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DISEASE IN WILDLIFE OR EXOTIC SPECIES

Dental and Temporomandibular Joint Pathology of the Steller Sea Lion (*Eumetopias jubatus*)

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Summary

Skulls from 112 Steller sea lions (*Eumetopias jubatus*) were examined according to predefined criteria. Of the specimens, 73 (65.2%) were from males, 29 (25.9%) from females and 10 (8.9%) were of unknown sex, with 50 adults (44.6%), 61 young adults (54.5%) and one of unknown age (0.9%). The number of teeth evaluated was 3,521. Adults had more acquired tooth loss than young adults (P <0.0001). A total of 1,660 teeth (47.1%) from 111 specimens (99.1%) had evidence of attrition or abrasion. Adults displayed more attrition or abrasion than young adults (P <0.0001). A total of 241 teeth (6.8%) from 47 specimens (42%) had tooth fractures. Adults had more fractured teeth than young adults (P <0.0001). Bony changes consistent with periodontitis affected 36.7% of teeth. Adults had more teeth affected by periodontitis than young adults (P <0.0001). Temporomandibular joint osteoarthritis lesions were found in 54 specimens (48.2%) with more in adults than in young adults (P <0.0001). Although the significance of our findings is unknown, the occurrence and severity of these lesions may play an important role in the morbidity and mortality of Steller sea lions.

Keywords: dental pathology; *Eumetopias jubatus*; Steller sea lion; temporomandibular joint pathology

Introduction

The Steller sea lion (*Eumetopias jubatus*), also known as the northern sea lion or Steller's sea lion, first identified in 1741 by George Wilhelm Steller, 1751), is the largest member of the family Otariidae (Schusterman, 1981) and the only known living member of its genus. It has marked sexual dimorphism. The average reported bodyweight and length of fully grown males and females are 1,120 kg and 3.25 m and 250 kg and 3.20 m, respectively (Loughlin, 1998). Adult males have a massive muscular neck and chest covered with thick and long coarse hair, as well as strong development of the sagittal crest by the age of 7 years (Fiscus, 1961). Stellar sea lions can live to about 16 years for males and 23 years for females (Trites, 2021).

The distribution of Steller sea lions historically ranges along the west coast of North America from California to Alaska, extending towards the Bering Strait and reaching the Asian coast (Burkanov and Loughlin, 2005). Several surveys have confirmed a steep decline of the Alaskan population (Merrick *et al*, 1987; Trites and Larkin 1996), which may be linked to changes in the quantity, quality and availability of preferred prey secondary to commercial fisheries or natural change of ecosystems (Merrick *et al*, 1997; Trites *et al*, 2007b; Atkinson *et al*, 2008).

Steller sea lions are opportunistic predators and feed near land or in relatively shallow water (Schusterman, 1981). Their typical diet includes

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various species of small fish and cephalopods, and varies according to their range, time of year, prey abundance and availability (Trites *et al*, 2007a). Steller sea lions use suction as their primary feeding mode but biting feeding was also observed (Marshall *et al*, 2015) (ie, they utilize their dentition to catch and hold prey). The food is not masticated but is swallowed either whole or, if too large, is first torn extra-orally into swallowable pieces.

The permanent dentition of Steller sea lions comprises 34 teeth. The dental formula is incisor teeth (I) 3/2, canine teeth (C) 1/1, premolar teeth (P) 4/4 and molar teeth (M) 1/1 (Fig. 1). 'Post canine' (PC) is a collective term used by zoologists for the premolar and molar teeth, as these teeth are of similar size and shape. In terms of tooth size, the first incisor tooth is the smallest, whereas the third incisor is the largest among the incisor teeth; the canine tooth is the largest tooth in the oral cavity (Wolsan *et al*, 2015), which may correlate with its use for display, combat, defending territory and competing for females by male Stellar sea lions. The crown of the maxillary first molar tooth is directed caudally and has no occlusal contact with the mandibular teeth (Loughlin, 2009; Wolsan *et al*, 2019). There is a marked space between the maxillary fourth premolar tooth and the maxillary first molar tooth, which may be caused by rapid growth and skull extension (Loughlin, 2009). Steller sea lions have the most integrated and occluding dentition but the least variable in tooth size compared with three other species of pinnipeds (*Histriophoca fasciata, Callorhinus ursinus* and *Phoca largha*) (Wolsan *et al*, 2015, 2019).

Dental anomalies reported for the Steller sea lion are very limited. A study of various samples of pinnipeds revealed a symmetrical absence of the first maxillary incisor teeth in a Steller sea lion skull (Drehmer *et al*, 2015). A recent study revealed variations of crown height and width in premolar and molar teeth, with the maxillary first molar tooth showing the

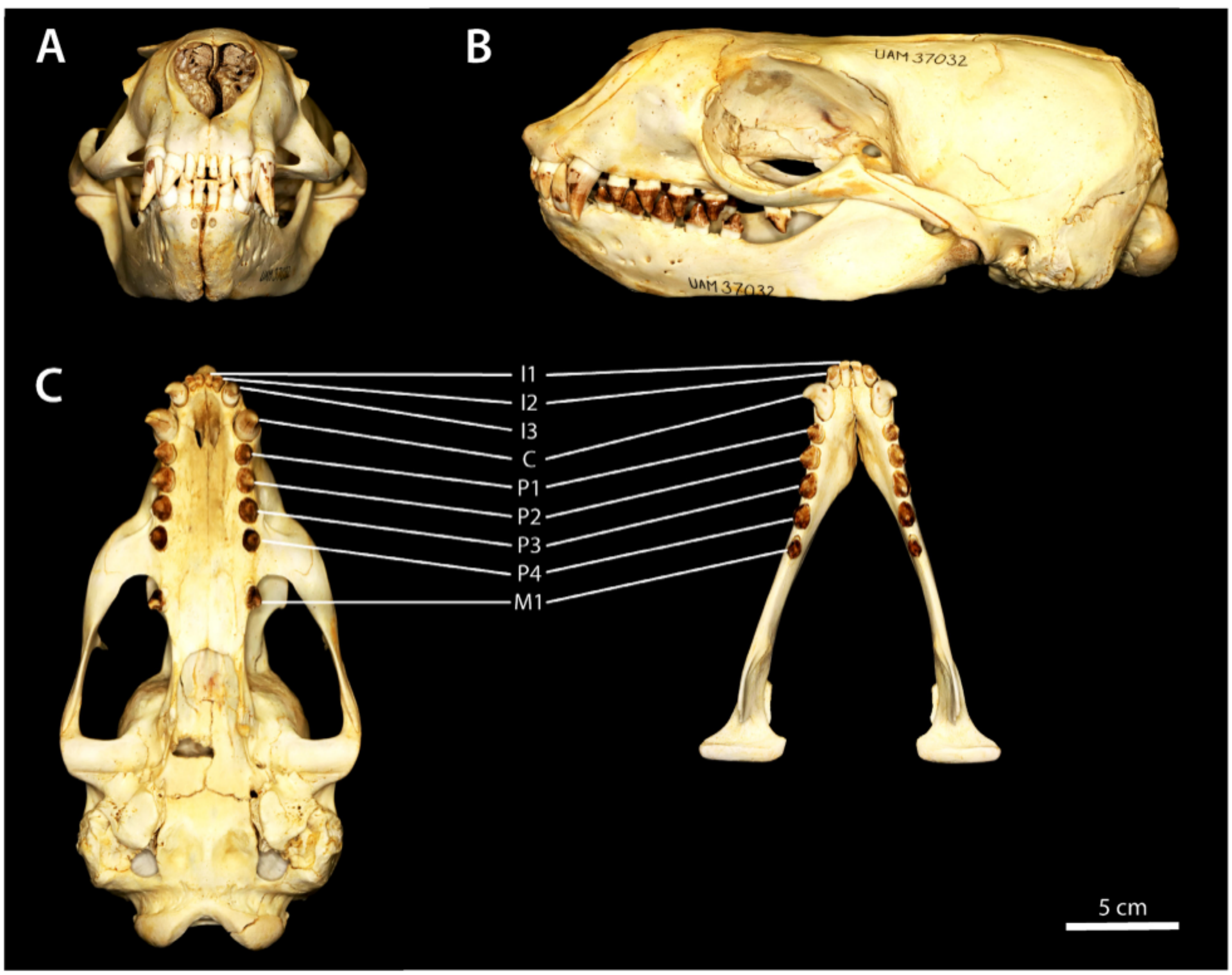

Fig. 1. (A–C) Representative dentition of a young adult female Steller sea lion (UMN 37032). The dental formula is incisor teeth (I) 3/2, canine teeth (C) 1/1, premolar teeth (P) 4/4 and molar teeth (M) 1/1.

Table 1
Congenital, developmental and acquired abnormalities in Steller sea lions and inclusion criteria for this study

Observation	*Criteria*
Tooth artefactually absent	Jaw fragment missing or tooth absent but a well-defined, sharp-edged, normal-shaped, empty alveolus present; no lesions visible in the alveolar bone; tooth presumed lost during preparation or post-mortem manipulation of the skull
Tooth absent (presumably acquired)	Tooth absent; alveolus or remnant of alveolus visible; alveolar bone has lesions (rounding of the alveolar margin, shallow alveolus, periosteal reaction on alveolar bone, increased vascular foramina)
Tooth absent (presumably congenital)	Tooth and alveolus absent; smooth, morphologically normal bone present at the site; no evidence of acquired tooth loss of adjacent teeth
Malformed tooth	Presence of an abnormal-shaped crown
Supernumerary tooth	Presence of a supernumerary tooth adjacent to the normal tooth
Number of roots	One, two or three roots
Persistent deciduous tooth	A persistent deciduous tooth adjacent to a fully erupted tooth
Attrition/abrasion	Rounding or flattening of the cusp tip; exposure of dentine, with or without tertiary dentine formation
Enamel fracture	A chip fracture or crack of the enamel only
Uncomplicated crown fracture	A fracture affecting enamel and dentine, but not exposing the pulp
Complicated crown fracture	A fracture affecting enamel and dentine, and exposing the pulp
Uncomplicated crown-root fracture	A fracture affecting enamel, dentine and cementum, but not exposing the pulp
Complicated crown-root fracture	A fracture affecting enamel, dentine and cementum, and exposing the pulp
Root fracture	A fracture affecting dentine, cementum and the pulp
Periapical lesions	Macroscopically visible periapical bone loss, root tip resorption, sinus tract formation originating periapically, or obvious focal periosteal reaction overlying the apex
Periodontitis stage 2	Evidence of increased vascularity at the alveolar margin (more prominent vascular foramina in, and slightly rougher texture of, the bone of the alveolar margin)
Periodontitis stage 3	Rounding of the alveolar margin; moderate horizontal or vertical bone loss
Periodontitis stage 4	Widening of the periodontal space; severe horizontal or vertical bone loss; tooth unstable in the alveolus
Enamel hypoplasia	Irregular pitting, or a band-shaped absence or thinning of the enamel, consistent with clinical signs of enamel hypoplasia

(Continued)

Table 1 *(continued)*

Observation	*Criteria*
Mild TMJ osteoarthritis	Evidence of early periarticular new bone formation/osteophytes with minimal or no subchondral bone change
Moderate TMJ osteoarthritis	Periarticular new bone formation and/or subchondral bone changes
Severe TMJ osteoarthritis	All previously described signs present and more pronounced; subchondral bone lysis present; partial or complete ankylosis may be observed

TMJ, temporomandibular joint.

highest variation (Wolsan *et al*, 2015). Several articles have been published on dental and/or temporomandibular joint (TMJ) pathology of marine mammal species; only four related to Otariidae in the Northern hemisphere (Sinai *et al*, 2014; Aalderink *et al*, 2015; Arzi *et al*, 2015a, b). Reported pathology included tooth wear (abrasion or attrition), tooth fractures, bony changes associated with periodontitis, acquired tooth loss, periapical lesions and TMJ osteoarthritis (TMJ-OA).

Presence of dental, TMJ or jaw pathology may interfere with a wild animal's ability to defend itself, prehend prey or intake food, contributing to morbidity and mortality. However, to the authors' knowledge, there has been no comprehensive study on the dental or TMJ pathology of Steller sea lions. Museum collections of skulls, such as those used in this study, are usually obtained from strandings, carcass recovery or donations by rehabilitation centres. An additional source of specimens is permitted hunting for subsistence (food or handicraft) purposes specific to Alaska Natives. The aim of this study was to investigate the nature and prevalence of dental and TMJ pathology in wild Steller sea lions by macroscopically and systematically examining museum specimen skulls.

Materials and Methods

Macroscopic examination was performed on 191 skull specimens from the University of Alaska, Museum of the North, Fairbanks, Alaska. The skull collections were obtained from carcass recovery and donations from other institutions and the public. Each skull was labelled with an identification number, collection date, location and sex. Categorization of specimens into adult and young adult age groups was determined by the degree of prominence of the cranial sutures and sagittal crest. Juvenile status was determined by incomplete eruption and resultant incomplete occlusion of the canine and incisor teeth. Neonate status was determined by the presence of physiological deciduous or mixed dentition. Specimens with skull fractures running through the sutures at the base of skull or obliteration of sutures were labelled as unknown age. Juveniles, neonates and incomplete skull specimens were excluded from the study.

The teeth surrounding bony structures and TMJs were examined and abnormalities classified according to previously defined criteria (Table 1) (Sinai *et al*, 2014; Aalderink *et al*, 2015; Arzi *et al*, 2015a; Winer *et al*, 2016). Congenital or developmental dental abnormalities were identified. Tooth form was determined by the shape of the crown, whereas the number of roots was determined by assessing the coronal portions. Teeth that were not glued into the alveoli were removed to complete the radicular examination. Supernumerary teeth and persistent deciduous teeth were recorded. Changes on the enamel indicative of enamel hypoplasia were also noted.

Acquired dental abnormalities were also assessed. Tooth wear such as attrition/abrasion, defined as smoothening and flattening of cusps and dentinal exposure with or without pulpal involvement, was recorded. Tooth fractures were evaluated according to the World Health Organization classification for tooth fractures in humans, as modified for use in carnivores (Verstraete, 2003), which consists of six different categories. Periapical lesions that were seen macroscopically were noted. Periodontal status of the teeth was categorized according to a classification system adapted for use on skulls (Verstraete *et al*, 1996a,b). The term stage 1 periodontitis was not used, as it indicates gingivitis, a condition that cannot be identified on skull specimens without soft tissue. The presence of bony lesions indicates periodontitis and the severity of the condition was classified into periodontitis stages 2, 3 or 4.

The TMJs, the mandibular head of the condylar process of the mandible and the mandibular fossa of the temporal bone were assessed on both sides for signs of OA and graded independently as mild, moderate or severe following a semiquantitative scoring system (Arzi *et al*, 2013, 2015a; Winer *et al*, 2016).

The data collected were first pooled with reference to tooth type and analysed descriptively. The data were also stratified by age and sex to assist in

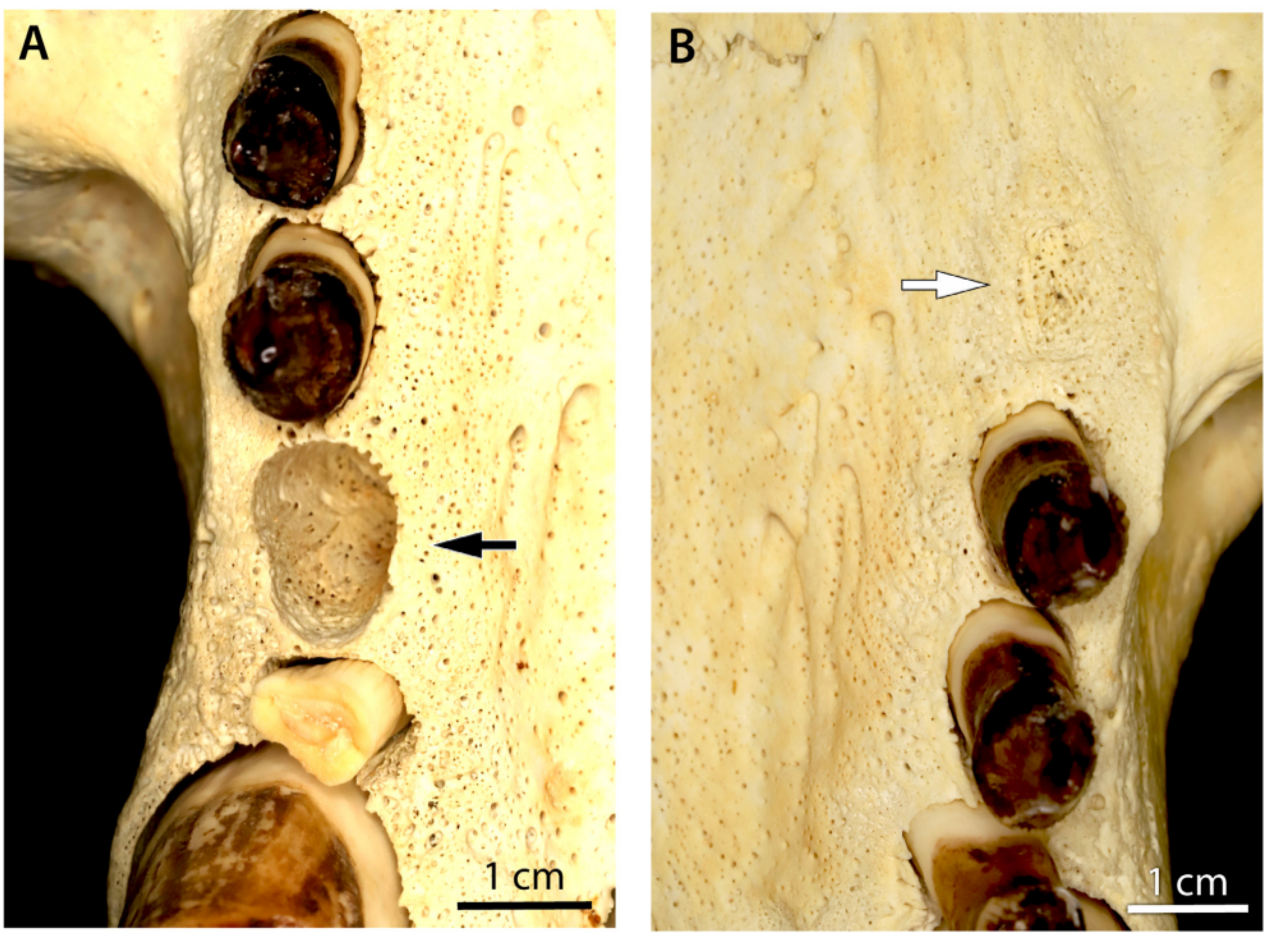

Fig. 2. Two types of tooth loss in an adult male Steller sea lion specimen (UMN 31955). (A) Artefactual loss of left maxillary second premolar tooth (arrow) as identified by a well-defined, sharp-edged, normal-shaped empty alveolus with no lesions visible in alveolar bone. (B) Acquired loss of right maxillary fourth premolar tooth (arrow) as identified by missing tooth and visible alveolus.

Fig. 3. Two-rooted right maxillary first molar tooth with stage 4 periodontitis in a young adult male Steller sea lion specimen (UMN 31959). Two distinct roots associated with the tooth, horizontal bone loss, rounding of alveolar margin (white arrow) and severe vertical bone loss at distal root (black arrows).

comparing the prevalence of dental pathology across various groups. Computer software (Prism version 9.0; GraphPad, www.graphpad.com) was used to perform all statistical analyses. Fisher's exact test was used to evaluate the relationship between groups (age or sex) and the presence of dental pathology. The Shapiro–Wilk test was used to assess the normality of data. The Mann–Whitney test was then used to investigate the relationship of age or sex with the number of teeth affected by the most common dental pathology (ie, tooth loss, attrition/abrasion, fractures, periodontitis, TMJ-OA). For all analyses, $P < 0.05$ was considered statistically significant.

Results

The dates of collection of the specimens ranged from 1953 to 2019. Of the 191 skull specimens available, 112 were included in the study. Forty-seven specimens were excluded due to excessive ante-mortem or post-mortem damage, 28 were omitted due to juvenile status as evidenced by the presence of mixed dentition, and four specimens were omitted due to a combination of both.

Of the 112 included specimens, 73 (65.2%) were from males, 29 (25.9%) from females and 10 (8.9%) from subjects of unknown sex. Fifty adult, 61 young adult and one specimen of unknown age corresponded to 44.6%, 54.5% and 0.9% of the studied population, respectively.

Presence of Teeth

The total number of teeth available for evaluation was 3,521 (92.5%) out of a potential maximum of 3,808 teeth. Artefactual absence (ie, loss in the specimen preparation process) accounted for 223 teeth (5.9%) and acquired tooth loss and congenital absence accounted for 55 teeth (1.4%) and nine teeth (0.2%), respectively (Fig. 2). Adults had significantly more acquired tooth loss than young adults ($P < 0.0001$) but no significant difference was found in terms of congenital absence between the age groups ($P = 0.37$). Males and females showed no significant difference in the number of congenital or acquired tooth loss ($P > 0.99$, $P = 0.86$, respectively). The most common tooth associated with acquired tooth loss in all specimens was the right mandibular first incisor tooth (n = 6; 10.9% of acquired missing teeth), followed by the left and right maxillary first incisor teeth and the right maxillary second incisor tooth (all n = 5; 9.1%). The maxillary first molar tooth was predominantly (n = 8; 88.9% of congenital missing teeth) associated with congenital absence, with a higher prevalence on the left maxillary first molar tooth (n = 5; 55.6%) than its contralateral tooth (n = 3; 33.3%). The other congenitally missing tooth identified was the right mandibular first molar tooth (n = 1; 11.1%).

Tooth Form

Only two teeth (0.06% of teeth) from two specimens (1.8% of skulls) had abnormal tooth form. These two teeth were right mandibular first premolar teeth in two different adult male specimens; they appeared small and minimally erupted past the surrounding alveolar bone, and therefore were described as vestigial teeth.

Number of Roots

One hundred and twenty-four teeth (3.5% of teeth) from 64 specimens (57.1% of skulls) were two rooted. All the two-rooted teeth identified were maxillary first molar teeth (Fig. 3); no other tooth type had supernumerary roots. Of the 104 right maxillary first molar teeth present for examination, 60 (57.7%) had two roots. Of the 104 left maxillary molar teeth available for evaluation, 64 (61.5%) had two roots. Bilateral

Fig. 4. Supernumerary right mandibular first premolar tooth (arrow) in a young adult male Steller sea lion specimen (UMN 73030). Note the relatively smaller size of the supernumerary tooth and dental crowding of the region due to its presence.

two-rooted maxillary first molar teeth were present in 60 specimens (53.6% of skulls). Of supernumerary roots, there was no significant difference between the two age groups ($P = 0.15$) or the two sex groups ($P = 0.87$).

Supernumerary Teeth

Three supernumerary teeth (0.09% of teeth) were identified in three specimens (2.7% of skulls). A young adult male specimen possessed a supernumerary right mandibular first premolar tooth (Fig. 4). The other two adult male specimens had a supernumerary right mandibular first molar tooth and a supernumerary right mandibular third premolar tooth, respectively. Localized crowding of teeth was seen in all three specimens with supernumerary teeth.

Persistent Deciduous Teeth

A persistent deciduous right mandibular canine tooth (0.06% of teeth) was observed in two specimens (1.8% of skulls) from young adult males. No other tooth type was found to be associated with the presence of persistent deciduous teeth.

Attrition and Abrasion

A total of 1,660 teeth (47.1% of teeth) from 111 specimens (99.1% of skulls) had evidence of attrition or abrasion. All adults ($n = 50$) and 98.4% of young adults ($n = 60$) had signs of dental attrition or abrasion. The only specimen that did not have dental attrition or abrasion was from a young adult male. The proportions of males and females affected by attrition or abrasion did not differ significantly ($P > 0.99$). Forty-three specimens (38.4% of skulls) had more than 50% of teeth affected by attrition or abrasion. Adults had significantly more teeth with attrition or abrasion than young adults ($P < 0.0001$). When comparing males and females, there was no significant difference between the number of teeth with attrition or abrasion ($P = 0.59$).

The incisor teeth accounted for almost half ($n = 824$; 49.6%) of the total tooth population with attrition or abrasion. The most common tooth displaying attrition or abrasion was the right mandibular first incisor tooth (n = 96; 85.7% of skulls), followed by the left mandibular first incisor tooth (n = 93; 83.0%), the left maxillary first incisor tooth (n = 90; 80.4%) and the right maxillary second incisor tooth (n = 89; 79.5%).

Tooth Fractures

A total of 241 teeth (6.8% of teeth) from 47 specimens (42.0% of skulls) had evidence of various types of tooth fracture. Tooth fractures were detected in most adults (n = 38; 76.0%) but only in 13.1% (n = 8) of young adults; this finding was statistically significant (P <0.0001). Similar proportions of males (n = 31; 42.5%) and females (n = 13; 44.8%) had tooth fractures. In total, adults accounted for 231 fractured teeth (95.9%) and young adults for nine fractured teeth (3.7%). One fractured tooth was identified in a specimen of unknown age. In total, males had 201 fractured teeth (83.4%), females had 37 fractured teeth (15.4%) and specimens of unknown sex had three fractured teeth (1.2%). Adult males had significantly more fractured teeth than adult females (P = 0.02). In terms of type of tooth fractures, complicated crown fractures were the most frequently identified (n = 69; 28.6% of fractured teeth), followed by complicated crown-root fractures (n = 65; 27.0%), uncomplicated crown fractures (n = 56; 23.2%), root fractures (n = 44; 18.3%) and uncomplicated crown-root fractures (n = 7; 2.9%), respectively. No enamel fracture was detected in any of the specimens. The incisor teeth accounted for more than half (n = 123; 51.0%) of the total tooth population with any type of tooth fracture, whereas only 3.7% (n = 9)of fractured teeth were seen in the molar teeth. The most common fractured teeth on the mandible were the left second incisor tooth (n = 16; 14.3% of skulls) and left first incisor tooth (n = 15; 13.4%), whereas on the maxilla they were the left second incisor tooth (n = 14; 12.5%) and left third incisor tooth (n = 14; 12.5%). The left mandibular first molar tooth was the only tooth in all the examined specimens that had no evidence of fracture.

Periapical Lesions

Eight periapical lesions were detected in five specimens (4.5% of skulls), all of which were specimens from adults (one female and four males). More than one lesion was identified in two specimens and were

Fig. 5. Mandibular heads in four adult Steller sea lion specimens. (A) Normal mandibular head (UMN 64001). (B) Mild temporomandibular joint osteoarthritis (TMJ-OA) lesion (UMN 32733). (C) Moderate TMJ-OA lesion with focal subchondral bone defect (UMN 87015). (D) Severe TMJ-OA lesion (UMN 86989).

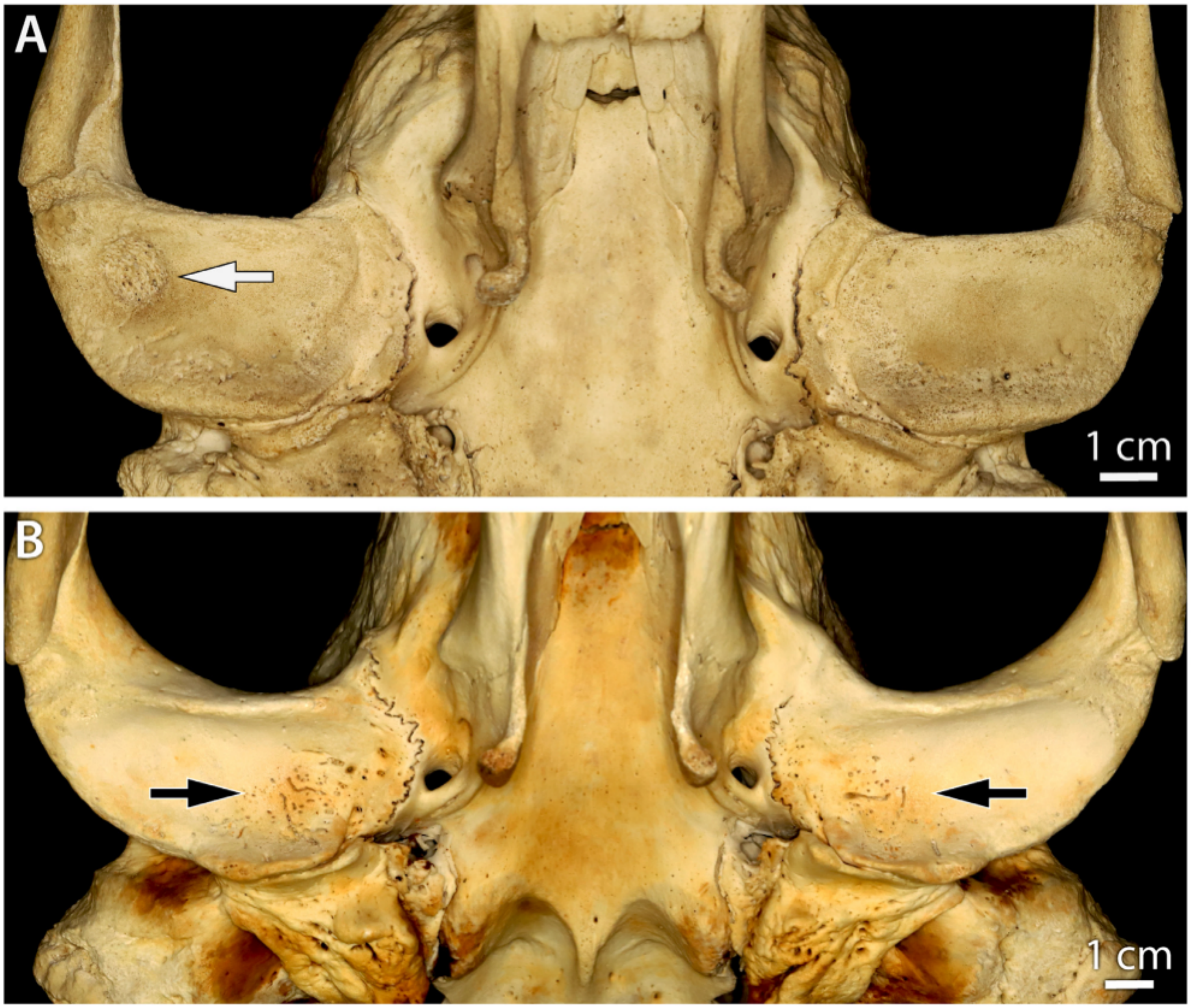

Fig. 6. Bilateral temporomandibular joint osteoarthritis (TMJ-OA) lesions in mandibular fossae in two adult Steller sea lion specimens. (A) Bilateral presentation with mild left TMJ-OA and moderate right TMJ-OA with focal subchondral bone defect (arrow) in a male adult specimen (UMN 85092). (B) Bilateral presentation with moderate TMJ-OA (arrows) in a male adult specimen (UMN 31955).

deemed to be associated with stage 4 periodontitis. Six of the eight lesions (75.0%) were seen in the maxilla. One of the periapical lesions identified in the mandible was deemed to be associated with severe attrition and abrasion of the left mandibular canine tooth.

Alveolar Bone Changes Consistent with Periodontitis

A total of 1,312 teeth (36.7%) out of 3,576 available for examination, with the addition of the acquired absent teeth, as presumably lost due to stage 4 periodontitis, had changes consistent with periodontitis. Various stages of periodontitis were detected in almost all adults (n = 49; 98.0%) but only in 55.7% (n = 34) of young adults; this finding was statistically significant (P <0.0001). A slightly higher proportion of females (82.8%) had periodontitis than males (72.6%) but the difference was not significant ($P = 0.32$). When taking all the teeth with periodontitis of different stages into account, adults had significantly more teeth affected by periodontitis than young adults (P <0.0001). This difference was not found between males and females ($P = 0.42$).

Among the teeth affected by periodontitis in all specimens, 55.9% (n = 734), 31.6% (n = 415) and 12.4% (n = 163) were categorized as stage 2, 3 and 4 periodontitis, respectively. While significantly more teeth with stage 2, 3 and 4 periodontitis were detected in adults than in young adults (P <0.0001, P

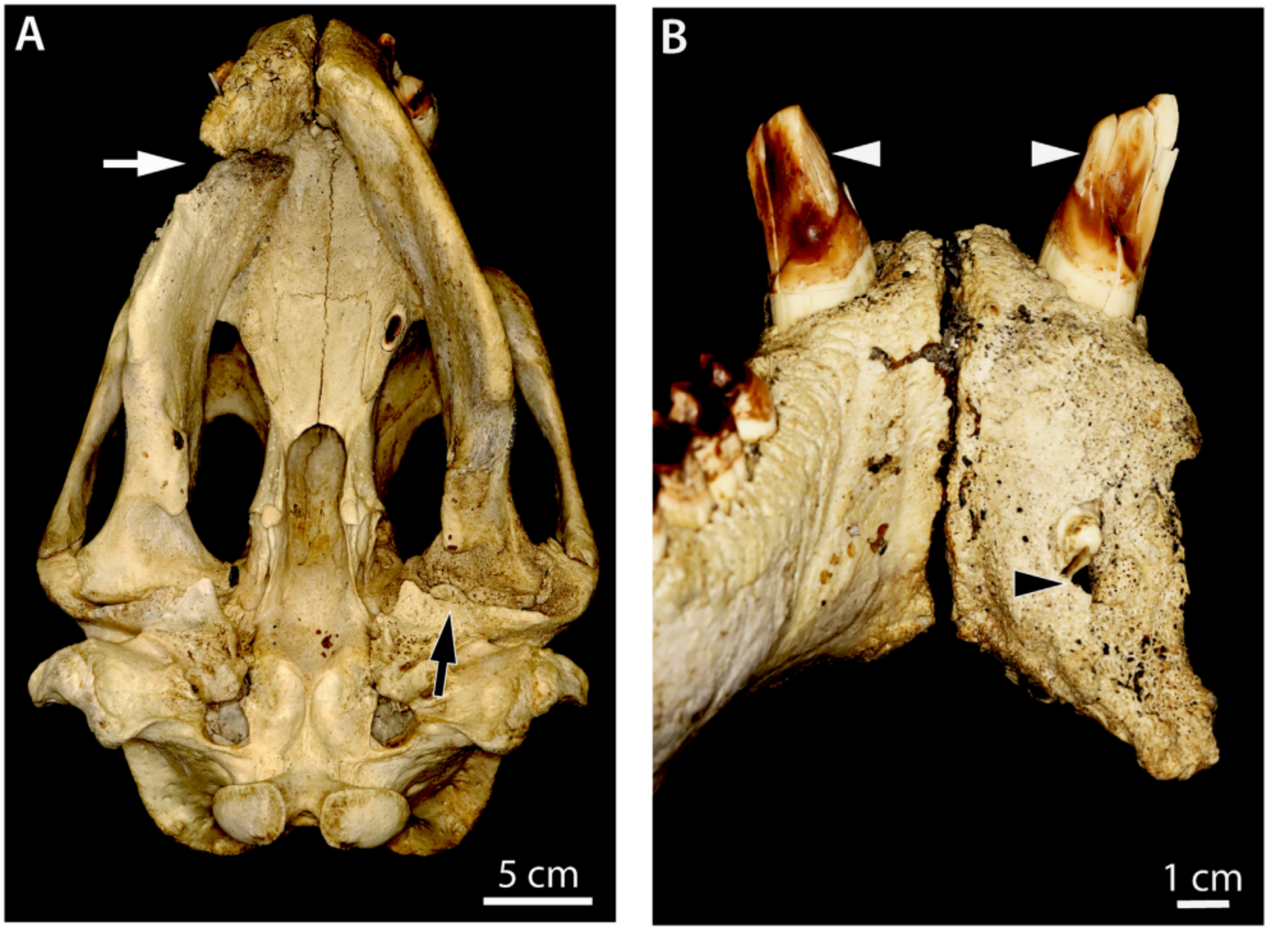

Fig. 7. An adult male Steller sea lion skull specimen (UMN 86969) with multiple lesions associated with teeth, temporomandibular joint (TMJ) and mandible. (A) Complete right mandibular fracture caudal to right mandibular canine tooth (white arrow). Note irregularities on left TMJ (black arrow). (B) Both left and right mandibular canine teeth have severe tooth wear (white arrow). Periapical lesion associated with the right mandibular canine tooth (black arrow) visible due to mandibular fracture.

<0.0001, $P<0.0001$, respectively), males and females showed no significant difference in terms of number of teeth with stage 2, 3 or 4 periodontitis ($P = 0.63$, $P = 0.25$, $P = 0.89$, respectively).

Enamel Hypoplasia

None of the 3,521 teeth examined had enamel hypoplasia.

Temporomandibular Joint Pathology

A total of 131 lesions consistent with TMJ-OA at different sites (a combination of left and/or right mandibular head and/or mandibular fossa of the temporal bone) were identified in 54 specimens (48.2% of skulls) (Fig. 5). At least one lesion was detected in most of the adults (n = 38; 76.0%) but only in 26.6% (n = 16) of the young adults, which was statistically significant ($P<0.0001$). More males (n = 41; 56.2%) than females (n = 10; 34.5%) were affected by TMJ-OA but the result was not significant ($P = 0.08$). Eighty-one lesions (61.8%) were seen in the mandibular fossae and 50 lesions (38.2%) in the mandibular heads. Bilateral TMJ-OA lesions were more commonly seen than unilateral presentation (Fig. 6). Bilateral TMJ-OA lesions were more frequently identified in the fossae, whereas unilateral TMJ-OA lesions were more frequently noted in the mandibular heads. Two adult male specimens had focal subchondral bone defects at the mandibular head and fossa that resembled osteochondritis dissecans (OCD) (Figs. 5C and 6A). Mild TMJ-OA was most frequently observed, accounting for 54.2% (n = 71) of all articular surfaces affected by TMJ-OA, followed by moderate TMJ-OA (n = 53; 40.5%) and severe TMJ-OA (n = 7; 5.3%). Thirteen specimens (11.6% of all skulls; 24.1% of specimens with TMJ-OA) had various degrees of TMJ-OA of all four articular surfaces; these specimens were all identified as adults, with most of them being male

(92.3%). Adults had significantly more mild and moderate TMJ-OA lesions than young adults (both P <0.0001), but no significant difference was found between the two age groups in the number of severe TMJ-OA lesions ($P = 0.33$). Males had significantly more mild TMJ-OA lesions than females ($P = 0.04$); no significant difference was found between the two sex groups in terms of number of moderate TMJ-OA lesions ($P = 0.70$) or severe TMJ-OA lesions ($P = 0.32$).

Other Findings

Three buccoverted first molar teeth were seen in two adult female specimens. A complete right mandibular fracture, caudal to the canine tooth, was seen in an adult male specimen (Fig. 7A). A periapical lesion was detected on the right mandibular canine tooth (Fig. 7B) as well as the presence of unilateral severe TMJ-OA lesions on the left mandibular head and fossa (Fig. 7A).

Discussion

The present study is the first to describe and characterize the nature and prevalence of dental and TMJ pathology in the Steller sea lion by systematic examination of a collection of skull specimens. The two most common dental pathologies identified were attrition and abrasion, and periodontitis. TMJ-OA was the third most common lesion in this study and was found in almost 50% of the examined specimens.

Congenital and developmental lesions were uncommon in this sample of Steller sea lions, with the exception of the presence of supernumerary roots. The prevalence of tooth malformation was 0.06%; this finding is comparable with that of the California sea lion (*Zalophus californianus*) (0.03%; Sinai *et al*, 2014). The northern fur seal (*C.allorhinus ursinus*) and the walrus (*Odobenus rosmarus*) had a slightly higher prevalence of tooth malformation (both 0.6%; Aalderink *et al*, 2015; Winer *et al*, 2016) than the Steller sea lion. Persistent deciduous teeth were deemed equally common in the Steller sea lion (0.06%) and the California sea lion (0.04%) (Sinai *et al*, 2014) but were slightly more frequently identified in the northern fur seal (0.4%) (Aalderink *et al*, 2015) and the southern sea otter (*Enhydra lutris nereis*) (0.6%) (Winer *et al*, 2013). A similar prevalence of congenital tooth loss was seen in the Steller sea lion (0.2%) and the California sea lion (0.1%) (Sinai *et al*, 2014). In contrast, supernumerary teeth were far less commonly seen in the Steller sea lion (2.7% of skulls) than in the California sea lion (25.4% of skulls) (Sinai *et al*, 2014).

More than 50% of the examined Steller sea lion specimens had at least one supernumerary root, which accounted for 3.5% of all teeth available for the study. The prevalence was higher than that reported in the California sea lion (0.2% of teeth) (Sinai *et al*, 2014), the northern fur seal (0.3%) (Aalderink *et al* 2015) and the southern sea otter (0.4%) (Winer *et al*, 2013). A supernumerary root was only identified in maxillary first molar teeth of the Steller sea lions, in contrast with findings in the California sea lion and the northern fur seal, in which two-rooted maxillary and mandibular first molar teeth were noted (Sinai *et al*, 2014; Aalderink *et al*, 2015). It is possible that these studies underreported the actual prevalence of supernumerary root when the teeth were glued into the alveoli after specimen preparation. Radiographic assessment would have assisted in detecting the presence of supernumerary root.

Acquired lesions were more frequently seen than congenital lesions. Among the acquired lesions, tooth loss and periapical lesions were rare. The prevalence of acquired tooth loss in the Steller sea lion was 1.4%, which is higher than reported in the California sea lion (0.4%) (Sinai *et al*, 2014), the southern sea otter (0.6%) (Winer *et al*, 2013) and the northern fur seal (0.8%) (Aalderink *et al*, 2015), but was lower than in the walrus (3.3%) (Winer *et al*, 2016). Adult Steller sea lions had more acquired tooth loss than young adults (P <0.0001). With advancing age, there is increased exposure to various inciting causes, enabling chronic pathological changes to develop. This may also account for our finding that periapical lesions were exclusively detected in adult specimens. Although these periapical lesions were only detected in 4.5% of the Steller sea lion skulls, similar to the California sea lion (5.8%) (Sinai *et al*, 2014) and the walrus (3.9%) (Winer *et al*, 2016), the prevalence may have been underreported. Radiographic examination would have likely revealed smaller and more subtle lesions beyond those detected during macroscopic examination.

Attrition/abrasion was the most common acquired lesion encountered, affecting almost all Steller sea lion specimens and 47.1% of teeth. This finding is consistent with the 42.4% of teeth with attrition/abrasion found in the California sea lion (Sinai *et al*, 2014) and the 52.0% detected in the southern sea otter (Winer *et al*, 2013) but differs remarkably from the 85.5% found in the walrus (Winer *et al*, 2016) and the 3.9% reported in the northern fur seal (Aalderink *et al*, 2015). Importantly, Steller sea lions do not masticate their food and the mechanical abrasion of food or other foreign items against teeth during foraging may be related to the extensive tooth wear. In addition, a large quantity of coarse gravel or fist-size rocks was commonly present in the stomach of Steller sea lions; it is suspected that such rocks and gravel would be regurgitated when the animals begin to forage (Thorsteinson and Lensink, 1962). Although the reason for stone intake is unknown, the initial ingestion, followed by regurgitation of stones, may possibly contribute to additional mechanical abrasion. Regurgitation may also cause acid demineralization of tooth substance, worsening the wear. Likewise, it has been speculated that excessive tooth wear in California sea lions is associated with a combination of mechanical abrasion against food items and acid demineralization secondary to regurgitation of food in order to remove the indigestible spines and bony structures of prey (Labrada-Martagón *et al*, 2007). Southern sea otters include hard food in their diet and, unlike pinnipeds, chew most of their shelled prey, which may explain the relatively high prevalence of tooth wear in this species (Kenyon, 1969). Walruses swallow soft-bodied prey whole and do not masticate (Fay, 1982). The high prevalence of tooth wear in the walrus may, therefore, be ascribed to abrasion by sand particles that enter the oral cavity while prey is procured from the ocean floor (Fay *et al*, 1977). Northern fur seals use a biting feeding mode and their teeth are developed for gripping slippery prey (Marshall *et al*, 2015). Their low prevalence of tooth wear is probably related to their diet and foraging behaviour. They feed on small schooling fish and squid in shallow water or midwater and swallow their prey (Gentry, 2009). Without the need for excessive chewing, it was proposed that attrition during normal occlusion contributed to tooth wear in the northern fur seal (Aalderink *et al*, 2015). Adult Steller sea lions had significantly more teeth with attrition/abrasion than young adults ($P < 0.0001$), which was probably associated with the additive effect of exposure to inciting causes over time with increasing age as previously described. Common wear patterns included coronal wearing in incisor teeth and mesial and distal wearing in canine teeth. Similar findings have been documented in the California sea lion (Sinai *et al*, 2014). It has been reported that male Steller sea lions older than 12 years might have difficulty defending their territories because of worn canine teeth (Thorsteinson and Lensink, 1962). Therefore, extensive tooth wear may contribute to the morbidity of the species, secondary to potential modification of feeding habits and behaviour.

Alveolar bony changes consistent with periodontitis were the second most commonly identified acquired lesion, affecting 75% of specimens and 36.7% of teeth. These findings differ from those reported in the California sea lion (19.4% of teeth affected) (Sinai *et al*, 2014) and the northern fur seal (18.6%) (Aalderink *et al*, 2015). Diagnosis of periodontal lesions from a dry skull is fundamentally flawed because soft tissue lesions are crucial in pathogenesis. However, the signs of periodontal disease can still be recognized because inflammatory hyperaemia results in more prominent, and an increased number of, vascular foramina, rough bone texture of the alveolar process and bone loss. Adult Steller sea lions were more commonly and severely affected by periodontitis than young adults (both $P < 0.0001$). Although periodontitis is more prevalent in adults, over 50% of the young adult population in our study had periodontitis, indicating that the disease process can begin at a young age and the lesions become substantial with advancing age. Similar findings have been reported in the California sea lion, the northern fur seal and the southern sea otter (Winer *et al*, 2013; Sinai *et al*, 2014; Aalderink *et al*, 2015).

Tooth fractures were identified in more than 40% of Steller sea lion specimens, affecting 6.8% of teeth. The prevalence is comparable to that found in the southern sea otter (4.5% of teeth) (Winer *et al*, 2013). In contrast, tooth fractures in the California sea lion (0.6%), the northern fur seal (1.1%) and the walrus (1.3%) were less prevalent (Sinai *et al*, 2014; Aalderink *et al*, 2015; Winer *et al*, 2016). The higher prevalence of tooth fractures in the Steller sea lion may be associated with the potentially large bite forces during biting feeding (Marshall *et al*, 2015) and the ingestion of stones and gravel, whereas in southern sea otters the higher prevalence may be secondary to chewing hard prey (eg, clams, mussels and sea urchins) (Murie, 1940). Adult Steller sea lions were more commonly and severely affected by tooth fractures than young adults (both $P < 0.0001$), in accordance with the findings in the California sea lion (Sinai *et al*, 2014). The cumulative effects of endogenous (eg, tooth wear secondary to abrasion and attrition that may result in cracks and craze lines predisposing teeth to fracture; thermal stresses that may result in fatigue; age-related changes in biomechanical properties of tooth substance due to degradation that may reduce fracture resistance) and exogenous factors (eg, trauma) may be more obvious in older Steller sea lions and possibly explain the observations. Adult male Steller sea lions had significantly more fractured teeth than adult females ($P = 0.02$). Similar findings were reported in the California sea lion and the southern sea otter (Winer *et al*, 2013; Sinai *et al*, 2014). This may be associated with the fact that adult males may engage in aggressive confrontation to establish dominance and defend their territory. Unlike California sea lions but like northern fur seals, the boundaries for male Steller sea lions are well defined and extremely stable (Gentry, 1970; Sandegren, 1970). It has been reported that 2,094 threat displays were observed but only 43 fights were seen among the male Steller sea lions in a given area (Gentry, 1970). Therefore, the significant difference observed in our study cannot be readily explained. Rostral teeth, the incisor teeth in particular, were most commonly fractured in the Steller sea lions, which is consistent with what has been described in the northern fur seal (Aalderink *et al*, 2015). Their location in the oral cavity may render them more prone to exogenous trauma, resulting in fractures.

TMJ-OA was present in 48.2% of the Steller sea lion specimens. Previous studies on TMJ-OA in the California sea lion (Arzi *et al*, 2015a) and the walrus (Winer *et al*, 2016) found a higher proportion (63.5% and 60.5%, respectively) of affected animals, while fewer northern fur seals (20.0%) (Aalderink *et al*, 2015) had TMJ-OA. It has been hypothesized that genetic factors may contribute to TMJ-OA occurrence and underlying processes such as progressive cartilage degradation, subchondral bone remodelling and chronic inflammation in the synovial tissue. However, the reason for the high prevalence of TMJ-OA in pinnipeds is unknown. Furthermore, it should be noted that osseous changes develop later in the disease process and hence the actual occurrence of TMJ-OA may be underestimated (Coan *et al*, 2010; Arzi *et al*, 2012). Significantly more adults had TMJ-OA than young adults (P <0.0001), as well as a significantly higher number of mild and moderate TMJ-OA lesions (both P <0.0001), indicating that age has a significant association with the presence of TMJ-OA in the Steller sea lion. This result agrees with the TMJ-OA findings in the northern fur seal but contrasts with observations in the California sea lion (Arzi *et al*, 2015a). Bilateral TMJ-OA and mild TMJ-OA were more commonly seen in the Steller sea lion, in agreement with findings in the California sea lion ((Arzi *et al*, 2015a). TMJ-OA lesions occurred more frequently in the mandibular head than in the mandibular fossa but no other specific consistent localization or distribution of TMJ-OA lesions was identified. The two focal OCD-like subchondral bone defects noted are an uncommon finding in the TMJ (Orhan *et al*, 2006) but this lesion has been reported in California sea lions (Arzi *et al*, 2015a). OCD is described as a separation of an articular cartilage—subchondral bone segment within a joint (Robertson *et al*, 2003). Although the reason for development of TMJ-OA is unknown, prolonged malocclusion/drifting of the mandible secondary to mandibular fracture may be a factor, as seen in an adult male Steller sea lion specimen with a concurrent fractured mandible and severe unilateral TMJ-OA on the contralateral side. It is speculated that the Steller sea lions that had moderate to severe TMJ-OA may have had discomfort or pain and a decreased range of motion that affected feeding habits and behaviour and potentially contributed to morbidity of the species.

In conclusion, understanding the dental pathology of Steller sea lions may help in the development of best husbandry practice for this species when in captivity, as longer life expectancy of captive animals is anticipated. Documenting the prevalence of various dental lesions in Steller sea lions consolidates our knowledge of dental disease in this species and contributes to a better understanding of their overall health.

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Conflict of Interest Statement

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Supplementary Data

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