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A B S T R A C T

Along the Dutch shores hundreds of harbour porpoises *Phocoena phocoena* are stranded each year. A recurrent phenomenon in the Netherlands is a surge of strandings in late winter and early spring of severely mutilated porpoises, that are mostly in good nutritional body condition (thick blubber layer). These mutilated porpoises have parts of the skin and blubber, and sometimes of the muscle tissue missing. By reviewing photographs of stranded animals taken at the stranding sites as well as autopsy results we found 273 mutilated animals from 2005 to 2012. Mutilations could be classified into several categories, but wounds had been mostly inflicted to the sides of these animals, in a zigzag fashion, or to the throat/cheek region. The stomach contents of 31 zigzags, 12 throats/cheeks and 31 control animals that were not mutilated, from the same age and blubber thickness categories were compared; all these animals had stranded between December and April, 2006–2012. The diet of individuals with zigzag lesions to their sides consisted for a large part of gobies, while animals that had wounds at the throat/cheek had been feeding predominately on clupeids. In comparison, animals without mutilations had a more varied diet, including gobies and clupeids, but also a large proportion of sandeels and gadoids. The finding that the type of mutilation corresponds to a certain diet suggests that porpoises that were feeding on different prey, or in different micro-habitats, were hit in different ways. Animals feeding at the sea floor (on gobies) apparently run a risk of being hit from the side, while animals supposedly feeding higher in the water column (on schooling clupeids), were predominantly hit from below, in the throat region. The wider variation in the diets of non-mutilated porpoises is suggestive of them using a larger variety of micro-habitats.

1. Introduction

Harbour porpoises *Phocoena phocoena*, being relatively large piscivores, are considered apex predators in the southern North Sea, where bigger marine predators such as large sharks or killer whales *Orcinus orca* are largely absent. Still, dozens of severely mutilated porpoises wash ashore yearly in the Netherlands. These animals have sharp, smoothly curved or erratic zigzag cuts over their bodies and have parts of the skin and blubber missing (Leopold et al., 2015). Earlier, such mutilations have been tentatively attributed to fishermen confronted with bycatches (Camphuysen and Oosterbaan, 2009; Haelters and Camphuysen, 2009; Leopold and Camphuysen, 2006), ship propeller strikes (Camphuysen and Siemensma, 2011, cf. Thompson et al., 2010), sand dredgers (Oudenaarden, 2012a,2012b) or scavenging grey seals *Halichoerus grypus* (Camphuysen and Siemensma, 2011). North Sea dolphins, particularly bottlenose *Tursiops truncatus* and white-beaked dolphins *Lagenorhynchus albirostris* have also been considered, as these may harm and even kill porpoises, but could be excluded as actors in this respect. Dolphins are rather rare in the SE North Sea and the lesions inflicted by these attacks are well described and quite different from those found in the mutilated porpoises in the Netherlands (Barnett et al., 2009; Haelters and Everaarts, 2011; Patterson et al., 1998; Ross and Wilson, 1996).

In the SE North Sea, grey seals were first implicated as predators of porpoises in Belgium and France (Bouveroux et al., 2014; Haelters et al., 2012). Two decades ago grey seals were seen incidentally to catch and partly consume harbour porpoises in the Isle of Man and in

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Northumberland, UK (Vodden, 1995). Van Bleijswijk et al. (2014) identified grey seal DNA in bite marks on harbour porpoise carcasses stranded in the Netherlands, linking the scarce observations of actual attacks to the large numbers of mutilated porpoises currently washing up dead in the SE North Sea.

Grey seals re-colonised Dutch waters around 1980 and the subsequent population development showed exponential growth (Brasseur et al., 2010; Reijnders et al., 1995). In 2012, 835 grey seals were counted in the Delta area in the southwest of the country (Strucker et al., 2013) and 3059 in the Dutch part of the Wadden Sea (Common Wadden Sea Secretariat, 2012). Grey seals range widely from their haul-out sites (Aarts et al., 2008; Brasseur et al., 2010; Russell et al., 2013) and occur anywhere off the Dutch and Belgian coastlines. Numbers of porpoises have also increased markedly in the southern North Sea in recent decades (Camphuysen, 2011; Camphuysen and Siemensma, 2011; Haelters and Camphuysen, 2009; Hammond et al., 2013; Scheidat et al., 2012) and therefore, interactions between seals and porpoises have potentially become much more frequent here in recent years.

Hundreds of stranded harbour porpoises are reported per year in the Netherlands and 25% of these bear the tell-tale marks of grey seal attacks (Leopold et al., 2015). Mutilations take different forms and several types are distinguishable, which may provide clues as to how these porpoises were attacked. In addition, the stomach contents of the mutilated animals may yield information on where the victims were feeding, when attacked. In this paper, we consider the different types of wounds inflicted, in concert with the stomach contents of mutilated porpoises to gain insight in the circumstances under which these porpoises were attacked.

2. Material and methods

2.1. Examining photographic evidence and autopsy data

The Dutch coastline (523 km, including the Wadden Sea and Western Scheldt) is mostly readily accessible to the public and most stranded cetaceans are probably reported, to www.walvisstrandingen.nl. Meta-information was collected for each animal, including date, location, and fate (animal collected or discarded). Since 2006, stranded porpoises were routinely collected for autopsy along several stretches of coastline, and incidentally elsewhere. Autopsies took place on Texel in 2006 (Leopold and Camphuysen, 2006) and from 2007 at the Faculty of Veterinary Pathology Medicine, Department of Pathobiology of Utrecht University (Gröne et al., 2012). From animals that went through autopsy, body length, sex and blubber thickness, taken dorsally, laterally and ventrally, just anterior of the dorsal fin were also recorded. These animals were all photographed, with special attention for external lesions.

In addition to the photographs taken during autopsies, all photographs of animals that were stranded between 2003 and 2012 that were made by the general public and uploaded to www.walvisstrandingen.nl were examined. For this study, we reviewed photographs of 1974 stranded porpoises, including 857 that went through autopsy. For each animal, we established, if possible, external damage. The state of decomposition at recovery (DCC: decomposition code) was established for all animals examined, on a 5-point scale: 1 = live stranding; 2 = fresh; 3 = visibly starting to decompose; 4 = rotten; 5 = remains (mere bones or "mummified"). Animals that were too rotten (mostly DCC 4 and 5 but also many DCC 3 animals) and animals for which only poor-quality photographs (taken at the strandings site) were available, were not analysed. Three observers assessed the photographs independently, categorising lesions as possibly inflicted by seals or probably caused by other agents such as ship propellers, knives or axes, and trauma inflicted by scavengers (birds, dogs, foxes, etc.). Data were entered into a database, discussed and amended afterwards if different observers had classed damaged porpoises differently.

Considering the traumas now known to have been inflicted by seals (Leopold et al., 2015; van Bleijswijk et al., 2014), we distinguished five types of wounds within the "major blubber defects" category:

a. Zigzag patterns: animals with multiple traumas inflicted mainly to the sides of the bodies, under various angles, with parts of the skin and blubber apparently torn off; some of these parts missing or hanging loose from the body (see Appendix A for photographs of these and other lesions);
b. Head–tails: animals with the head and tail sections largely intact, but with most of the soft parts in between lost;
c. Throat/cheek: animals with a large part of the skin and blubber missing from the side of the head, usually under the eye, extending to or from the throat area;
d. Circular body: animals with large cuts behind the head, at or near the widest part of the body and often with large sheets of the skin and blubber missing;
e. Body parts: loose pieces of the skin and blubber, loose dorsal fins, pectoral fins, flukes, or tailstocks, with or without loose pieces of the skin and blubber attached.

Lesions, considered not related to seals, were not used in the analysis. These included defects with very smooth edges that were supposedly inflicted with a cutting force, rather than a tearing force: animals cut straight in two, animals with amputated dorsal fins, pectoral fins or tail-flukes and cuts and stabs to the body apparently inflicted with knives (see: Haelters and Camphuysen, 2009). Small ($<5 \times 10$ cm diameter), often multiple lesions with irregular edges, with more superficial penetration were supposedly inflicted by scavenging birds, and not considered.

All photographs taken from the same animal were examined in concert. For each animal photographed, we noted if it showed a major blubber defect and if so, which type.

2.2. Selecting animals for stomach content analysis

Stomach content analysis was performed on three groups of porpoises: zigzag animals, animals with mutilations to the throat or cheek and animals that were not mutilated. Intact, non-empty stomachs were available for 36 zigzag animals. As most of these were juveniles (31 animals <130 cm total length, cf. Lockyer, 2003 for North Sea porpoises) that were found between December and April 2006–2012, this group was selected to reduce heterogeneity. Average blubber thickness of these 31 animals was 20.5 ± 5.3 mm and most was fresh or starting to decompose (DCC <3). For comparison, we used animals that had been mutilated at the throat or cheek (n = 12) and animals that were not mutilated (n = 31). Selection criteria for these were: juvenile, found between December and April 2006–2012, blubber layer >15 mm, DCC <3, intact, and non-empty stomach. For animals with "circular body lesions" or animals reduced to "head–tails" or to mere body parts, only 2, respectively 0 stomachs were available, so these groups were left out of the analyses.

2.3. Stomach content analysis

During autopsy, porpoise stomachs were removed and carefully cut open for a brief inspection for pathology. Stomachs were then bagged and stored frozen for later study. All food remains found in the fore stomach, the fundic stomach, and the pyloric stomach (Smith, 1972) and in the oesophagus were included in the analyses.

Relatively undigested prey were identified to the species level and measured directly. Most samples contained partly digested prey. These were collected in a large beaker. Prey hard parts were isolated by letting a gentle water flow make the beaker overflow, removing most of the soft particles. Care was taken to retain hard, but light parts that were useful for identification, such as squid beaks and shrimp claws. When a more or less clean sample of prey hard parts remained at the bottom of the beaker, this was sorted under a dissecting microscope. Alternatively, samples that contained large amounts of partly digested prey were packed in a 300-μm mesh bag, which in turn was put into a 120-μm mesh bag. The sealed package was then washed at 70 °C in a washing machine with standard washing powder. This procedure effectively removed soft material, while prey hard parts were retained within the inner bag. The 120-μm mesh bag served to protect the bones and otoliths in the inner bag from damage and provided an extra safety measure against loss of material that should have been retained in the inner bag. After washing, the samples were not spun dry in the washing machine, to prevent damage to the hard prey remains.

Prey remains used were: fish sagittal otoliths, bones, eye lenses and scales, cephalopod beaks, crustacean, and gadoid–parasite exoskeleton parts. First and foremost, otoliths were used to identify fish species, and to estimate fish length and weight, following Leopold et al. (2001). We used Clarke (1986), Härkönen (1986) and Leopold et al. (2001), as well as our reference collection of otoliths and fish bones for species identification. Prey remains were photographed with a Zeiss camera stereoscope (Stereo Discovery.V8 Achromat S, 0.63 × FWD 115 mm) and measurements were taken using Axiovision software (AxioVs 40 v.4.7 & 4.8). The minimum number of individual prey (MNI) was estimated for each prey species per porpoise. Otoliths were ordered in accordance with species, size and side (left/right). Pairs were made of otoliths that were visually assumed to originate from the same fish. The remaining single (left or right) otoliths were considered to represent one fish each. The upper and lower squid beaks and eye lenses were treated in a similar manner.

Other fish remains, such as vertebrae and premaxillae (see Watt et al., 1997), were also used to identify fish species and estimate their size and MNI. These other fish remains were used to complete and verify the findings by matching these to the paired otoliths. Remains of the parasitic copepod *Lernaeocera branchialis* were taken as proof of whiting *Merlangius merlangus* presence (Kabata, 1992; van Damme and Hamerlynck, 1999). In the absence of otoliths, fish eye lenses larger than 2 mm cross-section present in the same sample were considered to stem from whiting if *Lernaeocera* remains were present, and if no remains of other large fish were present. The regression: whiting length (in cm) = 8.4427 (fish eye lens length, in mm; Leopold et al., unpublished) was used to estimate fish length in such cases. Likewise, the presence of another parasitic copepod, the eye-maggot *Lernaeenicus sprattae* was taken as proof for the presence of sprat *Sprattus sprattus*, allowing in a few cases, worn clupeid vertebrae or otoliths to be used for identifying sprat as prey (Groenewold et al., 1996; Schram, 1991).

If stomachs contained very large (hundreds or thousands) numbers of goby *Pomatoschistus* sp. or sandeel *Ammodytes* sp. otoliths, these were sorted in 5–8 batches of similar size and wear (see below) which were counted. MNI per batch was taken as half the number of otoliths in that batch and per batch, the smallest and largest otoliths were measured. The sizes of the largest and smallest fish per batch were estimated from these, after correction for wear (see below) and the sizes of all other fish within that batch were estimated by linear intrapolation.

Even though sagittal otoliths are the parts of a fish that are most resistant to digestion, they do wear down in the acidic, grinding environment of a predator's stomach. Most retrieved otoliths are thus smaller than the original size and a correction is needed for an unbiased estimate of fish size (Tollit et al., 2004). All retrieved otoliths were examined for signs of wear and the amount of wear in each otolith was assessed as:

Wear class 0: no wear noticeable; otolith in pristine condition;

Wear class 1: slight wear, otolith shape still largely intact, but some wear at margins;

Wear class 2: moderate wear, otolith rounded but shape and otolith sulcus still well visible;

Wear class 3: severe wear; otolith badly worn, shape and size severely affected, sulcus barely visible.

Wear class 4: otolith worn down to such an extent that size is no longer related to original size.

Correction factors specific to each wear class 1–3 were obtained from a separate project on the diet of piscivorous predators (harbour porpoise, great cormorant *Phalacrocorax carbo* and Atlantic puffin *Fratercula arctica*) consuming considerable quantities of sand gobies *Pomatoschistus minutus*, whitings, smelts *Osmerus eperlanus*, herrings *Clupea harengus* and lesser sandeels *Ammodytes marinus*. This was accomplished by selecting predator stomachs that contained large numbers of otoliths of one of these fish species that were all of the same age group and that contained sufficient numbers of otoliths of all wear classes 0–3. Wear was assessed and length and width were measured for each individual otolith. Median sizes were calculated for each wear class and grade-specific correction factors were calculated by comparing median sizes of the various wear classes 1–3 to medium sizes of wear class 0 otoliths. For both length and width, and for all species except whiting, grade-specific correction factors were close to 1.05, 1.1 and 1.2 for wear classes 1–3, respectively and these values were used for all fish species, except whiting. Correction factors for whiting were determined as 1.06, 1.14 and 1.24 for wear classes 1–3, respectively. Lengths and widths of otoliths of wear classes 1–3 were corrected accordingly, before fish length and fish mass were calculated. Otoliths of wear class 4 were given the average size of all other otoliths, in the same sample or across samples for the same month of stranding, after correction for wear. Average size was only assigned to wear class 4 otoliths if their number was relatively small. If such numbers were larger (particularly in gobies) they got a randomly estimated size assigned to them from the other, less worn otoliths in the sample, thus preventing large peaks in numbers of otoliths of average size. In order to reduce heterogeneity (inter-observer differences), wear class was always assessed by the senior author.

Fish length was calculated from regression equations (Leopold et al., 2001), using lengths and width of both otoliths of presumed pairs, or length and width of single otoliths, or just length or just width of otoliths with damage preventing taking the other measurement. To obtain

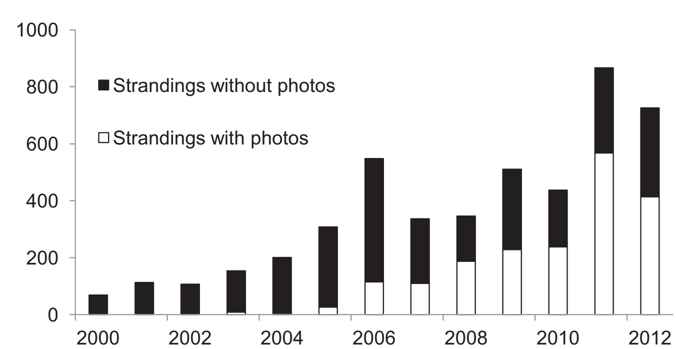

Fig. 1. Total numbers of reported strandings (n = 4724, 2000–2012) and the relative proportions of porpoises that were photographed (white), either on the autopsy table or at the stranding site, or both.

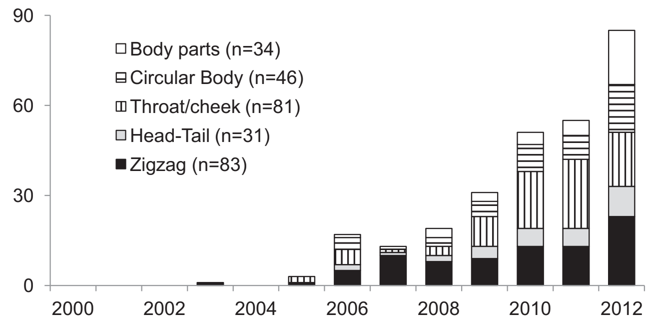

Fig. 2. Different types of major blubber defects among stranded porpoises in the Netherlands.

a single estimate for original total fish length, the average of all 4 (maximum) otolith measures was used. The total fish length value was then used to calculate the fresh wet weight of the fish (Leopold et al., 2001).

The number of cephalopods was defined as the more numerous number of the upper or lower beaks, or pairs of eyes. Because squid beaks are less sensitive to digestion (Phillips and Harvey, 2009; Sekiguchi and Best, 1997; Tollit et al., 1997), no corrections for wear were made of these remains. The length and weight of cephalopods were calculated from relationships between lower beak size according to Clarke (1986) or from our reference collection. When upper beaks were more numerous, squid size was estimated from the less numerous lower beaks. For the remaining upper beaks the average size of the other individuals within the same stomach was given.

When shrimp claws were found, the equation proposed by Doornbos (1984) was applied to estimate weight. For shrimp remains that could not be translated to shrimp size, such as shrimp eyes, a standard weight of 1.0 g was used, the average for all shrimps for which the size could be estimated.

2.4. Statistical analysis

For each porpoise stomach, the number of prey (MNI per species) was estimated, and from length–weight relationships (Leopold et al., 2001), total prey mass (Appendix B). Prey numbers and biomass data were fourth root transformed and the Bray–Curtis dissimilarity was calculated of each matrix. The resulting distance matrix was analysed using Principal Coordinate Analysis. Differences between groups were assessed using Permanova (Anderson, 2001; McArdle and Anderson, 2001). Analyses were performed using R (R core team, 2012) and the package vegan (Oksanen et al., 2012).

Table 2
Pairwise comparisons of diets of three groups of stranded porpoises: animals with zigzag lesions, with lesions to throat or cheek, and animals that were not mutilated. Permanova tests are used to test for differences.

Groups	T (prey biomass)	P (perm)	Perms	T (prey numbers)	P (perm)	Perms
Zigzag-throat	2.4661	0.001	997	2.8114	0.001	999
Zigzag-not mutilated	2.1211	0.002	999	2.3625	0.002	997
Throat-not mutilated	1.1914	0.249	999	1.1786	0.235	999

3. Results

3.1. Examining photographic evidence for seal inflicted trauma

Between 2000 and 2012 a total of 4724 harbour porpoise strandings were recorded in the Netherlands. From 2006 to 2012 857 animals were autopsied and these were all photographed. For 2005–2012, photographs were available for another 1117 animals on www.walvisstrandingen.nl. Over time, the proportion of animals that was photographed increased (Fig. 1).

Five types of major blubber defects have been identified from photographs (Fig. 2). Increasing numbers of mutilated animals were identified over the years, but this trend parallels the trend in general numbers stranded (Fig. 1). We found 273 porpoises with major blubber defects among reported porpoise strandings from 2005 to 2012, and a single earlier case in 2003. The largest proportions of mutilated animals were found in 2010 (21.4%) and 2012 (20.5%); the overall percentage of identified mutilated animals was 14.4%, or even 17% when only animals were considered that were autopsied (Leopold et al., 2015).

3.2. Animals used for stomach content analysis

A record number of animals with major blubber defects were stranded in 2012, including many with zigzag or throat/cheek lesions (Fig. 2). Zigzag lesions were most common and across all years, animals with these lesions were predominantly found in winter (December to April: Table 1).

The animals with zigzag lesions found from 2006 to 2012 and from December–April were predominantly juveniles (<130 cm, 91.5%) that were in a good nutritional body condition (average blubber thickness

Table 1
Numbers of identified porpoises with zigzag lesions per year and per month, 2003–2012. Order of months is centred around late winter. Grey highlight indicates the period selected for stomach content analyses.

Month	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	Totals
10					1	1			1		3
11								1			1
12						3				1	4
1			1	1			3	3	2	1	11
2					2		4	3	6	5	20
3	1			2	4	3	2	3	3	15	33
4				1	2						3
5				1							1
6											0
7					1	1			1		3
8								2			2
9								1		1	2
Totals	1	0	1	5	10	8	9	13	13	23	83

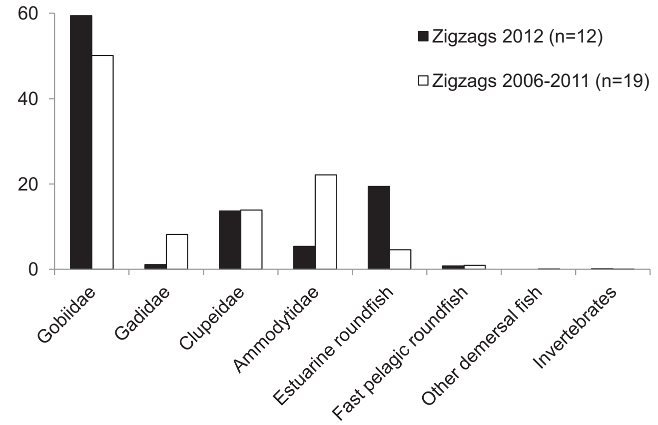

Fig. 3. Comparison of diets (summed prey masses) of porpoises found with zigzag lesions in 2012 and 2006–2011. Average reconstructed prey mass per stomach was 1010 ± 1176 g (2012), and 1507 ± 1066 g (2006–2011), respectively. Prey species included in each prey group are listed in Appendix B.

mostly >15 mm: Appendix B). Thirty-one zigzag juveniles were available from this period. For comparison, we selected all intact porpoises from our diet database, that were <130 cm long, had stranded between December and April 2006–2012, had >15 mm of blubber and a non-empty stomach (also 31 animals) and animals with throat/cheek lesions under the same criteria (12 animals).

3.3. Diet

The majority of zigzag animals available for the diet study were found in 2012 (Table 2). Therefore, we first compared the diet of 2012 zigzags (n = 12 stomachs, incidentally all found in March) with the diet of zigzags in earlier winters (n = 19). Both diets were dominated by gobies (Fig. 3) and in subsequent analyses all years were pooled.

Compared to the zigzag animals, the diet of the animals hit at the throat/cheek (n = 12) comprised a much larger proportion of clupeids (herring and sprat) and gadoids (mostly whiting) and a much smaller proportion of gobies (Fig. 4). We note, however, that the contribution of gadoids to the diet of porpoises wounded at the throat or cheek was mainly due to the stomach contents of one animal. The group of animals that were not mutilated (n = 31) had the most varied diet, with

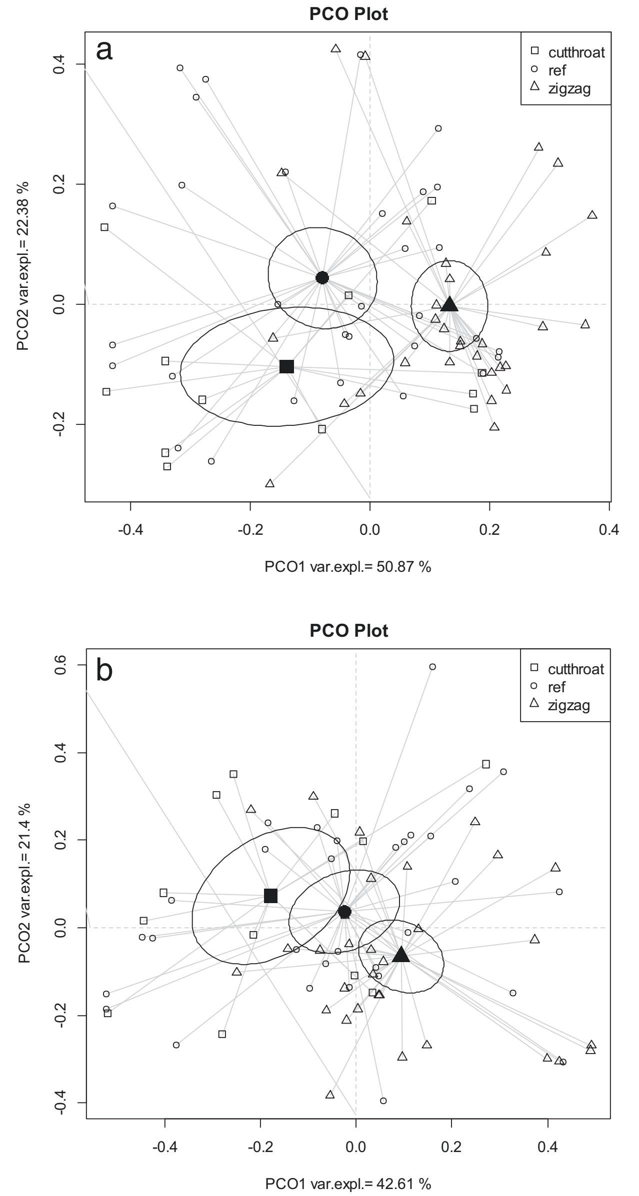

Fig. 5. a. PCO plots of the diet composition (prey numbers) of all porpoises analysed. Midpoints of groups in bold, 95% confidence ellipses are given around these centroids. b. PCO plots of the diet composition (prey mass) of all porpoises analysed. Midpoints of groups in bold, 95% confidence ellipses are given around these centroids.

rather equal proportions of gobies, clupeids, gadoids and sandeels, but also less full stomachs.

Comparing the three groups in concert, a Principal Coordinates Analysis (PCO) explains 73% of the variance in prey numbers within the total group of animals considered, and 64% of the variance of prey biomass (Fig. 5a, b). The differences between the prey spectra of zigzag and throat/cheek animals and between zigzag and non-mutilated animals were highly significant (Table 2); the difference between non-mutilated animals and throat/cheek animals was not significant.

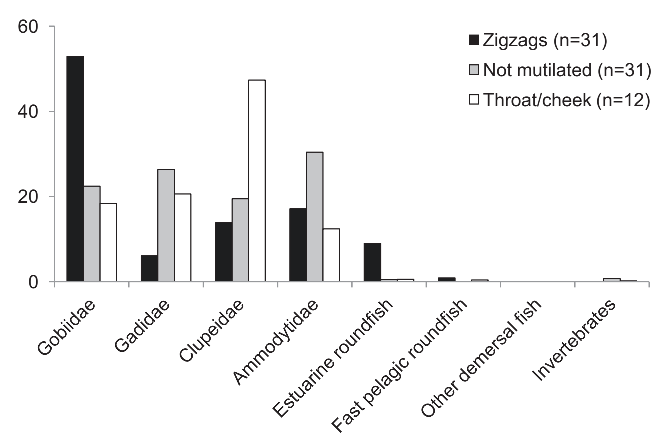

Fig. 4. Comparison of diets (summed prey masses) of porpoises found with zigzag lesions, lesions to the throat or cheek and animals that were not mutilated (all years combined in each category). Average reconstructed prey mass per stomach was 1315 ± 1117 g (zigzags), 1072 ± 809 g (throat/cheek), and 598 ± 680 g (not mutilated) respectively.

4. Discussion

In this study we investigated if the combination of specific wounds and stomach contents of mutilated porpoises would provide clues as to how and where these animals were attacked. This approach could only be successful if porpoises were feeding when being attacked, or at least, were still swimming in the same micro-habitat where they had been feeding last. The relatively full stomachs of mutilated individual suggest that this condition may have been met. Our study demonstrates that: 1) most affected animals were apparently in good nutritional body condition, and had comparatively full stomachs (Fig. 4), and 2) that their diet differed with the type of lesions inflicted. Porpoises with zigzag wounds had been feeding mostly on gobies, i.e., close to the sea floor. Animals with wounds to the throat or cheek had been feeding predominantly on clupeids, i.e., higher in the water column. The combination of attack wounds and attack-specific diets shows that porpoises are never safe from seal attacks and may be hit both at the sea floor and higher in the water column. The relationship between the specific attack wounds and diet cannot be explained by grey seals scavenging on already dead porpoises as a link with porpoise diet would have been lost. The difference in diets of porpoises with zigzag wounds and porpoises wounded in the cheek/throat region strongly indicates that the porpoises were attacked alive, while feeding. Their good nutritional body condition and filled stomachs would also indicate a sudden death. All these findings are consistent with predation during feeding, or shortly after feeding.

Non-mutilated animals, that is porpoises without major blubber defects, had the most varied diet. Net marks, i.e., thin linear impressions, either on the skin or on the lips, presumably from bottom-set gillnets (see: Haelters and Camphuysen, 2009), were found on eight of the 31 non-mutilated animals examined (Appendix B), indicating drowning as the cause of death. Incidentally, net marks were also found on one of the zigzags, and animal that also had a tailstock bite mark (UT047), from the teeth of a grey seal (see: Leopold et al., 2015; van Bleijswijk et al., 2014). This combination of lesions may indicate an attack on a porpoise stuck alive in a net, or a grey seal scavenging on a porpoise corpse, after this animal had drowned. Grey seals are known to take fish from set nets (Moore, 2003; Stenson et al., 2013) and it would seem a small step to start feeding from entangled porpoises.

Our findings indicate that the occurrence of mutilated harbour porpoises is much more common in the Netherlands than reported in bordering countries, and is seemingly rising, in concert with an increase in strandings. Major blubber defects were found on 17% of all stranded porpoises that were sufficiently fresh to be autopsied (Leopold et al., 2015). In some years this incidence was >20%, indicating that grey seal attacks are an important cause of death.

Both harbour porpoises and grey seals have greatly increased in numbers in Dutch nearshore waters in recent decades. The seals may have found porpoises to be a new food resource, carrying a large blubber store with a high energy density. Our results provide further arguments in favour of the hypothesis that grey seals cause these mutilations, now found on dozens of stranded porpoises per year. Alternative hypotheses, that porpoises were first by-caught in e.g. bottom set-nets (cf. Camphuysen and Oosterbaan, 2009) and mutilated later, either by fishermen or by scavenging seals, or that they were hit by ducted ship propellers (cf. Thompson et al., 2010), were not supported. This difference between anthropogenic causes of death and predation has important implications for policy making and mitigation measures for the protection of this vulnerable small cetacean, since predation, in contrast to man-induced mortality, is a natural phenomenon.

Acknowledgements

Every porpoise used in this study has its own history, from the moment it was found on the beach until it arrived at the autopsy table. Collecting dead porpoises, particularly mutilated ones, is by no means an easy or pleasant task. Animals have been collected by many individuals, always on a voluntary basis. This work cannot be appreciated too much and we would like to thank all people who reported, photographed and collected dead porpoises. This research was funded by the Dutch Ministry of Economic Affairs (140000353).

Appendix A. Examples of different lesions

Fig. A1. Zigzag (Jaap van der Hiele).

Fig. A2. Head–tail (Hans Verdaat, IMARES).

Fig. A3. Throat/cheek (Utrecht University).

Fig. A4. Circular body (Naturalis: www.walvisstrandingen.nl).

Fig. A5. Body parts (Arnold Gronert).

Fig. A6. Claw marks (Utrecht University).

Fig. A7. Tailstock bite mark (Kees Camphuysen, NIOZ).

Fig. A8. Cut in half (Utrecht University).

Fig. A9. Anthropogenic: knife cuts (Jaap van der Hiele).

Appendix B. Basic data for all porpoises included in the diet-part of this study, by mutilation category: zigzags, throat/cheeks and controls

ID: porpoise identifier; Marks: Minor marks, separate from major blubber defect, None (only when photographs showing all sides were available), Tailstock (bite) mark, Claw marks, Net marks, or unknown; Month and Year refer to stranding date, Lat and Long to stranding location; TBL is the total body length (cm), Sex: male (M), female (F), and unknown (?); Blubber is the average blubber thickness (see Material and methods section); Final columns give summed prey masses and prey numbers (in parentheses) for, respectively: gobies (common, Lozano's, sand, painted and transparent gobies), gadoids (bib, poor cod, whiting), clupeids (herring, sprat), Ammod. (Ammodytidae: greater, lesser and small sandeels), estuarine (estuarine roundfish: European perch, golden grey mullet, sand smelt, smelt, Nilsson's pipefish), fast pelgs (fast pelagic fish: Atlantic mackerel, Atlantic horse mackerel, European seabass), Demersal (other demersal fish: five-bearded rockling, viviparous blenny, flatfishes) and invert (invertebrates: brown shrimp, squids).

Cat.	ID	Marks	Month	Year	Lat	Long	TBL	Sex	Blubber	Gobies	Gadoids	Clupeids	Ammod.	Estuarine	Fast pelgs	Demersal	Invert
Zigzag	TX044	None	3	2006	51.8267	3.8438	119	F	17.7	1400.38 (1552)	0.00	69.61 (10)	30.48 (6)	61.54 (10)	196.67 (1)	0.00	0.00
Zigzag	TX024	?	4	2006	53.1781	4.8131	108	F	?	1244.35 (1979)	0.00	1.54 (1)	434.33 (298)	0.00	0.00	0.00	0.70 (1)
Zigzag	UT035	Claws	2	2007	52.9044	4.6915	130	F	24.3	95.77 (48)	0.00	606.80 (38)	431.92 (61)	0.00	0.00	0.00	0.00
Zigzag	UT008	?	3	2007	51.8516	3.9254	117	?	22.0	3312.06 (2578)	0.00	200.73 (13)	4.20 (3)	18.31 (1)	0.00	0.00	3.00 (3)
Zigzag	UT037	Tailstock	3	2007	51.8516	3.9254	~112	?	17.7	448.02 (1391)	0.00	0.00	2.63 (2)	0.00	0.00	0.00	4.88 (1)
Zigzag	UT038	Tailstock	4	2007	51.8267	3.8438	~88	?	16.0	1277.90 (1392)	37.40 (1)	0.00	0.00	59.17 (1)	22.85 (1)	0.00	1.00 (1)
Zigzag	UT047	Tailstock & net marks	3	2007	51.8516	3.9254	~100	M	11.0	428.93 (675)	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Zigzag	UT129	None	3	2008	51.4571	3.5094	103	F	30.0	164.85 (225)	784.37 (9)	164.03 (3)	12.14 (3)	0.00	0.00	0.00	6.00 (6)
Zigzag	UT130	Tailstock & claws	3	2008	51.8516	3.9254	113	M	22.0	164.99 (336)	0.00	9.21 (2)	42.22 (9)	0.00	0.00	0.00	0.00
Zigzag	UT131	Claws	3	2008	51.8516	3.9254	111	?	?	1790.52 (2163)	587.25 (6)	74.16 (7)	4.95 (2)	146.58 (7)	0.00	0.00	0.00
Zigzag	UT195	Tailstock & claws	12	2008	53.0796	4.7081	116	M	22.7	1.88 (3)	0.00	264.48 (20)	41.07 (2)	0.00	0.00	0.00	0.00
Zigzag	UT204	Tailstock & claws	2	2009	53.1781	4.8131	121	M	22.0	0.00	91.77 (1)	674.98 (56)	2721.90 (219)	42.65 (1)	0.00	0.00	0.00
Zigzag	UT207	Tailstock & claws	2	2009	51.8516	3.9254	102	M	19.3	15.02 (22)	0.00	4.24 (1)	0.00	652.10 (12)	0.00	0.00	0.00
Zigzag	UT208	Tailstock & claws	2	2009	51.4571	3.5094	114	F	25.0	0.33 (1)	736.18 (10)	243.28 (31)	292.03 (45)	112.66 (2)	16.24 (3)	0.00	1.84 (1)
Zigzag	UT227	?	3	2009	53.1781	4.8131	105	M	15.0	150.40 (230)	0.00	196.64 (25)	39.11 (7)	0.00	0.00	0.00	1.00 (1)
Zigzag	UT280	Claws	1	2010	52.3216	4.4578	92	F	13.7	429.11 (282)	0.00	195.62 (16)	0.00	223.69 (42)	27.35 (4)	28.84 (3)	0.00
Zigzag	UT386	?	3	2010	51.8516	3.9254	~100	?	?	999.87 (2285)	0.00	149.33 (8)	6.77 (1)	0.00	0.00	0.00	0.00
Zigzag	UT675	?	2	2011	52.859	4.6806	118	?	?	1082.92 (1226)	0.00	1127.66 (96)	0.00	0.00	0.00	0.00	0.00
Zigzag	UT674	Tailstock & claws	3	2011	53.0434	4.6850	110	M	23.0	767.87 (395)	102.73 (1)	0.00	2272.25 (484)	0.75 (1)	0.00	0.00	0.00
Zigzag	UT670	Claws	3	2012	53.4734	5.6038	104	M	23.7	1769.13 (2866)	0.00	753.60 (76)	485.65 (72)	79.04 (34)	0.00	0.00	9.98 (10)
Zigzag	UT693	None	3	2012	53.4287	5.8273	~110	F	13.0	3070.79 (5369)	42.55 (1)	0.00	111.66 (17)	27.92 (20)	0.00	0.00	0.00
Zigzag	UT697	T.stock? & claws	3	2012	51.8267	3.8438	104	M	?	6.01 (10)	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Zigzag	UT701	Claws	3	2012	51.8516	3.9254	109	M	30.0	87.00 (158)	0.00	27.03 (3)	0.00	18.87 (1)	0.00	0.00	0.00
Zigzag	UT702	Claws	3	2012	51.8267	3.8438	107	F	20.0	1224.27 (1691)	94.25 (1)	211.78 (23)	35.62 (4)	21.12 (3)	3.39 (2)	0.00	0.00
Zigzag	UT704	Tailstock & claws	3	2012	51.8567	4.0029	96	M	15.0	224.86 (383)	0.00	349.52 (27)	0.00	117.33 (11)	0.00	0.00	0.00
Zigzag	UT711	Tailstock	3	2012	51.8267	3.8438	112.5	F	30.0	257.29 (397)	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Zigzag	UT713	Tailstock	3	2012	51.8516	3.9254	101	F	21.0	45.95 (63)	0.00	120.24 (5)	15.94 (2)	478.08 (41)	0.00	0.00	4.51 (7)
Zigzag	UT714	Tailstock	3	2012	51.8516	3.9254	~99	M	22.7	45.93 (54)	0.00	96.07 (5)	0.00	1616.19 (89)	93.54 (10)	0.00	1.43 (4)
Zigzag	UT716	Tailstock	3	2012	51.8516	3.9254	123	F	16.0	465.94 (1014)	0.00	84.81 (8)	2.43 (1)	0.00	0.00	0.00	0.00

(continued on next page)

Appendix B. Basic data for all porpoises included in the diet-part of this study, by mutilation category: zigzags, throat/cheeks and controls (*continued*)

Cat.	ID	Marks	Month	Year	Lat	Long	TBL	Sex	Blubber	Gobies	Gadoids	Clupeids	Ammod.	Estuarine	Fast pelgs	Demersal	Invert
Zigzag	UT718	?	3	2012	51.8267	3.8438	~126	F	?	3.92 (5)	0.00	17.10 (1)	0.00	0.00	0.00	0.00	0.00
Zigzag	UT715	?	3	2012	51.8516	3.9254	~112	F	19.7	3.25 (5)	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Throat/Cheek	UT197	Tailstock & claws	2	2009	53.1781	4.8131	103	F	19.7	0.00	0.00	232.06 (55)	0.00	0.00	0.00	0.00	0.00
Throat/Cheek	UT182	Tailstock & claws	12	2008	51.5067	3.4115	111	M	21.7	0.00	60.31 (1)	619.53 (19)	8.53 (2)	0.00	0.00	0.00	1.00 (1)
Throat/Cheek	TX046	Tailstock & claws	3	2006	51.6858	3.8107	101	M	28.3	4.64 (8)	711.71 (8)	96.35 (3)	15.41 (2)	0.00	53.82 (4)	0.00	0.70 (1)
Throat/Cheek	UT198	Claws	1	2009	52.9867	4.6978	128	M	20.7	0.00	1207.07 (5)	885.89 (47)	0.00	0.00	0.00	0.00	1.00 (1)
Throat/Cheek	UT203	Tailstock & claws	2	2009	52.7421	4.6247	107	M	22.7	7.46 (11)	0.00	738.06 (125)	1422.32 (227)	0.00	0.00	0.00	0.00
Throat/Cheek	UT219	Tailstock & claws	2	2009	53.0796	4.7081	104	M	26.7	0.00	0.00	1.58 (1)	0.00	0.00	0.00	0.00	0.00
Throat/Cheek	UT221	Tailstock	3	2009	52.9748	4.7624	127	M	23.0	0.00	0.00	1029.24 (35)	24.28 (4)	0.00	0.00	0.00	1.00 (1)
Throat/Cheek	UT235	None	2	2009	52.3216	4.4578	103	M	21.3	27.10 (35)	321.65 (1)	0.00	12.23 (2)	0.00	0.00	0.00	11.73 (6)
Throat/Cheek	UT450	Claws	3	2011	52.1505	4.2969	116	M	21.7	496.31 (454)	352.43 (5)	1466.36 (179)	37.48 (10)	41.45 (5)	0.00	0.00	10.50 (11)
Throat/Cheek	UT452	None	3	2011	52.3768	4.4921	~97	M	15.3	478.97 (769)	0.00	72.98 (8)	9.04 (2)	3.72 (2)	0.00	0.00	0.00
Throat/Cheek	UT205	Tailstock & claws	2	2009	52.7421	4.6247	111	M	23.3	0.00	0.00	715.09 (76)	58.25 (4)	0.00	0.00	0.00	0.00
Throat/Cheek	UT454	Tailstock & claws?	3	2011	52.3768	4.4210	107	M	20.0	1351.70 (736)	0.00	235.87 (20)	9.37 (2)	28.40 (5)	0.00	0.00	0.00
Control	TX025	None	3	2006	53.0434	4.6850	99	F	16.0	3.70 (7)	0.00	2.71 (1)	0.00	0.00	0.00	0.00	0.00
Control	TX030	None	4	2006	53.1309	4.7543	~110	F	27.3	25.46 (13)	0.00	155.78 (10)	13.68 (3)	1.63 (1)	0.00	0.00	0.00
Control	TX033	None	3	2006	53.1035	4.9269	107	M	28.0	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.96 (1)
Control	TX057	Net marks	4	2006	52.7009	4.6138	102	M	18.3	35.02 (36)	0.00	38.17 (4)	45.82 (10)	0.00	0.00	0.00	1.96 (1)
Control	UT111	Net marks	3	2008	51.4571	3.5094	114	F	24.0	9.04 (11)	194.84 (5)	0.00	21.82 (7)	0.00	0.00	0.00	0.00
Control	UT114	None	3	2008	52.1505	4.2969	105	M	25.0	711.24 (713)	105.98 (3)	2.59 (1)	131.94 (58)	0.00	0.00	0.00	2.96 (2)
Control	UT120	None	2	2008	53.0434	4.6850	89	M	16.0	106.56 (255)	0.00	76.28 (5)	386.02 (27)	0.00	0.00	0.00	0.00
Control	UT209	None	12	2008	52.9867	4.6978	106	M	20.0	7.48 (11)	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Control	UT210	Tailstock & claws	2	2009	52.3768	4.4921	112	M	22.3	22.83 (16)	177.41 (3)	336.00 (59)	187.95 (53)	0.00	0.00	13.99 (1)	1.00 (1)
Control	UT211	Tailstock & claws	2	2009	52.7009	4.6138	119	F	25.7	0.00	0.00	200.16 (12)	1811.45 (207)	0.00	0.00	0.00	0.00
Control	UT212	Tailstock & Claws	2	2009	52.7421	4.6247	128	M	23.7	0.00	0.00	0.00	9.68 (1)	0.00	0.00	0.00	0.00
Control	UT213	Tailstock & claws	2	2009	52.8094	4.6539	107	M	26.3	0.00	0.00	283.38 (53)	0.00	0.00	0.00	0.00	0.00
Control	UT214	Claws?	2	2009	52.7421	4.6247	101	M	22.7	0.00	0.00	811.20 (27)	0.00	0.00	0.00	0.00	0.00
Control	UT216	Tailstock & claws	2	2009	52.859	4.6806	117	M	20.0	0.00	0.00	276.15 (7)	21.53 (3)	0.00	0.00	0.00	0.00
Control	UT220	Tailstock & claws	3	2009	52.8094	4.6539	98	M	22.7	0.83 (3)	135.33 (3)	280.06 (52)	806.79 (58)	0.00	0.00	0.00	0.00
Control	UT223	None	3	2009	52.7421	4.6247	92.5	M	20.3	39.04 (46)	0.00	273.57 (29)	27.66 (2)	0.00	0.00	0.00	1.00 (1)
Control	UT224	Tailstock & claws	2	2009	53.0796	4.7081	103.5	M	21.0	233.80 (156)	102.11 (1)	298.51 (34)	1442.21 (178)	0.00	0.00	0.00	1.00 (1)
Control	UT228	Net marks	12	2008	53.1781	4.8131	129.5	F	18.7	150.77 (104)	2238.15 (17)	70.27 (5)	0.00	0.00	0.00	0.00	2.46 (3)
Control	UT229	Net marks	3	2009	51.5067	3.4115	109	M	26.3	71.52 (45)	1399.54 (11)	0.00	2.56 (1)	0.00	0.00	0.00	5.00 (5)
Control	UT231	None	4	2009	52.9044	4.6915	121	F	24.0	0.57 (1)	41.27 (1)	172.00 (2)	126.56 (5)	0.00	0.00	0.00	0.00
Control	UT232	None	2	2009	52.1505	4.2969	102.5	F	18.0	0.00	0.00	0.00	0.00	0.00	0.00	0.00	7.78 (9)
Control	UT243	Claws?	12	2008	53.1309	4.7543	124.5	F	23.7	0.00	461.49 (8)	0.00	0.00	0.00	0.00	0.00	0.00
Control	UT393	None	1	2011	52.1505	4.2969	120	M	20.3	0.00	0.00	10.34 (1)	0.00	0.00	0.00	0.00	0.00
Control	UT395	None	3	2010	53.4734	5.6038	122	M	25.0	34.89 (41)	0.00	0.00	206.71 (41)	0.00	0.00	0.00	111.17 (48)
Control	UT421	Net marks	3	2011	53.4838	5.9180	117	F	20.3	407.76 (494)	0.00	34.46 (3)	293.37 (47)	4.29 (2)	0.00	0.00	0.00
Control	UT422	None	3	2011	52.0794	4.1988	108	M	15.0	9.75 (9)	23.35 (1)	0.00	0.00	14.88 (8)	0.00	0.00	0.00
Control	UT435	Net marks	4	2011	52.9044	4.6915	105	M	16.3	1080.66 (1169)	5.04 (2)	34.80 (4)	10.62 (2)	24.29 (5)	0.00	0.00	0.00
Control	UT453	Net marks	3	2011	52.3216	4.4578	125.5	F	24.3	0.00	0.00	141.19 (44)	34.76 (11)	0.00	0.00	0.00	0.00
Control	UT668	Net marks	3	2011	52.7421	4.6247	110.5	M	18.7	1167.43 (1185)	0.00	59.93 (4)	40.30 (3)	15.39 (4)	0.00	0.00	0.00
Control	UT669	Tailstock?	3	2011	52.1088	4.2103	105.5	M	20.0	36.67 (75)	0.00	53.37 (12)	19.13 (1)	27.53 (15)	0.00	0.00	0.00
Control	UT682	Claws?	3	2011	53.4838	5.9180	109.5	F	23.7	6.79 (10)	0.00	0.00	2.38 (1)	11.27 (3)	0.00	0.00	0.00

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