Suction or filter feeder? Morphology supports a combined feeding mechanism in the Little Auk (*Alle alle*)

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English abstract:

Little Auks (*Alle alle*) are the most abundant seabird in the Arctic, with their largest colonies in north-west Greenland sustained by foraging nearly exclusively on plankton. Given their high metabolic demands, adults must capture an approximate 60,000 copepods per day, raising long-standing questions about how this can be achieved efficiently, and with this, questions about the anatomical basis of prey capture and retention. Filter feeding has been proposed, but peer-reviewed morphological evidence remains absent. Experimental studies instead point to suction feeding of individual prey items, not sufficient to achieve the required prey consumption rate. Local Inughuit ecological knowledge has described tooth-like structures within the Little Auk's mouth, which aid foraging, a detail rarely, and where so, ambiguously, described in the peer-reviewed literature. We inspected two Little Auks that were taken for Inughuit subsistence use near Savissivik, Thule district. We took the opportunity to report here the first photographic documentation of the oral cavity of Little Auk. Agreeing with Inughit knowledge, we found the upper palate densely covered with posteriorly directed, cornified denticles, while the tongue remained smooth and thick. These observations support a combined suction-and-retention feeding mechanism of likely more than singular prey items, which might be similarly effective as filter feeding. This paper also highlights the value of integrating local ecological knowledge to resolve unanswered questions in Arctic seabird biology.

Keywords: seabirds, palatal denticles, prey retention, oral morphology, Inughuit ecological knowledge

Main text

Little Auks (*Alle alle*, Fig. 1a), known as Dovekies in North America, are the species among the family *Alcidae* that is most abundant in the Arctic (Wojczulanis-Jakubas et al., 2022). They breed at high latitudes, between 68–80°N, typically in large colonies on coastal scree slopes. The largest colonies occur in north-west Greenland, where estimates suggest a breeding population of between 10–33 million pairs (Freuchen & Salomonsen, 1958; Anker-Nilssen et al., 2000; Kampp et al., 2000). In this region, as in Svalbard and the other islands of the Barents Sea, Little Auks are primarily planktivorous, feeding mainly on copepods, particularly *Calanus glacialis* and *C. hyperboreus*, as well as amphipods and other zooplankton (Anker-Nilssen et al., 2000; Harding et al., 2009).

The exceptional abundance of Little Auks in north-west Greenland is thought to depend on the high productivity of the North Water Polynya, a recurrent area of open water in northern Baffin Bay that supports an early phytoplankton bloom and, consequently, large zooplankton populations (Hobson et al., 2002). By transporting marine-derived nutrients onto land, Little Auks also act as important ecosystem engineers, fertilizing terrestrial habitats and contributing to local biodiversity (González-Bergonzoni et al., 2017). Long-term colony persistence in this region further suggests that Little Auks may have influenced not only Arctic ecosystems over millennial timescales (Johansen, 2013) but are assumed to be a key factor to allow human settlement and persistance in the area (Mosbech et al., 2018).

Little Auk energetics, however, raise an unresolved question concerning prey capture efficiency. Because adults have high metabolic demands, they must capture large numbers of zooplankton to sustain both themselves and their chicks (Gabrielsen et al., 1991). Previous estimates suggest that an individual provisioning a chick may need to capture approximately 60,000 copepods per day, yet dive-based analyses indicate capture rates of roughly six copepods per second during underwater foraging (Harding et al., 2009). These values have prompted the question of how Little Auks are able to obtain sufficient prey within their behavioral time budget at that rate, which seems to be too inefficient.

One hypothesis is that Little Auks use a filter-feeding mechanism, with oral, barb-like structures retaining prey while water is expelled from the bill (Lovvorn et al., 2001; Harding et al., 2009). However, the anatomical basis for this idea remains uncertain (Enstipp et al., 2018). Earlier references to prey-retention structures are clearly documented in surface filter feeder species, in the South Pacific such as Short-tailed Shearwater (*Ardenna tenuirostris*, Morgan & Ritz, 1982), and Antarctic Prion (*Pachyptila desolata*, Prince, 1980). Experimental observations of Little Auks foraging in tanks stocked with copepods however did not support this, instead suggested suction feeding of individual copepods (Enstipp et al., 2018). In these tanks, birds using the gular pouch to generate strong suction to capture singular prey one-by-one (Enstipp et al., 2018). In those observations, birds fed at a maximum rate of three copepods per second, even in the presence of high prey densities, which is again not sufficient to meet their energetical requirements. The authors reported that no bill

adaptations for filter feeding were identified (Enstipp et al., 2018), but no further information was given. They suggest that Little Auk indeed forage on singular prey items using suction (Enstipp et al., 2018). However, these results also suggested that the time budget needs to be doubled, and it still did not sufficiently explain how Little Auk manage their daily energy demands. Thus, the question whether Little Auk have another, more efficient, mode of foraging, potentially aided by morphological palatal adaptation, remains.

Available scientific information on the oral morphology of Little Auk is however, limited. To our best knowledge, the only description we found is an early hand-drawn schematic, which depicts a smooth, non-cornified tongue, no conspicuous ridges or baleen-like structures along the bill margin, and small papillae across the palate (Bédard 1969). A non-peer-reviewed source suggests that Little Auks may have “barbs on the palate that retain food” (Boertmann et al., 2025), contradicting Enstipp et al., 2018 who state that comb-like structures along the edge of the beak do not occur in Little Auks. However, there is no photograph or schematic prodivde other than verbal description (Boertmann et al., 2025). There is also no comment on soft tissue functional traits of the oral cavity. We found no detailed modern photographs or morphological analyses of the beak that included soft tissue. Consequently, the morphological basis of prey capture and retention in Little Auk remains insufficiently documented. Yet, anecdotally, Inughuit have verbally suggested the presence of tooth-like structures within the bill of the Little Auk, and locals familiar with the species through long-term subsistence and hunting claim that structures on the tongue and/or palate are common knowledge known.

On 6 August 2026, the authors met in Savissivik (76.00°N, 65.16°W) in the Thule district of north-west Greenland, a region well known for its large Little Auk populations, and where local traditions of Little Auk hunting are alive (Flora et al., 2018; Mosbech et al., 2018). In their roles as polar guides and lecturer, JS, SI, and TH discussed with ALI about her knowledge on the matter during a visit alongside an expedition cruise. As it was hunting season, ALI had recently taken two Little Auk for subsistence use and presented them for opportunistic examination. Photographs were obtained of the tongue and palate (Fig. 1b, c), after removal of the large numbers of copepods from inside the bill and the area beneath the tongue, the gular pouch. Both birds’ oral cavities were consistent with verbal accounts and with the earlier description attributed to Bédard (1969). The palates were strongly cornified and densely covered with palatal denticles that extend across much of the palatal surface, with the denticles directed posteriorly (Fig. 1c). By contrast, the tongue appeared thick but smooth in both birds (Fig. 1b).

Fig. 1: A. Little Auk (*Alle alle*) with a full gular pouch in flight over open water near Savissivik, Thule district, Northwest Greenland. B. Oral cavity of a adult Little Auk taken for subsistence use, showing the thick, smooth tongue. C. Palate of the same specimen, showing dense fields of posteriorly directed palatal denticles, hypothesized to aid in prey retention.

These observations support the possibility that Little Auks use a suction-and-retention mechanism that allows for multiple prey intake, rather than a purely single-prey suction mechanism. Under this interpretation, birds may still use suction to take in multiple copepods into the bill, but then filter food by pressing them with its tongue against the denticulated palate while water is expelled. The retained prey could then be transferred into the gular pouch for subsequent transport to chicks. Such a mechanism would help explain how Little Auks achieve the high prey acquisition rates required by their energetic demands.

However, while the observation of posterior directed palatal denticles allows for such a mechanism to exist, it would also aid with the retention of single copepods during suction feeding, so this alone is not sufficient

evidence. In absence of direct observation, we still do not know if and how Little Auks forage on more than one prey item simultaneously.

Yet, together with the still unexplained need for an efficient ingestion mechanism, our observation builds on Enstipp et al. (2019) findings and strengthens the hypothesis that Little Auks may combine suction feeding with a form of prey retention functionally analogous to filtering, or at least similarly efficient. More broadly, it also illustrates the value of local Inughuit ecological knowledge in addition to older drawings for identifying biologically important structures and behaviors that have received little formal scientific attention. A fuller understanding of Little Auk feeding biology will require targeted morphological imaging, comparative anatomical study, and direct behavioral observations under natural foraging conditions. This is particularly important given the Little Auk's complex position between its relevance for modern science as a sentinel species of changes in the high Arctic and its thousand-year-long cultural importance for the local settlements (Mosbech et al., 2018).

Ethical note

No birds were killed, captured, or experimentally manipulated for the purposes of this study. The two Little Auks (*Alle alle*) examined were taken by AP and A-L, local Inughuit hunters from Savissivik, Thule district, Northwest Greenland, as part of ongoing subsistence hunting practices that occur independently of, and were not initiated for, this research. The photographs of the oral cavity were obtained opportunistically, post-mortem, after the birds had already been harvested for food, with the consent of the hunters involved, and as such, no permit was required. No live birds were captured, held, or otherwise disturbed during data collection, and no additional specimens were sourced or sacrificed for this study. The birds were returned to their originally intendent purpose after photographs were taken.

Competing interests

T.H. is employed by HX, a polar expedition travel operator. J.S. and S.D.I were short-term contractors for HX. All authors were present on the voyage during which the field observations reported here were made. HX had no role in the study design, data collection, analysis, interpretation, or the decision to publish this work. The remaining authors declare no competing interests.

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Reference list

Anker-Nilssen, T., Bakken, V., Strøm, H., Golovkin, A. N., Bianki, V. V. & Tatarinkova, I. P. (2000). The status of marine birds breeding in the Barents Sea region. *Norsk Polarinstitutt Rapportserie* No. 113. Tromsø: Norwegian Polar Institute.

Bédard, J. (1969). Adaptive radiation in Alcidae. *Ibis*, 111(2), 189–198. https://doi.org/10.1111/j.1474-919X.1969.tb02526.x

Boertmann, D., Egevang, C., Frederiksen, M., Johansen, K. L., Labansen, A. L., Linnebjerg, J. F., Merkel, F. R., Mosbech, A. (2025). The SEABIRDS of Greenland. Eds. Frederiksen, M. Alle alle publishing, Copenhagen.

Enstipp, M. R., Descamps, S., Fort, J. & Grémillet, D. (2018). Almost like a whale – first evidence of suction feeding in a seabird. *Journal of Experimental Biology*, 221(13), jeb182170. https://doi.org/10.1242/jeb.182170

Flora, J., Johansen, K. L., Grønnow, B. et al. (2018). Present and past dynamics of Inughuit resource spaces. *Ambio*, 47(Suppl. 2), 244–264. https://doi.org/10.1007/s13280-018-1039-6

Freuchen, P. & Salomonsen, F. (1958). *The Arctic Year*. New York: G. P. Putnam's Sons.

Gabrielsen, G. W., Taylor, J. R. E., Konarzewski, M. & Mehlum, F. (1991). Field and laboratory metabolism and thermoregulation in Dovekies (*Alle alle*). *The Auk*, 108(1), 71–78. https://doi.org/10.1093/auk/108.1.71

González-Bergonzoni, I., Johansen, K. L., Mosbech, A., Landkildehus, F., Jeppesen, E. & Davidson, T. A. (2017). Small birds, big effects: the little auk (*Alle alle*) transforms high Arctic ecosystems. *Proceedings of the Royal Society B*, 284(1849), 20162572. https://doi.org/10.1098/rspb.2016.2572

Harding, A. M. A., Egevang, C., Walkusz, W. et al. (2009). Estimating prey capture rates of a planktivorous seabird, the little auk (*Alle alle*), using diet, diving behaviour, and energy consumption. *Polar Biology*, 32, 785–796. https://doi.org/10.1007/s00300-009-0581-x

Hobson, K. A., Gilchrist, G. & Falk, K. (2002). Isotopic investigations of seabirds of the North Water Polynya: contrasting trophic relationships between the eastern and western sectors. *The Condor*, 104(1), 1–11. https://doi.org/10.1093/condor/104.1.1

Johansen, T. B. (2013). Foraging efficiency and small game: the importance of dovekie (*Alle alle*) in Inughuit subsistence. *Anthropozoologica*, 48(1), 75–88. https://doi.org/10.5252/az2013n1a4

Kampp, K., Falk, K. & Egevang Pedersen, C. (2000). Breeding density and population of little auks (*Alle alle*) in a Northwest Greenland colony. *Polar Biology*, 23, 517–521. https://doi.org/10.1007/s003000000115

Lovvorn, J. R., Baduini, C. L. & Hunt, G. L. Jr. (2001). Modeling underwater visual and filter feeding by planktivorous shearwaters in unusual sea conditions. *Ecology*, 82(8), 2342–2356. https://doi.org/10.1890/0012-9658(2001)082[2342:MUVAFF]2.0.CO;2

Morgan, W. L. & Ritz, D. A. (1982). Comparison of the feeding apparatus in the muttonbird, *Puffinus tenuirostris* (Temminck), and the fairy prion, *Pachyptila turtur* (Kuhl), in relation to the capture of the krill, *Nyctiphanes australis* Sars. *Journal of Experimental Marine Biology and Ecology*, 59(1), 61–75. https://doi.org/10.1016/0022-0981(82)90107-1

Mosbech, A., Johansen, K. L., Davidson, T. A. et al. (2018). On the crucial importance of a small bird: the ecosystem services of the little auk (*Alle alle*) population in Northwest Greenland in a long-term perspective. *Ambio*, 47(Suppl. 2), 226–243. https://doi.org/10.1007/s13280-018-1035-x

Prince, P. A. (1980). The food and feeding ecology of Blue Petrel (*Halobaena caerulea*) and Dove Prion (*Pachyptila desolata*). *Journal of Zoology*, 190(1), 59–76. https://doi.org/10.1111/j.1469-7998.1980.tb01423.x

Wojczulanis-Jakubas, K., Jakubas, D. & Stempniewicz, L. (2022). The Little Auk *Alle alle*: an ecological indicator of a changing Arctic and a model organism. *Polar Biology*, 45, 163–176. https://doi.org/10.1007/s00300-021-02981-7