Morphology and Biomechanics of the Pinniped Jaw: Mandibular Evolution Without Mastication

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ABSTRACT

Pinnipeds (seals, sea lions, and walruses) underwent a shift in jaw function away from typical carnivoran mastication to more novel marine behaviors during the terrestrial-aquatic transition. Here we test the effect of aquatic prey capture and male-male combat on the morphological evolution of a mammal jaw that does not masticate. Nine three-dimensional landmarks were taken along the mandible for 25 species ($N = 83$), and corpus and symphysis external and cortical breadths for a subset of five species ($N = 33$). Principal components analysis was performed on size-corrected landmark data to assess variation in overall jaw morphology across pinnipeds. Corpus breadths were input to a beam model to calculate strength properties and estimated bite force of specific species with contrasting behaviors (filter feeding, suction feeding, grip-and-tear feeding, and male-male combat). Results indicate that, although phylogenetic signal in jaw shape is strong, function is also important in determining morphology. Filter feeders display an elongate symphysis and a long toothrow that may play a role in filtering krill. Grip-and-tear feeders have a long jaw and large estimated bite force relative to non-biting species. However, the largest estimated bite forces were observed in males of male-male combative species, likely due to the high selection pressure associated with male success in highly polygynous species. The suction feeding jaw is weak in biting but has a different morphology in the two suction feeding taxa. In conclusion, familial patterns of pinniped jaw shape due to phylogenetic relatedness have been modified by adaptations to specialized behavior of individual taxa. Anat Rec, 296:1049–1063, 2013. © 2013 Wiley Periodicals, Inc.

Key words: Pinniped; geometric morphometrics; jaw biomechanics; marine feeding; sexual dimorphism

INTRODUCTION

The evolution of pinnipeds from a terrestrial ancestor to a fully aquatic mammal has involved numerous morphological and behavioral adaptations (Adam and Berta, 2002; Berta et al., 2006). While the postcrania have become specialized for swimming, the cranio-mandibular complex has assumed increased importance in

TABLE 1. Species sampling and ecological information

Family	Genus	Species	Morph, n	Biomech, n	Prey type	Technique	SSD	Harem size
Odobenid	*Odobenus*	*rosmarus*	3		Bivalve mollusks	Suction[a]	1.52	7.2
Otariid	*Arctocephalus*	*australis*	2		Cephalopods/fish	Pierce	1.88	6
Otariid	*Arctocephalus*	*forsterii*	1		Cephalopods/fish	Pierce	3.28	6.2
Otariid	*Arctocephalus*	*gazella*	2		Crustaceans/fish	Pierce	3.44	5.1
Otariid	*Arctocephalus*	*philippii*	1		Cephalopods/fish	Pierce	2.91	4
Otariid	*Arctocephalus*	*pusillus*	3		Cephalopods/fish	Pierce	4.1	13.8
Otariid	*Arctocephalus*	*tropacalis*	2		Cephalopods/fish	Pierce	3.14	4.4
Otariid	*Callorhinus*	*ursinus*	2		Cephalopods/fish	Pierce/suction[a]	4.2	22.7
Otariid	*Eumetopias*	*jubatus*	4		Cephalopods/fish	Pierce/suction[a]	3.48	11.8
Otariid	*Neophoca*	*cinerea*	2		Cephalopods/fish	Pierce/suction?	3.82	3.8
Otariid	*Otaria*	*byronia*	6	6	Cephalopods/fish	Pierce/suction?	2.08	6
Otariid	*Phocarctos*	*hookeri*	3		Cephalopods/fish	Pierce/suction?	3.17	12.9
Otariid	*Zalophus*	*californianus*	3		Cephalopods/fish	Pierce	3.02	14.9
Phocid	*Cystophora*	*cristata*	2		Cephalopods/fish	Pierce	1.54	1
Phocid	*Erignathus*	*barbatus*	1	7	Bivalve mollusks/ crustaceans	Suction[a]	0.96	1
Phocid	*Halichoerus*	*grypus*	5		Cephalopods/fish	Pierce	1.13	5
Phocid	*Histrophoca*	*fasciata*	2		Cephalopods/fish	Pierce	1.18	1
Phocid	*Hydruga*	*leptonyx*	4	7	Vertebrates/ crustaceans	Grip and tear/filter[a]	0.88	1
Phocid	*Leptonychotes*	*weddellii*	4		Cephalopods/fish	Pierce	1.01	3
Phocid	*Lobodon*	*carcinophagus*	4	5	Crustaceans	Filter[a]	0.98	1
Phocid	*Mirounga*	*angustirostris*		8	Cephalopods/fish	Pierce	4.66	13
Phocid	*Mirounga*	*leonina*	3		Cephalopods/fish	Pierce	6.2	48
Phocid	*Monachus*	*monachus*	2		Cephalopods/fish	Pierce	0.95	1
Phocid	*Monachus*	*tropacalis*	1		Cephalopods/fish	Pierce	1.13	?
Phocid	*Ommatophoca*	*rossii*	1		Cephalopods/fish	Pierce	0.94	1
Phocid	*Pagophilus*	*groenlandicus*	5		Cephalopods/fish	Pierce	1.04	1
Phocid	*Phoca*	*hispida*	2		Cephalopods/fish	Pierce	1.03	1
Phocid	*Phoca*	*largha*	2		Cephalopods/fish	Pierce	1.36	1
Phocid	*Phoca*	*vitulina*	3		Cephalopods/fish	Pierce	1.14	1
Phocid	*Pusa*	*caspica*	4		Cephalopods/fish	Pierce	1.28	1
Phocid	*Pusa*	*sibirica*	4		Cephalopods/fish	Pierce	1.05	1

Reproduced from Ferguson et al. (2006), with permission from Esperanza. SSD is sexual size dimorphism (male mass/ female mass). Prey type and feeding technique were taken from Adam and Berta (2001), except where [superscript a] direct observations of feeding technique have been made by Klages and Cockcroft (1990), Kastelein (1994), Marshall (2008), Hocking et al. (2013), Marshall (2013).

prey-acquisition and reproduction, with the development of novel feeding strategies, facial displays and combative behaviors (Adam and Berta, 2002); Jones and Goswami, 2010a). Simultaneously, the role of oral processing of food has decreased, leading to simplification of the dentition and loss of unilateral mastication (Berta et al., 2006). All these factors make pinnipeds a fascinating model for the study of cranio-mandibular functional morphology.

The Pinnipedia is made up of phocids (18 species), otariids (14 species), and odobenids (1 species) that diverged around 33 million years ago (Ma) (Arnason, 2006) and have undergone independent morphological evolution of both the cranium (Jones and Goswami, 2010a) and post-cranium (Berta et al., 2006). Within the Phocidae there are two subfamilies: phocines (10 species) and monachines (8 species) (Higdon, 2007). Phocines split from monachines about 22 Ma ago (Arnason, 2006) and have mostly adopted an ice-breeding habit. Pinnipeds make a particularly interesting mammalian model for testing non-masticatory adaptation of the jaw as they display a wide range of novel behaviors including marine prey-capture and extreme male-male combat. The majority of both phocids and otariids share a generalist "pierce-feeding" technique, catching squid and fish using sharp, homodont teeth, and swallowing them whole (Table 1). Phocid and otariid pierce feeders do not have systematic differences in diet though feeding is opportunistic and may vary depending on the season or locality (Tollit et al., 1998; Dellinger and Trillmich, 1999). However, a number of species have evolved novel prey acquisition methods (Klages and Cockcroft, 1990; Bonner, 1999; Adam and Berta, 2002; Reeves et al., 2002; Berta et al., 2006). Specialized suction feeding on bivalve mollusks is found in both the walrus and in one species of phocid (*Erignathus barbatus*) (Kastelein, 1994; Adam and Berta, 2002; Marshall, 2008). However, it is utilized to a lesser extent in other species to draw the prey toward the mouth before biting (Klages and Cockcroft, 1990; Marshall, 2013). In the walrus and bearded seal, soft-bodied mollusks are removed from their shells by powerful suction forces (up to 120 mpa in walrus) created by the rapid retraction of the tongue (Kastelein, 1994). A study examining evolution of discrete craniodental traits with different feeding strategies related suction feeding to a modified palate and fused mandibular symphysis in odobenids (Adam and Berta, 2002). The crabeater seal (*Lobodon carcinophagus*) uses filter

feeding to extract prey by gulping water then sieving out krill (King, 1961; Klages and Cockcroft, 1990; Berta et al., 2006). Filter feeding has been associated with the unusual shape and positioning (cuspate and interdigitate) of the teeth of *L. carcinophagus* (Klages and Cockcroft, 1990; Adam and Berta, 2002). Further, qualitative links have been made between filter feeding and elongation of the mandibular symphysis in this species, possibly relating this to modified insertions of the intrinsic tongue muscles (King, 1961). The leopard seal (*Hydrurga leptonyx*), has two disparate feeding modes (Hocking et al., 2013). It is well known for using its enlarged canines for grip-and-tear feeding, in which it holds large warm-blooded prey such as seal pups and penguins in its sharp teeth then shakes its head violently to rip off pieces of flesh that can be swallowed whole (Adam and Berta, 2002). In captivity, they have also been observed sucking prey into the mouth and using heavily cusped postcanine teeth for filtering, in a similar manner to the crabeater seal. This combination of feeding techniques allows the leopard seal to access a bimodal diet of prey both at the top (large vertebrates) and bottom (krill) of the marine food web (Hocking et al., 2013).

Polygyny involving extreme male combat behavior has evolved convergently in both phocid and otariid pinnipeds, and involves males defending their harems through violent clashes in which they rear up and bite each other's head and neck (Bartholomew, 1970; Berta et al., 2006). Included in this group are the elephant seals, in which males are on average six times larger in mass than females, representing amongst the largest known dimorphism in mammals (Reeves et al., 2002; Ferguson, 2006). Female elephant seals also interact aggressively although biting is rarer and less damaging than during male-male combat (Christenson and Le boeuf, 1978). Other pinnipeds are monogamous or display the less violent "resource-defense polygyny" (Berta et al., 2006).

Previous studies (Jones and Goswami, 2010a,b) used three-dimensional geometric morphometrics to assess the influence of phylogeny, ecology, and sexual dimorphism on cranial morphology in a large sample of extant pinnipeds. We showed that pinniped cranial morphology is very strongly influenced by phylogenetic history, with the three pinniped families, Phocidae (seals), Otariidae (fur seals and sea lions), and monospecific Odobenidae (walrus), occupying distinct regions of cranial morphospace. Superimposed on this phylogenetic pattern were possible functional signals relating to modification of the crania for facial displays and feeding behavior. Specifically, the grip-and-tear feeder (*H. leptonyx*) has a more elongate skull and greater interorbital breadth than other phocids, possibly relating to a more aggressive feeding strategy. Suction feeding (*E. barbatus)* and sediment feeding (*Halichoerus grypus*) phocids have broader, flatter snouts with larger nasal openings than most other phocids, which may relate to feeding at the sediment-water interface. Dimorphism of the cranium is very large in species with male facial displays. Male *Cystophora cristata* have a nasal bladder and *Mirounga leonina* have a proboscis, and males of both species display an enlarged nasal opening. *Otaria byronia* exhibits more cranial dimorphism than the other otariids studied.

Here, we apply this same method to the mandible to determine whether similar factors are influencing the evolution of both the cranium and the mandible. The analysis is further extended by assessing biomechanical parameters of the mandibular corpus. Whereas the cranium represents a very functionally complex unit that may be constrained by multiple requirements, including brain protection, sensory perception, and feeding (Cheverud, 1981; Hallgrimsson et al., 2007), the mandible has a direct link to the production of bite force and oral processing of food (Hylander and Johnson, 1994). Many studies have supported this interpretation of the mandible and thus used mandibular morphology to directly infer function (Hylander, 1979; Daegling and Grine, 1991; Biknevicius and Ruff, 1992a; Therrien, 2005b). Hence, when examining the pinniped jaw, more directly assessing its functional capabilities can enrich and refine our interpretation of the purely morphological data. Therefore, the original morphological dataset is augmented with additional biomechanical measures from species characterized by a variety of behaviors involving the jaw. Specifically, measures of strength of the mandibular corpus are calculated using cross-sectional properties and mechanical beam theory (Biknevicius and Ruff, 1992a,b; Therrien, 2005a,b).

Though many previous studies have examined mandibular function using biomechanical beam modeling, the primary emphasis has been on mastication and unilateral biting (Hylander, 1979; Daegling and Grine, 1991). A limited number of studies have considered biomechanical influences resulting from non-masticatory behavior, for example, sanguinivory and roost-excavating in bats (Davis et al., 2010; Santana and Dumont, 2011). Beam model analysis indicated that non-masticatory gouging behavior has not influenced cross-sectional properties of the primate mandible (Vinyard and Ryan, 2006), whereas cross-sectional data from humpback whale jaws indicated that they are optimized for resisting forces involved in lunge feeding in the absence of mastication (Field et al., 2010). Both jaw length and toothrow length are examined using landmark data. Jaw length has previously been related to diet and bite force production in primate taxa (Hylander, 1985; Ravosa, 2000) and gape in carnivores (Greaves, 1985, 2001). Toothrow length is shortened in pinnipeds, possibly relating to a release from the requirement of large bite force at the posterior teeth due to the lack of mastication (Greaves, 1983, 1988; Adam and Berta, 2002), though variation within the pinnipeds has not been examined.

Finally, morphology of the mandibular symphysis will be considered. The nature of the articulation between the two hemimandibles is highly variable in mammals. They may be linked by bone, strong cruciate ligaments, or looser fibrocartilagenous pads (Scapino, 1981). In masticating mammals, a fused symphysis transfers balancing side muscle forces to the working side and tends to be correlated with processing hard foodstuffs (Hylander et al., 2000, 2004; Scott et al., 2012). In primates, symphyses that are deeper superoinferiorly are thought to be strengthened against dorsoventral bending during anterior biting. Whereas, anteroposteriorly long symphyses may be resisting lateral forces during wishboning of the hemimandibles (Hylander, 1988; Daegling, 1989, 2001). These shape changes may be accomplished by both changing dimensions and orientation of the symphysis relative to the long axis of the jaw (Daegling, 1989, 2001). Pinniped symphyses are generally unfused (Adam and Berta, 2002; Scott et al., 2012), but,

depending on the nature of stiffness of the joint, shape may still reflect function. An elongate symphysis in *L. carcinophagus* has been suggested as a filter feeding adaptation (King, 1961); however, very little is known about pinniped symphyses compared to terrestrial carnivores (Scapino, 1981; Scott et al., 2012).

Morphometric data for 25 of 36 extant pinniped species are presented, representing all families and a wide range of ecologies. More detailed biomechanical data were collected for a subset of five of these species. Specifically, two species with male-male combat, an otariid (*O. byronia*) and a phocid (*M. angustirostris*) were selected due to their size dimorphism, aggressive behavior and to examine convergent instances of sexual selection (Bartholomew, 1970; Berta et al., 2006; Sanvito et al., 2007). Three species with specialized feeding behavior were also selected. Direct observations of feeding behavior are rare in this group; however, these three species are relatively well studied and have been previously highlighted for their unique feeding behavior in the literature. *E. barbatus* is one of two highly specialized suction feeding pinnipeds (Marshall, 2008). (The other, the walrus, we were unable to measure because the fused mandibles ruled out X-raying, see below.) *H. leptonyx* is the only pinniped to feed on large vertebrates using the grip-and-tear technique but also filter feeds, like *L. carcinophagus* (Hocking et al., 2013). Hence, the species included in this subset were chosen to best encompass the extremes of feeding and reproductive modes found in pinnipeds and to provide additional functional information relevant for understanding these unusual ecologies.

We hypothesize that variation in mandibular morphology between groups will show some similarities to that observed in the cranium (Jones and Goswami, 2010a,b). Specifically:

1. There should be strong contrasts between the morphology of the three pinniped families as observed in the cranium. Pierce feeding phocids and otariids may have distinctive morphology reflecting phylogenetic differences, despite strongly overlapping feeding habits. However, the correlation between phylogeny and morphology may be slightly weaker and function might play a larger role in the jaw than in the cranium due to its simpler structure and direct role in feeding.
2. *H. leptonyx*, which has a cranial morphology that diverges from the rest of the phocids, likely due to its grip-and-tear feeding technique, should also show distinctive jaw morphology. Specifically, *H. leptonyx* should have an enlarged coronoid for attachment of the temporalis muscle to produce a posteriorly directed muscle vector for resisting struggling prey (Smith and Savage, 1959; Weijs, 1980; Greaves, 1995), as well as a large gape for grasping large prey items. We expect morphological evidence of higher bite force production in this species than in those that do not utilize biting to capture prey (suction or filter feeding). Hence, dorsoventral mandibular strength relative to length will be increased in *H. leptonyx* relative to suction or filter feeders.
3. Previous qualitative observations of an elongated mandibular symphysis in *L. carcinophagus* that has been related to filter feeding will be tested (King, 1961). Since it has been suggested that toothrow

length is shortened in pinnipeds, related to the loss of mastication at posterior teeth (Adam and Berta, 2002), the secondary lengthening of the toothrow due to use of the posterior teeth in filtering krill will also be tested.
4. Similarities in jaw morphology between phocid and odobenid suction feeders due to their shared feeding ecology will be examined since this pattern is observed in the cranium. Suction feeding relieves the necessity for biting, and so adaptations might include reduced dorsoventral bite force and temporalis muscle attachment size.
5. We hypothesize that species using male combat will have more dimorphism in jaw shape than monogamous species, and that combative males will have jaws with large muscle attachment sites. Bite force (relative mandibular corpus strength) dimorphism between males and females will be greater in those species with combative male selection than in those with monogamous strategies.

MATERIALS AND METHODS

Specimens

Morphometric data for the mandible were taken in conjunction with previous cranial studies (Jones and Goswami, 2010a,b) on 83 specimens representing 25 of the 34 extant pinniped species (Table 1). Specimens were from the collections at the Natural History Museum, London, and the Cambridge Zoology Museum (Supporting Information Table S1). In contrast to the previous studies, juvenile specimens and specimens of unknown age were excluded because feeding changes drastically through ontogeny, which may affect interpretations of the relationship between feeding and jaw morphology. Additional biomechanical data were collected on a subset of the species using adult specimens from the Smithsonian Museum of Natural History, Washington DC (Table 1, Supporting Information Table S1). When comparing the biomechanical and morphometric data both species of the genus *Mirounga* are assumed to share similar morphological characteristics since both species are polygynous and combative. However, sampling limitations meant that only *M. leonina* could be included among our morphometric data, and only *M. angustirostris* among our biomechanical data.

Morphometric Data

Nine three-dimensional semi-landmarks were obtained using an Immersion Microscribe G2X digitizer (Immersion Corp., San Jose, CA) with 0.2 mm accuracy (Fig. 1, Table 3). Landmarks were selected to include all regions of the jaw (ramus and corpus) and to identify geometrically corresponding points among diverse taxa. Measurements were repeated three times on three specimens and landmarks with a standard deviation greater than 1 mm in repeated measurements were discarded as in the previous cranial study (Jones and Goswami, 2010a). Non-shape information (size, translation, and rotation) were removed from the landmark configurations using Procrustes Superimposition in Morphologika 2.5 (O'Higgins and Jones, 2006), and then Principal Components analysis (PCA) was used to describe the
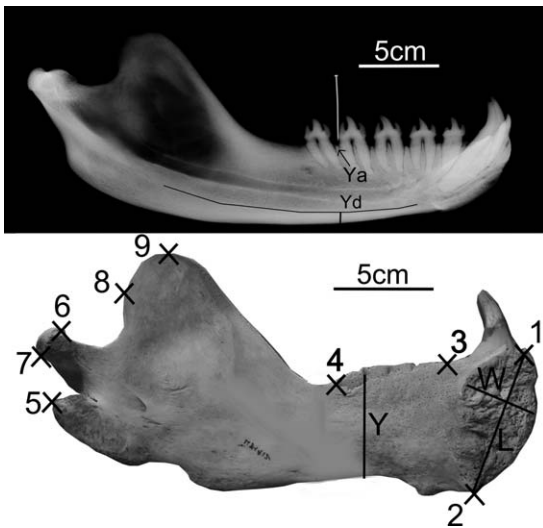
Fig. 1. Upper: internal corpus measures on *H. leptonyx*, specimen no. SM550359. Radiograph showing measurements of cortical thickness taken anterior to the most posterior tooth as indicated by a radiographic marker (nail, white line). Black lines represent the boundary between cortical and cancellous bone. Lower: external jaw measures on a jaw of *O. byronia*, specimen number SM484912. Numbers—landmark measurements for the morphometric analyses. Landmark names can be found in Table 3. Landmarks 3 and 4 are positioned based on alveolar sockets because cheek teeth are missing. Black line Y represents external corpus measurements for biomechanical analyses, taken at same position as measurements in (a). L, symphysis length; W, symphysis width; Ya, alveolar depth in the Y plane, a constant thickness of 0.5 mm was used for all specimens; Yd, inferior thickness of cortical bone in the Y plane.

major axes of variation in the dataset (Zelditch et al., 2004). PC loadings were obtained in PAST (Hammer et al., 2001), and the five landmarks contributing most to the variation on each axis were found. The influence of phylogeny on mandibular morphology was tested by correlating Euclidean distance between species (for males and females separately) on each PC axis with patristic distance output from Mesquite (Maddison and Maddison, 2010), using Spearman's rank correlation in PAST (Hammer et al., 2001), in the same manner as in the cranial study (Jones and Goswami, 2010a).

Mandibular and Toothrow Length Data

The landmarks were also used to calculate species averaged jaw length (L1 to L7, Table 2) and toothrow length (L1 to L4, Table 2). The centroid size calculated from 86 cranial landmarks from the same specimens was used as an overall measure of skull size. Phocids and otariids were compared using reduced major axis regressions of log jaw length on log cranial size for each family separately and then slopes were tested for similarity in SMATR (Warton and Weber, 2002). For slopes that were similar, elevation differences were tested in SMATR (Warton et al., 2006); however, for significantly different slopes a Fisher's exact test was conducted (Tsutakawa and Hewett, 1977). Since a significant difference in elevation was detected, only other members of the Phocidae when testing if *H. leptonyx* had a significantly longer jaw length based on its skull size. Species

averaged toothrow length was compared with jaw length to assess whether *L. carcinophagus* has a significantly longer toothrow than expected for its skull size. Phylogenetically robust outlier tests were conducted using least squares regression of independent contrasts that were placed back onto tip space to calculate associated 90% and 95% prediction intervals (Garland and Ives, 2000) in Mesquite (Maddison and Maddison, 2010). Slopes were calculated excluding the species being tested and a super-tree topology based on molecular data (Higdon, 2007) was the phylogeny used. This method takes into account the hierarchical non-independence of related species (Felsenstein, 1985; Garland and Ives, 2000).

Symphysis Morphology

Terrestrial carnivore symphyses have been well studied, and have been grouped into four categories based on their morphology (Scapino, 1981). A grade 1 symphysis is a flexible connection between the hemi-mandibles with a thick fibrocartilage pad and smooth endplates. Grade 2 has a thinner pad and more transverse supporting ligaments, limiting its flexibility and causing more rugosities on the endplate. Grade 3 has many deep, interlocking rugosities that are attachments for transverse and longitudinal ligaments, resulting in a stiff connection. Finally, grade 4 is synostosed, preventing any movement between the hemi-mandibles. Scott et al. (2012) classified many mammal symphyses according to this scheme, including the pinnipeds studied here: *E. barbatus, L. carcinophagus, H. leptonyx* and *M. angustirostris* (grade 1), and *O. byronia* (grade 2). We describe and compare the morphology of these symphyses. In addition, symphyseal length (L) and width (W) were measured using digital calipers to compare symphyseal size and shape between the species (Fig. 1). Size of the symphysis was measured by calculating the square-root of symphyseal area and scaling it by jaw length. Symphyseal shape was estimated by dividing the length of the symphysis by its width, to calculate its aspect ratio. The influence of species and sex on scaled area and aspect ratio of the symphyses was tested using a two-way ANOVA model in R. Pairwise differences were tested using a *post hoc* Tukey HSD test.

Biomechanical Data

Beam model. The mandibular corpus can be modeled as a beam that is deformed by bending forces about the dorsoventral (Y) and labiolingual (X) planes during biting (Hylander, 1979, 1988; Daegling, 1989; Daegling and Grine, 1991; Biknevicius and Ruff, 1992a; Daegling and McGraw, 2001; Therrien, 2005a,b; Therrien et al., 2005). Important loading regimes identified during unilateral biting in primates *in vivo* include parasagittal bending, dorsoventral shear and torsion (Hylander, 1988). We concentrate here on bending of the corpus in part to simplify the analysis (in the absence of *in vivo* mechanical studies of these taxa) and because bending strength of the mandible has been shown to discriminate between various carnivoran dietary groups (Biknevicius and Ruff, 1992a; Therrien, 2005a). An asymmetrical, hollow model is used as this more accurately captures the morphology of the mandibular corpus (Biknevicius and Ruff, 1992a,b). This assumes that the cortical bone

around the perimeter of the mandible is responsible for all the mechanical support, with no contribution from the cancellous bone in the center (Ruff, 1983; Daegling, 1989). Second moments of area (I) describe the distribution of bone about the sagittal and labiolingual axes and are proportional to bending rigidities (O'Neill and Ruff, 2004). The measures can also be converted into section moduli (Z), which are proportional to strength in bending, by factoring in the maximum distance from the neutral axis to the outermost fiber of the section (y):

$$Z = I/y. \tag{1}$$

When considering the mechanical functioning of the corpus we are most interested in bite force, as this is indicative of different *in vivo* behaviors (Valkenburgh and Ruff, 1987; Biknevicius and Ruff, 1992a; Therrien, 2005a,b). Bite force can be estimated using the section modulus of the corpus and a dimension proportional to the moment arm of the bite force, using the following relationships (Biknevicius and Ruff, 1992a; Therrien, 2005a,b; Therrien et al., 2005): Maximum bending stress (σ) is proportional to My/I, or M/Z, where M is the bending moment. Thus, if one assumes that σ for cortical bone remains constant in all species (Erickson, 2002) then M should be proportional to Z. The bite force moment, M, is a product of the bite force (F) and the moment arm of the force (L): $M = FL$. Thus,

$$FL \propto Z, \; or \quad F \propto Z/L. \tag{2}$$

Hence, the maximum bite force (F) that could be sustained by the specimens is estimated by scaling Z by the length of the moment arm (L). Here the moment arm is approximated by jaw length since this is the maximum effective distance from the force to the fulcrum (Biknevicius and Ruff, 1992a; Therrien, 2005a). Peak loads are assumed to be more important than cyclical loads in these taxa because mastication is related to cyclical loadings and is absent in these taxa (Hylander, 1979; Hylander and Johnson, 1994; Miller et al., 2007; Loch et al., 2010). While section moduli were calculated in both dorsoventral and labiolingual planes, we report here only dorsoventral section moduli, as they are likely to be the most important in terms of estimating bite force (Biknevicius and Ruff, 1992a; Therrien, 2005a), and because there was little variation in cross-sectional shape of the corpus between the species (Supporting Information Fig. S2).

This beam model is used to calculate the relative bite force which, when used in a relative sense, should provide useful comparisons of mechanically relevant parameters between species. This method assumes that mandibular form is optimized to resist mechanical loading, an assumption supported by several (Hylander, 1979, 1988; Ravosa, 1991; Biknevicius and Ruff, 1992a), although not all (Daegling and McGraw, 2001) previous studies. A great advantage of this approach is that it requires no assumptions regarding muscle architecture and positioning, which would be necessary for developing a full mechanical model, but which are not directly observable and difficult to estimate from skeletal material alone.

Measurements. Section properties of the mandibular corpus were determined using external measurements and radiographic images, in all cases measured immediately anterior to the most posterior tooth (Fig. 2). These data were collected in two planes: the dorsoventral plane (Fig.2, Y), which corresponds to the maximum depth of the corpus; and the labiolingual plane, which is perpendicular to it. Zx is calculated as strength about the labiolingual axis against forces in the dorsoventral plane, and Zy as strength about the dorsoventral axis against forces in the labiolingual plane. For the smaller specimens, *E. barbatus* and *L. carcinophagus*, X-rays were produced using a small, portable machine (Nomad Examiner CE) and detected using a small digital sensor (AFP Digital #2). For the larger specimens, *H. leptonyx, M. angustirostris*, and *O. byronia*, a mounted X-ray source (Kevex, PXS10-16W 130kVp 6 Micron Spot Micro-Focus) and a larger digital sensor (Varian PaxScan 4030R Std. GadOx DRZ-Plus Screen) was used. Cortical thicknesses were measured from the X-ray images using the "ImageJ" software (Rasband, 2004). The cortical thickness at the alveolar margin was difficult to observe because the bone there is very thin and often overlain (Biknevicius and Ruff, 1992b; Holmes and Ruff, 2011); however, measurements from radiographs with empty alveolar sockets indicate that a value of 0.5 mm is a reasonable estimate and was used for all specimens. External measurements of total corpus thickness (Y, Fig. 1) in the dorsoventral and labiolingual planes were taken using digital calipers (precision = 0.05 mm). These breadths were then entered into standard formulae for calculating second moments of area and section moduli employing a hollow asymmetric (or eccentric ellipse) model (Biknevicius and Ruff, 1992b), using an Excel macro available online (http://www.hopkinsmedicine.org/fae/CBR.htm); also see (O'Neill and Ruff, 2004). This model has been shown to provide an accurate representation of the cross-sectional geometry of the mammalian mandible (Biknevicius and Ruff, 1992b). Due to its very large size and correspondingly thick mandible, we were unable to clearly detect the endosteal boundaries of the cortical bone in the jaws of *M. angustirostris* (elephant seal). In this species a three-step process was used to estimate Z. First, a solid beam model using external breadths only was used to calculate a "solid Z" for all species (Therrien, 2005a,b; Therrien et al., 2005). Second, this solid Z was plotted against the hollow Z calculated as above for other species to generate least squares regressions ($HollowZx = 1.021 \; SolidZx - 0.288$, R^2; = 0.987, %SEE = 11.89%; $HollowZy = 1.00 \; SolidZy - 0.322$, R^2; = 0.979, %SEE = 15.34%; Supporting Information Fig. S1). Finally, these were used as predictive equations to convert the solid Z's for the elephant seals into predicted hollow Z values that could be compared with the other species. This assumes that relative cortical bone thickness in the elephant seal is similar to that of the other pinnipeds included in the study. Any errors resulting from this assumption are likely to be relatively minor, as bone strength (Z) parameters are heavily influenced by external dimensions (Stock and Shaw, 2007). There is also no evidence for unusually thick cortical bone in long bones of this species (Hayashi and Sawamura, 2011).

Jaw length of each disarticulated mandible was measured on an osteometric board (precision = 1 mm), and was defined as the maximum length from the tip of the jaw to the most proximal point of the articular condyle.
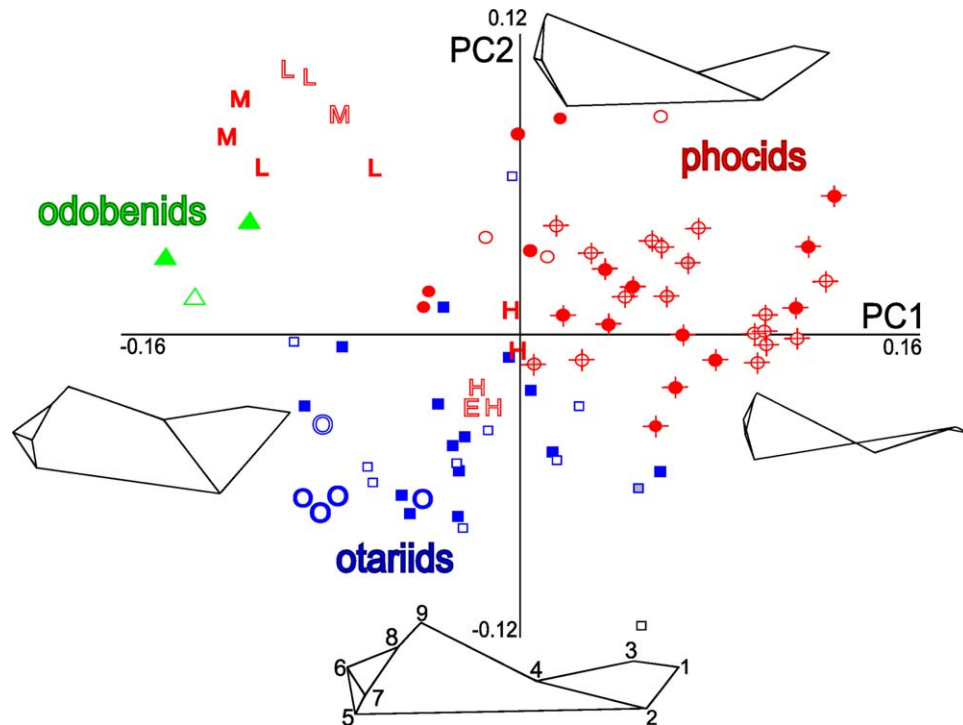
Fig. 2. Principal components analysis, PC1 and PC2. Red circle—Phocidae. Blue square—Otariidae. Green triangle—Odobenidae. Red circle with crosses—phocine phocids. Open symbols—female. Closed symbols—males. Letters—genera also represented in biomechanical analyses. Wireframes depict reconstructed shape at the extreme of each PC axis. Landmark numbers are shown on the wireframe at negative PC1. E, *E. barbatus*; H, *H. leptonyx*; L, *L. carcinophagus*; M, *M.angustirostris*; O, *O. byronia*.

Analyses. The influence of reproductive strategy and prey acquisition specialization on bite force was tested using a two-way ANOVA, with groupings of sex and species, in R (R Development Core Team, 2009). *Post hoc* Tukey HSD was used to test for pairwise differences between species or sexes.

RESULTS

Shape Analyses

Results of the morphometric analyses are summarized in Tables 2 and 3 and Figs. 2 and 3. In the PCA figures, each symbol represents a single specimen. Those genera with representatives in the biomechanical study are depicted with capital letters, and males are solid symbols (or letters). Wireframes represent shapes at the extremes of each PCA axis and are drawn as straight lines between the landmarks shown in Fig. 2. As a result, they are only approximations of actual mandibular shape (for example, lines connecting points 3 and 4, and 2 and 9, cross at the positive extreme of PC1, but this is a product of a very narrow symphysis and dorsoventral sloping of the toothrow, not a "negative" mandibular corpus height). Landmarks that contribute most to each PC and the relative importance of each PC to the overall shape variation are shown in Table 3.

The first four PCs explain 75% of the total variation of shape in the dataset. PC1 (39.6% of the total variation) is significantly correlated with phylogeny (male: $P = 0.014$, r = 0.14; female: $P = 0.0005$, r = 0.21),

although less so than PC2, and separates odobenids from otariids and most phocids. Negative scores on PC1, characteristic of odobenids (walruses), indicate a robust jaw with a large symphysis and low jaw joint. This morphology also characterizes the phocids *M. leonina* (elephant seal, M in Fig. 3) and *L. carcinophagus* (filter-feeding seal, L in Fig. 3). Phocine phocids score positively on this factor (circle with cross, in Fig. 2), with gracile jaws and short symphyses, along with a more inferiorly sloping cheek tooth row relative to the jaw joint. PC2 is the most strongly correlated with phylogeny (male: $P < 0.0001$, r = 0.46; female: $P < 0.0001$, r = 0.26), and reflects mainly variation in mandibular ramal morphology (Fig. 2). Phocids (positive PC2) tend to have a coronoid process that is more posteriorly placed relative to the angular and articular process, while otariids (negative PC2) have a more anteriorly placed coronoid. One otariid (female *Callorhinus ursinus*) occupies a position away from other otariids, including of the same species, within the phocid morphospace and may represent an anomalous data point. Odobenids are generally intermediate, but overlap more with phocids than with otariids.

Neither PC3 (male: $P = 0.092$, female: $P = 0.90$) nor PC4 (male: $P = 0.17$, female: $P = 0.64$) are significantly correlated with phylogeny, as is clear from the extensive overlap of the three families, as well as the phocid subfamilies, along these axes (Fig. 3). Instead, species with functional specializations occupy the morphological extremes. Negative scores on PC3 indicate an elongated toothrow, with a long symphysis and small muscle
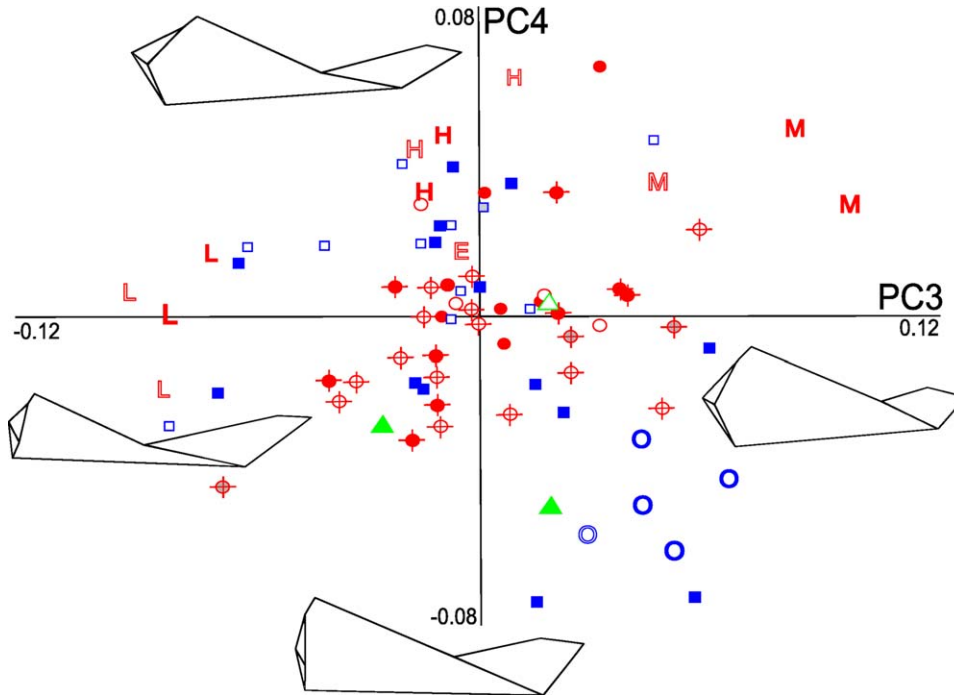
Fig. 3. Principal components analysis, PC3 and PC4. Symbols as in Fig. 2.

TABLE 2. Landmark numbers and descriptions as depicted in Fig. 2

Landmark number	Description
L1	Anterior most tip of jaw
L2	Ventral most point of the mandibular symphysis
L3	Anterior most point of cheek tooth row
L4	Posterior most point of cheek tooth row
L5	Posterior most point of angular process
L6	Labial extent of articular condyle
L7	Lingual extent of articular condyle
L8	Posterior most point of coronoid process
L9	Dorsal most point of coronoid process

TABLE 3. Eigenvalues and top five PC loadings describing the first four PCs shown in Figs. 2 and 3

	Eigenvalue (%)	Top five loadings
PC1	36.9	2(Z), 2(X), 4(Z), 3(Z), 2(Y)
PC2	19.1	5(Y), 5(X), 9(X), 9(Y), 5(Z)
PC3	11.7	3(Y), 4(Y), 4(X), 5(Z), 9(Z)
PC4	6.9	6(X), 9(Z), 7(Y), 8(Y), 7(Z)

attachments, and are most characteristic of the filter-feeder, *L. carcinophagus*. Positive scores on PC3 reflect a short tooth row and very large muscle attachment areas, and are most characteristic of males of male-fighting species, especially *M. leonina* but also *O. byronia* (M and O, Fig. 3). PC4 reflects the relative protrusion and rotation of the articular condyle, with *H. leptonyx* (leopard

seal, H in Fig. 3), the grip-and-tear feeder, exhibiting among the most positive (protruding) morphologies.

Mandibular and Toothrow Length Analyses

Mandibular lengths, relative to cranial size (species averages), are plotted in Fig. 4. Pinniped jaw length scales at slightly greater than isometry and there is no significant difference in slope (SMATR, $P = 0.214$) between phocids (slope = 1.183, 95% CI: 1.09–1.28) and otariids (slope = 1.348, 95% CI: 0.93–1.76) using reduced major axis regression. However, otariids tend to have longer jaws relative to cranium size than phocids (SMATR, $P < 0.001$). Moreover, the grip-and-tear feeding phocid, *H. leptonyx* (leopard seal, red dot), has a very long jaw relative to other phocids (between 90 and 95% prediction interval for phocids, Fig. 4) closer to the otariid condition. Toothrow length scales with slight negative allometry relative to jaw length (slope = 0.76, 95% CI 0.63–0.89) (Fig. 5). The filter feeder, *L. carcinophagus* (red dot, Fig. 5), has a longer toothrow than other pinnipeds (on the 90% prediction interval).

Symphysis Morphology

Figure 6a shows a box plot of scaled symphysis size for each species-sex group. ANOVA results indicate a significant effect of species ($P < 0.001$), but not sex, on symphysis size (Table 4). Specifically, *E. barbatus* has a smaller symphysis, whereas *M. angustirostris* and *O. byronia* have larger symphyses than the other species in the subset. Figure 6b shows a box plot of symphysis aspect ratio (*W/L*) for each species-sex group. Low values indicate an elongate, narrow symphysis, whereas high
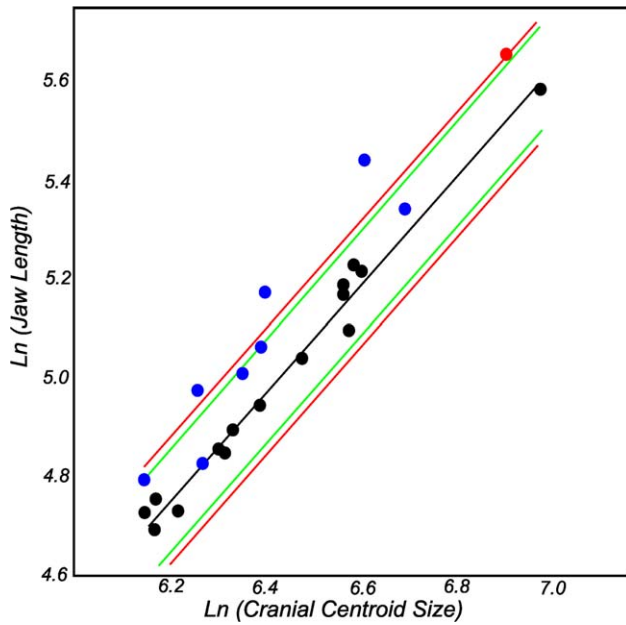
Fig. 4. Jaw length scaling (species means). Black circles—phocids, blue circles—otariids, red circle—*H. leptonyx*. Black line—least squares regression through phocid data excluding *H. leptonyx* calculated using phylogenetically independent contrasts and plotted back onto tip data as in Garland and Ives (2000). Green line—90% confidence interval (CI), red line—95% CI for outlier analysis.
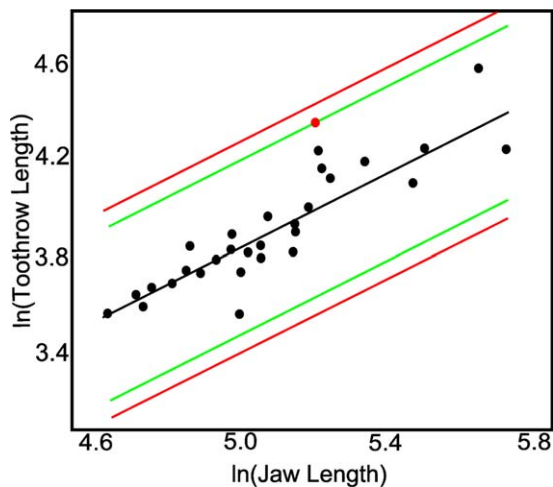

Fig. 5. Toothrow length scaling (species means). Black circles—all pinnipeds, red circle—*L. carcinophagus*, black line—regression through all data except *L. carcinophagus*, with method and CI's as in Fig. 4.

Fig. 6. **a.** Symphysis size as square root endplate area scaled by jaw length. **b.** Aspect ratio (*W/L*) of the endplate, indicating shape of the symphysis. Dark line—median. Box—interquartile range. Tail—range. Blue—males, pink—females.

symphyses than the other species. *L. carcinophagus* has a particularly long, narrow symphysis with an aspect ratio of around 0.2.

Photographs of the endplates of the symphysis for each of the five species are shown in Fig. 7. *E. barbatus* (a) has the smoothest endplate, with very few and very shallow rugosities. The filter feeder, *L. carcinophagus* (b) symphysis is smooth posteriorly but has slightly deeper rugosities antero-superiorly than *E. barbatus*. *M. angustirostris* (c) has a large round symphysis with smooth areas and some deep rugosities posteriorly. The endplate of the grip-and-tear feeder, *H. leptonyx* (d), has medium-deep rugosities that are evenly distributed. The rugosities of *O. byronia* (e) are the most-extensive and deepest of the pinnipeds sampled here, with many horizontal and pit-like interlocking ridges. Females of *M. angustirostris* and *O. byronia* were also examined (not shown) and in both cases had less developed rugosities than the males of the same species.

Biomechanical Analyses

Box plots of estimated maximum bite force are shown in Fig. 8 for each of the five species included in the biomechanical analyses. Males are represented by blue boxes and females by pink boxes (*L. carcinophagus* had only females). Results of two-way ANOVA of the effects of species and sex, and pairwise Tukey HSD tests are shown in Table 6. ANOVA indicates that both sex

values suggest a more circular shape. ANOVA results indicate there is a significant effect of species ($P <$ 0.001) on symphysis shape, but not an effect of sex (Table 4). The marginally significant interaction term ($P = 0.033$) indicates there is some difference in the symphysis dimorphism between species, and likely reflects the greater dimorphism of *M. angustirostris* relative to the other groups. *Post hoc* comparisons indicate that *E. barbatus* and *L. carcinophagus* have narrower
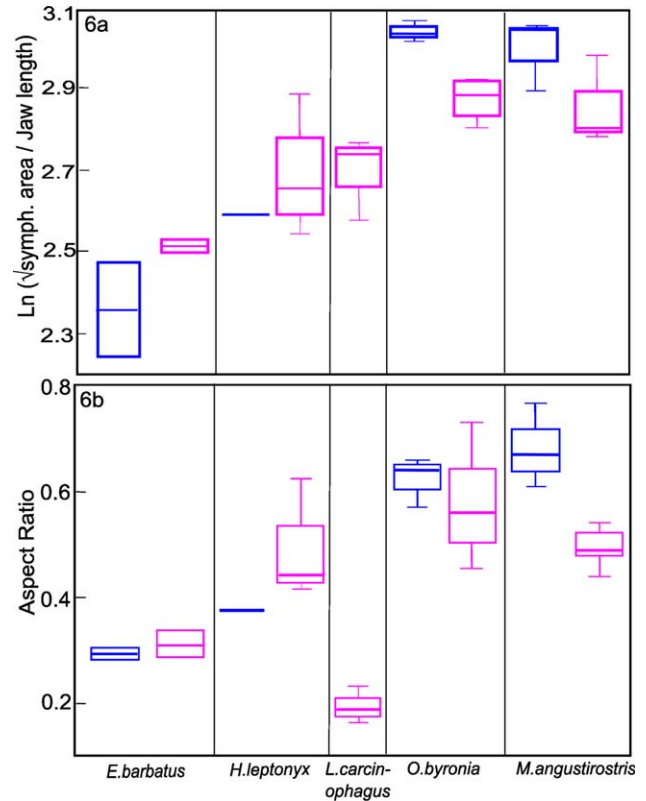
TABLE 4. Results of ANOVA on symphyseal size and shape data (Fig. 6) with Tukey's highly significant difference (*post hoc* pairwise comparison)

Variable	ANOVA	F	P	Pairwise significant differences (Tukey's HSD)
Aspect ratio	Species	22.44	1.3e-6	*E. barbatus* < all except *L. carcinophagus* *L. carcinophagus* < all except *E.barbatus*
	Sex	3.53	0.077	NA
	Interaction term	3.66	0.033	Same as above plus *M. angustirostris* (M) > *H. leptonyx* (M and F)

Symphysis size	Species	24.99	6.3e-7	*E. barbatus* < all others.
				   M. angustirostris and *O. byronia* > *L. carcinophagus*
				   and *H. leptonyx*

	Sex	2.68	0.119	NA
	Interaction term	2.37	0.093	NA

($P <$ 0.0001) and species ($P <$ 0.0001) have a significant influence on bite force (Table 5). There is also a significant interaction term ($P = 0.00012$) between species and sex. This means that although there is an overall difference between male and female bite force, this difference varies depending on species. *Post hoc* Tukey HSD tests reveal that male elephant seals (*M. angustirostris*) have a larger bite force than any other sex-species group (Table 5) including female elephant seals, though both males and females show high bite force relative to other species. Males of the other polygynous species, *O. byronia*, also have a very high bite force, higher than any other groups except male and female elephant seals. Female *O. byronia* have much lower bite force than males of the same species, similar to those of all other sex-species groups (except *M. angustirostris*) (Table 5). *H. leptonyx*, the grip-and-tear feeder, has a larger bite force than the very similar body-sized male *E. barbatus*, the suction feeder.

DISCUSSION

Our results indicate familial patterns of pinniped jaw shape due to phylogenetic relatedness are modified by adaptations to specialized behavior of individual taxa. Here, the morphological variations associated with each of these factors are summarized.

Phylogeny

Phocid versus otariid. Despite much dietary overlap, phocids and otariids display different jaw morphologies, confirming that, as with the cranium, there is a strong influence of phylogeny on shape. The otariid jaw has a more anteriorly positioned coronoid process and more posteriorly positioned angular process than that of phocids, suggesting differences in their muscular architecture. Specifically, some otariid pinnipeds have a larger and more anteriorly positioned origin for the temporalis on the cranium, with fibers attaching to the posterior side of the supraorbital process (Howell, 1929). This observation links the development of the supraorbital process in otariids noted in the cranium (Berta et al., 2006; Jones and Goswami, 2010a) with the anterior position of the coronoid found here, suggesting integration of phylogenetic features between the jaw and cranium. Examining jaw length scaling reveals that otariid pinnipeds also have longer jaws relative to skull size than phocids. However, comparing the results of the present morphospace analysis of the jaw with those of the

cranium (Jones and Goswami, 2010a) suggests that there is less morphological divergence of phocids and otariids in the jaw than in the cranium. The correlation of shape with phylogeny on those axes relating to phocid-otariid contrasts is lower in the jaw (PC2, male: r = 0.46, female: r = 0.25) than in the cranium (PC1, male: r = 0. 83, female: r = 0. 84), indicating fewer systematic differences between phocid and otariid pinnipeds in jaw morphology.

Walrus versus other pinnipeds. The walrus jaw displays a thick ramus, long symphysis and low jaw joint relative to other pinniped families. Although functional morphology of the walrus jaw has not been examined specifically, some of this robusticity may relate to pachyostosis of the mandible in relation to bottom feeding (Houssaye, 2009), as observed in other taxa (Domning and Debuffrenil, 1991). Examining the correlation of shape with phylogeny indicates that shape differences between walruses and other pinnipeds in jaw morphology are slightly more correlated with phylogeny (PC1, male: r = 0.14, female: r = 0.21) than are those in the cranium (PC2, male: r = 0.02, female: r = 0.16).

The three pinniped families show distinct jaw morphology as they do cranial morphology (Jones and Goswami, 2010a,b). Phylogenetically related factors include the relative position of the temporalis attachments between phocids and otariids, likely reflecting integration with cranial morphology via masticatory muscle architecture. These and previous data suggest that phocid and otariid pinnipeds are more morphologically distinct in the cranium than the jaw, but that walruses have the most distinctive jaw morphology.

Feeding

Grip-and-tear feeder. In contrast to the cranium, the grip-and-tear feeder, *H. leptonyx*, is not divergent from other phocids in (size-standardized) jaw shape, plotting within the range of morphospace of other species on PC1-3. However, its jaw is significantly longer than that of any other phocid relative to skull size. This osteological evidence suggests that *H. leptonyx* may be capable of a greater gape than other phocids if other morphological constraints on gape are constant across phocids. For example, the condyle is generally lower in species that are adapted to wide gapes (Herring, 1974; Dumont, 1997; Vinyard et al., 2003). Also, the positions of the chewing muscles affect gape; namely, muscles that pass closer to the center of rotation of the jaw facilitate
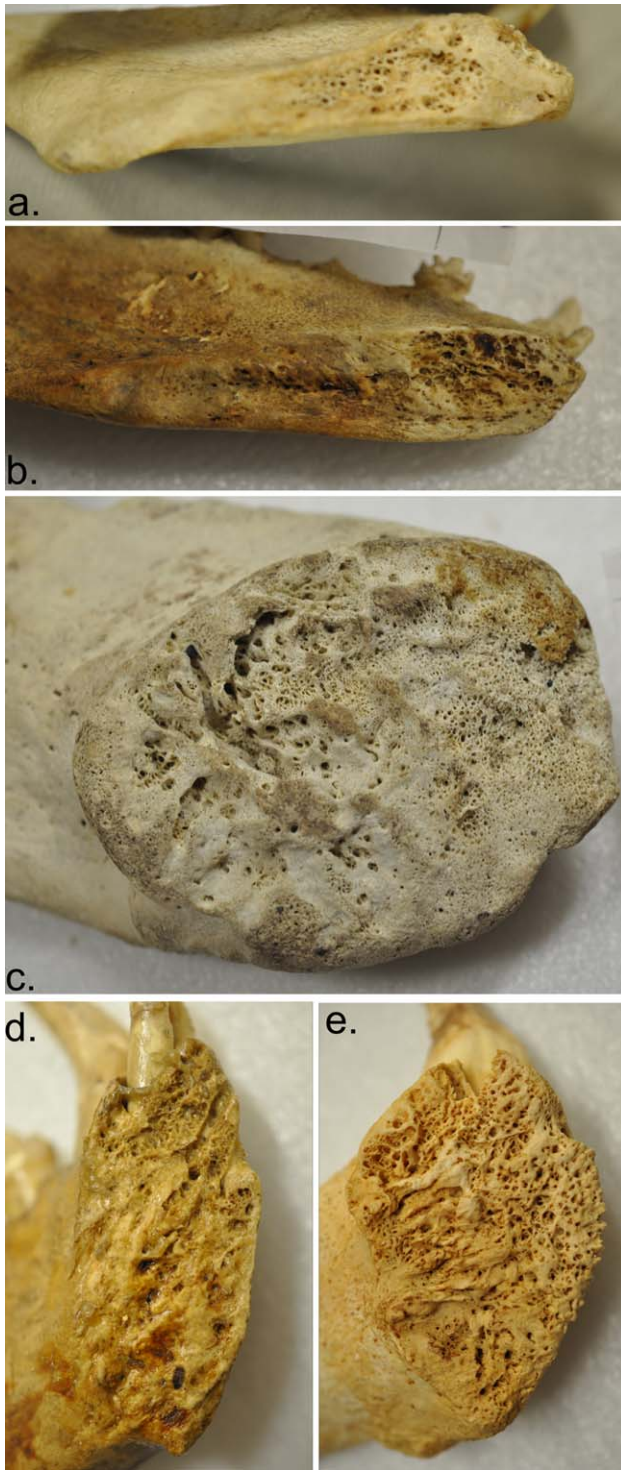
Fig. 7. Photographs of the endplates of representative specimens of each species for comparison. *W* is given for each specimen to indicate the scale of the images. **a.** *E. barbatus* USNM6569 (*W* = 12.81 mm); **b.** *L. carcinophagus* USNM115285 (*W* = 15.99 mm); **c.** *M. angustirostris* USNM21738 (male, *W* = 85.43 mm); **d.** *H. leptonyx* USNM3647 (*W* = 27.13); **e.** *O. byronia* USNM484912 (male, *W* = 49.46).

gape (Emerson and Radinsky, 1980; Greaves, 1983). Finally, the relative lengths of the chewing muscle fibers are known to affect gape (Perry et al., 2011).
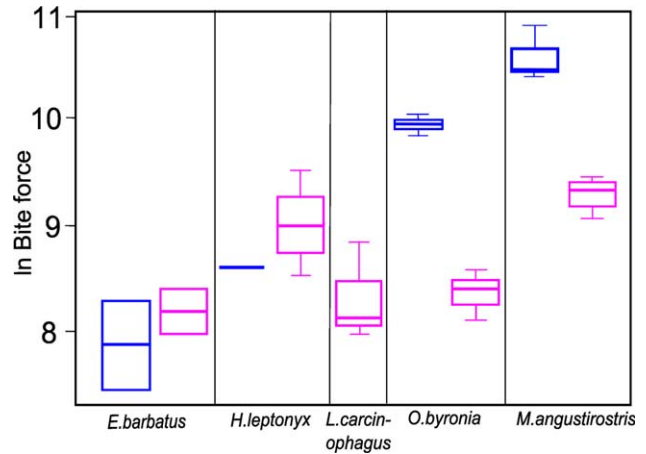

Fig. 8. Estimated bite force for five species of pinniped. Dark line—median. Box—interquartile range. Tail—range. Blue—males, pink—females.

Examination of the morphometric data do not suggest a very low jaw joint in *H. leptonyx* relative to the other taxa, which would be indicated by a negative score on PC1. Nor do they suggest a drastic shift in the antero-posterior position of the coronoid process, which is represented by variation on PC2. Hence, these data indicate that some of the other potential morphological influences on gape are not altered in *H. leptonyx*. Data on exact muscle attachments and fiber architecture were not available for the particular species included in our analyses, but could shed further light on the gape adaptation seen here in *H. leptonyx*. A wide gape in this species would allow large prey such as penguins to be captured and grasped in the mouth. We find some evidence to support the hypothesis that grip-and-tear feeders (*H. leptonyx*) can produce larger bite force than species with less violent prey capture techniques from this subset. Specifically, calculated bite force was larger than both suction and filter feeding species, though only significantly so for the suction feeder. This is true despite the longer jaw length of *H. leptonyx*, indicating that strong biting is important in this species. In addition, the symphysis of *H. leptonyx* has relatively more rugosities than either *L. carcinophagus* or *E. barbatus*.

Filter feeder. The jaw of the filter feeder, *L. carcinophagus*, has a distinctive morphology with a long symphysis and toothrow and small muscle attachment processes (Fig. 3). Filter feeding in *L. carcinophagus* has been linked to a shallowly sloping, elongated mandibular symphysis, possibly relating to increased area for attachment of tongue muscles (King, 1961). Our data quantitatively confirm that the symphysis is elongate anteroposteriorly (low aspect ratio), relative to other species in this subset (Fig. 6b). Further, the distribution of rugosities on the endplate suggests that the symphysis is most reinforced at its anterosuperior margin. This type of long symphysis might have several functional consequences. First, elongation may be a means of achieving overall greater symphyseal area—which would allow it to better resist lateral displacement of the two hemi-mandibles as water is forced laterally across the

TABLE 5. Results of ANOVA on estimated bite force data (Fig. 8) with Tukey's highly significant difference (*post hoc* pairwise comparison)

ANOVA	F	P	Pairwise significant differences (Tukey's HSD)
Species	39.98	1.9e-8	*M. angustirostris*>all others. *O. byronia*>*E. barbatus* and *L. carcinophagus*. *H. leptonyx*>*E. barbatus*
Sex	36.39	1.34e-5	Male>female
Interaction term	12.91	1.2e-4	*M. angustirostris* (M)>all others except *O. byronia* (M). *O. byronia* (M)>all except *M. angustirostris* (F & M). *M. angustirostris* (F)>*E. barbatus* (M & F), *L. carcinophagus* (F), *O. byronia* (F). *H. leptonyx* (M)>*E. barbatus* (F)

postcanine teeth during filter feeding. Second, because the symphysis is likely to be more calcified (and thus strongest) where tensile loads are greatest, it might indicate resistance to forces acting to ventrolaterally displace and externally rotate the hemimandibles. Such forces are consistent with those that might be generated by expulsion of water over the post-canine toothrow during filter feeding. However, our data demonstrate (Fig. 6a) that the overall size of the symphysis is not especially great in this species compared with others in our sample, contrary to expectation if the symphysis were mainly adapted to resist lateral displacement of the hemimandibles. Therefore, the mechanical consequences of the elongate symphysis in this species are still unclear. Loading experiments on fresh jaws with intact symphyses might help shed light on the function of the symphysis in the crabeater seal. These, and any related experimental feeding studies on pinnipeds, represent a fertile future avenue of research that would shed light on the unusual jaw morphologies seen in this group. Linear regression analyses reveal that the toothrow of this species is relatively long compared with its jaw length. A short toothrow is a synapomorphy of Pinnipedia and has been linked to the lack of mastication at the posterior teeth (Adam and Berta, 2002). Secondary elongation of the toothrow in filter feeders may be an adaptation to increase the area over which krill can be filtered. It was recently observed that *H. leptonyx* is also capable of filter feeding using its posterior dentition (Hocking et al., 2013). This species does not have a great toothrow length relative to jaw length, although the whole jaw is long relative to other phocids. Also, the symphysis does not have a lower aspect ratio as does *L. carcinophagus*. These differences plus the additional morphological characteristics described in the "grip-and-tear feeding" section above are present despite relatively close phylogenetic relatedness of these taxa. This disparate jaw morphology indicates that feeding on large vertebrate prey (exclusive to the leopard seal) has differentially influenced evolution of the jaw in *H. leptonyx*.

Suction feeder. Despite some cranial similarities (Adam and Berta, 2002; Jones and Goswami, 2010a), there is no evidence for morphological convergence between the bony jaws of the two suction feeding species (walrus and *E. barbatus)*. This may be because walruses are far more morphologically specialized for suction feeding on bivalve mollusks than *E. barbatus*. Walruses have a "heavy" (Kastelein and Gerrits, 1990), possibly pachyostotic mandible, which may assist in bottom feeding in this species. Alternatively, it may indicate that

they have slightly different mechanisms for producing suction. The bite force derived for the suction feeder, *E. barbatus*, was significantly lower than that of the grip-and-tear feeder, which may be attributable to the rarity of biting exhibited by this species during feeding (Marshall, 2008). Concordantly, this species also had significantly smaller endplates, indicating the presence of a smaller symphysis than the other species. The smoothness of the endplates indicates that its symphysis is also very flexible.

Comparison with the cranium. These results highlight the relative role of the jaw and cranium in aquatic feeding of pinnipeds. There are indications of grip-and-tear feeding in both the cranium and the mandible, i.e., an elongate skull and jaw with a strengthened mandibular corpus. The filter feeder has more distinctive jaw morphology than cranial morphology, modifying particularly the symphysis and dentition. Jaw adaptations for suction feeding are less consistent in the jaw than in the cranium. A short, blunt snout seems important; however, robustness of the jaw and fusion of the mandibular symphysis is found in odobenid but not phocid suction feeders. Pierce feeding taxa display a wide range of morphology in both the cranium and the jaw.

Fighting

M. leonina, M. angustirostris (both genus *Mirounga*), and *O. byronia* are highly polygynous species with combative male behavior (Berta et al., 2006). Our bite force data indicate that males of *M. angustirostris* and *O. byronia* can produce the largest bite forces of the sampled pinnipeds. Females of these species produce lower bite forces, more similar to males and females of non-polygynous species. This supports the hypothesis that combative species display greater bite force dimorphism than non-combative species. Part of the increased bite force in male elephant seals is due to their larger body size. However, this effect cannot account for the large bite force in male *O. byronia*, which has an average body mass similar to, or even smaller than that of most of the other sex-species groups. High bite forces are also consistent with observed symphyseal morphology in these species which suggests a more rigid connection between the hemimandibles. Both species have relatively round, large symphyses that could resist forces in the dorsoventral or transverse planes, in males and females. Deep rugosities, especially in *O. byronia*, may be indicative of a less flexible symphysis than found in the other species examined here. *M. angustirostris* has more symphysis shape dimorphism than *O. byronia*,

though females of both species have less rugose endplates than the males (not shown).

Given the large dimorphism in estimated bite force (based on cortical dimensions) in these taxa, there is relatively little dimorphism in overall external jaw shape. Males and females group almost as closely in morphospace as monomorphic species suggesting that these species are less dimorphic in jaw than cranial shape. Therefore, we do not find evidence to support the hypothesis that combative species show more overall shape dimorphism than monogamous species. However, results do suggest that both males and females of combative species have more robust jaw morphology. *M. leonina* and *O. byronia* have a short toothrow and expanded muscle attachment areas indicating that they have well-developed masticatory muscles and an increased muscle lever arm for producing high bite forces (Smith and Savage, 1959; Bramble, 1978; Weijs, 1980). This may indicate that male behavior may be driving general morphological evolution in the species, with female morphology in some way constrained by male-only selection (Lande, 1980). Alternatively, there may be aspects of jaw shape reflecting intra-specific strength differences that are not captured here, such as the inferior margin of the corpus which lacks distinctive points for the placement of homologous landmarks.

CONCLUSIONS

Pinnipeds provide an interesting model organism for the study of mandibular functional morphology because, unlike terrestrial mammals, they do not masticate. Released from the functional constraints imposed by mastication, the pinniped jaw is used for novel aquatic functions, such as filter and suction feeding. Here the influences of marine prey-capture and male-male combat on evolution of the pinniped jaw were investigated.

Phylogenetically distinctive features within phocids and otariids include the relative position of the muscle attachment processes, which is likely due to integration with the cranium via jaw muscle architecture. A low jaw joint relative to the toothrow and robust corpus makes the walrus jaw morphologically distinctive from that of other pinnipeds. By contrast, features related to function include the size of the attachment processes, bite force production, length of the toothrow, and symphysis morphology. Grip-and-tear feeders have a long jaw and large calculated bite force relative to non-biting species. Filter feeders display an elongate symphysis and long toothrow though which krill can be filtered. The suction feeding jaw is weak in biting in *E. barbatus* but has distinctive morphologies in the two suction feeding taxa. Male combat in polygynous species has resulted in very large bite force production in males relative to females or non-polygynous species with a range of feeding techniques. These males have strong jaws with large muscle attachment processes. These results indicate that generally, bite force production is more important in male combat than marine prey acquisition in pinnipeds, reflecting the fact that that biting is de-emphasized in most of these marine feeding techniques. Further, male combat likely acts as a strong evolutionary driver in these species because extreme polygyny results in large differences in male reproductive success which creates a strong selective pressure for male dominance.

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