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Oral suction of a Pacific walrus (*Odobenus rosmarus divergens*) in air and under water

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Abstract

Walruses mainly eat sessile bentic prey. Of bivalve molluscs, usually only the siphons and feet are found in walrus stomachs, and it is thought that walruses use oral suction to separate the molluscs from their shells. Low pressure in the buccal cavity is caused by retraction and depression of the tongue which acts like a piston. The pressure in the oral cavity of a female walrus was measured during several in-air and underwater suction tests. The lowest pressure recorded in air was −87.9 kPa (−0.879 Bar, almost vacuum) when the walrus sucked on the pressure transducer. The lowest pressure recorded under water was −118.8 kPa (−1.188 Bar) when the walrus was sucking on a mackerel. The walrus has good control over its tongue muscles and over both the pressure and the duration of suction.

Introduction

In contrast to most pinnipeds which prey on fish and squid, walruses mainly eat sessile bentic prey (Fay 1982). Of bivalve molluscs, usually only the siphons and feet are found in walrus stomachs. The bodies may be digested so quickly that they are difficult to detect. Vibe (1950) suggested that walruses use suction to separate the molluscs from their shells. Evidence to support this hypothesis was given by Oliver et al. (1983, 1985) who found intact empty shells on both sides of furrows in the ocean floor in walrus foraging areas. Kastelein and Mosterd (1989) observed walruses feeding on bivalve molluscs in a sandy substrate in a pool and leaving the empty shells on the bottom. Fay (1982) suggested that low pressure in the buccal cavity could be caused by retraction and depression of the tongue which could act like a piston. Kastelein and Gerrits (1990) showed that the buccal cavity of the walrus is relatively large due to the curvature of the maxilla and hard palate, and Kastelein et al. (1991) described the well-developed tongue muscles which are involved in producing oral suction.

The retraction speed of feet and siphons of molluscs depends on the species but the process is also temperature dependent. There is good evidence that *Serripes* (*Cardium*) *groenlandicus* is comparitively slow in retracting its feet. This may allow the walrus to remove the feet, and possibly the attached body, before they have retracted into the shells (Mansfield 1958). The suction force of the walrus, required to separate the body or body parts from the shells, probably depends on the degree of retraction and closure of the clam. It is probable that beyond a certain state of retraction, the Walrus is unable to extract the edible parts.

After detecting an object on the ocean floor, a walrus has a limited amount of time to identify (Kastelein and van Gaalen 1988; Kastelein et al. 1990), in certain cases excavate (Oliver et al. 1983; Kastelein and Mosterd 1989) and position the prey item between its lips (Kastelein et al. 1991), if it is to use the suction technique succesfully with a clam. This foraging technique has to be efficient because adult walruses in oceanaria eat about 50 kg of food per day (Kastelein pers. obs.). This would be about 3000 adult sand gapers (*Mya arenaria*) with an average soft body weight of 17 g. Born and Knutsen

(1990) even found 6401 individual prey items in a walrus stomach. A bivalve may detect the vibrations or current caused by an approaching walrus sooner than the walrus detects the clam, so the retraction of foot and siphon may have begun by the time the walrus touches the prey (KRISTENSEN 1957). So, the amount of time available for food processing is governed by the detection distance and retraction speed of the mollusc, as well as by the identification and excavation speed and suction power of the walrus. The prey identification speed of walruses was studied in a psychophysical study by KASTELEIN and VAN GAALEN (1988). The present study investigates the parameters determining suction force.

Material and methods

Animal

The study was done with a 10-year-old female Pacific walrus (*Odobenus rosmarus divergens*, code OrZH004) which was born in the wild, arrived at Harderwijk in 1985 and which has participated in educational performances since then.

Study area

A 50 cm × 50 cm square hole was made in a door between the walrus quarters and an adjacent room. In this room, a 50 cm × 50 cm × 50 cm water trough was placed on the floor beneath the hole. The walrus was trained to put her head through the hole in the door and into the water in the trough on command.

Experimental procedure

To measure the pressure changes in the walrus' mouth a Millar PC 350 catheter pressure transducer was used. This pressure transducer was chosen, because it is small (1.67 mm diameter), it has a linear relationship between pressure and output voltage, a broad bandwidth (about 3 kHz) and it is stabilized for temperature effects (VAN LEEUWEN and MULLER 1983). The output voltages were amplified with a differential amplifier (AD 610 K). The signals were stored on a Bell and Howell recorder (speed 30 inch/s, bandwidth 0–10 kHz), played back to be visualized on a Tektronix digital storage scope (type 2211) and plotted on a HP 7475A plotter (Hewlett-Packard).

The pressure transducer was inserted into a thawed fish. To protect the sensor, a hollow metal tube with a pointed end was first inserted through the body of the fish from the anus to the mouth. Then, the wirelike pressure transducer was threaded through the tube until the tip became visible. The tube was carefully removed and the sensor was placed so that its tip stuck out of the mouth of the fish by about 1 cm.

The pressure changes in the walrus' mouth were measured under various circumstances. When a fish containing the pressure transducer was held in front of the walrus' mouth, the animal gripped the rostral third part of the fish in its mouth, and then tried to suck it from the hand of the trainer (Fig. 1). The trainer kept a firm hold of two thirds of the fish until it broke or slipped from his hands. This could be done both in air and under water. Herring (*Clupea harengus*) and mackerel (*Scomber scombrus*) 20 to 25 cm in length were used.

In air, the pressure transducer was also offered while held along the trainer's finger, the walrus having been trained to suck the finger. In air, the transducer could also be held perpendicular to the cheek of the trainer. The walrus had been trained to "kiss" the trainer, and thus to suck the transducer, which extended about 6 cm into the walrus' mouth cavity. Both sucking the trainer's finger and "kissing" his cheek were known behaviours to the walrus because they were used in educational performances. In other experiments, the pressure transducer alone was offered to the animal. In all experiments, about 6 cm of the catheter tip was inside the walrus' mouth during suction.

The suction curves produced in this study consist of a zero level which is equal to the ambient air pressure, a descending part in which the pressure is dropping due to the depression and retraction of the tonge, a section in which maximum pressure is exerted, and an ascending part in which the pressure is returning gradually to ambient pressure because air or an object slips, or water flows, into the mouth cavity. For an example see figure 2. The following parameters were calculated:

Amp 0 = ambient pressure.
Amp 90 = 90 % of the maximum amplitude.
Amp 10 = 10 % of the maximum amplitude (10 % below ambient pressure).
Amp dif = Amp 90 – Amp 10.
Amp max = maximum amplitude.
T10 = Duration of the suction event at Amp 10.

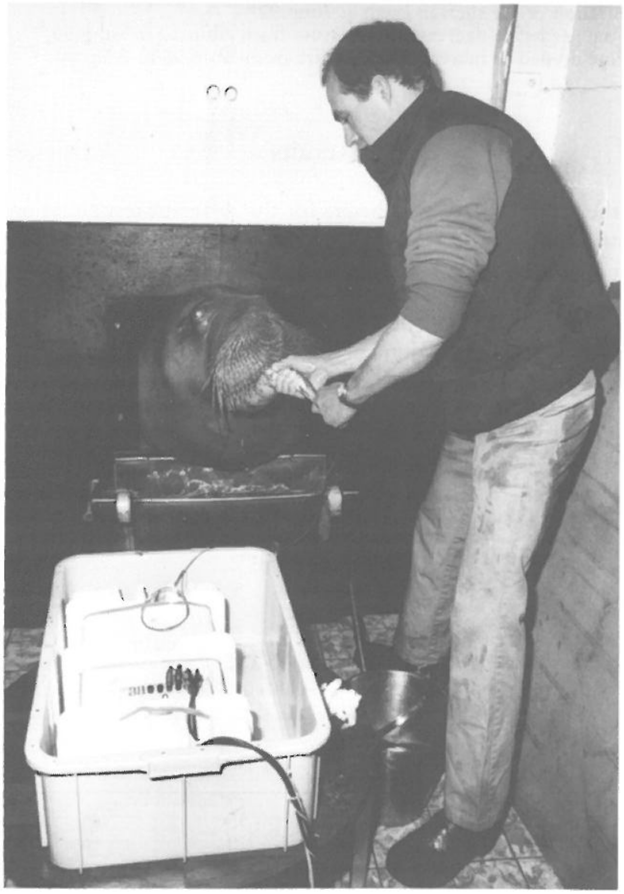

Fig. 1. The walrus sucking a fish containing the pressure transducer. The hole in the door is 50 × 50 cm (Photo: HENK MERJENBURGH)

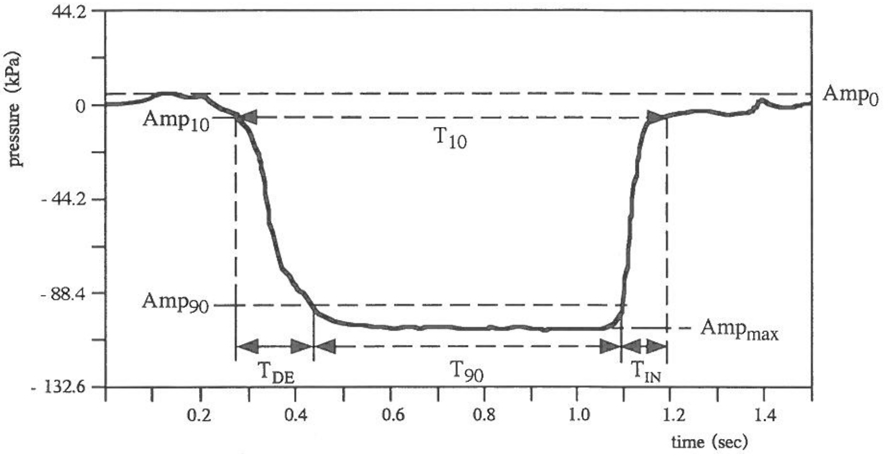

Fig. 2. An example of a curve showing the pressure changes in a walrus oral cavity during oral suction. (For abbreviations see text)

T90 = Duration of the suction event at Amp 90.
Tde = Time needed to decrease the pressure from Amp 10 to Amp 90.
Tin = Time needed to increase the pressure from Amp 90 to Amp 10.

Results

Table 1 shows the suction curve parameters for the different test situations which will be described in detail below.

Finger in air

On average the shortest T90 and smallest Amp 90 occurred when the walrus sucked the finger. A typical example of a suction curve is shown in figure 3A.

Cheek in air

On average the shortest T10, Tde and Tin and the largest Amp 90 occurred when the walrus "kissed" the trainer's cheek in air. Using this method, the suction parameters were less variable in each trial which is apparent from the relatively small standard deviations. A typical example of a suction curve is shown in figure 3B.

Table 1. **Average values (x) and standard deviations (S.D.) of suction parameters during a number of trials (N) in a 10-year-old female Pacific walrus**

Situation		In air				Under water
		Finger	Cheek	Transducer	Fish	Fish
Amp90 (kPa)	x	41	62	55	45	73
	S.D.	18	11	19	6	24
	N	8	11	5	4	19
Amp10 (kPa)	x	5	7	6	5	8
	S.D.	2	1	3	1	2
	N	8	11	5	4	19
Amp dif (kPa)	x	36	55	49	40	65
	S.D.	16	10	16	5	21
	N	8	11	5	4	19
Amp max (kPa)	x	46	69	62	51	81
	S.D.	19	12	21	6	26
	N	8	11	5	4	19
T10 (ms)	x	343	287	1310	1064	766
	S.D.	311	116	512	634	373
	N	8	11	5	4	19
T90 (ms)	x	73	103	339	266	241
	S.D.	56	60	239	226	164
	N	8	11	5	4	19
Tde (ms)	x	134	112	724	688	311
	S.D.	181	50	425	440	205
	N	8	11	5	4	19
Tin (ms)	x	140	68	233	115	218
	S.D.	203	40	208	82	207
	N	8	11	5	4	19

Pressure transducer alone

The T10, T90, Tde and Tin were the longest when the walrus sucked on the pressure transducer alone. The suction curves were quite irregular. An example is shown in figure 3C.

Fish in air

In each trial the animal usually sucked a few times without being able to move the fish. The final successful suck either pulled the entire fish from the trainer's hand, or the fish was pulled apart, leaving about half of it in the trainer's hand. In both events, the fish or a part of it was sucked over the sensor shortly after the suction was created. The values of the parameters measured during trials with herring and mackerel did not differ statistically, and therefore are analysed together.

Compared to the other test situations (except when the animal was sucking on the pressure transducer alone), the T90, Tde and Tin were on average long when the walrus sucked on fish in air. A typical example of a suction curve is shown in figure 3D.

Fish under water

The most conspicuous differences between under water and in-air suction on fish were the on average shorter T10 and Tde, the longer Tin and larger Amp 90 under water. The lines of the suction curves were smoother than when fish was sucked on in air. An example of a suction curve is shown in figure 3E.

Discussion

Physics

FAY (1982) reports on an anecdotal observation of a walrus which produced a pressure of around −91.4 kPa (−0.914 Bar) when sucking a tube which was connected to a mechanical pressure gauge. At the time of measurement, the animal was pulling air along the mouth piece. In the present study, using more sophisticated equipment, the lowest pressure recorded (Amp max) in air was −87.9 kPa (−0.879 Bar) when the walrus sucked on the pressure transducer. The minimum pressure reached while sucking under water was lower; −118.8 kPa (−1.188 Bar) when the walrus was sucking a mackerel.

The buccal cavity of a walrus can be regarded as a cylinder with a piston (the tongue). In rest, the tongue fills the buccal cavity almost entirely (KASTELEIN et al. 1991), so the initial volume of the cavity is practically zero. When the tongue is withdrawn to a caudal position, the volume of the buccal cavity is enlarged.

If the mouth cavity is filled with air, pressure (p) and mouth volume (V) are related by Boyle's law: $p_i \cdot V_i = p_f \cdot V_f$ (i = initial, f = final). As $V_f \gg V_i$ and p_i = the atmospheric pressure = 1 atm., it follows that p_f is close to 0 atm.; so the mouth cavity is close to vacuum. In air, the pressure cannot reach a value below 0 atm., so that a pressure transducer may record a pressure of maximally 1 atm. below the "baseline" of ambient pressure.

In water, the situation is different, and Boyle's law does not apply. When the piston is withdrawn to generate pressure of 0 atm., the water column will break after a certain short period and the cavity will be filled with water, water vapour and gas that was originally dissolved in the water. This phenomenon is unstable and is called "cavitation". At sufficiently low pressure, cavitation always occurs for a time, the length of which depends on the pressure and on the concentration of particles and dissolved gas in the water.

On a shorter time scale, the force applied to the piston may be transformed directly to

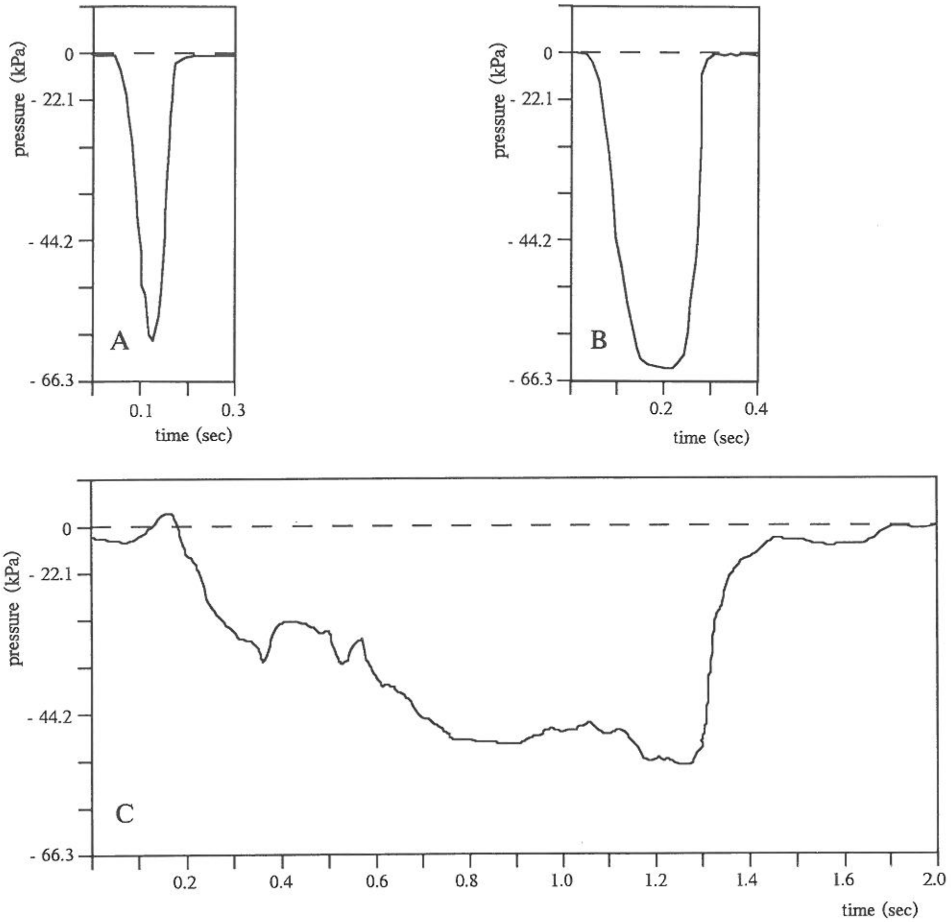

Fig. 3 A–C

pressure. So, a walrus may theoretically be able to generate a pressure of more than 1 atm. below ambient pressure for a short time.

In the above explanation, it is assumed that the flow through the mouth aperture is insignificant. In reality, food will be sucked into the oral cavity during tongue retraction and the pressure changes in the buccal cavity will be more complex.

Finger in air

The short T90 and small Amp90 are probably due to the fact that this was a trained behaviour in which the animal was rewarded for producing the "suction" sound, and not for the maximum suction power, or duration. From experience the animal probably knew it would not be able to suck in the object (= finger).

Cheek in air

The suction parameters between trials were rather similar when the animal sucked on a cheek in air. This is probably because other than the walrus' tongue, nothing moved into

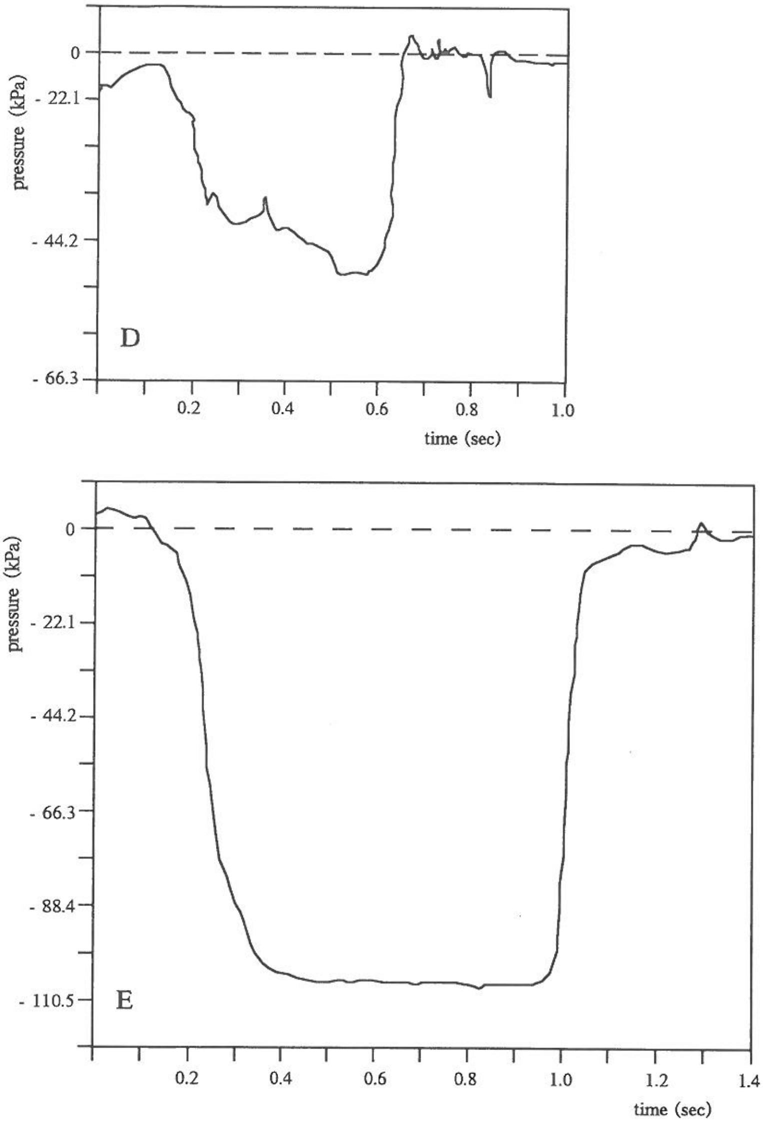

Fig. 3 (see also left side). Typical examples of suction curves on the same scales of time and pressure of A: Finger in air, B: Cheek in air, C: Pressure transducer alone, D: Fish in air, and E: Fish under water

the oral cavity and because the walrus controlled the entire situation. It started the trial by putting its lips against the cheek with a certain pressure, retracted its tongue, and allowed some air to enter the oral cavity to produce the "kiss" sound it was trained to produce in performances. The lips did not surround an object, but were pushed against the cheek of the trainer. This apparently also closed off the oral cavity tightly, resulting in a high Amp90. However, this parameter was not as high as when sucking fish under water. Air flows faster into the oral cavity than water, thus the pressure amplitudes in air are less negative than in water.

Pressure transducer alone in air

The long duration of the suction event when sucking the transducer alone in air can be explained by the fact that the transducer only filled a minute portion of the oral cavity, leaving a large volume of air to be expanded. This allowed the tongue to retract completely, which took more time. The relatively large Amp90 indicates that the walrus is able to close its lips tightly, even around such a small diameter pressure transducer. However, some air probably leaked into the oral cavity causing the irregularities in the suction curves.

Fish in air

The suction curves produced on fish in air are irregular. Pressure changes are probably caused by air leaking around the fish while it was sliding into the oral cavity. The suction events are long probably because the walrus attempted to swallow the fish. The irregularities at the end of the suction event in figure 3D are caused by the fish slipping over the pressure transducer.

Fish under water

During suction on fish under water the Tde was shorter, the Amp90 much higher, and the Tin longer than in air, probably because water flowed into the oral cavity more slowly than air. During the Tin the fish was pulled from the hand quickly and some water probably flowed into the oral cavity. The irregularity at the end of the suction event in figure 3E is caused by the fish slipping over the pressure transducer.

Correlations between suction parameters

To determine the level of control the walrus has over the different suction parameters, the correlations between these parameters were calculated. The correlations between the different suction curve parameters in all situations in air and under water are shown in table 2. The parameters within the following pairs are positively correlated both in air and under water: T10-Tde, T10-T90 and T10-Tin. This means that the longer the entire suction event (T10), the longer each of its 3 time components (Tde, T90 and Tin). Under water the parameters of the following 2 parameters pairs are positively correlated: Amp90-T90 and Tin-Tde. These are not correlated in air. This is probably due to the high density of water

Table 2. **The correlation between the different suction parameters in air (A) and under water (B)**
A – indicates no significant correlation. A + indicates significant correlation ($p < 0.05$)

A. Suction in air ($N = 29$, significance at $r > 0.306$)

	T10	T90	Tde	Tin
T90	+			
Tde	+	+		
Tin	+	+	–	
Amp90	–	–	–	+

B. Suction in water ($N = 17$, significance at $r > 0.412$)

	T10	T90	Tde	Tin
T90	+			
Tde	+	–		
Tin	+	–	+	
Amp90	–	+	–	–

compared to air. Water passes between the object and the lips with more difficulty, causing a higher force to retract the tongue which causes a slow sliding movement of the prey. In air, probably too much air leaks into the oral cavity, and the animal may not be able to maintain a large Amp90 for a long period without air leaking into the oral cavity. In air, the parameters of the following 2 pairs are positively correlated: Tde-T90 and Tin-T90. These are not correlated under water. This is probably due to the different shapes of the suction curves; in air, they are often V-shaped, while under water they are usually U-shaped.

Ecological significance

The present study shows that at least 3 parameters influence the shape of the suction curve (Tab. 3). The Tde is influenced by the retraction speed of the tongue, the tightness of the lips on the food item, and the presence of sealing mucus. The T90 is influenced by the time the animal can keep or decides to keep its tongue retracted, the tightness of the lips on the food item, and by the toughness and slipperiness of the food item and the strength of the trainer. The Amp90 is influenced by the strength and volume of the tongue, the initial position of the tongue in the buccal cavity, the fit of the tongue in the buccal cavity, the tightness of the lips around the food item and also by the shape, firmness and toughness of the food item and the presence of sealing mucus.

Table 3. **Parameters which influence the shape of the suction curve**

	Tde	T90	Amp90
Walrus	1. Retraction speed of tongue 2. Tightness of lips on food item	1. Time the animal can keep or decides to keep its tongue retracted 2. Tightness of lips on food item	1. Strength of tongue 2. Initial position of tongue 3. Fit of tongue in buccal cavity 4. Volume of tongue 5. Tightness of lips on food item
Food item	Sealing mucus	1. Toughness 2. Slipperiness	1. Shape 2. Firmness 3. Toughness 4. Sealing mucus
Trainer		Strength	

In air, the walrus normally uses its capacity for oral suction mainly during its suckling period. Ray (1960) describes a walrus calf which emptied a 225 ml baby bottle in 15 seconds, and often sucked the plastic container flat. Walruses have a relatively long suckling period of at least 15 months (Fay 1982), and suckling probably occurs both on land and under water (Miller and Boness 1983). Some walruses sometimes eat seals and use in air and under water oral suction to process their prey. Only strips of skin and blubber are found in walrus stomachs, indicating that these parts only are sucked off without mastication (Collins 1940; Breshin 1958; Perry 1967; Lowry and Fay 1984; Fay et al. 1990; Timoshenko and Popov 1990).

When a walrus encounters a clam in the sea bed, whether the clam will be eaten or not depends on the behaviour of both organisms. For the clam, its shape, firmness and toughness and the ability to detect a walrus are of importance. Shape and firmness are fixed properties of a clam, but the toughness of the siphon may depend on its retraction state. The more retracted, the more difficult it is to suck the clam out of its shell. For the walrus the volume, strength and retraction speed of the tongue and the firmness of the lips on a food item are of importance. The volume seems to be a fixed property, unless the walrus can retract the tongue partly during a suction event. The walrus can probably determine the strength and retraction speed of its tongue and the pressure on the clam with its lips. The pressure of the funnel-shaped lips should be sufficient to prevent water from flowing around the prey into the oral cavity, but low enough to prevent the clam's shells from breaking. Depending on the toughness of its prey, the walrus may retract its tongue faster, or use more muscle bundles. Possibly, the walrus has an expectation of the toughness of its prey before it sucks. If that is true, the Tde is mainly consciously determined by the walrus. This explains also part of the correlations in table 2. If a siphon is slowly stretched during a suck, the toughness is slowly decreased until the siphon breaks off the clam's body. This might explain the function of the long T90's found in the present study (in air 625 ms and under water 658 ms); because the walrus was eager to swallow the fish, she kept her tongue retracted for a longer time.

The present study provides insight into the control a walrus has over its oral suction power, speed and duration. Whether the walrus can process bivalve molluscs at all stages of siphon and foot retraction remains to be determined.

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Zusammenfassung

Orales Saugvermögen eines Pazifischen Walrosses (Odobenus rosmarus divergens) in Luft und unter Wasser

Walrosse fressen hauptsächlich sessilen tierischen Benthos. Von zweischaligen Weichtieren werden normalerweise nur die Siphonen und Füße in Walroßmägen gefunden. Es wird allgemein angenommen, daß Walrosse durch ihr Saugvermögen Weichtiere von deren Schalen trennen können. In der Mundhöhle kann Unterdruck dadurch erzeugt werden, daß die wie ein Kolben funktionierende Zunge zurück- und heruntergezogen wird. Während mehrerer Über- und Unterwasser-Saugtests wurde der Druck in der Mundhöhle einer Walroßkuh gemessen. Durch Saugen am Druckübermittler konnte über Wasser als niedrigster Druck – 87,9 kPa (−0,879 bar; fast Vakuum) gemessen werden. Beim Ansaugen einer Makrele unter Wasser konnte als niedrigster Druck −118,8 kPa (−1,188 bar) registriert werden. Da das Walroß seine Zungenmuskeln präzise kontrollieren kann, sind Druck und Dauer des Saugaktes gut regulierbar.

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