

How seals divide up the world: environment, life history, and conservation

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Received: 25 November 2005 / Accepted: 20 June 2006 / Published online: 25 July 2006
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Abstract Pinnipeds display a remarkable variation in life history adaptations while successfully inhabiting almost every marine environment. We explore how they have done this by grouping the world's pinniped species according to their environmental conditions, mating systems, lactation strategies, and timing of life histories. Next, we tested whether any of these clusters provide information about risk of extinction (using the International Union for Nature and the Conservation of Natural Resources status ranks). Seals at risk were not characterized by differences in lactation pattern (22% short vs. 46% long), mating system (24% multi-male vs. 35% harems), or timing of life history events (23% fast vs. 42% slow) but did differ based on four environmental groupings. Grouping traits (rather than seals) described two clusters: one that included the environmental trait, primary productivity, and a second one that included all other environmental variables (seasonality, latitude, and temperature). Based on this result and theoretical considerations, we plotted seals according to energy (primary productivity) and variation (seasonality) and found a pattern analogous to that of the same four groups determined by cluster analysis of all environmental variables. Of the two pinniped groups representing low variation (equatorial

and high productivity), ten of 21 seal species have been designated at risk, in contrast to none of the 13 seal species adapted to high variation. We conclude that seals appear to be best adapted to seasonal environments and thus, conservation efforts may benefit by concentrating on species inhabiting less variable environments.

Keywords Body size · Extinction risk · Geographic range · Lactation · Life history evolution

Introduction

Species are non-uniformly distributed across the world. This has provided evolutionary ecology with an interesting puzzle and intense debate as to its causes (Menge and Southerland 1976; Harvey and Godfray 1987; Sugihara 1989). One approach to understanding species distribution is to first remove the confounding problems of body size (Peters 1983) and phylogeny (Harvey and Pagel 1991), thereby leaving the primary evolutionary and ecological forces leading to species-level adaptation. A prediction derived from this logic is that removing space (body size) and time (phylogenetic momentum) provides a perspective of species adaptations to environmental selection pressure due to the distribution of energy (primary productivity; Stevens 1989; Tuljapurkar 1990; Ferguson and Larivière 2002). Furthermore, understanding how species' risk of extinction [International Union for Nature and the Conservation of Natural Resources (IUCN) status ranks] falls along the continuum of energy availability and distribution would facilitate a formidable conservation tool. Most fisheries resources are overexploited

Communicated by Craig Osenberg

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(Fay et al. 1989; Gerber and Hilborn 2001; Pauly et al. 2002), necessitating methods to timely identify species or populations vulnerable to extinction and devise and execute appropriate countermeasures (Jennings et al. 1999; Ando et al. 1998; Ceballos and Ehrlich 2002).

The pinnipeds are a monophyletic group consisting of three families: Otariidae (14 species of fur seals and sea lions), Phocidae (19 species of “true” seals), and Odobenidae (the walrus). Pinnipeds live around the world in mostly salt water oceans and seas. Tagging experiments have found seals far from land and capable of feeding in mid-ocean (Stewart and DeLong 1993; Hindell et al. 2003), suggesting that many species are not limited to proximity to land for at least parts of their annual cycle. How did a group considered to have made trade-offs to allow feeding in the ocean while breeding on land manage to evolve to live in so many diverse marine habitats? Here we address that question while considering the conservation consequences of life history adaptations for 34 world pinniped species (one extinct). Understanding how seals are distributed would likely help to understand why some species are at risk of extinction while others are not. Such knowledge would help concentrate conservation efforts on species currently in peril in addition to those that may be predisposed to eventual danger.

First, we cluster pinnipeds based on a number of trait groupings and then test which groupings of species are more at risk relative to those species deemed not vulnerable. We grouped pinnipeds on traits related to environment, mating system, lactation pattern, and chronology in life history events. We use the comparative method that controls for body size and phylogeny where necessary. Second, we clustered all species' traits to distinguish the ultimate environmental selection pressures. Finally, from this determination we mapped pinniped clusters onto an energy-variation continuum resulting in “rule-of-thumb” descriptions of relative risk of extinction for groups adapted to four marine ecosystems.

Materials and methods

We used the phylogenetic tree proposed by Bininda-Emonds et al. (1999). These data consisted of three families and 34 species of world pinnipeds (Table 1). We obtained data on life history and behavioural traits from published sources (Kovacs and Lavigne 1986, 1992; Lindenfors et al. 2002; Schulz and Bowen 2004; Ferguson 2006). Data included traits for environment (latitude, seasonality, primary productivity, temperature), mating system (harem size, sexual size dimor-

phism), lactation pattern (lactation duration, percent fat in milk, neonate growth rate, neonate size), and life history chronology (gestation length, age at maturation, interbirth interval, longevity).

Latitude of the midpoint of each species' historical distribution was approximated visually using maps from Mammalian Species accounts and world carnivore maps (see Ferguson and Larivière 2004). Species geographic ranges were from historic maps that included ranges before commercial exploitation. Seasonality and temperature at the centre point of each species' historical distribution were obtained from Wilmott et al. (1985) (<http://www.climate.geog.udel.edu/~climate>). Seasonality was calculated as the coefficient of variation of monthly ($n = 12$) values of actual evapotranspiration (Ferguson 2002), whereas temperature was calculated as the mean of 12 months. We used the absolute values for latitude to compare similar latitude locations in the northern (positive) and southern (negative) hemispheres. Annual global marine primary productivity was obtained from Rutgers (State University of New Jersey) Institute of Marine and Coastal Sciences ocean primary productivity estimates (<http://www.marine.rutgers.edu/opp/>) based on ^{14}C uptake and stimulated fluorescence techniques (Behrenfeld et al. 1996; primary productivity $\text{g C m}^{-2} \text{ year}^{-1}$). All environmental variables were \log_{10} transformed to normalize residuals.

We used cluster analysis to define groups of similar pinniped species based on: (1) the environment they live in, (2) mating system, (3) lactation pattern, and (4) life history timing traits. The standardized matrix of objects (seal species) and attributes were used to compute values of Euclidean distance as a measure of resemblance (Romesburg 1984). Average linkage clustering processed the resemblance coefficients to create a dendrogram displaying the hierarchy of similarities among species. We measured distances between clusters at each step of the amalgamation procedure with semi-partial R^2 -values (PROC CLUSTER; SAS 1999). Semi-partial R^2 -values are the sum of ANOVA sum-of-squares with clusters as “treatment” variables and measured traits as “response” variables. The level at which the dendrogram should be cut to create a reasonable number of clusters was determined by the relative R^2 -value increase at each cluster amalgamation step (Romesburg 1984). We also used R -analysis, a type of cluster analysis, as a method of clustering environmental attributes based on species rather than clustering species based on environmental attributes. Here, the purpose was to group species' traits to locate a separation among traits that reflected redundancy.

Table 1 Species' traits and environmental measures from species' geographic distribution. *SD* Sexual size dimorphism (male mass/female mass), *N/A* not available

Code	Family	Genus	Specific name	Male mass ^a	Female mass ^a	SSD	Harem size	Latitude	Temperature ^b	Product ^c	Seasonality ^d	Neonate mass ^a	Lactation ^e	Growth rate ^f	Milk fat ^g	Maturity ^h	Gestation	Longevity ⁱ	Inter-birth
OR	Odobenidae	<i>Odobenus</i>	<i>rosmaris</i>	12,330	8,115	1.52	7.2	73	-13.2	355	189.3	63,400	720	0.45	26	2,373	330	480	24
AA	Otariidae	<i>Arctocephalus</i>	<i>australis</i>	910	485	1.88	6.0	-25	+7.3	300	24.2	4,400	365	0.06	44	1,095	236	252	12
AF	Otariidae	<i>Arctocephalus</i>	<i>forsteri</i>	1,250	381	3.28	6.2	-41	-8.8	120	42.9	3,875	285	0.04	N/A	1,825	233	180	12
AG	Otariidae	<i>Arctocephalus</i>	<i>galapagoensis</i>	645	274	2.35	5.9	0	+15.5	125	29.3	3,500	540	0.07	29	1,460	210	264	36
AP	Otariidae	<i>Arctocephalus</i>	<i>philippii</i>	1,400	481	2.91	4.0	-33	+6.9	120	27.4	5,433	210	0.08	41	N/A	N/A	N/A	12
AT	Otariidae	<i>Arctocephalus</i>	<i>townsendi</i>	1,120	496	2.26	6.2	-29	+5.3	190	65.1	7,800	285	0.10	43	N/A	N/A	288	12
AZ	Otariidae	<i>Arctocephalus</i>	<i>gazella</i>	1,550	450	3.44	5.1	-54	-8.1	205	34.0	8,000	116	0.08	41	1,278	233	276	12
AR	Otariidae	<i>Arctocephalus</i>	<i>tropicalis</i>	11,600	350	3.14	4.4	-38	+15.3	215	49.1	5,200	300	0.04	43	1,734	232	276	12
AS	Otariidae	<i>Arctocephalus</i>	<i>pusillus</i>	2,630	641	4.10	13.8	-34	+15.3	310	27.3	4,700	270	0.06	31	1,232	240	252	12
NC	Otariidae	<i>Neophoca</i>	<i>cinera</i>	3,000	786	3.82	3.8	-40	+12.6	200	37.1	5,500	520	0.11	31	1,095	255	192	18
PK	Otariidae	<i>Phocarcos</i>	<i>hookeri</i>	3,640	1,147	3.17	12.9	-50	+7.6	340	46.3	21,100	365	N/A	N/A	N/A	N/A	N/A	12
OB	Otariidae	<i>Otaria</i>	<i>byronia</i>	3,000	1,440	2.08	6.0	-40	-14.0	340	55.7	7,700	548	0.21	32	1,460	255	274	12
EJ	Otariidae	<i>Eumetopias</i>	<i>jubatus</i>	10,000	2,875	3.48	11.8	55	+7.6	250	73.6	12,820	320	0.35	22	1,825	240	360	12
ZC	Otariidae	<i>Zalophus</i>	<i>californianus</i>	2,445	810	3.02	14.9	46	+9.6	350	40.7	7,600	330	0.13	36	2,099	240	360	12
CU	Otariidae	<i>Callorhinus</i>	<i>ursinus</i>	1,400	333	4.20	22.7	55	+7.7	330	69.0	8,300	118	0.065	42	1,460	240	420	12
PC	Phocidae	<i>Phoca</i>	<i>caspicus</i>	705	550	1.28	1.0	42	+0.8	290	44.4	22,000	23	2.2	N/A	1,825	330	600	12
PH	Phocidae	<i>Phoca</i>	<i>hispidus</i>	840	812	1.03	1.0	74	-8.5	215	168.9	35,500	39	0.35	38	2,191	225	552	12
PS	Phocidae	<i>Phoca</i>	<i>sibirica</i>	895	850	1.05	1.0	54	-7.6	290	132.0	16,060	60	N/A	N/A	1,643	270	672	12
PL	Phocidae	<i>Phoca</i>	<i>largha</i>	970	713	1.36	1.0	46	-1.5	285	54.0	35,000	18	N/A	N/A	1,461	248	426.1	12
PV	Phocidae	<i>Phoca</i>	<i>vitulina</i>	971	852	1.14	1.0	60	-2.7	400	132.0	27,100	27	0.48	50	1,278	248	480	12
HG	Phocidae	<i>Halichoerus</i>	<i>grypus</i>	2,330	2,058	1.13	5.0	60	+7.6	380	56.3	30,700	16	2.3	50	1,643	242	560.1	12
PF	Phocidae	<i>Phoca</i>	<i>fasciata</i>	948	804	1.18	1.0	69	-6.6	350	156.4	41,100	25	0.34	N/A	1,278	234	365.3	12
PG	Phocidae	<i>Phoca</i>	<i>groenlandica</i>	1,450	1,390	1.04	1.0	51	+2.1	305	116.9	42,600	12	2.2	46	1,825	233	504	12
CC	Phocidae	<i>Cystophora</i>	<i>cristata</i>	3,432	2,225	1.54	1.0	58	-1.7	320	144.9	22,000	4	6.8	59	1,095	234	420	12
EB	Phocidae	<i>Erigonathus</i>	<i>barbanus</i>	3,125	3,260	0.96	1.0	75	-13.7	250	193.0	10,700	24	3.3	47	2,008	270	377.4	18
HL	Phocidae	<i>Hydrurga</i>	<i>leptonyx</i>	3,240	3,670	0.88	1.0	-72	-14.2	180	180.9	N/A	29	N/A	N/A	1,205	276	312	18
LC	Phocidae	<i>Lobodon</i>	<i>carcinophagus</i>	2,205	2,240	0.98	1.0	-72	-9.5	200	181.5	27,000	17	4.2	51	1,278	255	468	12
LW	Phocidae	<i>Leptonychotes</i>	<i>weddellii</i>	4,500	4,470	1.01	3.0	-75	-19.5	190	182.2	5,000	50	1.95	45	1,095	263	300	12
OR	Phocidae	<i>Ommatophoca</i>	<i>rossii</i>	1,538	1,640	0.94	1.0	-70	-18.4	190	234.7	10,500	30	N/A	N/A	1,323	248	252	12
MA	Phocidae	<i>Mirounga</i>	<i>angustirostris</i>	22,750	4,880	4.66	13.0	34	+15.3	375	63.9	10,800	26	4	43	1,186	230	243.5	12
ML	Phocidae	<i>Mirounga</i>	<i>leonina</i>	35,100	5,657	6.20	48.0	-60	+8.5	240	228.2	5,400	23	4.05	34	1,171	225	276	12
MS	Phocidae	<i>Monachus</i>	<i>schauinslandi</i>	1,730	2,722	0.64	1.0	20	+18.4	110	25.9	11,300	38	N/A	N/A	1,825	330	360	15.4
MT	Phocidae	<i>Monachus</i>	<i>tropicalis</i>	1,800	1,600	1.13	N/A	22	+27.8	90	21.6	3,050	N/A	N/A	N/A	N/A	N/A	N/A	18
MM	Phocidae	<i>Monachus</i>	<i>monachus</i>	2,600	2,750	0.95	1.0	18	+17.5	160	55.5	10,300	42	N/A	N/A	1,461	330	284	24

^aFemale (x100), male (x100), and neonate mass in g

^bTemperature in °C (mean of 12 months)

^cProduct is primary productivity (g m⁻² year⁻¹)

^dSeasonality = coefficient of variation in monthly actual evapotranspiration (mm m⁻² year⁻¹) values

^eLactation duration in days

^fGrowth rate in kg days⁻¹

^gMilk fat as percentage

^hAge at sexual maturity for females in days

ⁱLongevity in months

We tested for significant differences among clusters using conventional and phylogenetic methods. Conventional statistical tests assumed that all pinniped species originated from a single common extinct ancestor without any intermediary species. Analysis of covariance (ANCOVA; Sokal and Rohlf 1995) was performed with log female body mass as the covariate. The ANCOVA was adjusted for differences associated with body mass between groups, enabling the assessment of differences in traits with variation in body mass statistically removed from the analysis.

Phylogenetic corrections are necessary when variation in the data is due to phylogenetic structure, which violates the statistical assumption of independence in general linear models (Harvey and Pagel 1991). Therefore, a second set of analyses assumed that pinniped species are part of a hierarchical, branching phylogeny (Bininda-Emonds et al. 1999). Simulations were performed at a log-transformed scale using a simple Brownian motion model of trait (e.g. life history) evolution and the default values in the PDSIMUL module of the Phenotypic Diversity Analysis Programs version 5 (Garland et al. 1993, 1999). One thousand Monte Carlo simulations were used to generate phylogenetically based null distributions of *F* statistics for ANCOVAs using the PDANOVA module. From this distribution of *F*-values for the simulated data, the 95th percentile was computed and used as the phylogenetically informed critical value. This process recalibrates the critical value increasing the criterion

for significance. To control for phylogeny we used corrected critical values (PDANOVA) of differences due to clusters set at $\alpha = 0.05$ from the 95th percentile of the simulated distribution (Ferguson et al. 1996). We report results of both conventional and phylogenetically based statistical analyses, as recommended by Garland et al. (1999). Using the derived clusters, we tested whether the groups were related to extinction risk (IUCN extinction risk categories) using goodness-of-fit test statistics.

Results

Grouping seals

First, we grouped the 34 pinniped species according to the environmental variables characterising their geographic range. The amalgamation of four clusters was the best fit to the grouping of environmental data according to the semi-partial R^2 -values (Fig. 1a). Differences among the four groups were significant using conventional ANCOVA (Table 2). This result is not surprising as cluster analysis separated the groups according to Euclidean distance, which maximizes intergroup differences. A more conservative test that controls for phylogeny found significant difference among the four groups based on temperature, primary productivity, seasonality, and latitude (Table 2).

Fig. 1 Dendrogram from cluster analysis of **a** environment variables, **b** mating system, **c** lactation pattern, and **d** timing of life histories for 34 pinniped species. See Table 1 for explanation of pinniped species codes

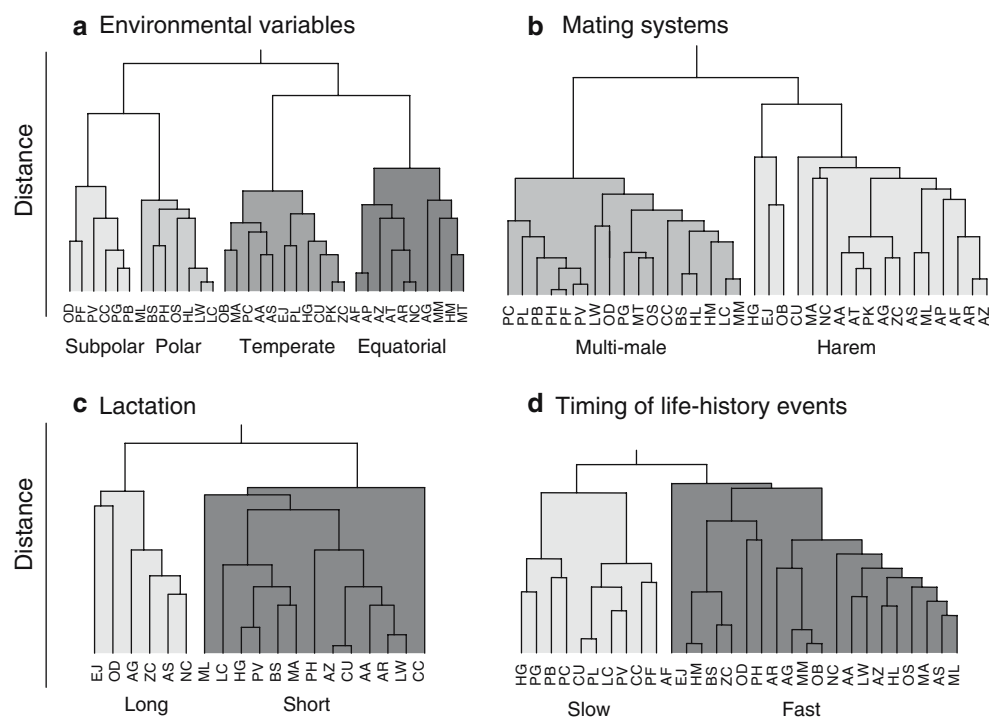


Table 2 Tests for differences among groups of pinniped species identified using cluster analysis of traits for: environment (latitude, seasonality, temperature, primary productivity); mating system (harem size, sexual size dimorphism); lactation (growth rate, lactation, % fat in milk, neonate size); and timing (longevity, interbirth interval, age at maturity, gestation). The covariate in the analysis of covariance (ANCOVA) is female body mass. Models of evolutionary change were no phylogenetic (conventional ANCOVA) or gradual evolutionary change with differences proportional to branch lengths (phylogenetic ANCOVA)

Variable	Groups	n	Conventional		Phylogenetic	
			F	P	Critical F	P
Environmental variables						
Latitude	4	34	20.9	0.0001	7.5	0.0001
Temperature	4	34	65.1	0.0001	7.6	0.0001
Primary productivity	4	34	41.3	0.0001	7.2	0.0001
Seasonality	4	34	138.3	0.0001	7.3	0.0001
Mating system						
Sexual size dimorphism	2	34	59.6	0.0001	31.0	0.0001
Harem	2	33	98.7	0.0001	32.3	0.0001
Lactation						
Growth rate	2	22	31.9	0.0001	7.5	0.0001
Lactation duration	2	33	103.2	0.0001	4.3	0.0001
% Fat in milk	2	23	21.2	0.0001	4.8	0.001
Neonate mass	2	33	15.7	0.0004	5.0	0.002
Life history timing						
Longevity	2	31	15.7	0.0005	5.5	0.001
Interbirth interval	2	34	10.2	0.003*	5.5	0.01
Age at maturity	2	30	51.1	0.0001	5.5	0.0001
Gestation length	2	30	9.8	0.004	5.8	0.02

*Significant interaction between female mass and interbirth interval and therefore Type III sum of squares reported

One group of ten pinnipeds lived in more equatorial regions, hereafter referred to as “equatorial”, and was characterized by low latitude, low seasonality, warm temperatures, and low productivity (Fig. 2). A second group, hereafter referred to as “temperate”, consisted of 11 pinnipeds living in more productive waters, at low latitude, low seasonality, and warm temperatures (Table 3). A third group of seven seals lived at high latitudes, hereafter referred to as “polar”, primarily phocids ($n = 5$) in the northern hemisphere ($n = 4$), characterized by large seasonality, low temperatures, and low primary productivity. A fourth group of six seals, hereafter referred to as “subpolar”, lived at mid-latitudes characterized by high seasonality, low temperatures and high primary productivity.

Cluster analysis according to mating system discerned two groups of pinnipeds based on R^2 criteria: one with large harems and great sexual size dimorphism, and a second one with smaller harems and less dimorphism (Fig. 1b). Using residual analysis to

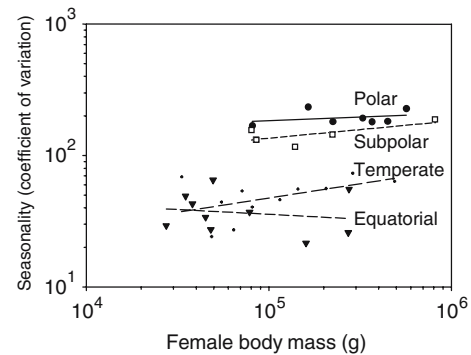


Fig. 2 Differences in seasonality (amount of variation in monthly primary productivity) among four groups of pinnipeds, polar ($n = 7$), subpolar ($n = 6$), temperate ($n = 11$), equatorial ($n = 10$). Pinnipeds were grouped based on cluster analysis of four environmental variables: latitude (absolute value), temperature, seasonality, and primary productivity

control for male body size resulted in a division into two groups based largely on phylogeny, with all otariids in the harem-mating cluster and all but three phocids in the multi-male mating cluster. The exceptions are noteworthy given the relatively consistently different mating systems between otariids (polygynous) and phocids (multi-male). The two phocid elephant seal species (northern, *Mirounga angustirostris* and southern, *Mirounga leonina*) grouped with otariids. Three species grouped as a subgroup of the harem mating cluster and included one phocid (grey seal, *Halichoerus grypus*) and two otariids: the Steller sea lion (*Eumetopias jubatus*) and South American seal lion (*Otaria byronia*). This group was characterized by intermediate harem size (7.6) and sexual size dimorphism (2.23).

Next, we clustered residual lactation traits (duration, pup growth rate, % fat in milk, and neonate size) that controlled for female body size differences (Fig. 1c). Due to a limited number of species with measured lactation traits only 19 species were initially grouped according to lactation. When controlling for body size only Odobenidae and Otariidae species grouped into long lactation, and only phocids grouped into short lactation, with the exception of four otariids: *Arctocephalus gazella*, *A. australis*, *A. tropicalis*, and *Callorhinus ursinus*, which grouped as having relatively short lactation. We re-ran the cluster analysis on fewer traits (deleting juvenile growth rates and percent fat in milk) to align the missing species within the two groups. This procedure limits some of our results for grouping according to lactation (Table 4). Results designated one group of 12 pinniped species as characterized by long lactation duration, fast growth rate, high fat content, and large neonate size in contrast

Table 3 Differences among groups (least square mean ± SE) of pinniped species identified using cluster analysis: environment (latitude, seasonality, temperature, primary productivity); mating system (harem size, sexual size dimorphism); lactation (growth rate, lactation, % fat in milk, neonate size); and timing (longevity, interbirth interval, age at maturity, gestation). *MMM* Multi-male mating

Environment	<i>n</i>	Latitude	Seasonality	Temperature	Primary productivity
Polar	7	73.6 ± 2.0 (7)	195 ± 9.8 (7)	−192 ± 34.5 (7)	209 ± 10.3 (7)
Temperate	11	44.6 ± 3.5 (11)	50 ± 4.8 (11)	142 ± 15.7 (11)	323 ± 12.0 (11)
Equatorial	10	27.0 ± 4.3 (10)	39 ± 4.5 (10)	225 ± 19.9 (10)	154 ± 14.5 (10)
Subpolar	6	59.6 ± 4.9 (6)	145 ± 10.4 (6)	−44 ± 26.7 (6)	336 ± 16.3 (6)
Mating	<i>n</i>	Harem size	Sexual size dimorphism		
MMM	17	1.5 ± 1.1 (17)	1.11 ± 0.22 (17)		
Harem	17	11.5 ± 1.1 (17)	3.42 ± 0.21 (17)		
Lactation	<i>n</i>	Growth rate	Lactation	% Fat	Neonate size
Short	21	1.59 ± 1.12 (14)	35.5 ± 1.2 (21)	45.3 ± 1.0 (13)	11,663 ± 1.1 (21)
Long	12	0.68 ± 1.13 (8)	396.3 ± 1.2 (12)	32.0 ± 1.1 (10)	11,015 ± 1.0 (12)
Timing	<i>n</i>	Longevity	Interbirth interval	Age at maturity	Gestation
Fast	22	302 ± 1.1 (20)	13.1 ± 1.0 (22)	1,282 ± 1.0 (19)	247 ± 1.0 (19)
Slow	12	475 ± 1.1 (11)	13.9 ± 1.1 (12)	1,851 ± 1.1 (11)	253 ± 1.0 (11)

to a second group of 21 seals characterized by “slow” lactation (Table 3).

We clustered pinnipeds using traits associated with life history timing (gestation length, age at maturity, interbirth interval, and longevity) after controlling for body size using residual regression analysis (Fig. 1d). Two groups were identified. One group was represented by seals with fast chronology: short gestation, early age at maturity, short interbirth interval and short lifespan. The second grouping showed slow chronology with a spreading out of the temporal traits over the seal’s life. Only two otariids, *Eumetopias jubatus* and *Zalophus californianus*, grouped with the slow species (Table 4).

Vulnerability

Next, we tested for differences within the four clusters according to vulnerability to extinction. Only environmental groupings differed relative to risk of extinction, with equatorial (six of ten) and temperate (four or 11) species at risk of extinction compared to polar (none of seven) and subpolar (none of six) species (*G*-test: $\chi^2 = 13.3$, $P = 0.004$). No difference was observed between the two groups of mating systems (*G*-test: $\chi^2 = 0.57$, $P = 0.35$), lactation (*G*-test: $\chi^2 = 2.02$, $P = 0.16$), and life history chronology (*G*-test: $\chi^2 = 1.34$, $P = 0.94$) relative to the distribution of vulnerable seals.

Conservation “rules-of-thumb”

We tested for groupings of traits and found two major groups of variables (Fig. 3). One included primary

productivity together with traits associated with timing of life histories. The second included the other three environmental variables (seasonality, latitude, and temperature) and the species’ traits associated with mating system and lactation pattern. We consider seasonality to be the single variable best representing the three environmental traits from this latter group, as all three were highly intercorrelated (latitude and seasonality $r = 0.69$, temperature and latitude $r = -0.62$, seasonality and temperature $r = -0.65$). Plotting primary productivity against seasonality separated out the four groups identified by cluster analysis (Fig. 4). Here, the two groupings that included pinniped species living in equatorial and temperate environments were most at risk of extinction (60% of species) and together lived in less seasonal environments. In contrast, none of the seals living in polar and subpolar environments characterized by high seasonality were at risk of extinction.

The equatorial species that are most at risk live in environments characterized by both low seasonality and low primary productivity. Only Odebenidae and Phocidae lived in the highly seasonal environments, whereas all otariids lived in temperate and equatorial regions characterized by low seasonality. Phocids living in less seasonal environments included the three monk seals that live in equatorial regions and are characterized by extreme risk of extinction, with one species extinct (West Indian monk seal, *Monachus tropicalis*) and the Mediterranean monk seal (*M. monachus*) considered one of the most endangered mammals (IUCN 1996). Of the equatorial seals, species not currently at risk included *Neophoca cinerea*, *Arctocephalus tropicalis*, and *A. gazella* (all classed as “lower risk” by IUCN).

Table 4 Pattern that describes how seals divide up the world: matching species to groupings according to environment (latitude, seasonality, temperature, primary productivity); mating system (*Mating*; harem size, sexual size dimorphism); lactation pattern (*Lactation*; growth rate, lactation, % fat in milk, neonate size); timing of life history events (*Timing*; longevity, interbirth interval, age at maturity, gestation); International Union for Nature and the Conservation of Natural Resources listing (*Listing*). *LR* Lower risk, *VU* vulnerable, *EN* endangered, *CR* critically endangered, *EX* extinct; for other abbreviations see Tables 1 and 3

Species	Environment	Mating	Lactation	Timing	Listing
OR	Subpolar	MMM	Long	Slow ^a	LR
AA	Temperate	Harem	Short	Fast	LR
AF	Equatorial	Harem	Long ^a	Fast	LR
AG	Equatorial	Harem	Long	Fast ^a	VU
AP	Equatorial	Harem	Long ^a	Fast ^a	VU
AT	Equatorial	Harem	Long ^a	Fast ^a	VU
AZ	Equatorial	Harem	Short	Fast	LR
AR	Equatorial	Harem	Short	Fast ^a	LR
AS	Temperate	Harem	Long	Fast	LR
NC	Equatorial	Harem	Long	Fast ^a	LR
PK	Temperate	Harem	Long ^a	Fast ^a	VU
OB	Temperate	Harem ^a	Long ^a	Fast	LR
EJ	Temperate	Harem ^a	Long	Slow	EN
ZC	Temperate	Harem	Long	Slow	LR
CU	Temperate	Harem	Short	Fast	VU
PC	Temperate	MMM	Short ^a	Slow ^a	VU
PH	Polar	MMM	Short	Slow	LR
PS	Subpolar	MMM	Short ^a	Slow	LR
PL	Temperate	MMM	Short ^a	Fast	LR
PV	Subpolar	MMM	Short	Fast	LR
HG	Temperate	Harem ^a	Short	Slow	LR
PF	Subpolar	MMM	Short ^a	Fast	LR
PG	Subpolar	MMM	Short ^a	Slow	LR
CC	Subpolar	MMM	Short	Fast	LR
EB	Polar	MMM	Short	Slow	LR
HL	Polar	MMM	Short ^a	Fast	LR
LC	Polar	MMM	Short	Fast	LR
LW	Polar	MMM	Short	Fast	LR
OR	Polar	MMM	Short ^a	Fast	LR
MA	Temperate	Harem	Short	Fast	LR
ML	Polar	Harem	Short	Fast	LR
MS	Equatorial	MMM	Short ^a	Slow ^a	EN
MT	Equatorial	MMM	Short ^a	Slow ^a	EX
MM	Equatorial	MMM	Short ^a	Slow ^a	CR

^aSpecies grouped based on reduced number of trait values due to incomplete data

Discussion

Our most important finding is that understanding how species are distributed according to two key ecological characteristics—energy and its temporal distribution—provided groupings of species that related to risk of extinction. Knowledge of the amount of energy in an environment (measured as primary productivity) and variation (measured as seasonality) (Boyce 1979; Ferguson and McLoughlin 2000) will help to concentrate conservation efforts according to species not only in

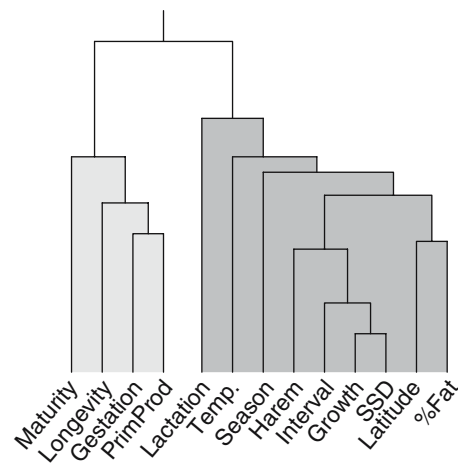


Fig. 3 Dendrogram representing similarity of 11 traits of pinniped species based on cluster analysis. *PrimProd* Primary productivity, *Temp.* temperature, *SSD* sexual size dimorphism

peril now but species that may be predisposed to eventual danger (Kotiaho et al. 2005). Previously, assessing extinction vulnerability required knowledge of population dynamics (Purvis et al. 2000; Norris 2004), which limits rapid assessment. Currently, the population parameters considered important, such as intrinsic rate of increase *r*, require considerable quantitative data on population status to estimate reliably, and are costly to obtain (Harwood and Rohani 1996; Wickens and York 1997; Reynolds et al. 2001). The problem is greatest for equatorial regions with developing countries where some of the greatest species diversity is found but where monitoring is poor (Jennings et al. 1998). Ecological and life history traits, which have evolved to ensure individual fitness under considerable biotic and abiotic variability, can serve as “rule-of-thumb” proxies to evaluate the intrinsic vulnerability of animals (Saether et al. 1996; Jennings et al. 1998; Ferguson and Larivière 2002).

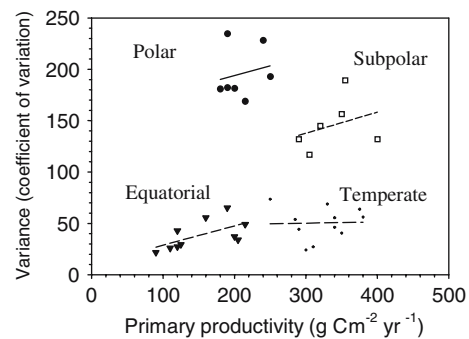


Fig. 4 Relationship between mean energy (measured as primary productivity) and temporal variation of energy (seasonality) of four clusters of pinniped seals based on environment: polar (filled circle), subpolar (open square), temperate (dot), equatorial (filled inverted triangle). *yr* Year

Extinction risk combines intrinsic vulnerability and exposure to extrinsic factors (McKinney 1997), and natural and anthropogenic factors often work in concert (Naves et al. 2003; Cardillo et al. 2004). Intrinsic factors include life history adaptations to environmental perturbations (including anthropogenic mortality, e.g. by-catch) that relate to the species' intrinsic rate of increase and strength of density dependence (Fowler 1981, 1990). Particular life history traits and ecological conditions are correlated with intrinsic vulnerabilities (Cheung et al. 2005), and considered as "rules-of-thumb" to triage vulnerable species (Dulvy et al. 2004). Information for the majority of species is incomplete, necessitating indices of extinction vulnerability derived from more easily accessible life history and ecological characteristics estimated using conventional techniques. Our findings follow this approach and provide a means to assess conservation priorities for pinnipeds. As an illustrative example using phocids within the North Atlantic: the ringed seal (*Phoca hispida*) living in a polar environment is not vulnerable, the harp seal (*Phoca groenlandica*) in a subpolar environment is not at risk, the grey seal (*Halichoerus grypus*) in a temperate environment is not at risk, and the West Indian monk seal that once lived in an equatorial environment is extinct (all based on IUCN status ranks). A conservation implication derived from this analysis is that a management approach of caution should focus on the future vulnerability of the grey seal.

Why would energy, and variation in its temporal distribution, relate to vulnerability of species to extinctions? The three physical dimensions are space, time, and energy (Allen et al. 2002). Spatial and temporal distribution of energy are major environmental selection pressures at the species level (Liou et al. 1993). We found a pattern of how seal species are distributed around the world according to a relationship between primary productivity and seasonality (temporal dispersion of energy; Slobodkin and Sanders 1969). Future research should consider the spatial distribution of energy as an important factor in explaining the distribution of organisms as an approach to understanding conservation risk.

There are some limitations of the approach we have used. Comparative methods have stimulated research into ecological mechanisms underlying conservation, but comparative analyses of extinction risk have tended to be too general in scale to assist specific efforts required to conserve individual endangered species (Fisher and Owens 2004). The collected species' level factors are viewed as rough indicators of vulnerability and we expect that they will only explain a fraction of

the variance in population trends among species. An alternative hypothesis to environment explaining seal extinction risk postulates that seal species face extinction in areas with greater human population (Engelhard et al. 2002). The majority of extinction risks for seal species are anthropogenic in nature (Arnould et al. 2003). However, humans co-occur with pinnipeds throughout the world, and have for centuries, particularly because of the importance of coastline, islands, and estuaries to both species (Weber et al. 2004). Also, some of the most intense marine mammal harvesting has occurred in sub-polar waters as documented first in the North Atlantic, then the North Pacific and finally the Antarctic (Jackson et al. 2001), not in the low-latitude areas where pinnipeds are at risk. Human density effects on extinction risk are not a recent phenomenon, and humans have been part of the ecosystem for thousands of years (McDonnell and Pickett 1993). The growth and expansion of pre-human and human populations displaced species and led to extinctions throughout the Pliocene and Holocene (Klein 2000; Alroy 2001; McKee 2001, 2003). To ensure effective conservation, human interventions should not perturb ecosystem components beyond the natural boundaries of variation (Mangel et al. 1996).

We believe environmental adaptation by pinnipeds is the ultimate explanation for conservation risk, which would include proximate causes such as human harvesting (Hucke-Gaete et al. 2004), habitat loss (Pastor et al. 2004), and pollution (Tsydenova et al. 2004). While mammalian population extinctions are concentrated in areas with high human population densities (Ceballos and Ehrlich 2002), phylogenetic comparative methods have shown that extinction risk in carnivores is predicted more strongly by biology than human exposure (Cardillo et al. 2004).

Another concern is that using the species' centre point as the location representative of geographic range is an approximation that may not adequately represent the range of a species' adaptation to environmental variability. Our results indicate that environmental features related to risk of extinction better than life history traits (cf. Cardillo et al. 2004). This may be the case if environmental selection pressure is the first line of evolution resulting in the strongest signal, which may explain why the other groupings (lactation, mating system, and timing of life histories) did not relate to risk of extinction. Environment likely exerts the dominant evolutionary pressure on species adaptations (Branke 2002) and life history correlates are secondarily influenced or are under strong resistance to change due to phylogenetic inertia (i.e. species are not perfectly adapted).

Last, we have documented species-level patterns that should be considered separate from population-level comparisons, as there is no reason to expect patterns at the species level to be similar to patterns observed at the population level (Ferguson and McLoughlin 2000). Thus, our results will not help discern relative risk of extinction among populations of a single species of seal (e.g. McMahon et al. 2005). However, the approach may succeed if species and population patterns are nested (Donlan et al. 2005).

Natural selection acting on complex systems, such as life histories, can develop separable modules (Fodor 1983) defined as patterns of strong internal connections combined with weaker or fewer external links (Raff and Sly 2000). Subjectively, we grouped life history traits into modules of traits associated with lactation, mating behaviour, and the chronology of life history events. However, an objective clustering of traits uncovered different evidence for modules or traits that grouped together: primary productivity grouped with life history traits associated with the chronology of life events such as age at maturity and life span; whereas other environmental features, such as seasonality, grouped with lactation and mating traits. Future research into the adaptive part of evolution of life histories requires consideration of the relationship between developmental processes and environmental traits (Klingenberg 2002).

Also, consideration is required of the units of selection and whether the IUCN categories, which rely on global ranks, may require population assessment since a species classed as lower risk globally may be endangered locally. After species have been identified as of potential concern using a “rules-of-thumb” type analysis, detailed demographic analyses are required before the status of species and populations can be fully understood. Only long-term studies are capable of accurate estimation of demographics for many long-lived species, including pinnipeds (e.g. Pistorius et al. 2001, 2004). A disadvantage of long-term mark-recapture studies is that long periods must elapse before sufficient data become available (Hindell 1991). This again speaks to the value of rapid assessments such as this study, to identify species of potential future concern and begin long-term demographic studies before species become endangered.

Otariids appear to be more susceptible to risk of extinction with five of 14 (36%) vulnerable versus four of 19 (21%) for phocids. All otariids breed in dense colonies and have relatively long periods (i.e. 4–20 months) of neonatal dependence (Riedman 1990; Boness et al. 2002). Also, all otariids forage throughout lactation (i.e. “income” breeders; Bowen 1991), which

may relate to food availability controlling population rate of increase relative to phocids (Eberhardt and Siniff 1977; Wickens and York 1997). Relative to phocids, otariids live in environments that are less seasonal (44.4 ± 14.3 versus 124.9 ± 12.3 , $F_{1,32} = 18.2$, $P = 0.002$) but not significantly different in primary productivity (1216 ± 154 vs. 883 ± 132 , $F_{1,32} = 2.7$, $P = 0.11$). Understanding the evolution of different pinniped life histories requires an understanding of the interactions between environmental food distribution and mating systems relative to breeding substrate (Ferguson 2006). Ancestral phocids and otariids apparently responded to environmental selection pressure in different ways with early phocids evolving larger size (Wyss 1994), possibly as a response to cold temperatures and risk of predation (Costa 1993), enabling adaptations to cold, seasonal, and productive oceans (Schulz and Bowen 2005). In contrast, ancestral otariids retained smaller body size while breeding on isolated rookeries, thereby reducing exposure to terrestrial predators while gaining proximity to more predictable (temporal variation) prey resources (Schulz and Bowen 2005).

Our results provide some implications relative to conservation of biodiversity. The search for generality in ecological systems dictates the emphasis on species assemblages and ensures future research will continue to focus on community-level patterns. Where conservation patterns exist, the imminent challenge is to identify the mechanism(s) that underlies these patterns—why does the pattern observed here occur? We recommend the following types of investigations. First, what are the primary environmental selection pressures shaping the groups adaptations? Second, what are the life history consequences for these adaptations? Third, what are the conservation outcomes of this relationship? This includes exploring the relationships between life histories and environment in further detail to see if species groups adapted to particular environments show modules of life history traits tuned to those circumstances that may have conservation implications (e.g. bet-hedgers, producers, survivors, and competitors; Ferguson and Larivière 2002). The “rules-of-thumb” can be adjusted or weighted with the availability of new evidence or experts’ opinions. For example, benthic foraging seals have smaller populations and lower population growth rates compared to seal species that forage pelagically, and this may provide another environmental consideration important to conservation and management (Costa et al. 2004).

The comparative approach identified the environmental imprint on vulnerable species, which may

provide more focused management and conservation efforts. The environmental imprint uncovered is that pinnipeds may be best adapted to seasonality because of their evolutionary past. Early pinnipeds (pinnipedimorphs) originated in the North Pacific during the late Oligocene (34–24 million years ago) (Wyss 1988; Berta and Sumich 1999; Deméré et al. 2003; Schulz and Bowen 2005). Otariids and walrus both evolved in the North Pacific, in the early late Miocene (ca. 11–5 million years ago) and late early Miocene (ca. 21–16 million years ago), respectively (Deméré et al. 2003). The first phocid fossils are from the middle Miocene (ca. 16–14 million years ago) in the North Atlantic (Barnes et al. 1985), although Deméré et al. (2003) postulate a North Pacific origin. Once in the North Atlantic, phocids underwent a dramatic diversification event in the late Miocene (Deméré et al. 2003), radiating and diversifying throughout highly seasonal environments. Possibly as a result, those living in equatorial or temperate regions, characterized by high productivity–low variation, are at relatively greater risk. This scenario identifies general ecological principles underlying mechanisms that cause conservation problems (Fisher and Owens 2004).

The system of providing intrinsic vulnerability estimates from environment and life history can provide a priori indicators of species' vulnerability. This knowledge imparts a prioritization of species according to their potential extinction vulnerabilities and helps allocate limited research and monitoring resources required to develop effective conservation policies (Sæther 1988; Purvis et al. 2000; Dulvy et al. 2004). In conclusion, we suggest the approach described here as a useful tool to predict intrinsic vulnerability of species according to risk of extinction associated with environmental and life history characteristics of the species. However, like all surrogate approaches, the application of “rules-of-thumb” is limited and must be treated with caution (Sibly and Calow 1985). Integration of other factors such as degradation of critical habitat, climate change and the impacts of high human densities can contribute significantly to extinction risk, and should therefore be considered in evaluating overall extinction risk (Fisher and Owens 2004). Connecting environmental selection pressures with risk combines evolution and ecology and provides insights into both how nature works and how anthropogenic threats can impact species differently.

Acknowledgements An NSERC Discovery Grant (250465-03) and ArcticNet supported this research. M. Mangel and an anonymous reviewer improved earlier drafts of this paper.

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