring wintering grounds estimated a minimum of 700 killer whales to be foraging and feeding on NSS herring, at least seasonally (Kuningas et al., 2014). More recent work has led to an updated estimate of around 1,900 killer whales at dynamic herring wintering grounds between 2012 and 2019 (Jourdain et al., 2021). Being one of the largest fish stocks worldwide, the NSS herring has been shown to play key roles in the marine ecosystems of the Norwegian and the Barents Seas and is also of major economic importance (Varpe et al., 2005). Its long-term sustainability in view of multiple pressures, such as fisheries and killer whale predation, therefore, appears crucial. Understanding the predation effects of killer whales on NSS herring should not only contribute to improving fisheries management advice, but would also allow predictions on how other varying exploitation pressures may impact these predators (Bogstad et al., 1997).

Past studies have shown that killer whales in Norway use a variety of techniques to feed on herring. The most commonly observed are carousel and seiner feeding. In carousel feeding behavior, individuals cooperatively steer the fish into a tight, ball-shaped school near the surface. Using underwater tail slaps, killer whales strike the school to stun and facilitate the capture of fish, which they eat one by one (Domenici et al., 2000; Similä, 1997; Similä & Ugarte, 1993; Simon et al., 2005; Van Opzeeland et al., 2005). In seiner feeding behavior, killer whales noncooperatively feed on herring discards, i.e., dead or stunned fish that may slip from the nets during haul in and haul out operations, around purse seiners (Similä, 2005; Van Opzeeland et al., 2005). By providing prey that can be captured with minimum effort, fisheries may substantially supplement killer whales' daily food intake, or replace other feeding behaviors, and may in some cases lead to positive effects on reproductive output and demographics at the population level (Esteban et al., 2016; Tixier et al., 2015, 2017). Likely driven by variation in schooling behavior and distribution of their herring prey, killer whales in Norway may also use other feeding techniques, such as deep feeding or subsurface feeding, but these have been described to a lesser extent (Samarra & Miller, 2015; Similä, 1997). In these techniques, killer whales also display convoluted swimming but do not bring the herring to the surface, and only rarely use tail slaps for prey capture (Samarra & Miller, 2015). Feeding dives to deep prey fields are also common in other killer whale ecotypes, as revealed in fish-eating Southern and Northern Residents in the North Pacific (Tennessen et al., 2019; Wright et al., 2017).

To what extent killer whales in Norway may use or benefit from the herring fisheries for their daily food intake is unknown. Similarly, how individuals acquire their food to meet their energy requirements by adopting behavioral specializations or rather showing plasticity in response to changes in herring schooling behavior has been poorly investigated (but see Samarra & Miller, 2015). Quantifying feeding bouts, relative use of different feeding behaviors, and prey acquisition rates would provide a baseline for assessing feeding success and how it can be impacted by environmental factors and anthropogenic disturbance.

Previous studies in Norway used surface and underwater behavioral observations to characterize killer whale feeding activity (Domenici et al., 2000; Samarra & Miller, 2015; Similä, 2005, 1997; Similä & Ugarte, 1993; Simon et al., 2005; Van Opzeeland et al., 2005). In this study, we use a novel combination of data logger and animal borne video data to quantify feeding activity for five adult male killer whales at herring wintering grounds in northern Norwegian fjords. Specifically, the objectives of this study were: (1) to estimate the scope of feeding activity during a day, (2) to characterize the different behaviors used and quantify the relative use of each, and (3) to estimate prey consumption rates to further explore their relative profitability and overall feeding success.

2 | MATERIALS AND METHODS

2.1 | Data collection

Killer whales were tagged at herring wintering grounds at Vengsøy ($69^{\circ}51'36.09''\text{N}$, $18^{\circ}34'12.17''\text{E}$) in November 2016 and at Skjervøy ($70^{\circ}4'57.78''\text{N}$, $21^{\circ}10'23.47''\text{E}$) in November 2017, northern Norway. Fjords in which killer whales were encountered in Vengsøy had depths mostly <150 m, with a maximum of ~ 300 m. Fjords in Skjervøy were deeper with waters commonly reaching ~ 250 m to a maximum of ~ 350 m.

Killer whales were approached in a 6 m aluminum research vessel. Data loggers from Customized Animal Tracking Solutions (CATS; <https://www.cats.is/>; Cade et al., 2016; Goldbogen et al., 2017) had a 4K GoPro video camera integrated into a housing (Figure 1a) that contained a suite of inertial measurement unit (IMU) sensors (details below). Tags were attached noninvasively using suction cups (Figure 1a) and delivered by a handheld carbon fiber pole. To minimize disturbance, approaches were conducted with the engine off and using the current to drift into a group of feeding killer whales. Intended placement of the data logger on the killer whales was between the blowhole and the dorsal fin, and with the camera lens facing forward. The camera with a 130° field of view was turned on immediately before deployment and was set to record continuously for approximately 5 hr (maximum battery life). Video and data were recorded onto high-capacity microSD cards so that data collection was limited by battery life, not by card capacity. The battery of the data logger allowed for diving data to be recorded for up to 5 days. No time was preset on the tag for the suction to release and tags therefore remained on the whales for varying durations from a few hours to up to 4 days. When the tag was released from the animal, an inbuilt VHF transmitter allowed it to be tracked when floating upright at the sea surface, facilitating recovery. Photographs of the dorsal fin and adjacent saddle patch were used to identify tagged individuals from a catalog of known killer whales in the study area (Jourdain & Karoliussen, 2021), using natural scarring and pigmentation patterns, following protocols introduced by

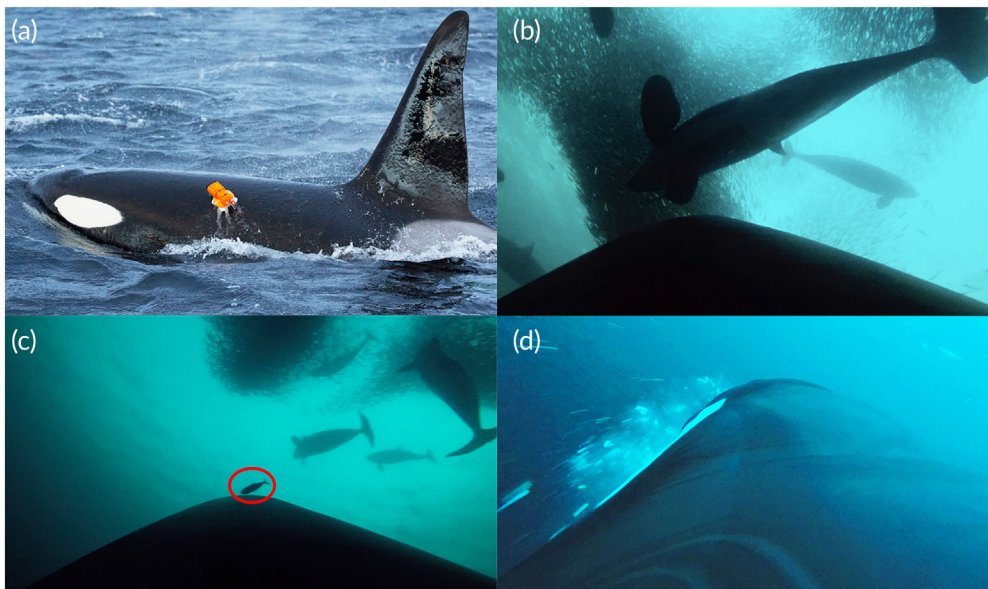


FIGURE 1 (a) Photograph showing the data logger with integrated 4K video attached with suction cups to adult male killer whale NKW-752 in November 2016 in Vengsøy. (b) View showing NKW-752 positioned below the herring school when carousel feeding alongside other killer whales. (c) View showing NKW-752 swimming towards a single debilitated herring prey (indicated by red ellipse) before consuming it. (d) View confirming feeding by NKW-752 as indicated by head movements and plumes of debris exiting the mouth upon successful capture and consumption of a single herring prey.

Bigg (1982). Tagging was conducted in compliance with Norwegian animal ethics regulations and under permit (FOTS ID 10176).

Tag accelerometers were sampled at 400 Hz, magnetometers and gyroscopes at 50 Hz, and pressure, light, temperature, and GPS at 10 Hz. Audio was recorded at 48 kHz as part of the video from a microphone embedded within the 4K GoPro video camera.

2.2 | Data analysis

2.2.1 | Video/audio data

We first sought to examine the occurrence and frequency of feeding-related behaviors using video and audio data from the animal borne GoPro (Figure 1b,c,d). Video (11.3 hr) was collected at 4K resolution and audio was recorded simultaneously with video. Video data were transcribed using event logging software BORIS v7.0.13 (Friard & Gamba, 2016). Each behavior was defined as either a point (no duration) or state (limited duration, with recorded start and stop time) event (Table 1). Point events included prey capture, respiration, and underwater tail slaps. Underwater tail slaps were considered indicative of prey capture attempts (Domenici et al., 2000; Samarra & Miller, 2015; Similä & Ugarte, 1993; Simon et al., 2005; Van Opzeeland et al., 2005). State events covered feeding and traveling (Table 1). During video data processing, behavior state was recorded to the nearest second and both state and point events were marked as they occurred. Examining videos concurrently with spectrograms derived from the video's audio data allowed for identification of specific sounds associated with certain behaviors. Specifically, an increasing flow noise followed by a clear “hit” sound, produced as a result of cavitation and/or physical contact with the herring (Domenici et al., 2000; Simon et al., 2005), characterized underwater tail slaps; and “crunch” sounds were associated with prey consumption. Video indicated that killer whales typically consumed one herring at a time (Figure 1c,d). Once validated from videos with fair lighting conditions, these signature sounds allowed for underwater tail slaps and prey consumption events also to be unequivocally distinguished in darker sequences. To avoid misidentification, only behavioral events for which identification was audio based but was supported by preceding contextual video data were accepted. For example, with a whale swimming towards a stunned herring (Figure 1c), if the fish became indiscernible due to filming conditions changing from bright to dark, a crunch sound provided a high confidence that the tagged whale had consumed the fish. This also ensured that identified signature sounds reflected the behavior of the tagged individual and not that of adjacent whales. Video helped to validate behavior indicative of prey capture attempts and allowed for identification of associated kinematic signatures (see below). These signatures were then used to identify killer whale feeding behavior from the entire tag deployment

TABLE 1 Definitions of behavioral categories used for coding video events. Point behaviors (P) had no duration. State behaviors (S) had a recorded start and finish time. Modified from Similä and Ugarte (1993) and Ford (1989).

Behavior	Point or state event	Description
Prey capture	P	Whale consumed the prey, as indicated by physical opening and closing of the mouth, sharp head movements, crunching sounds and/or plumes of debris exiting mouth (Figure 1d).
Respiration	P	Whale took breath at surface.
Tail slap	P	Whale performed an underwater tail slap to stun prey. Fluke slap usually followed acceleration towards the herring school, rapid tilting of camera axis and a short, sharp snapping sound.
Feeding bout	S	Whale engaged in carousel or seiner feeding (Figure 1b). Started with fluke slap, or prey consumption and ended after a period of repeated respiration with little/no deep diving. Did not include suspected prey searching.
Traveling	S	Whale was moving at consistent pace and heading.

data, including when video was not available. Video behavioral states (feeding, traveling) were then matched via timestamp to general diving characteristics (mean dive speed, duration, depth) recorded by the data logger (see below) and compared using two sample *t* tests for each whale to allow comparison between seiner and carousel feeding (two sample *t* test: depth ~ state, speed~state, duration~state).

To explore prey consumption rates for all filmed feeding bouts (defined in Table 1), we recorded the number of herring taken per minute of feeding activity for each tagged killer whale (Figure 1c). Gross energy intake during feeding bouts was then estimated using two sources of data. Using fishery catch data on herring size for the two tagging areas, Vengsøy (2016) and Skjervøy (2017), we calculated minimum, maximum, and mean mass (grams) of the herring fed upon. Energy contained in each herring was calculated by multiplying mean fish mass (grams) by energy density. The latter was estimated using the equation $E_{dt} = -0.053t + 25.771$ from Varpe et al., (2005), covering days 196–295 of the year and where *ED* is energy density (kilojoules/gram) and *t* is the day of the year (Bachiller et al., 2018; Varpe et al., 2005). In this study, average deployment day (*t*) = 326 (November 22) fell beyond the model range. Because the rate of energy density loss is expected to decrease in herring after cessation of feeding from September, our estimates may be negatively biased, as most fat depletion occurs after wintering during the spawning migration (Slotte, 1999). Total prey consumption was then used to calculate the mean, minimum, and maximum gross energy intake per feeding bout in Vengsøy in 2016 and in Skjervøy in 2017.

2.2.2 | Data logger

All tag data were decimated to 10 Hz, tag orientation (e.g., pitch, roll, heading, and relative x, y, z position) on the animal was corrected for, and animal orientation was calculated using custom written scripts in MATLAB 2014a (as per Cade et al., 2021). Animal speed for all deployments was determined using the amplitude of tag vibrations (Cade et al., 2018) as well as flow noise when audio was available (Goldbogen et al., 2006). Video data were synched to 3D orientation and motion data using breath timing from the pressure sensor (as per Cade et al., 2021). Bench test calibrations were applied to the data to convert all raw outputs to engineering units, and in situ calibrations were performed on the accelerometer and magnetometer data streams using spherical calibration procedures from <https://www.animaltags.org> using scripts from Cade et al. (2021). Only bench calibrations were used for gyroscope data, so magnitude between deployments could not be compared.

Animal pitch, roll, and heading (calculated from the accelerometers and magnetometer) and rotational motion (from gyroscope signals) associated with underwater tail slaps detected in video were used to identify a characteristic kinematic signature for feeding events. Notably, underwater tail slaps in this study were produced in a foraging context (as confirmed by video) and are contextually and kinematically distinct from tail slaps noted in surface observations (for example Noren et al., 2009). Underwater tail slaps were found to have kinematic signatures characterized by double humped y-axis gyroscope signals, similar to the two phased tail slaps noted by Domenici et al. (2000), and usually were associated with maneuvers such as roll, pitch, and heading changes (Figure 2). The remainder of the IMU data (lacking video data) was then audited for these characteristic signals to reliably identify underwater tail slaps indicative of foraging activity. K-means clustering was applied to the timing between underwater tail slaps to group the slaps into feeding bouts. Slaps that were more than 9.7 min apart were determined to be part of separate events.

Carousel feeding behavior was inferred using tails slaps and the kinematic signatures of orientation and motion of an animal throughout a dive. Typically, carousel feeding showed repeated circling behavior interspersed with tail slaps (Figure 2). Duration of carousel feeding bouts was determined from the start of the dive containing the first tail slap in an event to the end of the dive containing the last tail slap in an event.

Dives containing discrete instances of high jerk and maneuvering, but with no stereotypical two humped signature of underwater tail slaps associated with carousel feeding (MathWorks, 2014), were identified as deep feeding dives (Tennessen et al., 2019; Wright et al., 2017). Figure 3 highlights relevant IMU data for a deep feeding dive in NKW-561.

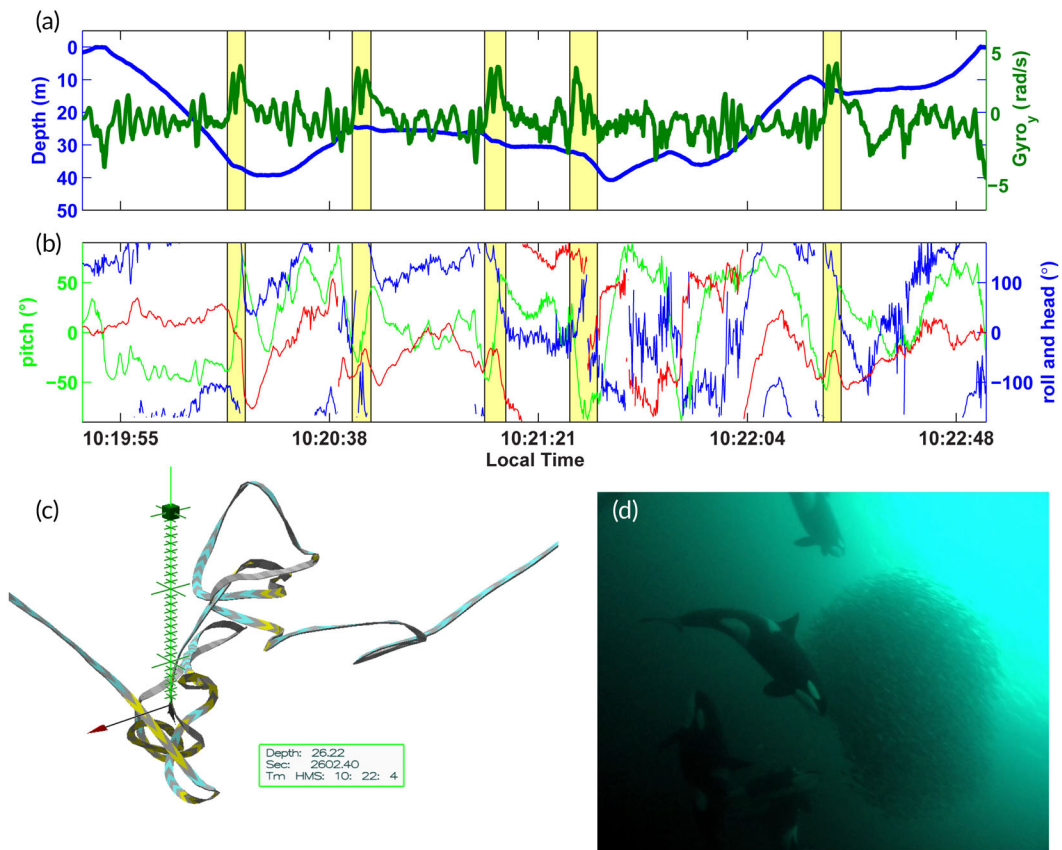


FIGURE 2 Kinematic signature of underwater tail slapping behavior. (a) Depth and y-axis (sway axis) gyroscope rotations for tag attached near the head of NKW-561. Highlighted regions are periods of tail slaps observed in the video. Slaps tended to be deep in the water column and were associated with a distinct 2-humped y-gyroscope signal. (b) Pitch (green), roll (red), and heading (blue) of the same animal showing changes in rotation during the feeding event. Tail slaps were associated with a rolling maneuver $>20^\circ$ or absolute roll position $>45^\circ$. (c) Trackplot (Ware, 2006) showing the movement patterns from part A and B visualized in three dimensions. (d) Image of the herring school under predation in panels a–c.

Seiner feeding bouts were not analyzed kinematically, as there was a lack of video data for any seiner feeding whale. This prevented kinematic analyses, and therefore further extrapolation, of seiner feeding bouts.

Sunrise, sunset, and civil twilight periods used to calculate percentage time feeding were defined by calculated solar elevation angle using the MATLAB package “Sunrise/Sunset” (Garrison, 2021). Twilight was defined as the period of time when solar elevation is $<6^\circ$ below the horizon.

To explore prey profitability with regard to each feeding behavior, tentative estimates of adult male field metabolic rate (FMR) were calculated. Data from Christensen (1984) provided the length to age relationship of killer whales found along the Norwegian coast (mean adult length of 6.7 m for males). The body length to mass relationship described in Bigg and Wolman (1975) was then used to calculate mean mass in kilograms for adult male killer whales in Norway using the equation $M = 0.000208L^{2.577}$, where M = mass in kilograms and L = length in centimeters. Following methods in Noren (2011), we produced upper and lower bound estimates of killer whale FMR and DPER (daily prey energy requirements) using $5\times$ and $6\times$ Kleiber’s (1975) predicted basal metabolic rate (BMR) in kilocalories/day, where $BMR = 70M^{0.75}$ and M = mass in kilograms.

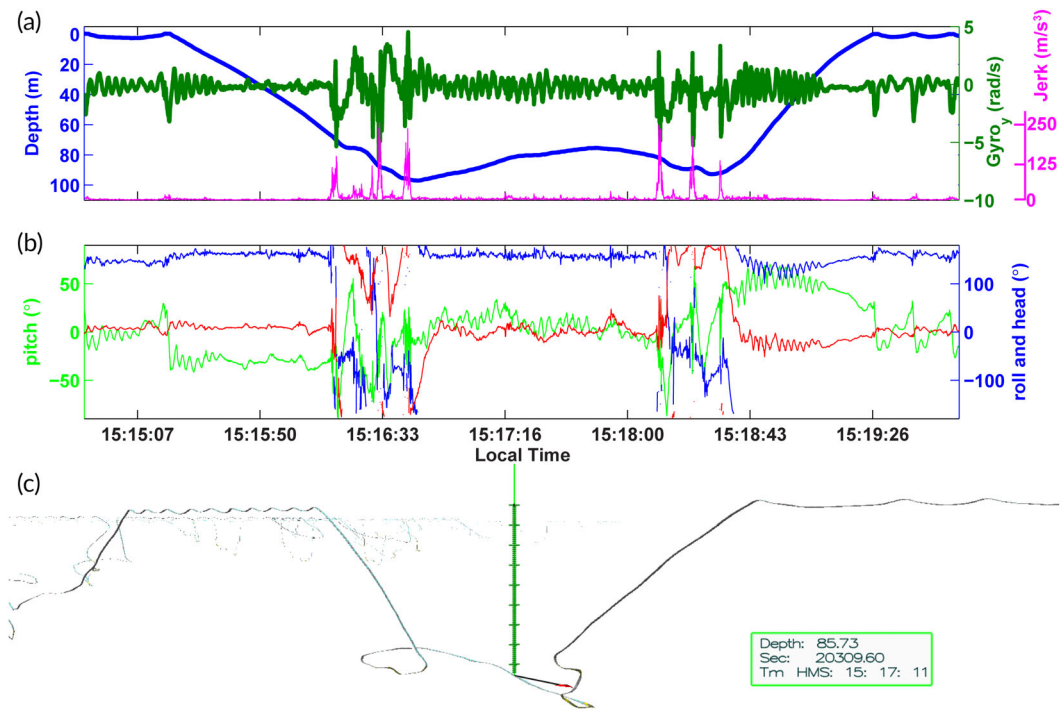


FIGURE 3 Deep feeding exhibited by NKW-561. (a) Depth (blue), y-axis (sway axis) gyroscope rotations (green), and jerk (magenta) during a deep feeding event. (b) Plot of pitch (green), roll (red), and heading (blue). (c) Trackplot (Ware, 2006) of the 3D movement during the deep dive from panels A and B.

Unless otherwise stated, data processing was done in MATLAB v2014a, and statistical analyses were done in R v.3.5.1 (R Core Team, 2018).

3 | RESULTS

3.1 | Data summary

Data were collected from four adult male killer whales (NKW-335, NKW-561, NKW-718, and NKW-752) at Vengsøy in November 2016 and from one adult male killer whale (NKW-028) at Skjervøy in November 2017, all five from different social groups. Due to technical mistakes/misfunctions, one tag recorded video but no data log (NKW-028), while another tag recorded data log but no video (NKW-718). Overall, data loggers provided a total of 11.3 hr of video (1.7–4.9 hr, $n = 4$) and 132.9 hr of logger data (0.9–96.3 hr, $n = 4$).

3.2 | Video data

During video, killer whales preyed exclusively on herring and engaged in two types of feeding: carousel feeding (NKW-561 and NKW-752; Figure 1b,c,d) and seiner feeding (NKW-028 and NKW-335). Carousel feeding was identified by the presence of large herring school(s), typically with neighboring killer whales circling the perimeter of these schools (Figure 1b). Seiner feeding was identified by the presence of purse seiner(s) on the surface, which the tagged whale loosely followed. Each tagged whale used one of the two feeding methods during

video, but not both. The proportion of total video time spent carousel feeding (mean \pm SD: 39.9% \pm 25.9%, n = 6 feeding bouts between two whales; Table S1) was greater than the time spent seiner feeding (mean \pm SD: 10.0% \pm 9.0%, n = 3 bouts between two whales; Table S1). Over the total video duration showing carousel feeding, individuals NKW-561 and NKW-752 performed a total of 11 and 20 underwater tail slaps, respectively, equivalent to a rate of 0.4 \pm 0.2 slaps per minute, and 5.2 \pm 3.5 slaps per bout. Each underwater tail slap led to an average consumption of 1.4 \pm 1.1 herring for NKW-561 (range: 0–3), and of 4.6 \pm 2.0 herring for NKW-752 (range: 0–7). When seiner feeding, individuals NKW-028 and NKW-335 did not use underwater tail slaps. Overall, the average number of herring prey consumed per minute of feeding bout was 0.76 \pm 0.45 and, more specifically, 1.08 \pm 0.43 when killer whales engaged in carousel feeding and 0.43 \pm 0.07 when engaged in seiner feeding.

3.3 | Logger data

Data logger analysis of general diving characteristics showed that killer whales swam at speeds ranging between 0.6 and 7.3 m/s (Table 2). Individuals spent the majority of their time in the upper 10 m of water, however, deep dives of up to 221 m were recorded (Figure 4, Table 2). Kinematic signatures of underwater tail slaps (Figure 2) allowed for detection of further carousel feeding for NKW-335, NKW-561, NKW-718, and NKW-752 outside of video hours (mean \pm SD; 5 \pm 2 additional bouts identified, range: 2–7). Mean carousel feeding bout duration was 23.5 \pm 27.8 min (range: 1.7–119.4 min), with 12 \pm 15 underwater tail slaps recorded per bout. Mean slap depth during carousel feeding was recorded at 14.3 \pm 10.3 m (range: 1.6–33.0 m; Figure 2a). In addition, logger data for these whales (except NKW-718) revealed deep feeding dives (52 \pm 80 number of deep feeding dives, range: 0–170) as shown in Figure 3. Mean deep feeding dive duration was 212 \pm 37 s with a mean depth of 64.9 \pm 48.0 m (range: 10.6–221.3 m). No fluke slaps were recorded during these dives. Individual NKW-335 engaged in both seiner feeding and deep feeding over logger deployment, showing that all tagged whales switched between various feeding behaviors.

During daylight hours, percentage time spent carousel feeding was 35% \pm 19% and percentage time conducting deep feeding dives 7% \pm 6%. During twilight hours, killer whales spent 15% \pm 21% of their time carousel feeding and 5% \pm 1% of their time deep feeding. During dark/night hours, no carousel feeding bouts were detected, however, whales spent 8% \pm 5% of time deep feeding. Deep feeding dives were recorded at all light levels.

Using the two killer whales with deployment duration greater than 24 hr to capture a full diurnal cycle (NKW-561 and NKW-335; Table 2), percentage time spent deep feeding over a 24 hr period was calculated as 17% for NKW-561 and 35% for NKW-335. Percentage time spent carousel feeding over 24 hr was 20% for NKW-561 and 30% for NKW-335. As a result, without accounting for seiner feeding (not possible to quantify due to instrument limitations), the whales spent at least 37%–65% of time per day feeding.

TABLE 2 Summary of dive information over full logger duration for the four adult male herring-feeding killer whales tagged in Vengsøy in November 2016 for which logger data were available.

Whale ID	Video deployment duration (hr)	Logger deployment duration (hr)	Feeding type	Mean dive depth (m) \pm SD	Maximum dive depth (m)	Mean swim speed (m/s) \pm SD	Maximum swim speed (m/s)
NKW-752	1.1	9.8	C, D	9 \pm 12	155	1.5 \pm 0.5	3.9
NKW-718	0.0	0.9	C	10 \pm 2	13	1.3 \pm 0.1	1.73
NKW-561	2.3	25.9	C, D	9 \pm 18	221	1.5 \pm 0.7	7.3
NKW-335	4.9	96.3	C, D, S	10 \pm 20	196	1.4 \pm 0.5	6.9

Note. C: carousel feeding, D: deep feeding, S: seiner feeding.

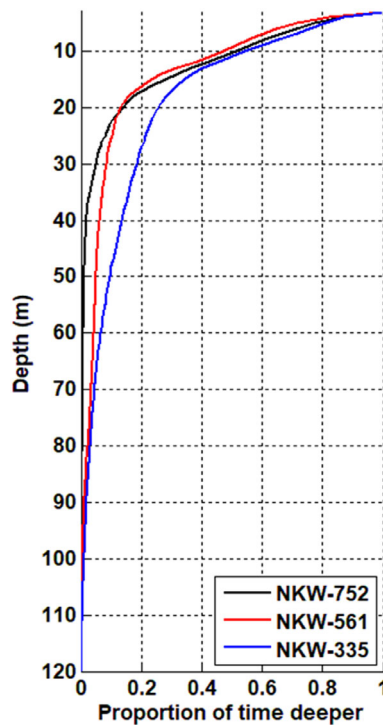


FIGURE 4 Proportion of time spent at various depths (meters) for three of the five adult male killer whales tagged at herring wintering grounds in Vengsøy in November 2016.

Over the video duration, where dive characteristics could be related to specific state behaviors, mean dive depth was greater when feeding than when traveling in all tagged individuals (Table S1, Figure 5a) but the difference over all whales was not significant ($t[2.8] = 1.8, p = .2$). There was no such pattern for mean dive speed or dive duration (Table S1, Figure 5b,c; swim speed: $t(4.0) = 0.6, p = .6$; dive duration: $t(3.9) = 0.9, p = .4$).

When comparing seiner and carousel feeding using video output, mean dive depth and swim speed during feeding were greater in carousel feeding whales (NKW-752, NKW-561) compared to the seiner feeder (NKW-335) (Table S1, Figure 5a,b) but these differences were not statistically significant (Table S1, Figure 5a,b,c; dive depth: $t(2.8) = 1.8, p = .2$; swim speed: $t(4.0) = 0.6, p = .6$; dive duration: $t(3.9) = 0.9, p = .4$).

3.4 | Prey profitability

Herring captured by purse seiners operating out of Vengsøy in November 2016 had mean mass of 358 ± 14 g (range: 230–391 g; data provided by Norges Sildesalgslag, on request) and mean estimated energy content per individual of 3.0 ± 0.1 MJ (range: 1.9–3.3 MJ) (Varpe et al., 2005). Herring caught in Skjervøy in November 2017 had mean mass of 215 ± 9 g (range: 180–250 g; data provided by Norges Sildesalgslag, on request) and mean estimated energy content per individual of 1.8 ± 0.1 MJ (range: 1.5–2.1 MJ). Carousel feeding NKW-752 consumed the highest number of herring ($n = 93$) in 1.1 h (Table 3), equivalent to 279.0 MJ energy intake. Carousel feeding NKW-561 consumed 15 herring in 0.3 hr equivalent to 45.0 MJ energy intake (Table 3). Seiner feeding NKW-028 consumed the lowest number of herring ($n = 13$) over 0.5 hr, equivalent to 23.4 MJ energy intake over the video recorded feeding bouts (Table 3).

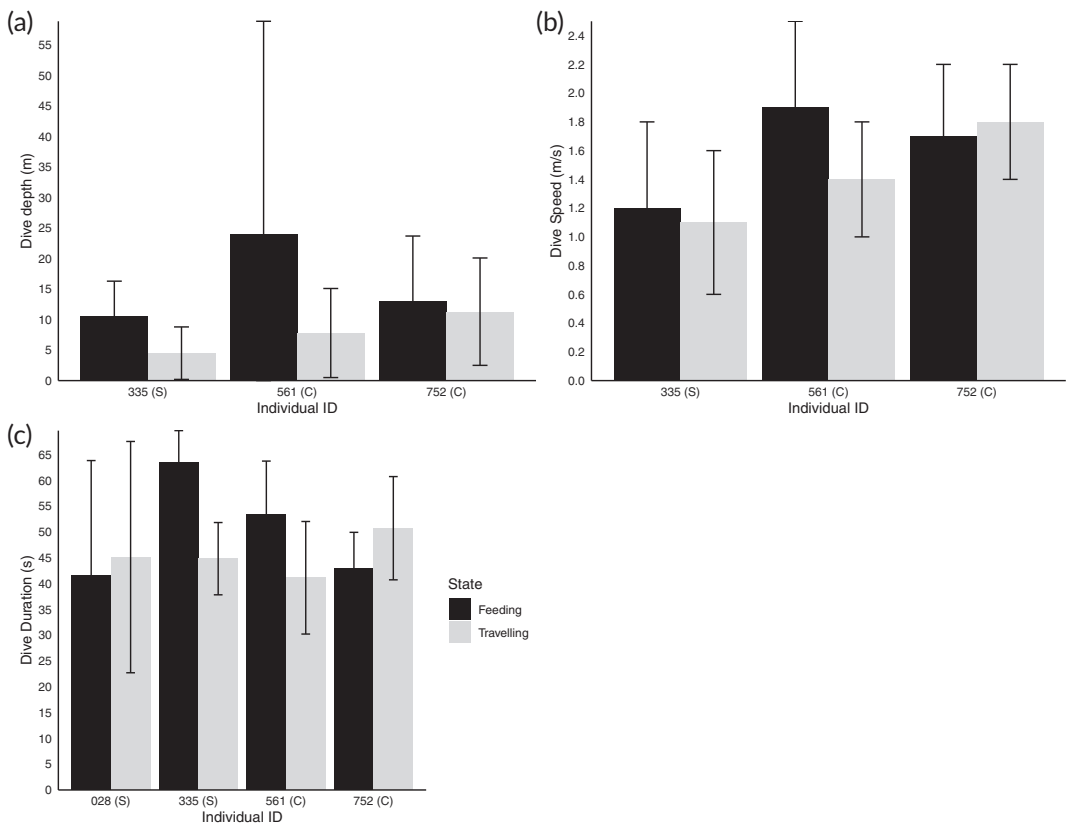


FIGURE 5 Dive characteristics associated with feeding (black) and traveling (gray) states for the three tagged killer whales for which data loggers and video, or just video were available, i.e., NKW-335, NKW-561, NKW-028, and NKW-752 (C: carousel feeding, S: seiner feeding). Means (\pm SD) are calculated over the video duration only. Differences between the two behavioral states were not statistically significant (two sample t-tests).

The mass of an adult male killer whale in Norway was estimated to be 3,988 kg. By calculating $5\times$ and $6\times$ Kleiber's (1975) predicted BMR, FMR range was 735–882 MJ/day with DPER of 867–1,041 MJ/day. Given these values, it would take the average adult male killer whale 285–342 herring in Vengsøy, or 482–578 herring in Skjervøy to balance DPER. Using mean feeding rate derived from the video data (0.76 prey per minute), it would take 375–450 min daily feeding activity (26%–31% of day length) in Vengsøy to balance DPER. In Skjervøy an individual would require 634–761 min of daily feeding activity (44%–53% of day length) to balance DPER. Using only carousel feeding, the average adult male would take 264–535 min daily feeding activity (18%–37% of day length) to balance DPER. Using only seiner feeding, it would take 663–1,344 min of daily feeding activity (46%–93% of day length) to balance DPER.

4 | DISCUSSION

The recent development of data loggers that couple three dimensional sensors with animal borne video allows for novel use of logging data, beyond the usual behavioral descriptions (Goldbogen et al., 2017). Despite a small sample size, our use of data loggers with 4K video has revealed new aspects of killer whale underwater activities in a major

TABLE 3 Number of Atlantic herring consumed and estimated gross energy intake during feeding events (C: carousel feeding, S: seiner feeding) based on video data collected from four adult male killer whales tagged in November 2016 ($n = 3$) and November 2017 ($n = 1$) in northern Norway. NKW-718 had no video data and so was excluded from the table.

Whale ID	Video footage duration (hr)	Time spent feeding (hr)	Feeding type	Total prey consumption	Prey consumed per minute	Minimum energy intake (MJ)	Average energy intake (MJ)	Maximum energy intake (MJ)
NKW-752	1.7	1.1	C	93	1.4	176.7	279.0	306.9
NKW-561	2.3	0.3	C	15	0.8	28.5	45.0	49.5
NKW-028	2.4	0.5	S	13	0.5	19.5	23.4	27.3
NKW-335	4.9	0.04	S	1	0.4	1.9	3.0	3.3

seasonal feeding ground in northern Norway and provided the first estimates of prey acquisition rates in North Atlantic killer whales.

4.1 | Feeding techniques and usage patterns

Logger data spanning over 24 hr for two deployments indicated killer whales may spend at least 37%–65% of the day feeding when at herring wintering grounds. Data were insufficient to quantify time spent seiner feeding, so this should be taken as a lower bound estimate. Regardless, our findings indicate carousel feeding, seiner feeding, and deep feeding as main feeding techniques at herring wintering grounds, although the relative importance of each cannot be quantified with our limited data.

The tagged killer whales did not use a single feeding behavior, but rather a combination of behaviors following apparent diurnal patterns. Seasonal plasticity in feeding behavior, as induced by variations in herring antipredator strategies across life stages (wintering, spawning, feeding), was previously suggested for herring feeding killer whales (Samarra & Miller, 2015). Here, we found diurnal variations in the use of feeding techniques, which may reflect differences in profitability for each relative to the time of day, most likely owing to variations in herring behavior and/or light conditions.

Of the entire tag deployment duration, carousel feeding was only detected during daylight and twilight hours. Mean depth of slap production during carousel feeding in this study was 14.3 ± 10.3 m, which equals the 14.3 ± 11.8 m depth reported for killer whales tagged at former herring wintering grounds in Vestfjord, Lofoten, in November 2005 and 2006 (Samarra & Miller, 2015). Depth of slap production also aligns with previous sonar observations reporting carousel feeding within the upper 10 m of the water column (Similä & Ugarte, 1993). Therefore, carousel feeding always seems to occur near the surface (Similä & Ugarte, 1993; Simon et al., 2005), regardless of environmental context, suggesting that the profitability of this feeding technique may be tied to the availability of light and subsequently, the ability to use visual cues. During daylight hours, killer whales can use their white undersides to flash the herring. This can promote herring schooling behavior and a more compact ball formation (Similä & Ugarte, 1993; Simon et al., 2005). Tighter schooling improves the effectiveness of underwater tail slaps, as more herring are likely to be stunned by the flukes during carousel behavior.

Although not light dependent, carousel feeding near the surface also creates a shallow prey patch, thus minimizing depth, dive duration, and ultimately, the energy expenditures for breath hold mammals like killer whales. While herding a herring ball from the depths to the surface likely represents a high energy investment (whales dive from 160 to 180 m depth to penetrate herring fields), energy expenditure per whale is lower when group size is larger (Nøttestad et al., 2002). It was observed that all group members in a pod actively participate in herding and preventing schools from escaping back to the depths (Simon et al., 2005). This may offer individuals intermittent

but repeated prey capture opportunities over relatively long feeding bouts (range: 1.7–110.4 min in this study; range: 10–295 min in Similä & Ugarte, 1993). However, when using visual cues becomes impossible outside of daylight hours, the advantage to carousel feeding may be lost and other feeding techniques may become more profitable.

As detected in video, killer whales foraged on herring discards around purse seiners as another feeding technique (Mul et al., 2020; Similä, 2005; Van Opzeeland et al., 2005). The lack of underwater tail slaps detected during seiner feeding bouts confirms that, in close vicinity to fishing vessels, killer whales access herring that are already stunned or dead and thus benefit from low expenditure prey captures. Seiner feeding was not extrapolated outside of video hours given the short sample of video data, and thus kinematic signatures, that were needed to infer further bouts. Because tags were deployed during carousel feeding (see Materials and Methods), our results likely underestimate the importance of seiner feeding for killer whales at herring wintering grounds. Of note, fishing activity at herring wintering grounds typically starts after twilight (Jourdain et al., 2021) when the herring ascend to the upper water column (Røttingen et al., 1994). Therefore, it cannot be ruled out that no detection of carousel feeding during the hours of darkness is caused by killer whales preferentially scavenging around fishing vessels as the vessels become active, rather than killer whales not carousel feeding at night at all. In fact, satellite tagging data have suggested that killer whales may be able to acoustically detect herring fishing vessels from 30 to 40 km distance and modify their behavior to approach them (Mul et al., 2020). However, lower prey capture rates estimated for seiner feeding individuals, relative to carousel feeding, suggested a lesser importance of seiner feeding to meet DPERs.

Our findings indicate that killer whales may also perform deep feeding dives (mean \pm SD: 64.9 \pm 48.0 m). This is consistent with observations of killer whales interacting with herring schools at depths ≥ 100 m at former herring wintering grounds (Samarra & Miller, 2015; Similä, 1997). Similar to previous studies, the kinematics during deep feeding dives were characterized by elevated jerk signals and high angular deviation in heading, (e.g., Figure 3) which suggested prey pursuit and feeding attempts (Samarra & Miller, 2015; Tennessen et al., 2019). However, the lack of underwater tail slaps detected during deep feeding dives suggested killer whales may employ various techniques to capture individual prey as a response to differences in herring behavior, which themselves may be influenced by school size, school depth, and other environmental factors (Similä, 1997).

4.2 | Costs/benefits of feeding techniques

Carousel feeding killer whales NKW-561 and NKW-752 had higher mean swim speeds and depths in comparison to seiner feeding NKW-335 (Figure 5, Table S1). During carousel feeding, the whales also repeatedly performed underwater tail slaps and herding dives, which is expected to make carousel feeding behavior more energetically costly than other feeding types (Domenici et al., 2000; Similä & Ugarte, 1993). However, mean swim speeds adopted during carousel feeding only represented a 0.3–0.6 m/s increase in swim speeds compared to NKW-335 when seiner feeding (Table S1). These values fall within the range of modified swim speeds for which associated energetic cost was estimated negligible by Noren et al. (2016). In contrast, the seiner feeding individual was observed to be slower swimming and closer to the surface and did not need to use high speeds nor tail slaps to capture herring discards from fishing operations (Van Opzeeland et al., 2005). While these observations indicated reduced metabolic costs associated with seiner feeding, prey acquisition rates revealed a much lower feeding efficiency for this technique (0.43 ± 0.07 prey consumed/minute) compared to carousel feeding (1.08 ± 0.43 prey consumed/minute) (Table 4). However, the small sample size and large variability around our results precludes any robust conclusion. In addition, video footage of seiner feeding was always in low light levels. Our strict identification of feeding bouts during video may have led to an underestimate in feeding efficiency for seiner feeding whales, due to potential prey capture events being discounted. More notably, the profitability of each technique may greatly depend on the size of the catch, the number and predictability of fishing vessels and the number of killer whales feeding around the nets. Further logger deployments with inbuilt video are needed for kinematic

characterization of seiner feeding and further identification of seiner feeding over entire logger duration. This would allow investigation of differences in characteristics and relative prey acquisition rates for each feeding type, a full estimate of percentage time spent feeding over 24 hr and highlight any preference in feeding type that may be present.

4.3 | Prey acquisition rates and implications

The whales spent at least 37%–65% of their time feeding over 24 hr, which was higher than the estimated feeding duration needed to balance DPER for an average adult male in Vengsøy (26%–31%) and fell within the duration estimated for an adult male in Skjervøy (44%–53%). However, the prey consumption rate used to estimate time needed to balance DPER was based on carousel and seiner feeding, while actual time spent feeding considered carousel and deep diving behavior. Therefore, it is likely that there is large variability in prey acquisition rates for each behavior, which was not adequately accounted for.

Tagging locations were both part of the wintering grounds of the NSS herring at time of tagging (Vengsøy in 2016, Skjervøy in 2017) but held different year classes (ICES, 2018). Herring in the fjords of Vengsøy in November 2016 had an average mass of 358 g. The recruitment of the 2013 year class to the stock resulted in wintering areas shifting from Vengsøy to Skjervøy in November 2017, leading to the younger herring found nearshore whereas the older portion of the stock wintered offshore (ICES, 2018). Despite a requirement to capture nearly twice as many fish to balance DPER (see Results), in Skjervøy some killer whales remained in the fjords and targeted the younger herring instead of the older herring offshore, possibly owing to benefits from using the shallow bottom topography for hunting wintering herring (Nøttestad, 2002). This highlights how prey fluctuations (distribution and stock composition) may affect killer whales' energetics. In this respect, and because whale watching and swim-with activities take place all winter in these fjords (International Whaling Commission, 2020), our findings call for further research on how human activities may impact killer whales' behavior. If vessel disturbance led to displacement from feeding spots, foraging efficiency could be compromised and energetic costs to killer whales could be important (Williams et al., 2006).

By quantifying feeding activity and estimating prey profitability, this study begins to highlight the flexible use of carousel, seiner, and deep dive feeding behaviors among killer whales at herring wintering grounds in Norway. Such data allow us to establish a baseline for understanding feeding behavior and feeding success for the various techniques over time. This can be used to investigate the impact of environmental and anthropogenic stressors or changes in the future.

ACKNOWLEDGMENTS

Tagging was conducted as part of the making of the BBC television series *Blue Planet II* and under permit FOTS ID 10176 granted by Mattilsynet to Norwegian Orca Survey. Fieldwork was supported by grants from the Sea World and Busch Gardens Conservation fund and Sea World and Parks Entertainment. E.J. and R.K. were contracted by BBC to deploy data loggers on killer whales. Data loggers with 4K video were designed by Customized Animal Tracking Solutions (CATS, Oberstdorf, Germany) for the BBC. The CATS team was very generous with their time to assist with technical help on the tagging project. Additional kinematic analyses were completed with help from Arianna Torello, University of California, Santa Cruz, CA.

AUTHOR CONTRIBUTIONS

Aimee Matika: Conceptualization; formal analysis; investigation; methodology; visualization; writing – original draft. **Eve Jourdain:** Conceptualization; data curation; funding acquisition; investigation; project administration; resources; supervision; writing – original draft. **Dave Cade:** Conceptualization; formal analysis; investigation; methodology; resources; software; validation; visualization; writing – review and editing. **Richard Karoliussen:** Conceptualization; data curation; funding acquisition; investigation; resources; writing – review and editing. **Philip Hammond:**

Conceptualization; formal analysis; investigation; methodology; project administration; supervision; validation; writing – review and editing.

ORCID

Eve Jourdain  <https://orcid.org/0000-0003-2619-7799>

David E. Cade  <https://orcid.org/0000-0003-3641-1242>

REFERENCES

- Bachiller, E., Kjell, R. U., Teunis, J., & Geir, H. (2018). Bioenergetics modeling of the annual consumption of zooplankton by pelagic fish feeding in the northeast Atlantic. *PLoS ONE*, 13(1), 1–29. <https://doi.org/10.1371/journal.pone.0190345>
- Bigg, M. (1982). An assessment of killer whale (*Orcinus orca*) stocks off Vancouver Island, British Columbia. *Reports of the International Whaling Commission*, 32, 655–666.
- Bigg, M., & Wolman, A. (1975). Live-capture killer whale (*Orcinus orca*) fishery, British Columbia and Washington, 1962–73. *Journal of the Fisheries Research Board of Canada*, 32(7), 1213–1221. <https://doi.org/10.1139/f75-140>
- Bogstad, B., Kjellrun, H. H., & Øyvind, U. (1997). MULTISPEC - a multi-species model for fish and marine mammals in the Barents Sea. *Journal of Northwest Atlantic Fishery Science*, 22, 317–341. <http://doi.org/10.2960/J.v22.a23>
- Cade, D. E., Barr, K. R., Calambokidis, J., Friedlaender, A. S., & Goldbogen, J. A. (2018). Determining forward speed from accelerometer jiggle in aquatic environments. *Journal of Experimental Biology*, 221(2), jeb170449. <https://doi.org/10.1242/jeb.170449>
- Cade, D. E., Friedlaender, A. S., Calambokidis, J., & Goldbogen, J. A. (2016). Kinematic diversity in orca whale feeding mechanisms. *Current Biology*, 26(19), 2617–2624. <https://doi.org/10.1016/j.cub.2016.07.037>
- Cade, D. E., Gough, W. T., Czapskiy, M. F., Fahlbusch, J. A., Kahane-Rapport, S. R., Linsky, J. M. J., Nichols, R. C., Oestreich, W. K., Wisniewska, D. M., Friedlaender, A. S., & Goldbogen, J. A. (2021). Tools for integrating inertial sensor data with video bio-loggers, including estimation of animal orientation, motion, and position. *Animal Biotelemetry*, 9(1), 34. <https://doi.org/10.1186/s40317-021-00256-w>
- Christensen, I. (1982). Killer whales in Norwegian coastal waters. *Reports of the International Whaling Commission*, 32, 633–641.
- Christensen, I. (1984). Growth and reproduction of killer whales, *Orcinus orca*, in Norwegian coastal waters. *Reports of the International Whaling Commission, Special Issue 6*, 253–258.
- Domenici, P., Batty, R. S., Similä, T., & Ogam, E. (2000). Killer whales (*Orcinus orca*) feeding on schooling herring (*Clupea harengus*) using underwater tail-slaps: kinematic analyses of field observations. *Journal of Experimental Biology*, 203(2), 283–294. <https://doi.org/10.1242/jeb.203.2.283>
- Esteban, R., Verborgh, P., Gauffier, G., Giménez, J., Guinet, C., & Stephanis, R. (2016.) Dynamics of killer whale, bluefin tuna and human fisheries in the Strait of Gibraltar. *Biological Conservation*, 194, 31–38. <https://doi.org/10.1016/j.biocon.2015.11.031>
- Estes, J. A., Heithaus, M., McCauley, D. J., Rasher, D. B., & Worm, B. (2016). Megafaunal impacts on structure and function of ocean ecosystems. *Annual Review of Environment and Resources*, 41(1), 83–116. <https://doi.org/10.1146/annurev-environ-110615-085622>
- Ford, J. K. B. (1989). Acoustic behaviour of resident killer whales (*Orcinus orca*) off Vancouver Island, British Columbia. *Canadian Journal of Zoology*, 67(3), 727–745. <https://doi.org/10.1139/z89-105>
- Ford, J. K. B. (2018). Killer whale *Orcinus orca*. In B. Würsig, J. G. M. Thewissen, & K. M. Kovacs (Eds.). *Encyclopedia of marine mammals* (3rd ed., pp. 650–656). Academic Press.
- Friard, O., & Gamba, M. (2016). BORIS: A free, versatile open-source event-logging software for video/audio coding and live observations. *Methods in Ecology and Evolution*, 7(11), 1325–1330. <https://doi.org/10.1111/2041-210X.12584>
- Garrison, D. (2021). *Sunrise/Sunset* [Computer software]. MATLAB Central File Exchange. <https://www.mathworks.com/matlabcentral/fileexchange/55509-sunrise-sunset>
- Goldbogen, J. A., Cade, D. E., Boersma, A. T., Calambokidis, J., Kahane-Rapport, S. R., Segre, P. S., Stimpert, A. K., & Friedlaender, A. S. (2017). Using digital tags with integrated video and inertial sensors to study moving morphology and associated function in large aquatic vertebrates. *Anatomical Record*, 300(11), 1935–1941. <https://doi.org/10.1002/ar.23650>
- Goldbogen, J. A., Calambokidis, J., Shadwick, R. E., Oleson, E. M., McDonald, M. A., & Hildebrand, J. A. (2006). Kinematics of foraging dives and lunge-feeding in fin whales. *Journal of Experimental Biology*, 209(7), 1231–1244. <https://doi.org/10.1242/jeb.02135>
- ICES. (2018). *Report of the Working Group on Widely Distributed Stocks (WGWIDE)*, 28 August–3 September 2018. International Whaling Commission. (2020). Norway. <https://www.handbook.iwc.int/en/country-profiles/norway>

- Jourdain, E., Goh, T., Kuningas, S., Similä, T., Vongraven, R., Karoliussen, D., Bisther, A., & Hammond, P. (2021). Killer whale (*Orcinus orca*) population dynamics in response to a period of rapid ecosystem change in the eastern North Atlantic. *Ecology and Evolution*, 11, 17289–17306. <https://doi.org/10.1002/ece3.8364>
- Jourdain, E., & Karoliussen, R. (2021). Photo-identification catalogue of Norwegian killer whales 2007–2021 [Data set]. *Figshare*. <https://doi.org/10.6084/m9.figshare.4205226.v4>
- Kleiber, M. (1975). *The fire of life: An introduction to animal energetics*. Robert E. Kreiger Publishing.
- Kuningas, S., Similä, T., & Hammond, P. S. (2014). population size, survival and reproductive rates of northern Norwegian killer whales (*Orcinus orca*) in 1986–2003. *Journal of the Marine Biological Association of the United Kingdom*, 94(6), 1277–1291. <https://doi.org/10.1017/S0025315413000933>
- MathWorks. (2014). MATLAB V2014a. [Computer software]. <https://www.mathworks.com/products/matlab.html>
- Mul, E., Blanchet, M. A., McClintock, T., Grecian, J. W., Biuw, M., & Rikardsen, A. (2020). Killer whales are attracted to herring fishing vessels. *Marine Ecology Progress Series*, 652, 1–13. <https://doi.org/10.3354/meps13481>
- Noren, D. P. (2011). Estimated field metabolic rates and prey requirements of resident killer whales. *Marine Mammal Science*, 27(1), 60–77. <https://doi.org/10.1111/j.1748-7692.2010.00386.x>
- Noren, D. P., Holt, M. M., Dunkin, R. C., Thometz, N. M., & Williams, T. M. (2016). Comparative and cumulative energetic costs of odontocete responses to anthropogenic disturbance. *Proceedings of Meetings on Acoustics*, 27(1), 040011. <https://doi.org/10.1121/2.0000357>
- Noren, D. P., Johnson, A. H., Rehder, D., & Larson, A. (2009). Close approaches by vessels elicit surface active behaviors by Southern Resident killer whales. *Endangered Species Research*, 8(3), 179–192. <https://doi.org/10.3354/esr00205>
- Nøttestad, L. (2002). Killer whales (*Orcinus orca* L.) and saithe (*Pollachius virens* L.) trap herring (*Clupea harengus* L.) in shallow water by taking advantage of steep bottom topography. *ICES Theme Session N: 20 Environmental Influences on Trophic Interactions*, 1–11.
- Nøttestad, L., Fern, A., Axelsen, B. (2002). Digging in the deep: killer whales' advanced hunting tactic. *Polar Biology*, 25(12), 939–941. <https://doi.org/10.1007/s00300-002-0437-0>
- Pauly, D., Trites, A. W., Capuli, E., & Christensen, V. (1998). Diet composition and trophic levels of marine mammals. *ICES Journal of Marine Science*, 55(3), 467–481. <https://doi.org/10.1006/jmsc.1997.0280>
- R Core Team. (2018). *R: A language and environment for statistical computing* [Computer software]. R Foundation for Statistical Computing.
- Røttingen, I., Foote, K. G., Huse, I., & Ona, E. (1994). Acoustic abundance estimation of wintering Norwegian spring spawning herring, with emphasis on methodological aspects. *International Council for the Exploration of the Sea*, CM1994/(B+D+G+H): 1, 1–17.
- Samarra, F. I. P., & Miller, P. J. O. (2015). Prey-induced behavioural plasticity of herring-eating killer whales. *Marine Biology*, 162(4), 809–821. <https://doi.org/10.1007/s00227-015-2626-8>
- Similä, T. (1997). Sonar observations of killer whales (*Orcinus orca*) feeding on herring schools. *Aquatic Mammals*, 23(3), 119–126.
- Similä, T. (2005). Interactions between herring fishery and killer whales in northern Norway. *International Council for the Exploration of the Sea*, CM 2005/R: 03, 3–6.
- Similä, T., Holst, J. C., & Christensen, I. (1996). Occurrence and Diet of killer whales in northern Norway: seasonal patterns relative to the distribution and abundance of Norwegian spring-spawning herring. *Canadian Journal of Fisheries and Aquatic Sciences*, 53(4), 769–779. <https://doi.org/10.1139/f95-253>
- Similä, T., & Ugarte, F. (1993). Surface and underwater observations of cooperatively feeding killer whales in northern Norway. *Canadian Journal of Zoology*, 71(8), 1494–1499. <https://doi.org/10.1139/z93-210>
- Simon, M., Wahlberg, M., Ugarte, F., & Miller, L. A. (2005). Acoustic characteristics of underwater tail slaps used by Norwegian and Icelandic killer whales (*Orcinus orca*) to debilitate herring (*Clupea harengus*). *Journal of Experimental Biology*, 208(12), 2459–2466. <https://doi.org/10.1242/jeb.01619>
- Slotte, A. (1999). Differential utilization of energy during wintering and spawning migration in Norwegian spring-spawning herring. *Journal of Fish Biology*, 54, 338–355. <https://doi.org/10.1111/j.1095-8649.1999.tb00834.x>
- Springer, A. M., Estes, J. A., Van Vliet, G. B., Williams, T. M., Doak, D. F., Danner, E. M., Forney, K. A., & Pfister, B. (2003). Sequential megafaunal collapse in the North Pacific Ocean: An ongoing legacy of industrial whaling? *Proceedings of the National Academy of Sciences of the United States of America*, 100(21), 12223–12228. <https://doi.org/10.1073/pnas.1635156100>
- Tennessen, J. B., Holt, M. M., Hanson, M. B., Emmons, C. K., Giles, D. A., & Hogan, J. T. (2019). Kinematic signatures of prey capture from archival tags reveal sex differences in killer whale foraging activity. *Journal of Experimental Biology*, 222(3), jeb191874. <https://doi.org/10.1242/jeb.191874>
- Tixier, P., Authier, M., Gasco, N., & Guinet, C. (2015). Influence of artificial food provisioning from fisheries on killer whale reproductive output. *Animal Conservation*, 18(2), 207–218. <https://doi.org/10.1111/acv.12161>

- Tixier, P., Barbraud, C. Pardo, D., Gasco, N., Duhamel, G., & Guinet, C. (2017). Demographic consequences of fisheries interaction within a killer whale (*Orcinus orca*) population. *Marine Biology*, 164(8), 170. <https://doi.org/10.1007/s00227-017-3195-9>
- Van Opzeeland, I. C., Corkeron, P. J., Leyssen, T., Similä, T., & Van Parijs, S. M. (2005). Acoustic behaviour of Norwegian killer whales, *Orcinus orca*, during carousel and seiner foraging on spring-spawning herring. *Aquatic Mammals*, 31(1), 110–119. <https://doi.org/10.1578/AM.31.1.2005.110>
- Varpe, Ø., Fiksen, Ø., & Slotte, A. (2005). Meta-ecosystems and biological energy transport from ocean to coast: the ecological importance of herring migration. *Oecologia*, 146(3), 443–451. <https://doi.org/10.1007/s00442-005-0219-9>
- Ware, C., Arsenault, R., Plumlee, M., & Wiley, D., (2006). Visualizing the underwater behavior of humpback whales. *IEEE Computer Graphics and Applications*, 26(4), 14–18. <https://doi.org/10.1109/MCG.2006.93>
- Williams, R., Lusseau, D., & Hammond, P. S. (2006). Estimating relative energetic costs of human disturbance to killer whales (*Orcinus orca*). *Biological Conservation*, 133(3), 301–311. <https://doi.org/10.1016/j.biocon.2006.06.010>
- Williams, T. M., Estes, J. A., Doak, D. F., & Springer, A. M. (2004). Killer appetites: assessing the role of predators in ecological communities. *Ecological Society of America*, 85(12), 3373–3384. <https://doi.org/10.1890/03-0696>
- Wright, B. M., Ford, J. K. B., Ellis, G. M., Deecke, V. B., Shapiro, A. D., Battaile, B. C., & Trites, A. W. (2017). Fine-scale foraging movements by fish-eating killer whales (*Orcinus orca*) relate to the vertical distributions and escape responses of salmonid prey (*Oncorhynchus* spp.). *Movement Ecology*, 5, 3. <https://doi.org/10.1186/s40462-017-0094-0>

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

How to cite this article: Matika, A. F., Jourdain, E., Cade, D. E., Karoliussen, R., & Hammond, P. S. (2022). Feeding characteristics and prey profitability in five herring-feeding killer whales (*Orcinus orca*) in northern Norway. *Marine Mammal Science*, 1–16. <https://doi.org/10.1111/mms.12931>