

## SHORT COMMUNICATION

# Almost like a whale – first evidence of suction feeding in a seabird

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## ABSTRACT

Little auks (*Alle alle*) are one of the most numerous seabird species in the world and feed primarily on copepods in arctic waters. Their high daily energy requirements leave them vulnerable to current changes in the arctic plankton community, where a smaller, less-profitable copepod species (*Calanus finmarchicus*) becomes increasingly abundant. Little auks have been estimated to require ~60,000 copepods per day, necessitating prey capture rates of ~6 copepods per second underwater. To achieve such performance, it has been suggested that little auks capture their prey by (non-visual) filter feeding. We tested this hypothesis by exposing little auks to varying copepod densities within a shallow experimental pool and filming their prey capture behaviour. At none of the copepod densities tested did birds filter feed. Instead, all birds captured copepods by what we identified as visually guided suction feeding, achieved through an extension of their sub-lingual pouch. Suction feeding is very common in fish and marine mammals, but to the best of our knowledge, this is the first time that it has been specifically identified in a seabird species. While presumably less efficient than filter feeding, this behaviour may allow little auks to foster higher resilience when facing the consequences of arctic climate change.

**KEY WORDS:** Foraging, Little auks, Copepods, Diving, Climate change, Feeding mechanism

## INTRODUCTION

Trophic flow and food web architecture are conditioned by prey capture techniques (Garvey and Whiles, 2016). In the marine environment, many predators use raptorial feeding, seizing prey items individually, yet the largest of all marine predators, e.g. sharks and whales, evolved a filter-feeding apparatus, allowing them to catch high numbers of plankton organisms simultaneously (Werth, 2006). Seabirds are mainly piscivorous (Shealer, 2002) and the minority of species that feed on plankton seldom show filter-feeding capabilities. Based on studies concerning bill morphology, head hydrodynamics and diet composition, filter feeding has been suggested for a number of prion species (*Pachyptila*) and short-tailed shearwaters (*Puffinus tenuirostris*) (Prince, 1980; Morgan and Ritz, 1982; Klages and Cooper, 1992; see also Lovvorn et al., 2001). Broad-billed prions

(*Pachyptila vittata*) have been observed to filter feed at the surface (Harper, 1987) but direct observations of underwater foraging are lacking. Other planktivorous seabird species (e.g. alcids) are assumed to use raptorial feeding (Lovvorn, 2010), which is puzzling considering the very high numbers of zooplankton that they are supposed to ingest. Notably, Harding et al. (2009) estimated that the little auk, *Alle alle* (Linnaeus 1758), a 150 g diving seabird of the North Atlantic, should ingest 59,800 copepods per day to cover its energy requirements, thereby catching 6 prey items per second underwater. Further, the little auk, one of the most numerous seabirds in the world (60–80 million individuals) and a climate change sentinel in the Arctic, is expected to respond to ocean warming by feeding on even smaller prey items and further increasing its capture rates (Grémillet et al., 2012; Descamps et al., 2017; Weydmann et al., 2018). As it seemed improbable that little auks achieve such predatory performance by raptorial feeding, we hypothesized that they are capable of filter feeding. This species has never been observed feeding in the wild, and we therefore tested the prediction of filter feeding in an experimental setup.

## MATERIALS AND METHODS

Experiments were conducted at the Ny-Ålesund research station in Svalbard (78°55'25"N, 11°54'37"E). In July 2014, a self-standing Intex pool (5.5×2.7 m, 1.2 m deep; Intex Development Company, Wan Chai, Hong Kong), enclosed within a metal frame and fine mesh netting, was set up for experimentation. The pool was continuously supplied with seawater from the adjacent Kongsfjorden and drained through a surface-skimming system that maintained good water quality. An underwater video array allowed the observation of birds without human presence. It consisted of four black and white (b/w) video cameras (Lorex, Markham, ON, Canada) connected to a monitor for live view and a DVR (Bascom, Paris, France) for recording, which was supplemented with two GoPro cameras [Hero 3, set to a resolution of 1280×960 pixels (960p), a recording rate of 100 frames s<sup>-1</sup>, and an ultra-wide field of view; GoPro, San Mateo, CA, USA] that provided high-density and fast-speed video footage. Zooplankton (predominately *Calanus glacialis* and *Calanus finmarchicus*) was caught on several occasions from a vessel within Kongsfjorden using a WP3 net (mesh size: 1000 µm). Plankton was maintained in 40 l buckets filled with fresh seawater (continuously aerated) inside a temperature-controlled (5°C) dark room, until used in the trials. Live copepods were added to the pool ~8 h before a trial. Their numbers were estimated by counting all copepods within subsamples (~350 ml, three replicates) from each storage bucket and extrapolating mean values to the bucket volume. Copepod density in the pool was then estimated by dividing the number of added copepods by the water volume. Copepod loss through the drainage system and mortality in the pool before a trial were considered to be low. Little auks were caught at a nearby colony (Feiringfjellet) using noose traps, transported by boat to Ny-Ålesund, weighed and banded upon arrival, and allowed to rest overnight. The following morning, birds were released into the pool and all activity was filmed continuously with the b/w cameras. At first, birds typically preened

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and explored the pool by swimming and flying, before spontaneously starting to dive and forage. At this point, the GoPro cameras were triggered and submerged at opposing ends of the pool, without disturbing the birds. Filming with the GoPro cameras was restricted to ~2.5 h, after which a trial was stopped, the birds caught and released immediately from shore. The average time between capture in the colony and release from shore was 32 h (range: 20.5–47.5 h). All birds tolerated temporary captivity extremely well, appeared to be in good health when released and ~40% of them were re-sighted during later colony visits.

We conducted a total of seven trials with 17 birds (typically, two birds per trial) that were exposed to copepod densities ranging between 450 and 8300 copepods  $m^{-3}$  (density differed for each trial). The dive and foraging behaviour of 10 birds was included in our analysis (three birds did not forage during a trial, while insufficient marking prevented consistent identification of the others). First, for our dive behaviour analysis (Table 1), we extracted start and end times of all dives conducted during a trial to the nearest second from the b/w footage. Unlike the GoPro cameras, the b/w cameras provided a continuous view of all individuals during a trial. We calculated dive duration and subsequent surface duration between dives, as well as the resulting dive:pause ratio (dive duration/surface duration; Table 1). We used a bout-ending criterion of 30 s to distinguish individual dive bouts, based on a log-survivorship plot of surface durations (Slater and Lester, 1982). Accordingly, surface intervals exceeding 30 s were removed from the calculation of mean surface interval duration. Second, for our foraging behaviour analysis (Table 2), the GoPro footage (100 frames  $s^{-1}$ ) was viewed in GoPro Studio (GoPro) and selected foraging sequences were analysed on a frame-by-frame basis. We randomly selected 10 dives per bird from the first hour of a ~2.5 h foraging trial and extracted the time interval between successive capture events ('capture interval') as an index of prey capture rate (Table 2). Given the small size of copepods, their translucent appearance and film speed limitations, actual copepod ingestion was not always obvious. However, the distinct attack pattern used by little auks (see below), especially head striking and gular depression, allowed a clear identification of prey capture events. Occasionally, a bird disappeared from the GoPro camera

**Table 1. Summary of all displayed dive behaviour during foraging trials**

Bird	$M_b$ (g)	No. of dives	Dive duration (s)	Surface duration (s)	Dive: pause ratio
YMRG	150	230	9.8±0.2 (20)	4.5±0.3	3.5±0.2
YMRY	130	171	14.7±0.3 (24)	6.2±0.4	3.8±0.2
YMYO	142	194	14.6±0.5 (29)	8.3±0.4	2.5±0.1
YWYM	162	30	18.0±0.7 (26)	11.7±1.8	2.4±0.4
YMRO	142	268	13.3±0.3 (25)	5.8±0.2	2.8±0.1
YMYB	152	326	9.2±0.3 (24)	2.2±0.1	5.9±0.2
YMRB	151	380	7.3±0.1 (17)	3.4±0.2	3.7±0.1
LMYN	162	150	12.7±0.4 (24)	6.3±0.5	3.8±0.3
LMNO	144	154	11.0±0.4 (25)	5.0±0.4	3.5±0.2
LMNY	144	291	11.5±0.2 (21)	3.0±0.2	5.6±0.2
Grand mean	147.9±3.1	219.4±32.1	12.2±1.0	5.6±0.9	3.8±0.4

Body mass ( $M_b$ ), total number of dives conducted during a trial, dive duration (maximum value in parentheses), the duration of the subsequent surface interval and the resulting dive:pause ratio (dive duration/surface duration) for 10 birds are presented. Dive behaviour analysis was conducted using the black and white (b/w) footage. Surface durations exceeding 30 s were removed (bout-ending criterion) when calculating mean surface durations for individual birds. Values are means±s.e.m. for individual birds. The grand mean±s.e.m. was established from individual bird means.

**Table 2. Summary of observed prey capture behaviour**

Bird	Dive duration (s)	Capture interval (s)	Capture rate (copepods $s^{-1}$ )	No. of captures observed ( $N$ )
YMRG	9.6±1.1	0.69±0.05	1.51±0.09	95
YMRY	17.3±1.0	0.78±0.05	1.33±0.08	122
YMYO	16.1±1.0	0.86±0.08	1.26±0.12	94
YWYM	21.4±1.2	1.03±0.09	1.03±0.08	120
YMRO	11.3±1.2	0.60±0.03	1.70±0.09	84
YMYB	12.8±0.9	0.71±0.06	1.49±0.11	89
YMRB	9.2±0.9	0.60±0.07	1.85±0.18	76
LMYN	14.9±0.6	0.89±0.06	1.17±0.07	143
LMNO	11.0±0.9	1.00±0.09	1.07±0.09	82
LMNY	13.8±1.2	0.98±0.06	1.06±0.07	92
Grand mean	13.7±1.2	0.81±0.05	1.35±0.09	99.7±6.8

Dive duration of analysed dives (10 per bird) was determined from the b/w footage, which provided a continuous view on all individuals during a trial. Capture interval is the measured time interval between successive capture events during a dive and serves as an index of prey capture rate (calculated as 1/capture interval). The number of captures observed does not necessarily represent the sum of all prey captures that occurred during the 10 analysed foraging dives, as sequences during a dive when a bird was not clearly visible in the GoPro footage were excluded from the foraging behaviour analysis. Values are means±s.e.m. for individual birds based on 10 foraging dives per bird, selected from the first hour of a ~2.5 h foraging trial. The grand mean±s.e.m. was established from individual bird means.

view during a foraging dive. These periods, during which prey captures might have occurred, were excluded from the analysis. Hence, we only included sequences, when a bird was clearly visible in the footage of at least one GoPro camera and when successive capture events could be identified. Accordingly, reported prey capture rates (Table 2) exclude periods before the first detected capture (i.e. descent), after the last (i.e. ascent), and when a bird disappeared from view. For filter feeding to occur, we expected birds to swim through copepod concentrations while alternately opening and closing their beak to take in prey-laden water (Morgan and Ritz, 1982). Furthermore, when filter feeding, birds will not visually detect, pursue and attack individual prey items but will indiscriminately take in a gulp of water from which prey items are strained. All values below are presented as means±s.e.m.

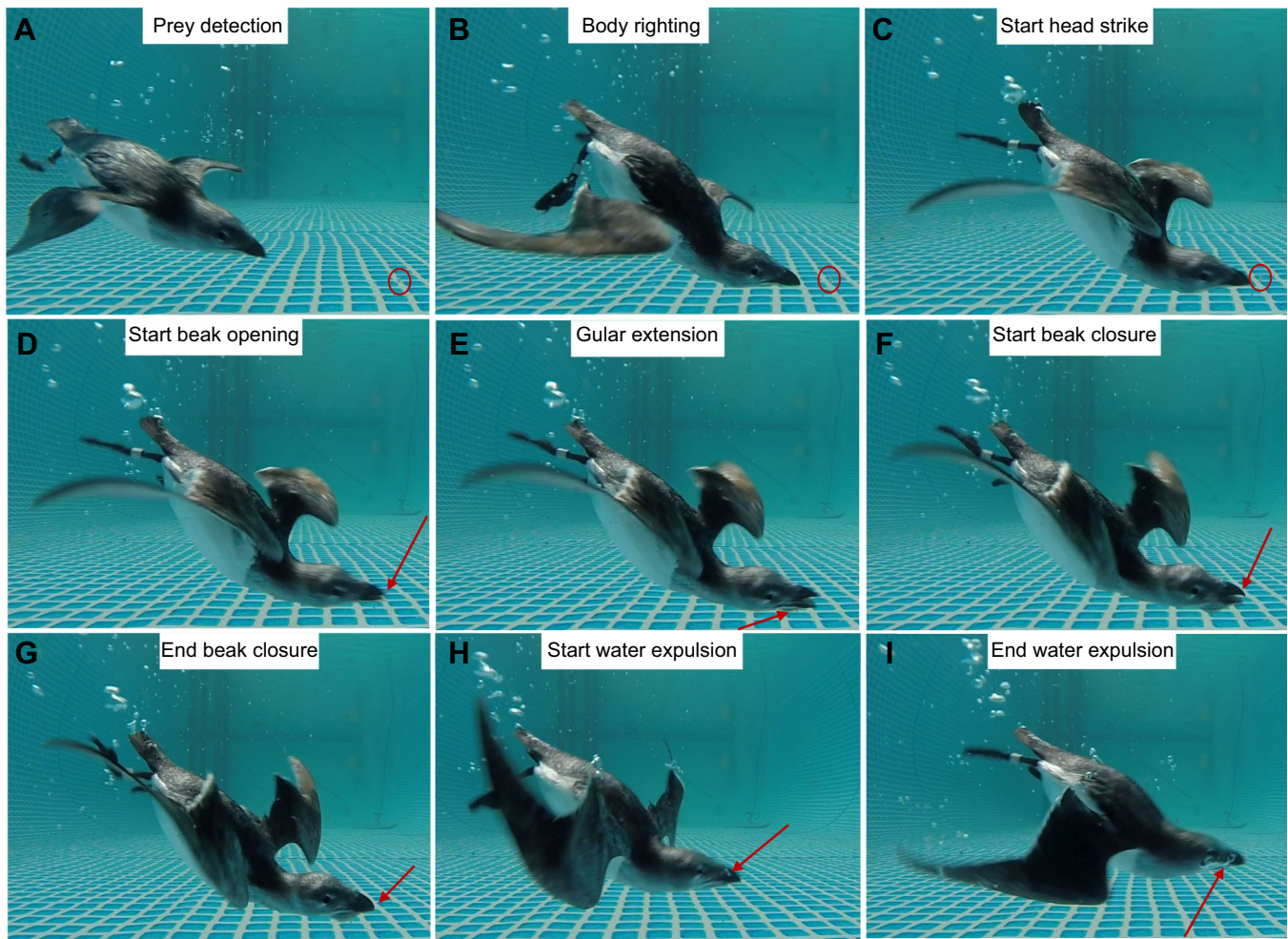
All field procedures were approved by the Norwegian Animal Research Authority (ref. no. 2013/63807-2) and the Governor of Svalbard (ref. no. 2014/00482-4, a.512).

## RESULTS AND DISCUSSION

During a trial, birds were highly motivated and conducted an average of 219.4±32.1 dives (range: 30–380 dives), lasting on average 12.0±1.0 s (maximum 29 s; Table 1). The time spent at the surface between dives was on average 5.6±0.9 s but at times considerably shorter (~1–2 s), resulting in a high dive:pause ratio (3.8±0.4; Table 1). Foraging occurred throughout the water column in distinct bouts that lasted up to ~1.5 h, after which birds preened and floated on the water or rested on the pool rim.

Our foraging behaviour analysis showed that birds did not filter feed, even at the highest copepod density provided (0% of 997 observations from 10 birds; Table 2). By contrast, birds caught prey by what we identified as visually guided suction feeding. Birds visually detected and approached copepods individually and upon attack, when they extended their neck, the small beak opening and gular suppression probably created a suction flow, which drove individual prey items into their oral cavity. While prey items were retained within the oral cavity or the gular pouch, excess water was expelled through the nostrils or from the back of their bill. A typical





**Fig. 1. Typical prey capture sequence of a little auk, catching a copepod.** The sequence is characterized by five distinct phases: (1) prey detection and preparation for capture (A,B); (2) head strike and beak opening (C,D); (3) gular depression, when the sub-lingual pouch is extended and prey is taken in (E); (4) beak closure, while the pouch is still extended (F,G); and (5) water expulsion through the nostrils (H,I). The entire sequence occurred within 420 ms, while phases 2–4 (C–G) occurred within 50 ms. The red circle in A–C shows the position of the copepod.

prey capture sequence is illustrated in Fig. 1 (see also Movie 1) and was characterized by five distinct phases: (1) prey detection and preparation for capture (body righting); (2) neck extension and beak opening; (3) gular depression (extension of sub-lingual pouch) and prey capture; (4) beak closure; and (5) water expulsion through the nostrils/from the back of the bill, after which the bird searched for new prey. Typically, phases 2–4 of a prey capture sequence occurred within 40–80 ms (mean:  $64.0 \pm 6.3$  ms), while the duration of phases 1 and 5 varied (mean:  $151.9 \pm 11.7$  ms and  $210.6 \pm 7.3$  ms, respectively). For example, the entire prey capture sequence shown in Fig. 1(A–I) occurred within 420 ms (mean time for all capture events:  $426.5 \pm 13.6$  ms). When prey capture occurred in very quick succession, water expulsion did not necessarily occur after each capture but after 2–3 events.

This capture behaviour was observed in all birds and across all copepod densities (100% of the 997 observed feeding events; Table 2). However, as birds moved rapidly throughout the water column, feeding behaviour differed from that of a stationary ('sit and wait') predator, where the creation of a strong water current is the only means of capturing prey. Instead, prey capture in little auks was dynamic so that head striking – reducing the distance between the beak of the bird and the copepod to a few centimetres (~1–5 cm) – and the presumed creation of a suction flow (based on the observed

gular pouch extension) were both elements of a capture event. The combination of these elements might be important in facilitating copepod intake, as copepods are capable of fast escape responses. Upon detection of hydrodynamic disturbances created by an approaching predator, they are able to accelerate rapidly to great velocities that might propel them out of danger (Kjørboe et al., 2010; Svetlichny et al., 2018). Escape responses of copepods and subsequent failure of capture were observed occasionally during video analysis.

During foraging, little auks captured copepods in quick succession. The time between successive prey captures, mostly representing search time, averaged  $0.81 \pm 0.05$  s (minimum and maximum time between two events: ~0.20 and 6.0 s, respectively), resulting in a capture rate of  $1.35 \pm 0.09$  copepods per second (Table 2). This, of course, only considers the active foraging time underwater and neglects transit times (descent/ascent), which were short in our shallow pool but might be considerably longer in the wild. At times, little auks engaged in up to three independent capture events per second during trials. Despite this, birds foraging within our shallow pool never achieved estimated prey capture rates of ~6 copepods per second underwater (Harding et al., 2009). This 'failure' during our trials might be explained by (1) an overestimation of required prey capture rates by Harding et al. (2009) and/or (2) birds

deploying a filter-feeding mechanism when foraging in the wild, despite its absence during our trials (see below). Harding et al. (2009) provided a first estimate of food requirements and associated prey capture rates for chick-rearing little auks. This estimate was based on the energy expenditure of adult birds (doubly labelled water study), chick diet composition and the dive behaviour of four adults (over 1–2 days). Each of these components for the overall capture rate estimate is potentially associated with inaccuracies that might have affected the overall estimate. The most critical points that might have caused an overestimation of prey capture rate are (1) the relatively short time birds spent foraging in the study (~2.7 h underwater per day), (2) the assumption that adult birds themselves feed on the same prey as that delivered to the chicks, and (3) the assumed energy density of prey species (taken from the literature), which differs considerably between developmental stages and throughout the seasons. The estimated required daily copepod intake of ~60,000 individuals exceeds the content of 35 full gular pouches delivered to chicks (table 2 in Harding et al., 2009), illustrating the scope of the estimate, and the authors themselves were aware that their estimate might be ‘artificially inflated’.

Under the experimental conditions investigated, we found no evidence for filter feeding in little auks. Rather, all birds displayed visually guided suction feeding across the range of zooplankton densities to which they were exposed ( $n=997$  observations from  $N=10$  birds; Table 2). Suction feeding is very common in fish and marine mammals (Muller and Osse, 1984; Werth, 2000; Wainwright et al., 2007) but, to the best of our knowledge, this is the first time that it has been specifically identified in a seabird species.

Captive little auks dived voluntarily and extensively, yet their dive depths and durations were lower than in the wild, where birds reach 10 m on average, thereby staying 52 s underwater (Harding et al., 2009). However, as birds demonstrated suction feeding in all cases in our experimental setup, we find no reason why they should not also do so at sea. Copepod densities in our pool corresponded well with densities reported in the literature for little auk foraging areas in Svalbard (from a few individuals up to ~6000 individuals  $m^{-3}$  for the relevant size classes; Kwasniewski et al., 2010; Trudnowska et al., 2012, 2016). However, as plankton densities are typically averaged over the entire water column or big parts thereof, information concerning the fine-scale spatial distribution within the water column is rare. Copepods might be concentrated by distinctive oceanographic features at a specific depth and, hence, occur at much greater densities than was possible to achieve within our experimental pool. Consequently, we cannot exclude the possibility that individual spacing of copepods in our pool might have been below a potential threshold that triggers a switch to filter feeding. Hence, while we did not observe filter feeding in our experimental setup, this does not prove the absence of such a feeding mechanism in the wild. However, the lack of specific morphological adaptations for filter feeding (see below) does not lend support to its suggested presence.

Moreover, light conditions in our shallow pool might have differed from conditions at sea. In our pool, birds were able to visually detect single copepods, while light attenuation with increasing depth might make visual detection at sea challenging. However, most dives of little auks at sea are relatively shallow (Harding et al., 2009), probably allowing visual detection. Furthermore, in a study modelling the foraging profitability of auklets (Cassin’s auklets, *Ptychoramphus aleuticus*, and least auklets, *Aethia pusilla*) in pelagic prey patches, Lovvorn (2010) found that changes in light condition over a depth range of 20 m had

little effect on intake rates of zooplankton prey, as intake rates were limited by capture time (pursuit and handling after detection) and not by prey visibility.

Filter-feeding broad-billed prions show specific morphological adaptations in the form of palatal lamellae: comb-like structures along the edges of the beak (Klages and Cooper, 1992). Such structures do not occur in little auks but this species has an extensible sub-lingual gular pouch, allowing it to suck prey-laden water into its oral cavity. Water is probably subsequently pressed out by their fleshy tongue, while prey is kept within the gular pouch. Harding et al. (2009) reported up to ~4300 prey items in gular pouches of little auks (95% of which were *Calanus* copepods), illustrating the volume of the gular pouch and its potential for creating strong suction.

In planktivorous alcids, the seabird family to which little auks belong, prey transportation to the nest in an extensible gular pouch is common. We therefore anticipate that suction feeding may occur across this group. Our findings have strong implications for the trophic ecology of little auks in a warming Arctic: unlike filter feeding, raptorial feeding requires individual prey captures. Suction feeding, however, may allow multiple prey intakes during one strike, thereby enhancing foraging profitably, when compared with raptorial feeding. While presumably less efficient than filter feeding, this mechanism may become crucial for birds facing smaller zooplankton prey as a consequence of climate change (Daufresne et al., 2009; Descamps et al., 2017; Weydmann et al., 2018). Therefore, little auks may show higher resilience than expected (Grémillet et al., 2012), contrary to simulations forecasting the decline of 40% of their breeding colonies as a consequence of global warming (Karnovsky et al., 2010).

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#### Competing interests

The authors declare no competing or financial interests.

#### Author contributions

Conceptualization: M.R.E., S.D., J.F., D.G.; Methodology: M.R.E., S.D., D.G.; Software: M.R.E.; Validation: M.R.E.; Formal analysis: M.R.E.; Investigation: M.R.E.; Resources: M.R.E., S.D.; Data curation: M.R.E.; Writing - original draft: M.R.E., D.G.; Writing - review & editing: M.R.E., S.D., J.F., D.G.; Visualization: M.R.E.; Supervision: S.D., D.G.; Project administration: S.D., D.G.; Funding acquisition: M.R.E., S.D., D.G.

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#### Supplementary information

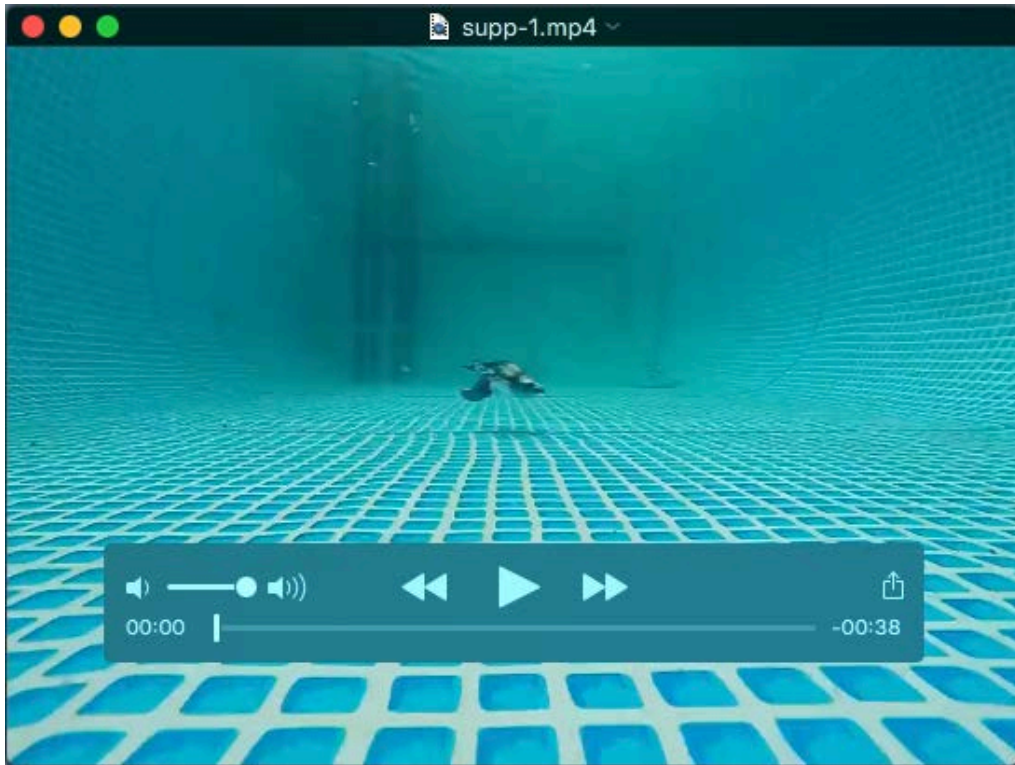
Supplementary information available online at <http://jeb.biologists.org/lookup/doi/10.1242/jeb.182170.supplemental>

#### References

- Daufresne, M., Lengfellner, K. and Sommer, U. (2009). Global warming benefits the small in aquatic ecosystems. *Proc. Natl. Acad. Sci. USA* **106**, 12788–12793.
- Descamps, S., Aars, J., Fuglei, E., Kovacs, K. M., Lydersen, C., Pavlova, O., Pedersen, Å. Ø., Ravolainen, V. and Strøm, H. (2017). Climate change impacts on wildlife in a High Arctic archipelago – Svalbard, Norway. *Glob. Change Biol.* **23**, 490–502.

- Garvey, J. E. and Whiles, M. (2016). *Trophic Ecology*. Boca Raton, FL, USA: CRC Press.
- Grémillet, D., Welcker, J., Karnovsky, N. J., Walkusz, W., Hall, M. E., Fort, J., Brown, Z. W., Speakman, J. R. and Harding, A. M. A. (2012). Little auks buffer the impact of current Arctic climate change. *Mar. Ecol. Prog. Ser.* **454**, 197-206.
- Harding, A. M. A., Egevang, C., Walkusz, W., Merkel, F., Blanc, S. and Grémillet, D. (2009). Estimating prey capture rates of a planktivorous seabird, the little auk (*Alle alle*), using diet, diving behaviour, and energy consumption. *Polar Biol.* **32**, 785-796.
- Harper, P. C. (1987). Feeding behaviour and other notes on 20 species of Procellariiformes at sea. *Notornis* **34**, 169-192.
- Karnovsky, N., Harding, A., Walkusz, W., Kwaśniewski, S., Goszczko, I., Wiktor, J., Jr, Routti, H., Bailey, A., McFadden, L., Brown, Z. et al. (2010). Foraging distributions of little auks *Alle alle* across the Greenland Sea: implications of present and future Arctic climate change. *Mar. Ecol. Prog. Ser.* **415**, 283-293.
- Kjørboe, T., Andersen, A., Langlois, V. J. and Jakobsen, H. H. (2010). Unsteady motion: escape jumps in planktonic copepods, their kinematics and energetics. *J. R. Soc. Interface* **7**, 1591-1602.
- Klages, N. T. W. and Cooper, J. (1992). Bill morphology and diet of a filter-feeding seabird: the broad-billed prion *Pachyptila vittata* at South Atlantic Gough Island. *J. Zool.* **227**, 385-396.
- Kwasniewski, S., Gluchowska, M., Jakubas, D., Wojczulanis-Jakubas, K., Walkusz, W., Karnovsky, N., Blachowiak-Samolyk, K., Cisek, M. and Stempniewicz, L. (2010). The impact of different hydrographic conditions and zooplankton communities on provisioning little auks along the west coast of Spitsbergen. *Prog. Oceanogr.* **87**, 72-82.
- Lovvorn, J. R. (2010). Modeling profitability for the smallest marine endotherms: auklets foraging within pelagic prey patches. *Aquat. Biol.* **8**, 203-219.
- Lovvorn, J. R., Baduini, C. L. and Hunt, G. L., Jr. (2001). Modeling underwater visual and filter feeding by planktivorous shearwaters in unusual sea conditions. *Ecology* **82**, 2342-2356.
- Morgan, W. L. and Ritz, D. A. (1982). Comparison of the feeding apparatus in the mutton-bird, *Puffinus tenuirostris* (Temminck) and the fairy prion, *Pachyptila turtur* (Kuhl) in relation to the capture of the krill, *Nyctiphanes australis* Sars. *J. Exp. Mar. Biol. Ecol.* **59**, 61-75.
- Muller, M. and Osse, J. W. M. (1984). Hydrodynamics of suction feeding in fish. *Trans. zool. Soc. Lond.* **37**, 51-135.
- Prince, P. A. (1980). The food and feeding ecology of Blue petrel (*Hulobaeno caerdea*) and Dove prion (*Pachyptila desolara*). *J. Zool. Lond.* **190**, 59-76.
- Shealer, D. A. (2002). Foraging behaviour and food of seabirds. In *Biology of Marine Birds* (ed. E.A. Schreiber and J. Burger), pp. 137-177. Boca Raton: CRC Press.
- Slater, P. J. B. and Lester, N. P. (1982). Minimising errors in splitting behaviour into bouts. *Behaviour* **79**, 153-161.
- Svetlichny, L., Larsen, P. S. and Kjørboe, T. (2018). Swim and fly: escape strategy in neustonic and planktonic copepods. *J. Exp. Biol.* **221**, jeb167262.
- Trudnowska, E., Szczucka, J., Hoppe, L., Boehnke, R., Hop, H. and Blachowiak-Samolyk, K. (2012). Multidimensional zooplankton observations on the northern West Spitsbergen Shelf. *J. Mar. Syst.* **98-99**, 18-25.
- Trudnowska, E., Gluchowska, M., Beszczynska-Möller, A., Blachowiak-Samolyk, K. and Kwasniewski, S. (2016). Plankton patchiness in the Polar Front region of the West-Spitsbergen Shelf. *Mar. Ecol. Prog. Ser.* **560**, 1-18.
- Wainwright, P., Carroll, A. M., Collar, D. C., Day, S. W., Higham, T. E. and Holzman, R. A. (2007). Suction feeding mechanics, performance, and diversity in fishes. *Integr. Comp. Biol.* **47**, 96-106.
- Werth, A. J. (2000). Feeding in marine mammals. In *Feeding: Form, Function, and Evolution in Tetrapod Vertebrates* (ed. K. Schwenk), pp. 487-526. San Diego, CA, USA: Academic Press.
- Werth, A. J. (2006). Odontocete suction feeding: experimental analysis of water flow and head shape. *J. Morphol.* **267**, 1415-1428.
- Weydmann, A., Walczowski, W., Carstensen, J. and Kwaśniewski, S. (2018). Warming of Subarctic waters accelerates development of a key marine zooplankton *Calanus finmarchicus*. *Glob. Change Biol.* **24**, 172-183.





Movie S1