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# Leopard seals (*Hydrurga leptonyx*) use suction and filter feeding when hunting small prey underwater

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**Abstract** Leopard seals (*Hydrurga leptonyx*) are unusual among apex predators in that they feed at both the top and near the bottom of marine food webs; they capture and consume marine amniotes (seals and penguins) as well as krill. This is thought to be achieved with their unusual dentition: rostral caniniform teeth function to grip large prey and tricusate postcanines function to sieve krill. The use of canine teeth is known, yet until now, the function of the postcanines has never been documented. Here, we present the first direct observations of filter feeding in leopard seals. Suction was used to draw small prey into the mouth followed by expulsion of ingested seawater through the sieve formed by postcanine teeth. Individuals show abrasive wear on canines and incisors, but not postcanines. This suggests that postcanines are not systematically used for piercing prey during macrophagous feeding, confirming that the postcanines primarily serve a sieving function. Rather than being less efficient at feeding as a result of its polarized diet, the leopard seal is well adapted towards two disparate feeding modes.

**Keywords** Dentition · Foraging behaviour · Pinnipedia · Suction feeding

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## Introduction

Optimal foraging theory predicts that large predators focus their hunting efforts on prey that maximizes energy intake per hunting investment (Stephens and Krebs 1986; Fossette et al. 2011). This has been found in both terrestrial and marine environments, with predator body mass being positively correlated with prey mass across a range of predator species (Carbone et al. 1999; Costa 2009). Yet, in aquatic environments, the opposite is often true with large predators, such as mysticete whales, focusing part or all of their feeding on abundant small prey, thereby maximizing their energy intake in a different way (Heithaus and Dill 2009; Fossette et al. 2011). Aquatic predators employ specialized feeding modes often closely linked with their intended prey: raptorial, suction and filter feeding (Werth 2000a). Most species utilize one of these strategies as the dominant prey capture mode; for example, teuthophagous odontocetes are often specialized suction feeders, and mysticetes employ bulk filter feeding to capture planktonic prey (Heithaus and Dill 2009). Of these feeding modes, bulk filter feeding is considered the most efficient when feeding on small schooling prey. Yet, filter feeding generally requires such morphological specialization that species become obligate filter feeders (Sanderson and Wassersug 1993). Few species are known to successfully switch between prey capture strategies at will.

Antarctic leopard seals (*Hydrurga leptonyx* Blainville 1820) are known for their predatory habits, using a raptorial ‘grip-and-tear’ feeding style to kill and process amniote prey, including penguins and other seals (Hamilton 1939; Adam and Berta 2002; Ainley et al. 2005; Edwards et al. 2010). Nevertheless, much of their diet is not composed of vertebrates but instead consists of krill, a small euphausiid crustacean (Øritsland 1977; Siniff and Stone 1985; Lowry

et al. 1988; Hall-Aspland and Rogers 2004; Casaux et al. 2009). The ability to feed on both large and extremely small prey is thought to be dependent upon their use of specialized dental morphology (Fig. 1): robust canines and caniniform incisors grip and tear large prey, whereas multi-cusped postcanines are hypothesized to sieve smaller prey from seawater as has also been observed in crabeater seals (*Lobodon carcinophaga*; Ross et al. 1976; Øritsland 1977; Klages and Cockcroft 1990). Hence, besides hunting both large and small prey, leopard seals seem capable of changing feeding modes when feeding on these two disparate size classes of prey, allowing them to take advantage of whichever prey is locally available. Yet, despite many accounts of macrophagy in leopard seals (Hamilton 1939; Edwards et al. 2010), no description of underwater predation on small prey has been reported.

Here, we present the first detailed description of underwater feeding on small prey by leopard seals, based on observations of captive specimens at Taronga Zoo, Australia. These data permitted testing of the hypothesis that leopard seals use suction and filter feeding during capture of small prey underwater, rather than the raptorial grip-and-tear behaviours for which this species is more commonly known. This hypothesis was then further tested by surveying the dental wear observed on the teeth of wild caught museum specimens, allowing us to better understand and interpret how these behaviours might be used in their wild setting when feeding upon natural prey.

## Materials and methods

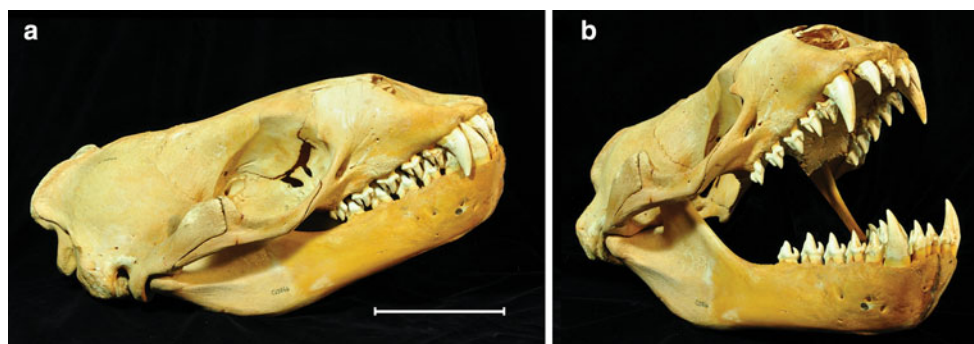
### Feeding trials

Detailed observations were made during captive feeding trials using 2 leopard seals held at Taronga Zoo in Sydney, Australia, during February–March 2011. These seals were a 4-year-old male (Casey: ARKS#A70508) and a 6-year-old female (Sabine: ARKS#A70509). Feeding data were

collected over 6 days with both seals participating in 1 or 2 experimental feeding sessions per day. All trials were performed individually for each seal to prevent competition between animals. As the seals share a pool, a seal keeper offered a fish reward to the non-focal animal to keep it at the other end of the pool. This method was successful and no interaction between animals occurred during the trials.

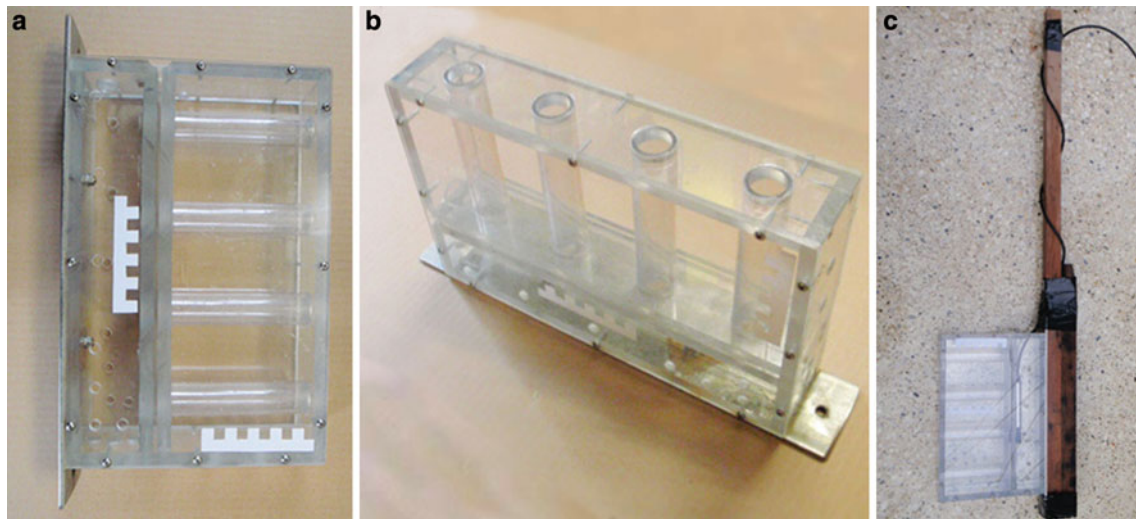
The focal seal was presented with fish in an experimental feeding apparatus that tested its ability to use suction during prey capture. The experimental feeding apparatus was a polycarbonate plastic box (355 × 30 × 75 mm) with four 25 mm internal-diameter tubes inserted into the side (Fig. 2a–b). The box was fixed to a wooden pole so that it could be held below the water by a keeper during the trial and easily raised for reloading with fish between feeding attempts (Fig. 2c). Fish were placed into the four tubes head facing outward to prevent the spines from the fish irritating the seal's throat as they were swallowed. The fish were placed protruding out of the tubes by approximately 1 cm so that the seal could identify the front of the box (when fish were placed fully inside the box, the seals often attempted to capture the fish through the clear sides of the box). During these trials, the seals were fed a mixed fish diet including yellowtail mackerel (*Trachurus novaezelandiae*), Australian herring (*Arripis georgianus*) and whiting (*Sillago* sp.), each between 8 and 15 cm in length. We also attempted to use smaller fish (whitebait) or chopped fish in order to better approximate the size of krill for our trials; however, the leopard seals rejected these small prey items and let them sink to the bottom of the pool without displaying interest. As captive animals, these seals were selective in only eating prey that they were familiar with and that constituted their regular captive diet. Finally, we also performed scatter feeds with whole fish thrown loose into the water before the seal was released and allowed to consume the free-floating fish.

Experimental trials were performed in the leopard seal pool in the Great Southern Ocean Precinct at Taronga Zoo. Observations were made through an acrylic underwater



**Fig. 1** Leopard seal skull (*Hydrurga leptonyx*; NMV C13866) showing robust canines and caniniform incisors and the sieve created by the postcanines in occlusion. Scale bar = 10 cm





**Fig. 2** **a–b** Polycarbonate feeding apparatus used during the trials. **c** Feeding apparatus attached to wooden pole as used at Taronga Zoo. Note the hydrophone positioned inside the rear compartment of the box

viewing window that allowed us to film the feeding behaviours displayed by the seals without the need for underwater camera equipment. All feeding attempts made during the trials were filmed using a Sony HVR-Z1P Camcorder at HDV 1080/50i resolution (25 full frames/fields per second). Audio was recorded to camera using a CR-80-40 Hydrophone (sensitivity:  $-166 \text{ dB} \pm 5 \text{ dB}$  re  $1 \text{ V/uPa}$ ; frequency range:  $7 \text{ Hz}$  to  $80 \text{ kHz}$ ) run through a HP-A1 series mixer-amplifier with a  $12 \text{ dB/octave}$  band-pass noise reduction filter (Burns Electronics Hydrophone Systems). This hydrophone was placed inside the rear of the feeding apparatus.

Individual feeding events were chosen for further analysis using the camera's frame rate to calculate the duration of the different phases of the feeding cycle. Only feeding events where the seal approached the box and successfully drew out and consumed the prey item in a single attempt were chosen for analysis. Durations were recorded by using Final Cut Pro 7.0.3 (Apple Inc., Cupertino, California) to place markers (m) into the video footage to identify key events within the feeding cycle including: (mA) head-strike start, first frame with rapid forward motion of the head towards the prey item; (mB) head-strike end, first frame after the end of rapid forward motion, generally just before suction; (mC) mouth open, first frame where the mouth is visibly open; (mD) suction, first frame where the prey item visibly moves towards the mouth; (mE) maximum gape, first frame at which the maximum gape is achieved for that feeding event taken as the distance between the tip of the upper and lower lips; (mF) fish gone, first frame where the fish is completely inside the oral cavity and out of view; (mG) water expulsion start, the first frame after fish gone (mF); (mH) water expulsion end, end of the feeding cycle

taken as the frame where the lips and jaws return to their pre-feeding position with no further signs of water expulsion. These markers were used to calculate the duration of phases within the feeding cycle by counting the number of frames between markers with each frame equalling  $40 \text{ ms}$  ( $25 \text{ frames per second}$ ): (mA–mB) duration of head-strike; (mC–mD) time to suction; (mC–mE) time to maximum gape; (mD–mF) duration of suction; (mG–mH) duration of water expulsion phase; (mA–mH) total length of feeding cycle. At maximum gape (mE), the distance between the tip of the upper and lower jaws was measured to provide an estimate of the maximum gape used during the feeding event. This was measured from a still image using ImageJ  $1.45 \text{ s}$  (National Institutes of Health, USA). Maximum gape during a feeding event was then compared with the absolute maximum gape length for both individuals as estimated from photographs of each seal performing a trained behaviour where they opened their mouth to full gape. This is a routine veterinary technique that permits regular inspection of the seal's oral health. ImageJ was also used to measure gape and distance between the prey item and the head and shoulder. Some degree of parallax error in these measurements will be apparent, because the seals often did not directly approach the box in a plane perpendicular to the camera view. Therefore, estimates of velocity and acceleration will be underestimates of the true values in three-dimensional space. Maximum velocity and maximum average acceleration were taken from data smoothed with a moving window average of 5 frames. Maximum velocity was the highest value reached during the strike towards or away from the prey. Maximum average acceleration was the average of the acceleration data throughout the head-strike either towards or away from the prey.

## Dental morphology

Twenty-six leopard seal skulls of varying ages were examined to determine the extent and cause of dental wear observed on both the anterior (canines) and the postcanine teeth (Table 1). All available specimens were included except those in which (1) dentition was severely damaged or missing; (2) significant pathology was manifest; or (3) the frontal sutures were not closed, signalling early ontogenetic stage. Three measurements were taken from each skull in addition to dental wear parameters. These were condylobasal length (CBL), bizygomatic width (BZW) and tooth row length (TRL). CBL was measured from the anterior edge of the premaxilla to the posterior edge of the occipital condyle. BZW is the maximum width of the skull measured across the exterior edges of the zygomatic arches. TRL was measured along the sagittal plane from the posterior edge of the alveoli for the upper 5th

postcanine to the anterior edge of the alveolus for the first upper incisor.

For each skull, the dental wear state of the canines and postcanines was examined to determine whether they showed signs of abrasive wear and/or dental attrition. Abrasive wear surfaces usually develop when a tooth penetrates a food item and thus form on tooth apices as a smooth, rounded wear surface without an opposite on the opposing tooth row; additionally, abrasive wear may be caused by abiotic factors such as abrasion on ice (Stirling 1969). In contrast, dental attrition is caused by tooth-on-tooth contact and is indicated where the wear surfaces on the lower teeth match opposing wear surfaces on the uppers. The wear surface itself is often relatively flat and polished and restricted to points of contact with the opposing teeth. Fractures were identified as either pre- or postmortem by the presence of signs of use (either abrasion or attrition) on the broken surface, indicating that the

**Table 1** Leopard seal (*Hydrurga leptonyx*) skulls used in this study

| Specimen               | CBL  | BZW  | TRL  | Sex | Collection location                 | C Frac | C Abra | C Attr | PC Frac | PC Abra | PC Attr |
|------------------------|------|------|------|-----|-------------------------------------|--------|--------|--------|---------|---------|---------|
| NMV C31561             | 30.7 | 16.5 | 12.2 | U   | Geelong (Aus.)                      | 0      | 0      | 0      | 0       | 0       | 0       |
| NMV C7401              | 31.8 | 16.5 | 12.8 | M   | Macquarie Is.                       | 0      | 0      | 0      | 0       | 0       | 0       |
| NMV C7375              | 31.9 | 16.3 | 11.5 | F   | Heard Is.                           | 0      | 0      | 0      | 0       | 0       | 0       |
| NMV C27418             | 32.3 | 17.0 | 12.3 | F   | Sunday Is. (Aus.)                   | 0      | 0      | 0      | 0       | 0       | 0       |
| NMV C7402              | 32.7 | 17.0 | 12.2 | M   | Macquarie Is.                       | 0      | 0      | 0      | 0       | 0       | 0       |
| NMV C7380              | 33.2 | 17.4 | 13.1 | M   | Heard Is.                           | 0      | 0      | 0      | 0       | 0       | 0       |
| NMV C25043             | 33.7 | 17.4 | 12.1 | M   | Port fairy (Aus.)                   | 0      | 1      | 0      | 1       | 0       | 1       |
| NMV C10955             | 35.1 | 18.7 | 13.2 | U   | Manns Beach near port albert (Aus.) | 1      | 0      | 0      | 0       | 0       | 1       |
| NMV C7536              | 35.2 | 18.1 | 13.3 | M   | Buckles bay beach (Macquarie Is.)   | 1      | 1      | 0      | 0       | 0       | 1       |
| NMV C23589             | 35.4 | 17.7 | 13.2 | U   | Macquarie Is.                       | 0      | 0      | 0      | 0       | 0       | 1       |
| NMV C33802             | 35.6 | 18.7 | 13.6 | F   | 90 Mile beach (Aus.)                | 0      | 1      | 0      | 0       | 0       | 0       |
| NMV C13866             | 37.1 | 20.0 | 13.6 | M   | Macquarie Is.                       | 0      | 1      | 0      | 0       | 0       | 1       |
| NMV C23590             | 37.3 | 20.6 | 14.7 | U   | Macquarie Is.                       | 0      | 0      | 0      | 0       | 0       | 1       |
| NMV C7378              | 38.1 | 20.1 | 14.0 | M   | Heard Is.                           | 0      | 0      | 0      | 1       | 0       | 1       |
| NMV C34063             | 38.9 | 21.5 | 14.2 | U   | Mallacoota inlet (Aus.)             | 1      | 1      | 1      | 1       | 0       | 1       |
| NMV C7381              | 39.0 | 21.9 | 13.9 | F   | Heard Is.                           | 0      | 1      | 1      | 1       | 0       | 1       |
| NMV C7376              | 39.1 | 21.2 | 13.7 | M   | Atlas cove (Heard Is.)              | 1      | 1      | 1      | 0       | 0       | 1       |
| NMV C7377              | 39.2 | 21.3 | 13.6 | M   | Heard Is.                           | 1      | 1      | 1      | 0       | 0       | 1       |
| NMV C7383              | 39.3 | 22.3 | 13.9 | F   | Atlas cove (Heard Is.)              | 1      | 1      | 1      | 1       | 0       | 1       |
| NMV C7379              | –    | –    | 14.5 | M   | Atlas cove (Heard Is.)              | 1      | 1      | 1      | 0       | 0       | 1       |
| NMV C7382              | –    | –    | 14.6 | F   | Atlas cove (Heard Is.)              | 1      | 1      | 1      | 0       | 0       | 1       |
| NMV C33801             | 40.1 | 23.4 | 14.7 | F   | Safety beach (Aus.)                 | 1      | 1      | 1      | 1       | 0       | 1       |
| NMV C7540              | 40.3 | 22.5 | 14.3 | F   | Corinthian bay (Macquarie Is.)      | 1      | 1      | 1      | 0       | 0       | 1       |
| NMV C7403              | 40.8 | 22.9 | 14.1 | F   | Macquarie Is.                       | 0      | 1      | 1      | 0       | 0       | 1       |
| NMV C7384              | 40.9 | –    | 14.8 | F   | Heard Is.                           | 1      | 1      | 1      | 0       | 0       | 1       |
| NMV C7412              | 41.7 | 22.1 | 14.9 | F   | Heard Is.                           | 1      | 1      | 1      | 0       | 0       | 1       |
| Number of individuals: |      |      |      |     |                                     | 12     | 16     | 12     | 6       | 0       | 19      |

NMV C Museum Victoria Mammalogy Collection, Melbourne, Australia. CBL condylobasal length; BZW bizygomatic width; TRL tooth row length. All measurements in centimetres. Sex is male (M), female (F) or unknown (U). Aus. Australia; Is. Island. C canine; PC postcanine; Frac fracture; Abra abrasion; Attr attrition. Wear states: 0 absent; 1 present

animal was still alive and using the tooth after the break. Teeth with postmortem breaks were not included in the survey.

In order to understand how the soft tissue relates to cranial osteology, we also dissected a leopard seal that died in captivity at Taronga Zoo (Brooke: ARKS#990269). This permitted inspection of orofacial soft tissues, especially the gingivum invading spaces between the teeth that are visible in prepared skulls. This was also compared with photographs of the soft tissue anatomy of the live seals at Taronga Zoo. All osteological specimens were sourced from the Mammalogy Collection of Museum Victoria (NMV C), Melbourne, Australia.

## Results

### Feeding trials

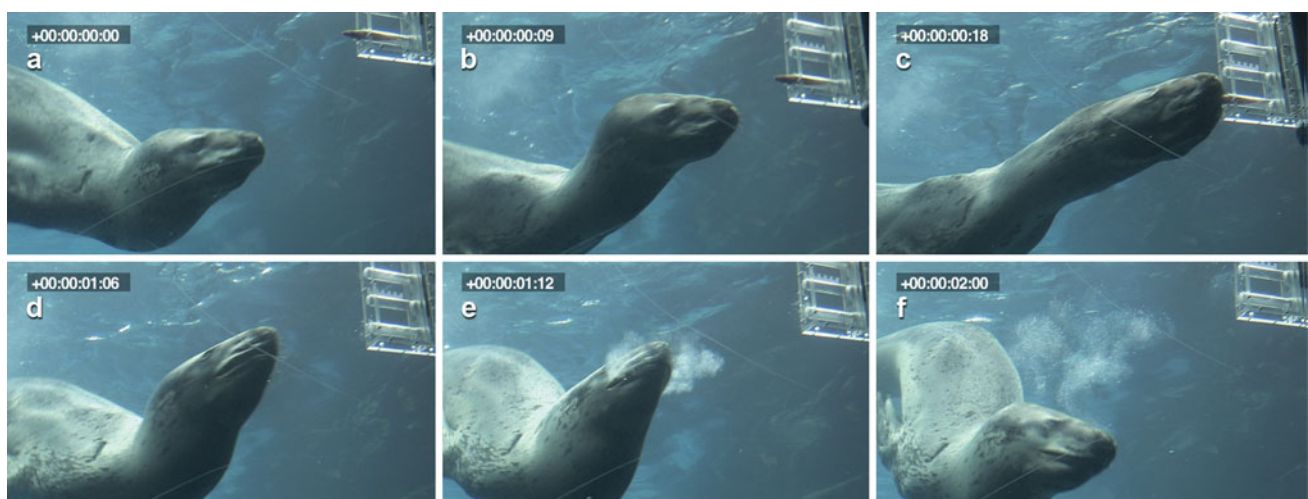
Leopard seals were found to use suction to draw fish out of the feeding apparatus during trials before expelling water out via the sides of the mouth in a sieving action (Fig. 3; Online Video Resource: ESM\_1.mp4). The feeding event began with the seal approaching the box apparatus containing the prey. In the female individual, this was marked with a clearly identifiable ‘head-strike’ where she rapidly accelerated her head towards the box, used suction to acquire the prey and then drew back to her initial position where the water was expelled (Figs. 3a–c, 4). In contrast, the male individual slowly approached the fish and often nudged and gently mouthed the fish with his lips before using suction and sieving to consume it. In no trial did

either seal attempt to break apart the fish either by chewing or by shaking. The female closed her eyes during her rapid ‘head-strike’ phase, and they remained closed until after the completion of suction. The male occasionally closed his eyes during suction; however, in some events, they remained open throughout the feeding cycle.

On approaching the prey, the mouth was opened to a small maximum gape of 3–5 cm before suction commenced within approximately 5 cm of the box. In most feeding events, suction did not commence until the anterior lips were close to contacting the prey and no suction occurred at a distance of more than 5 cm. In contrast to the small gape used during underwater feeding, the maximum gape (measured between the anterior tip of the upper and lower jaws) for these seals during dental inspection was approximately 30 cm for both individuals.

Suction appeared to be generated by the depression and retraction of the tongue and hyoid apparatus (Fig. 3c), which coincided with rapid movement of the prey into the mouth (mD–mF). Because of the seal’s thick neck and because they did not approach the box from a consistent position, it was not always possible to visually discern when gular depression occurred and so suction could only be identified as occurring from the onset of movement of the prey item towards the mouth (mD), until the fish was completely out of view inside the oral cavity (mF).

Lateral water expulsion followed suction, where water was expelled from the sides of the mouth through the teeth, presumably allowing the seal to swallow the fish without ingesting copious amounts of seawater (mG–mH, Fig. 3d–f). The initial pulse of water expulsion often appeared to be concentrated to the corners of the mouth



**Fig. 3** Underwater feeding cycle of the leopard seal (Sabine: ARKS#A70509). **a** Begins head-strike, **b** rapidly extends long S-shaped neck, **c** neck reaches full extension, prey is sucked into the mouth, **d** neck retracts, lips are parted to commence lateral water

expulsion, **e** water expelled (note the cloud of bubbles and turbid water that is ejected from the sides of the mouth through the postcanine tooth row), and **f** end of feeding cycle when lips and jaws return to pre-feeding position

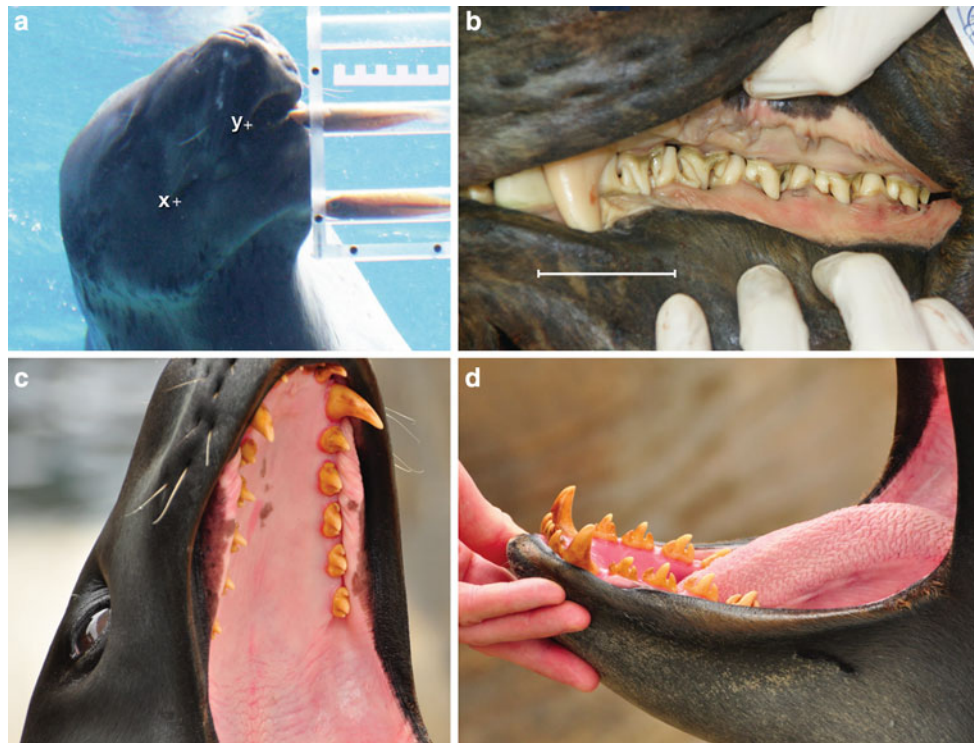
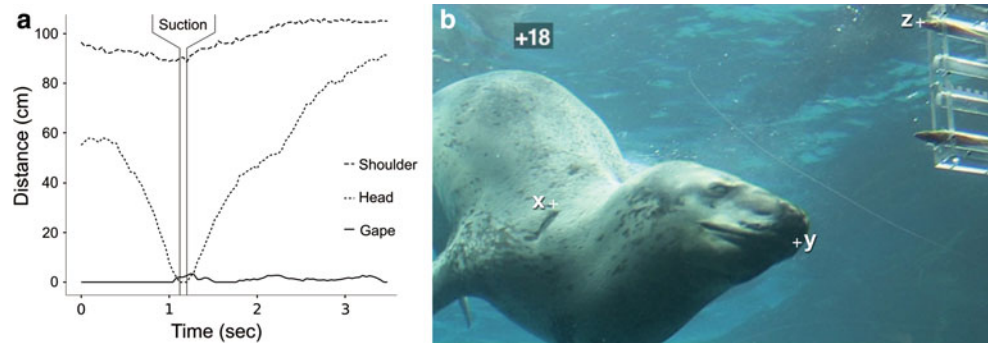


where the lips focused most of the flow through the main section of the postcanine sieve (Online Video Resource: ESM\_1.mp4). Water was expelled out of both sides of the mouth at the same time, and a second pulse of water was often seen where the anterior lips were slightly parted, allowing water to escape along the full mouth margins including the front of the mouth. In a number of trials, the tail of the fish protruded out of the mouth between the incisors during this second pulse, drawn out with excurrent flow. However, rather than escaping with the excurrent, the fish appeared to be retained within the mouth by the small gape. The fish was then drawn back into the mouth either by another pulse of suction or perhaps physically by the tongue.

It was not possible to precisely identify the moment when the fish was swallowed within the feeding cycle from these trials; however, given that the fish was still in the mouth behind the barrier formed by the teeth as the water is expelled, it is likely that it is swallowed somewhere near the end of the feeding cycle with minimal excess water.

During both suction and lateral water expulsion, the thick mobile lips appear to play an important role, firstly in concentrating suction forces to the anterior of the mouth by occluding the lateral lip margins (Fig. 5), and secondly by controlling the release of water through the cheek tooth row (Fig. 3e). Kinematic variables are summarized in Table 2. The same combination of suction and water

**Fig. 4** Head movement and gape during head-strike, showing distance between a marker (*scar*) on the seal's shoulder and the fish/box (X–Z) and between a marker at the tip of the seal's snout and the fish/box (Y–Z). The gape distance was measured between the anterior tip of the *upper and lower lips*. Vertical bars indicate the start and end of suction (mD–mF)



**Fig. 5** **a** Seal commencing suction (Sabine: ARKS#A70509). Lip pursing occludes gape from the corner of mouth (X) to position of the canines (Y), concentrating suction forces to the front of the mouth. **b** Sieve created by tight occlusion of postcanines when in life position

with gingival tissue occupying the space between the teeth that is present in prepared skulls (Brooke: ARKS#990269) Scale bar = 5 cm. **c–d** View of soft tissue and dentition of a leopard seal during a routine dental check (Casey: ARKS#: A70508)



**Table 2** Summary of kinematic variables for leopard seals

| Markers kinematic variables |                                   | Male (Casey)  | <i>N</i> | Female (Sabine) | <i>N</i> |
|-----------------------------|-----------------------------------|---------------|----------|-----------------|----------|
| mA-mB                       | Duration of head-strike (s)       | n/a           | n/a      | 0.335 ± 0.023   | 16       |
| mC-mD                       | Time to suction (s)               | 0.107 ± 0.027 | 6        | 0.080 ± 0.012   | 16       |
| mC-mE                       | Time to maximum gape (s)          | 0.267 ± 0.034 | 6        | 0.163 ± 0.025   | 15       |
| mD-mF                       | Duration of suction (s)           | 0.287 ± 0.035 | 6        | 0.150 ± 0.016   | 16       |
| mG-mH                       | Duration of water expulsion (s)   | 3.107 ± 0.363 | 6        | 1.850 ± 0.148   | 16       |
| mA-mH                       | Total length of feeding cycle (s) | 3.540 ± 0.378 | 6        | 2.120 ± 0.150   | 16       |
| mE                          | Maximum gape (cm)                 | 4.736 ± 1.680 | 4        | 3.345 ± 0.390   | 13       |

See text for explanation of Marker abbreviations. *s* seconds  
Values are mean ± standard error

expulsion was used when feeding on free-floating fish during the scatter feeds.

### Dental morphology

Of the 26 skulls surveyed, 20 were found to display some dental wear and the remaining 6 represented younger individuals with unworn teeth (Table 1). Abrasive wear was found to be the main type of wear present on the apices of the canines with 16 individuals having clear evidence of abrasion (tooth-food wear) on their anterior teeth with some individuals losing up to 20 % of their canine crown height, resulting in much shorter and blunter canines (Fig. 6a–b). The tips of the canines do not come into contact with another tooth during normal jaw motion hence any major loss of height must be the result of fracture or abrasive wear, both of which were found to be common. Abrasive wear was also found on the apices of the robust caniniform incisors (Fig. 6c–d). Attritional wear was also found in 12 individuals on the sides of the canines and incisors where they came into contact with opposing teeth at full occlusion.

In contrast, no evidence of systematic abrasive wear was found on the postcanine teeth of any individual, including individuals with severe abrasion to their anterior teeth. The postcanine teeth interlock so that each tooth sits between its two opposing teeth. In young animals, they are held in occlusion with very minimal contact between postcanines, which are held apart by the locked anterior dentition. With increased wear and loss of crown height in anterior teeth, the occlusion of the postcanines becomes closer (Fig. 7). This results in the postcanines contacting each other, leading to attritional wear at points of occlusion. Initially, this is mostly restricted to the sides of the accessory cusps as these are the first points of contact (Fig. 6e). As the anterior teeth wear down, attrition on the postcanines becomes more severe and can result in the accessory cusps being completely obliterated (Fig. 6f). Hence, attrition to the postcanines was most severe in individuals with heavy abrasive wear to the anterior teeth. Loss in height to the canines in particular meant that the postcanines came to rest closer together than they would have when the anterior

teeth were unworn, leading to increasingly severe postcanine attritional wear.

Tooth fracture was also fairly common on the postcanine teeth with 6 individuals having a fracture on one or more of their postcanines. The only postcanine that did occasionally show some signs of abrasive wear was the posterior cusp of the upper PC5 (Fig. 6f). This is most likely the result of contact with the occluding gingivum rather than from tooth-food abrasion as none of the other postcanines in the tooth row showed equivalent evidence of abrasion.

By studying a dissected leopard seal head, we found that tooth occlusion was more precise in the dissected individual than in the osteological specimens resulting in smaller spaces between teeth (Fig. 5b). This is likely due to movement of teeth in alveoli as the skull dries, which often causes the bone to warp slightly. Teeth are also removed and then glued in place in some museum specimens, distorting occlusal relationships from the *in vivo* condition.

## Discussion

### Feeding trials

During underwater feeding, the leopard seal's feeding cycle showed stages or phases similar to those seen in other suction feeding marine mammals, including odontocete cetaceans and other pinnipeds (Werth 2000b; Bloodworth and Marshall 2005; Marshall et al. 2008; Kane and Marshall 2009). Four phases have been identified in this previous work: (I) preparatory, where the animal approaches the food while slowly opening its jaws to a partial gape (10–30 % of maximum gape); (II) jaw opening, a more rapid jaw opening phase, where the jaws move to maximum gape; (III) gular or hyolingual depression, where suction is generated by retraction of the tongue and hyoid apparatus; and (IV) jaw closing and water expulsion, leading to the end of the feeding cycle (Werth 2000b; Bloodworth and Marshall 2005; Marshall et al. 2008; Kane and Marshall 2009).



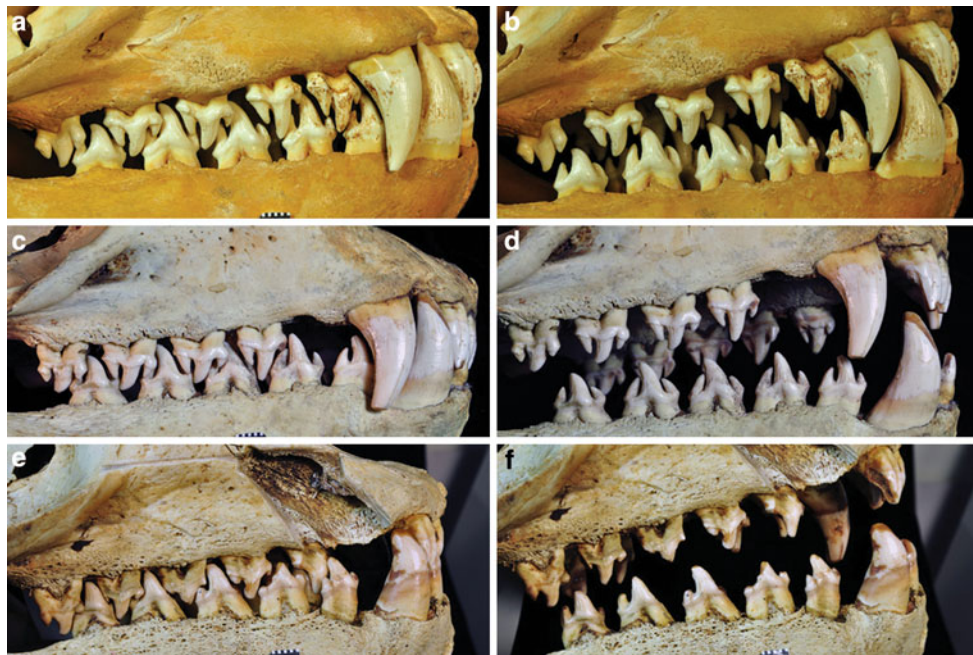
**Fig. 6** Lateral view of *upper* (a) and *lower* (b) canines displaying apical abrasion (NMV C7376). c–d Upper canine and incisors showing signs of both apical abrasive wear and attrition in occlusal view (c) and with slight rotation (b) that allows a better view of loss of height from the canine (NMV C7376). e Lingual view of light

attrition to the anterior accessory cusp of a postcanine (NMV C7384). f Buccal view of severe attrition to *upper* and *lower* PC5 with half of *upper* PC5 being worn away (NMV C7376). Note the smoothed apex of the posterior cusp on the *uppers* PC5. This abrasion is likely caused by contact with the occluding gingivum. Scale bars in mm divisions

In these studies, the preparatory phase is one of slow mandibular abduction, where the mouth is opened to a fraction of maximum gape, before the second jaw opening phase (II) sees rapid jaw opening through to maximum gape for that feeding event. Kane and Marshall (2009) found that during this preparatory phase, beluga and pilot whales expel any residual water from their mouth before commencing suction so as to maximize the volume change and hence amount of suction pressure generated with the onset of suction in phase III. This initial expulsion was identified by bubbles expelled from the lateral lip margins and through direct measurement of a suprambient pressure spike at the start of the feeding cycle. However, unlike these studies, leopard seals were observed to keep their mouths closed as they approached the prey item, with rapid jaw opening (II) occurring in one movement through to maximum gape. Hence, from these trials, it appears that leopard seals feeding on small prey underwater do not display a distinct preparatory phase involving slow jaw opening, prior to a more rapid jaw opening phase as identified in other suction feeding marine mammals.

Leopard seals also differ in having a long mobile neck with which they can perform a ‘head-strike’ behaviour

during the final approach to the prey. Both seals were observed to perform this behaviour, where the head was rapidly extended towards the prey, the food was sucked into the mouth and the head was withdrawn to its initial position for water expulsion and swallowing. This behaviour may allow these seals to feed more effectively on small elusive schooling prey like fish and krill, by allowing them to strike into the middle of a shoal of krill, while being able to withdraw and strike out again rapidly. This behaviour could potentially be detected in wild leopard seals using animal mounted accelerometers that measure the relative acceleration of the head and body during feeding (Naito 2010; Skinner 2009; Viviant et al. 2010). Figure 4 shows the distance between the prey/apparatus and two points on the female leopard seal: the approximate position of the pectoral girdle as marked by a scar on the shoulder, and the rostral apex. While the head accelerates rapidly towards and away from the box during the head-strike, the body does not (approximate maximum average acceleration of head relative to body during outward strike towards prey was found to be  $167 \text{ cm/sec}^2$  over 0.48 s and  $299 \text{ cm/sec}^2$  over 0.12 s while withdrawing from box; absolute maximum velocity outward is 86 cm/sec and



**Fig. 7** **a, b** Light (NMV C13866), **c, d** moderate (NMV C7384) and **e, f** heavy abrasion (NMV C7376) to canines with jaws in occlusion and slightly open (viewed laterally). When anterior teeth are in good condition, the postcanines are held apart by the occluded anterior

teeth; however, as these teeth wear, the postcanines come closer together, leading to increased tooth–tooth attrition. Scale bars in mm divisions

56 cm/sec while withdrawing). Short-necked marine mammal species, such as odontocete cetaceans, are probably unable to perform this type of head-strike behaviour during suction feeding.

Jaw opening (II) and suction (III) in the leopard seal appear very similar to that in other suction feeding marine mammals (Bloodworth and Marshall 2005; Werth 2000b; Marshall et al. 2008; Kane and Marshall 2009). Leopard seals were observed to suck in fish from a very short distance with both individuals approaching the prey (with or without head-strike) before sucking it in from a distance of generally less than 5 cm. In most cases, the fish is almost touching the anterior lips before the mouth rapidly opens and the fish is sucked in. In contrast, captive crabeater seals have been found to be able to suck pilchards out of a channel (section of pipe cut in half) from a distance of up to 50 cm, although more than one suction cycle was required for greater distances (Klages and Cockcroft 1990). Klages and Cockcroft (1990) suggest that this ability may be an adaptation that allows crabeater seals to capture krill hiding in caverns or crevices underneath ice floes during winter months when krill is less easily caught in the water column. While we did not test leopard seal's ability to acquire prey from a distance, it is possible that through their use of suction they share this ability. Similar specialist foraging behaviours have been seen in other pinnipeds that feed on prey hiding beneath ice floes; Weddell seals (*Leptonychotes weddelli*) have been observed blowing

bubbles into crevices in the ice to flush fish out of hiding so that they could be pursued and captured in open water (Davis et al. 1999).

Through using the lateral lips to seal the sides of their mouth, leopard seals were able to effectively concentrate suction to the pursed lips at the anterior of the mouth. This is essential for suction feeding because if unsealed, the long jaw length would weaken suction forces at the anterior of the mouth as water was drawn into the oral cavity via the whole length of the jaw. Leopard seals must retain this long jawline and ability to open to a wide gape so that they are able to capture and feed on large prey, whereas obligate suction feeders that do not routinely take large prey often possess shorter and broader snouts in combination with highly mobile facial musculature, as seen in beluga whales (*Delphinapterus leucas*) and walruses (*Odobenus rosmarus*; Kastelein et al. 1991; Werth 2006a, b; Marshall et al. 2008; Kane and Marshall 2009).

Before swallowing, the leopard seals expelled the seawater that had been drawn into their mouths along with the prey item. It is at this point that the tall, tricuspid teeth appear to play an important role, retaining prey against the excurrent flow of water out of the mouth. During their observations of captive feeding in crabeater seals, Ross et al. (1976) and Klages and Cockcroft (1990) observed similar expulsion behaviours where prey was sucked into the mouth before the excess water was expelled in a 'lip-smacking' action. In these trials, the seal held its head above



the water's surface as it waited for the next fish, and as a result, water expulsion was clearly visible out of the sides of the mouth. Klages and Cockcroft (1990) suggest that the tongue may be important in holding prey against the palate while water is expelled. However, given that the tongue is likely the main driver of water expulsion as it is raised to the palate, it is more likely that the crabeater seal's blunt, heavily cusped postcanines are acting as a sieve to retain the prey against the water flow. Teeth were also found to be important in retaining prey by Bloodworth and Marshall (2005) who report pygmy and dwarf sperm whales (*Kogia* spp.) gripping prey between their teeth to retain squid as water is expelled at the end of the suction feeding cycle.

Water expulsion at the end of the feeding cycle has been described as 'hydraulic jetting' in odontocetes (Bloodworth and Marshall 2005; Kane and Marshall 2009). However, this term is also used to describe the focused, water-squirting behaviours used by walruses and possibly the bearded seal, where powerful jets of water are used to stir benthic sediments and excavate prey during foraging (Kastelein and Mosterd 1989; Kastelein et al. 1991; Werth 2000a; Marshall et al. 2008). This term is, therefore, considered inappropriate for the gentler water expulsion observed in leopard seals at the end of their feeding cycle, where water was slowly expelled over the full length of the jaw, rather than as a focused 'jet' of water. We recommend that 'hydraulic jetting' be reserved for describing a focused jet of water, with 'water expulsion' being a more general term for any behaviour where water is expelled from the mouth during the feeding cycle.

In leopard seals, the water expulsion phase was found to be the longest part of the feeding cycle (Table 2). Similar water expulsion has been observed in other suction feeding marine mammals with both the long-finned pilot whale (*Globicephala melas*; Werth 2000b) and *Kogia* spp. (Bloodworth and Marshall 2005) being reported to maintain a partial gape subsequent to the end of the main jaw closure. Bloodworth and Marshall (2005) suggest that this slow jaw closure probably functions to allow water to exit at the end of the feeding cycle. In contrast, Werth (2000b) describes the water expulsion in pilot whales as being extremely rapid and visible only in slow motion playback. However, given that the whales' jaws were also seen to close very slowly after the feeding event, it is possibly that after an initial rapid pulse, slow water expulsion was still occurring throughout jaw closure in a similar way to what we observed in leopard seals. Werth also found that the ejected water was only clearly visible when the whale was near the surface or had raised its head out of the water, which may explain why he did not detect water expulsion during the slow jaw closure. Water expulsion is often very difficult to see underwater as the excurrent water may not be distinguishable from surrounding water. Fortunately, in

most of our trials, water expulsion could be clearly identified from bubbles and turbid water that was ejected from the mouth. Kane and Marshall (2009) also observed water expulsion as bubbles being expelled from the entire length of the lateral lip margin at the end of the feeding cycle in beluga whales, long-finned pilot whales and Pacific white-sided dolphins (*Lagenorhynchus obliquidens*), with the lips not returning to their resting position until after the completion of water expulsion.

The final water expulsion phase is an important component of the suction feeding cycle as the animal 'reloads' its feeding apparatus in readiness for future suction feeding attempts, as described by Werth (2000b). This is something that fish, the other main group of suction feeding marine animals, avoid through the use of a continuous flow system where prey is sucked into the mouth before the water is expelled via the gills (Sanderson and Wassersug 1993). All aquatic mammals must either swallow water drawn in with their prey or expel it prior to prey swallowing and thus risk losing the prey with the excurrent flow. Perhaps, the selection pressure of this risk played a crucial role in leading toothed filter feeders like the leopard and crabeater seal to evolve their complex dentition.

The results of these captive trials appear to confirm that leopard seals are able to use suction and water expulsion/sieving when feeding on small prey underwater. While these results are compelling, they are only preliminary and based on two captive specimens feeding on thawed fish rather than schooling wild krill. Future research should focus on observing foraging behaviour when feeding on large as well as small prey. Until these behaviours are also observed in a wild setting, it is still possible that the suction feeding behaviours observed here are learned behaviours that have developed in response to feeding on non-evasive dead prey rather than being representative of wild feeding.

#### Dental morphology

The lack of abrasive wear on the postcanine dentition supports the hypothesis that these teeth, and their long sharp cusps, are primarily used for sieving, rather than for piercing prey during grip-and-tear feeding as suggested by Adam and Berta (2002). Abrasive wear on the canines and incisors is congruent with descriptions of these teeth being used to pierce and hold large prey as it is shaken apart prior to swallowing (Hamilton 1939; Edwards et al. 2010); since the postcanines do not show similar amounts of abrasive wear, they probably are not frequently used in a similar fashion. The relatively delicate morphology of the leopard seal's multi-cusped postcanines (when compared to other grip-and-tear feeding marine mammals such as the killer whale) may constrain this species' predatory capacity by leading them to adopt their prey shaking, grip-and-tear



handling technique when dealing with large prey. Although slower and energy intensive (Rogers 2009), this method involves holding large prey with the robust anterior teeth during shaking and thus limits postcanine abrasion or fracture, which could otherwise reduce efficiency of the postcanine teeth in retaining small prey during the water expulsion and sieving that follows suction.

While some food piercing by the postcanines is inevitable when prey is captured and held in the mouth (as possibly indicated by the presence of fractured postcanines in 6 of the specimens examined), the discrepancy in the presence of abrasive wear on the rostral and postcanine teeth supports the hypothesis that these two sets of teeth were performing different primary functions during wild feeding; canines and incisors being used for piercing, and postcanines being used for sieving. This is consistent with our observations of live animals and strongly supports the hypothesis that the postcanine teeth of leopard seals are primarily used in filter feeding rather than grip-and-tear feeding.

There is also some evidence to support the hypothesis that the leopard seal's tricuspid postcanines may function more efficiently at retaining small prey than a simpler tooth shape. During our experiments with the leopard seals, we were also able to make some opportunistic observations of California sea lions (*Zalophus californianus*) feeding on small chopped fish (whitebait) out of our feeding apparatus (Online Video Resource: ESM\_1.mp4). California sea lions have near-homodont postcanines with a single main cusp. The captive sea lions were observed using suction to draw prey out of the box apparatus. During water expulsion, many of the small prey items sucked into the mouth were subsequently expelled along with the excurrent water flow. These prey items were then sucked back into the mouth individually before being swallowed. These preliminary observations require further exploration, as it is possible that their apparent inefficiency at retaining prey during suction feeding may reflect this species' simpler, single-cusped postcanine teeth. Unfortunately, it was not possible to repeat these observations using the leopard seals as both individuals rejected these small prey items in favour of larger, un-chopped fish. Nonetheless, we anticipate that if this experiment were repeated, the leopard seal's taller and more complex postcanines may prove more effective at retaining these small prey items. We could then better estimate how the teeth might function when feeding on multiple small prey items at once. This has been a point of contention in the past with some authors questioning whether these 'toothed filter feeders' (including both leopard and crabeater seals) are able to feed on multiple small prey in bulk (batch feeding) or whether each prey item is taken individually (Sanderson and Wassersug 1993; Fitzgerald 2006). Only direct observation will

confirm that prey are indeed taken in bulk during wild feeding, although circumstantial evidence corroborates this hypothesis with Lowry et al. (1988) finding over 10,000 freshly caught krill in the stomach of a leopard seal, which is a lot of krill to have been individually caught.

An alternative explanation for the abrasion seen on the canines of the leopard seal skulls is abiotic ice abrasion. This is commonly seen on the procumbent incisors and canines of the Weddell seal (*Leptonychotes weddelli*), which uses these teeth to maintain breathing holes in the ice (Stirling 1969). The constant deliberate abrasion leads to heavy wear on the apical surfaces of the teeth, similar to what is observed on leopard seal canines. However, the incisors and canines of leopard seals are not procumbent, and these seals are not known or suspected to maintain ice holes, living as they do in the pack ice, generally never far from the water's edge. It is considered likely, therefore, that the abrasive wear seen on the teeth of the leopard seals in this survey is the result of piercing during grip-and-tear processing of large prey, rather than abiotic ice abrasion.

The leopard seal's specialized dental morphology and their unusual mixed feeding mode, combining suction and sieving, allow these seals to exploit krill, an abundant Antarctic resource that would otherwise be unavailable to a large exclusively raptorial predator. Their unusual ability to switch between this feeding mode and the raptorial grip-and-tear feeding style, for which they are better known, appears to be key to their success and survival by allowing them to feed on locally available prey. Leopard seals are more than simple generalists; they are highly adapted towards two disparate feeding modes, allowing them to function as both a top predator and a planktivore within the Antarctic ecosystem.

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## References

- Adam PJ, Berta A (2002) Evolution of prey capture strategies and diet in the Pinnipedimorpha (Mammalia, Carnivora). *Oryctos* 4:83–107

- Ainley DG, Ballard G, Karl BJ, Dugger KM (2005) Leopard seal predation rates at penguin colonies of different size. *Antarctic Sci* 17:335–340. doi:[10.1017/s0954102005002750](https://doi.org/10.1017/s0954102005002750)
- Bloodworth B, Marshall CD (2005) Feeding kinematics of *Kogia* and *Tursiops* (Odontoceti: Cetacea): characterization of suction and ram feeding. *J Exp Biol* 208:3721–3730. doi:[10.1242/jeb.01807](https://doi.org/10.1242/jeb.01807)
- Carbone C, Mace GM, Roberts SC, Macdonald DW (1999) Energetic constraints on the diet of terrestrial carnivores. *Nature* 402:286–288. doi:[10.1038/46266](https://doi.org/10.1038/46266)
- Casaux R, Baroni A, Ramón A, Carlini A, Bertolin M, DiPrinzio CY (2009) Diet of the leopard seal *Hydrurga leptonyx* at the Danco Coast, Antarctic Peninsula. *Polar Biol* 32:307–310. doi:[10.1007/s00300-008-0567-0](https://doi.org/10.1007/s00300-008-0567-0)
- Costa GC (2009) Predator size, prey size, and dietary niche breadth relationships in marine predators. *Ecology* 90:2014–2019. doi:[10.1890/08-1150.1](https://doi.org/10.1890/08-1150.1)
- Davis RW, Fuiman LA, Williams TM, Collier SO, Hagey WP, Kanatous SB, Kohin S, Horning M (1999) Hunting behavior of a marine mammal beneath the Antarctic fast ice. *Science* 283:993–996. doi:[10.1126/science.283.5404.993](https://doi.org/10.1126/science.283.5404.993)
- Edwards EWJ, Forcada J, Crossin GT (2010) First documentation of leopard seal predation of South Georgia pintail duck. *Polar Biol* 33:403–405. doi:[10.1007/s00300-009-0709-z](https://doi.org/10.1007/s00300-009-0709-z)
- Fitzgerald EMG (2006) A bizarre new toothed mysticete (Cetacea) from Australia and the early evolution of baleen whales. *Proc R Soc B* 273:2955–2963. doi:[10.1098/rspb.2006.3664](https://doi.org/10.1098/rspb.2006.3664)
- Fossette S, Gleiss AC, Casey JP, Lewis AR, Hays GC (2011) Does prey size matter? Novel observations of feeding in the leatherback turtle (*Dermochelys coriacea*) allow a test of predator—prey size relationships. *Biol Letters*. doi:[10.1098/rsbl.2011.0965](https://doi.org/10.1098/rsbl.2011.0965)
- Hall-Aspland SA, Rogers TL (2004) Summer diet of leopard seals (*Hydrurga leptonyx*) in Prydz Bay, Eastern Antarctica. *Polar Biol* 27:729–734. doi:[10.1007/s00300-004-0662-9](https://doi.org/10.1007/s00300-004-0662-9)
- Hamilton JE (1939) The leopard seal *Hydrurga leptonyx* (De Blainville). *Discovery Reports* 18:239–264
- Heithaus MR, Dill LM (2009) Feeding strategies and tactics. In: Perrin WF, Würsig B, Thewissen JGM (eds) *Encyclopedia of marine mammals*, 2nd edn. Academic Press, San Diego, pp 414–423
- Kane EA, Marshall CD (2009) Comparative feeding kinematics and performance of odontocetes: belugas, Pacific white-sided dolphins and long-finned pilot whales. *J Exp Biol* 212:3939–3950. doi:[10.1242/jeb.034686](https://doi.org/10.1242/jeb.034686)
- Kastelein RA, Mosterd P (1989) The excavation technique for molluscs of Pacific walruses (*Odobenus rosmarus divergens*) under controlled conditions. *Aquat Mamm* 15(1):3–5
- Kastelein RA, Gerrits NM, Dubbeldam JL (1991) The anatomy of the walrus head (*Odobenus rosmarus*): part 2. Description of the muscles and of their role in feeding and haul-out behavior. *Aquat Mamm* 17:156–180
- Klages NTW, Cockcroft VG (1990) Feeding behaviour of a captive crabeater seal. *Polar Biol* 10:403–404. doi:[10.1007/BF00237828](https://doi.org/10.1007/BF00237828)
- Lowry LF, Testa JW, Calvert W (1988) Notes on winter feeding of crabeater and leopard seals near the Antarctic Peninsula. *Polar Biol* 8:475–478. doi:[10.1007/BF00264724](https://doi.org/10.1007/BF00264724)
- Marshall CD, Kovacs KM, Lydersen C (2008) Feeding kinematics, suction and hydraulic jetting capabilities in bearded seals (*Erignathus barbatus*). *J Exp Biol* 211:699–708. doi:[10.1242/jeb.009852](https://doi.org/10.1242/jeb.009852)
- Naito Y, Bornemann H, Takahashi A, McIntyre T, Plötz J (2010) Fine-scale feeding behavior of Weddell seals revealed by a mandible accelerometer. *Polar Sci* 4:309–316
- Øritsland T (1977) Food consumption of seals in the Antarctic pack ice. In: Llano GA (ed) *Adaptations within antarctic ecosystems*, Proceedings of the Third SCAT symposium on Antarctic Biology, Smithsonian Institution, Washington DC, pp 749–768
- Rogers TL (2009) Leopard seal *Hydrurga leptonyx*. In: Perrin WF, Würsig B, Thewissen JGM (eds) *Encyclopedia of Marine Mammals*, 2nd edn. Academic Press, San Diego, pp 673–674
- Ross GJB, Ryan F, Saayman GS, Skinner J (1976) Observations on two captive crabeater seals *Lobodon carcinophagus* at the Port Elizabeth Oceanarium. *Intl Zoo Yearbook* 16:160–164
- Sanderson SL, Wassersug R (1993) Convergent and alternative designs for vertebrate suspension feeding. In: Hanken J, Hall BK (eds) *The Skull*, vol 3. University of Chicago Press, Chicago
- Siniff DB, Stone S (1985) The role of the leopard seal in the trophodynamics of the Antarctic marine ecosystem. In: Siegfried WR, Condy PR, Laws RM (eds) *Antarctic nutrient cycles and food webs*. Springer, Berlin, pp 555–560
- Skinner JP (2009) Head striking during fish capture attempts by Steller sea lions and the potential for using head surge acceleration to predict feeding behaviour. *Endangered Species Research* 10:61–69. doi:[10.3354/esr00236](https://doi.org/10.3354/esr00236)
- Stephens DW, Krebs JR (1986) *Foraging theory*. Princeton University Press, Princeton NJ
- Stirling I (1969) Tooth wear as a mortality factor in the Weddell seal, *Leptonychotes weddelli*. *J Mammal* 50:559–565
- Viviant M, Trites AW, Rosen DAS, Monestiez P, Guinet C (2010) Prey capture attempts can be detected in Steller sea lions and other marine predators using accelerometers. *Polar Biol* 33:713–719. doi:[10.1007/s00300-009-0750-y](https://doi.org/10.1007/s00300-009-0750-y)
- Werth AJ (2000a) Feeding in marine mammals. In: Schwenk K (ed) *Feeding: form function and evolution in tetrapod vertebrates*. Academic Press, San Diego, pp 487–526
- Werth AJ (2000b) A kinematic study of suction feeding and associated behaviour in the long-finned pilot whale, *Globicephala melas* (Traill). *Mar Mamm Sci* 16:299–314. doi:[10.1111/j.1748-7692.2000.tb00926.x](https://doi.org/10.1111/j.1748-7692.2000.tb00926.x)
- Werth AJ (2006a) Mandibular and dental variation and the evolution of suction feeding in Odontoceti. *J Mamm* 87:579–588. doi:[10.1644/05-MAMM-A-279R1.1](https://doi.org/10.1644/05-MAMM-A-279R1.1)
- Werth A (2006b) Odontocete suction feeding: experimental analysis of water flow and head shape. *J Morphol* 267:1415–1428. doi:[10.1002/jmor](https://doi.org/10.1002/jmor)