

Field-Based Age Estimation of Juvenile Galapagos Sea Lions (*Zalophus wollebaeki*) Using Morphometric Measurements

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Abstract

Information about the age of juvenile pinnipeds is necessary for an understanding of ontogeny-specific patterns and strategies. Exact age determination of juvenile cohorts from wild populations is best achieved through birth observations and subsequent marking, but this involves a considerable time lag during which juveniles mature. A combination of body and teeth measurements of known-age Galapagos sea lion juveniles taken during brief routine captures in the field was used to create age prediction models. Several general linear models (GLMs) produced reliable age estimates for male and female juveniles up to an age of 2 y. Teeth measurements were important predictors of age: male age was best estimated using upper canine length (CL), mass, and girth, while the best predictors for female age were CL, canine width (CW), body length (SL), body mass, and an interaction between CL and CW. The presented method of aging wild unmarked juveniles in the field is applicable during routine captures, requires little equipment, and yields a considerable increase of information for studies involving brief sampling periods in the field. We suggest its adjustment, testing, and application in studies of juveniles of other species.

Key Words: age estimation, field method, tooth measurements, general linear models, Galapagos sea lion, *Zalophus wollebaeki*

Introduction

Studies of the behaviour and ecology of species in the wild often require knowledge of the age of the animals. During the juvenile stage, substantial changes in physiology, morphology, and behaviour take place and are connected to increasing age. In pinnipeds, for example, oxygen stores increase (Fowler et al., 2007; Trillmich et al., 2008), age-specific growth rates change (Chabot & Stenson, 2002), and animals begin diving and feeding (Horning & Trillmich, 1997; Jørgensen et al., 2001; Guinet et al., 2005; Fowler et al., 2006).

Traditionally, seals have been sorted in broad age categories according to their pelage and size (Wilson, 1974; Blundell & Pendleton, 2008). A more reliable approach is to mark cohorts of pups just after birth, providing a pool of known age individuals (McMahon et al., 1999; Bradshaw et al., 2000b). This technique yields exact information on the study animals but requires substantial field effort and leads to a considerable time lag between the initial marking and the potential field study on known-aged animals.

Another method is based on counts of growth layer groups in the dentine or cementum of sectioned canines, incisors, or post canine teeth (Mansfield & Fisher, 1960; Mansfield, 1991; Arnbom et al., 1992; Lawson et al., 1992; Bernt et al., 1996; Oosthuizen, 1997; Blundell & Pendleton, 2008). However, this technique is invasive, with potential disadvantages for the study animals resulting in the irreplaceable loss of an important morphological structure. Moreover, age cannot be estimated on site.

Field methods for age estimation using models based on morphological measurements of known-age juvenile Steller sea lions (*Eumetopias jubatus*) and harbour seals (*Phoca vitulina*) have recently been published (King et al., 2007; Blundell & Pendleton, 2008), but the study subjects needed to be anaesthetized in order to perform the necessary measurements. Chemical immobilization of pinnipeds has become increasingly safe and applicable in field conditions (Heath et al., 1997; Gales & Mattlin, 1998; Gales et al., 2005), and it is routinely used during lengthy instrument deployments or sampling procedures (Fowler et al., 2007; Villegas-Amtmann et al., 2008). Still, even the currently favoured method using gas anaesthetics requires a considerable amount of time for immobilization procedures, wake-up period, and post immobilization animal monitoring (Raum-Suryan et al., 2004; Gales et al., 2005), and there is a risk of a negative impact on the health and behaviour of the study animal (Lynch et al., 1999; Engelhard et al., 2002). In species where body size and behaviour allow, researchers physically

restrain study animals for brief periods of time without chemical immobilization (Boltnev et al., 1998; Beuplet et al., 2005).

Herein we investigate the accuracy of a field-based age estimation method for juvenile Galapagos sea lions (*Zalophus wollebaeki*), applicable during such brief captures. The aim was to establish a reliable, fast, and easily applicable technique for estimating age in the field that had minimal impact on the study animals and that did not involve their chemical immobilization. Galapagos sea lions are born during an exceptionally long pupping season spanning at least 5 mo and show variable mass and size at birth which largely depends on oceanic conditions (Trillmich, 1990; Trillmich & Dellinger, 1991; Mueller et al., in press). Therefore, the physical appearance of juveniles aged between 1 and 3 y is variable but does not necessarily reflect different age classes, which is illustrated by considerable overlap in body mass (Mueller et al., in press). However, it has been suggested that skeletal structure and especially teeth grow more conservatively (King et al., 2007), and a combination of body and teeth measurements should contain sufficient age-specific information for accurate age determination. We test this prediction by creating age determination models based on morphological measurements for known-age Galapagos sea lion juveniles.

Materials and Methods

Sampling Procedure

Measurements were taken as part of a demographic study on Caamaño Islet, Galapagos Islands, Ecuador, from October through December 2007 and 2008, coinciding with the reproductive season of the Galapagos sea lion. (For details on the study location, see Wolf et al., 2005.) Since 2003, newborn Galapagos sea lions of this population were individually marked by fur clipping and later recaptured and tagged using numbered ALLFLEX® tags. A subsample of the juveniles with known birth dates is recaptured each year for estimation of growth patterns. For this study, we recaptured and measured 66 known-age Galapagos sea lions (birth date known to the nearest week) between the ages of 11 and 27 mo (34 females, 32 males). Additionally, we took measurements of 15 3-y-old animals to determine whether age estimation is feasible for this older age class as well. The animals were captured in the morning or evening with hoop nets (Fuhrmann Diversified, Seabrook, TX, USA), weighed with a digital scale (Kern, HUS 300K100) hanging from a tripod, and briefly restrained in a lying position on a restraint board without chemical immobilization (Gentry & Kooyman, 1986). We measured the dorsal straight

standard length, here termed SL (McLaren, 1993), with a metal measuring pole to the nearest 1 cm. The axillary girth was measured just caudal to the axilla of the thoracic flippers to the nearest 0.5 cm with a measuring tape. The partial length of the thoracic flipper (FL) was measured as a straight line from the radio-carpal joint to the tip of the longest digit along the anterior edge, flipper width (FW) as a straight line along the width of the flipper at the radio-carpal joint, and head length (HL) as a straight line from the tip of the snout to the upper end of the external occipital protuberances (Figure 1A). Flipper and head measurements were made with a metal ruler to the nearest 0.5 cm. For tooth measurements, we placed a cloth covered wooden pole gently between the sea lion's jaws to expose the teeth while the head of the animal was firmly held. To reduce handling stress, we covered the eyes of the restrained animal with a towel. Teeth measurements were taken with a digital caliper to the nearest 0.01 mm. Upper canine length (CL), upper third incisive length (IL), and lower canine length (LCL) were measured as a straight lateral line from the gum to the tip of the crown. Width of canine (CW), upper third incisive (IW), and lower canine (LCW) were measured laterally from the caudal to the cranial base of the tooth at the gum level (Figure 1B). All measurements were taken from the right body side of the animal. Total handling time was about 10 to 15 min from capture to release, and sea lions spent at most 8 min on the restraint board being measured. All animals were released immediately after completion of teeth measurements by gently opening the upper flap of the restraint board, while the personnel silently retreated several metres away. All animals continued sitting on or beside the restraint board for several minutes. Frequently, animals explored the restraint board and surrounding measurement tools before slowly moving away. Some animals lay down and rested on the restraint board. In this case, we waited until the sea lion had left the immediate area before beginning another capture, or delayed further captures until the following day. We measured the teeth of 19 animals two to four times and the FL, FW, and SL of 17 animals twice to determine the measurement error. Repeated teeth measurements resulted in a mean maximum measurement error of 0.08 ± 0.05 cm (coefficient of variation: 0.54); repeated FL, FW, and SL measurements produced a mean maximum measurement error of 0.7 ± 0.6 cm, 0.4 ± 0.4 cm, and 4.0 ± 4.0 cm (coefficients of variation: 0.87, 1.24, and 1.02, respectively).

Statistical Analysis

We used a principal component analysis to reduce the number of variables. All variables were highly

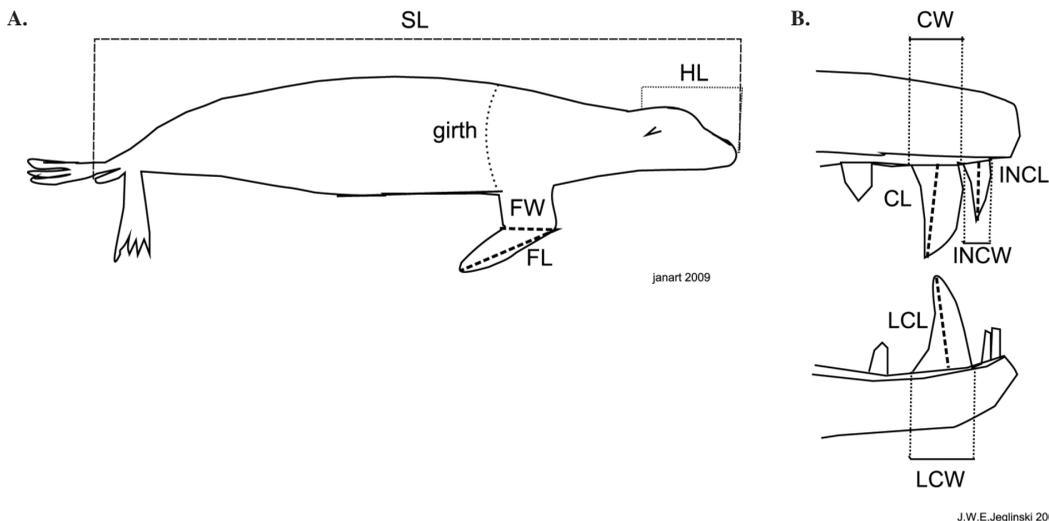


Figure 1. Body (A) and teeth measurements (B) taken from juvenile Galapagos sea lions (*Zalophus wollebaeki*) < 28 mo; for further description, see text. Abbreviations are explained in the “Materials and Methods” section.

correlated and formed only one component. However, IL and IW explained the smallest proportion of the variance and were excluded from the analysis. General linear models were constructed to predict the age of the 66 1- and 2-year-old animals, and separate models included the 15 older animals. The factor *season* (the year in which an animal had been captured) was included in all models to check if there were year-specific differences in morphometric measurements.

Galapagos sea lions exhibit significant sexual size dimorphism and sex-specific growth patterns, so we analysed males and females separately. We fitted a series of simple models using one predictor at a time and models containing one predictor and its quadratic term (King et al., 2007). We then fitted more complex models containing the most important single predictors and reduced the models in a stepwise manner using AIC. We also tested a model containing only body measurements (SL, FL, FW, HL, mass, and girth) as estimating age using these measures alone would reduce handling time substantially. A further model containing SL, mass, and girth was tested to determine whether this approach could be used as successfully in otariids as in harbour seals (Blundell & Pendleton, 2008). We calculated the maximum residuals between known age and estimated age and the standard deviation (SD) of the residuals for all models to determine the applicability of the models for age prediction (see Table 1). Model selection was based on AIC and model simplicity (Bozdogan, 1987; Crawley, 2007) as well as on the discrepancy between modelled and true age of animals (King et al., 2007). We considered

models producing an SD of residuals of calculated age below 4 mo as appropriate for reliable age estimation because a misclassification of ± 4 mo still assigns pulse breeders like the Galapagos sea lion into the correct age class. We decided against using maximum over- and underestimation (King et al., 2007) to reduce the weight of single outliers. Statistical analysis was performed using R, Version 2.11.1 (R Development Core Team, 2005).

Results

Sampling year had no significant influence in any of the age prediction models and was consequently removed during model simplification. Models including all animals up to the age of 3 y had higher AIC values than models containing only 1- and 2-year-old animals and exceeded the 4 mo limit of the SD of the residuals. Three-year-old juveniles were therefore excluded from subsequent modelling. Male age could successfully be determined using a model containing only CL or CL², while simple models containing only one predictor were not sufficient to estimate age of 1- and 2-year-old females reliably (see Table 1). In single predictor models, those containing CL, CW, or LCL had the lowest AIC values and SD of residuals for male age, while LCW, SL, and mass were the best single predictors in females. A number of more complex models, containing more than one predictor, estimated age within our range of acceptable accuracy for both sexes.

The best model in males contained CL, mass, and girth. In female juveniles, the best model

contained the predictors CL, CW, SL, mass, girth, and an interaction between CL and CW (Table 1). Figure 2 shows a linear regression between true and estimated age of 1- and 2-y-old Galapagos sea lions using the best models for males and females.

In all models, the SD of residuals was larger in females than in males, and models for female juveniles were more complex than models for males. Models containing only body measurements or condition measurements did not perform well enough for estimating age in both sexes (Table 1). Table 2 shows the equations for age estimation of the three best models. Likelihood ratio tests of the best models for male and female juveniles,

respectively, revealed no significant differences between the models. We suggest, therefore, based on the smallest AIC and SD of residuals, the use of equation M 1.1 for males and M 2.1 for females (Table 2) to obtain reliable age estimates for 1- and 2-y-old Galapagos sea lion juveniles.

Discussion

Our results show that it is possible to estimate the age of juvenile Galapagos sea lions between 11 and 27 mo using body and teeth measurements taken during routine captures without chemical immobilization of the animals. The duration of restraint was well below the time required by studies

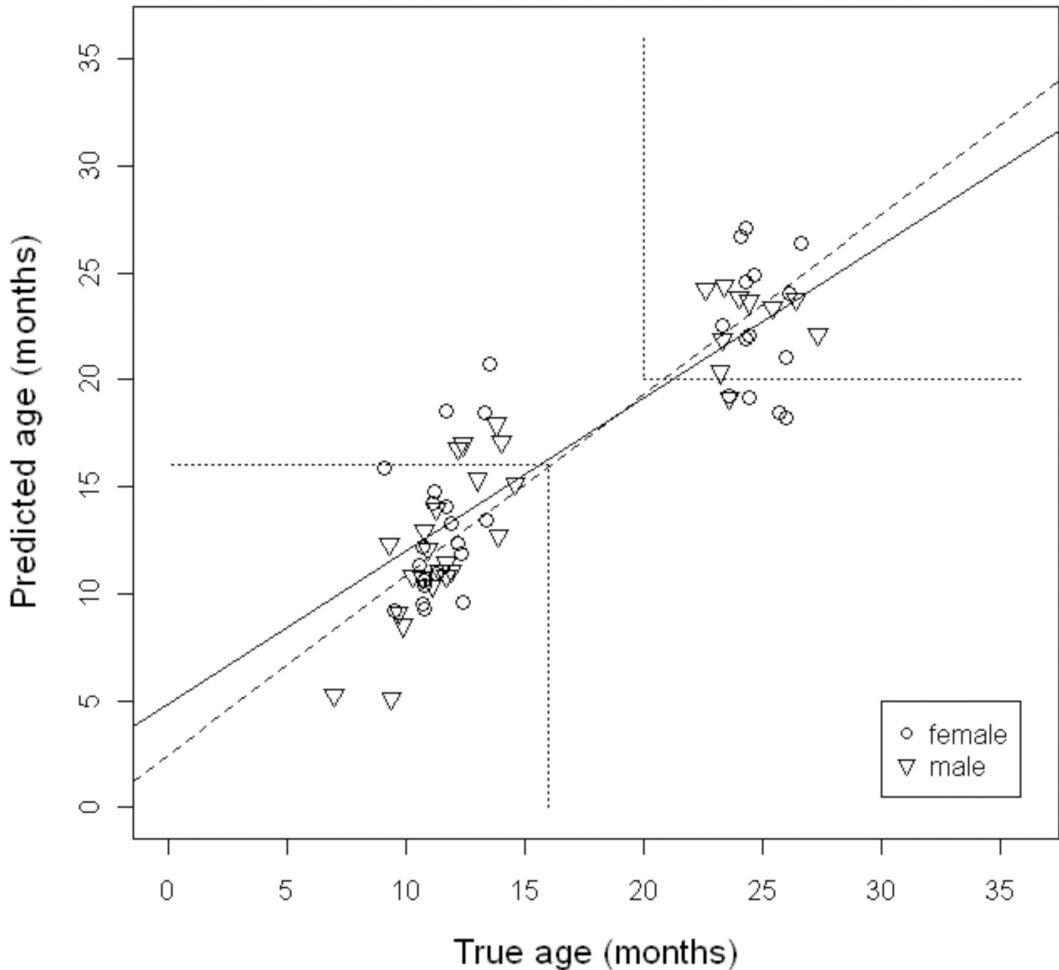


Figure 2. Linear model of true age and predicted age for male (dashed: $R^2 = 0.8386$, $p < 0.01$) and female (solid: $R^2 = 0.7076$, $p < 0.01$) Galapagos sea lion juveniles; dashed boxes limit age class 1 y (lower left box, based on a standard age of 12 mo + 4 mo of tolerated overestimation) and age class 2 y (upper right box, based on a standard age of 24 mo - 4 mo of tolerated underestimation). Note that due to the seasonality of the breeding season, all animals outside the boxes apart from one female would still be assigned to the correct age class (in years).

Table 1. Performance of the best age prediction models (M 1.1, M 1.2, M 1.3, M 2.1, M 2.2, and M 2.3), condition models (M 1.4 and M 2.4), and body measurement models (M 1.5 and M 2.5) for Galapagos sea lions < 28 mo; condition and body measurements model (M 2.4 and M 2.5) in females result in the same set of most important predictors. SD = standard deviation of the residuals of estimated age, Max.U = maximum underestimate, and Max.O = maximum overestimate. Age is given in months.

Model	Predictors	AIC	SD	Max.U	Max.O
<i>Males</i>					
M 1.1	CL + mass + girth	158.9	2.5	4.6	5.1
M 1.2	CL ²	159.9	2.7	8.6	6.6
M 1.3	CL	164.1	2.9	8.7	6.0
M 1.4	SL	204.6	5.5	8.1	9.8
M 1.5	Mass + girth + HL	203.1	5.0	7.0	9.3
<i>Females</i>					
M 2.1	CL + CW + SL + mass + CL*CW	198.7	3.6	6.5	7.1
M 2.2	CL + SL + CL*CW	199.8	3.9	6.5	7.1
M 2.3	CW + LCW + mass + girth	200.2	3.9	7.9	7.1
M 2.4/2.5	SL + mass	202.2	4.3	8.3	9.9

CL = canine length, CW = canine width, LCL = lower canine length, LCW = lower canine width, FL = flipper length, FW = flipper width, SL = standard length, and HL = head length; all measurements are in cm, and mass is in kg.

Table 2. Equations of the three best age prediction models for Galapagos sea lions < 28 mo; age is given in months. Further abbreviations are cited in Table 1.

Model	Formula
<i>Males</i>	
M 1.1	Age = 12.045 + (18.578*CL) + (0.378*mass) – (0.419*girth)
M 1.2	Age = 3.890 + (7.972*CL ²)
M 1.3	Age = -6.375 + (18.699*CL)
<i>Females</i>	
M 2.1	Age = 42.137 – (48.359*CL) – (56.147*CW) + (0.195*SL) + (0.556*mass) – (0.395*girth) + (73.823*[CL*CW])
M 2.2	Age = 16.956 – (43.175*CL) + (0.304*SL) – (57.929*CW) + (68.814*[CL*CW])
M 2.3	Age = 3.097 + (21.70*LCW) + (26.801*CW) + (0.681*mass) + (0.525*girth)

involving immobilization (Raum-Suryan et al., 2004; Gales et al., 2005) and within the range of physical restraint periods reported in other studies (Wolf et al., 2007). The behaviour of the animals did not suggest that the procedure put them under unacceptably high stress. Galapagos sea lions are very docile animals that can be approached, after brief habituation, up to a distance of 1 m for capture and observation without showing signs of distress, fear, or aggression (Jeglinski, pers. obs.). Size and/or behaviour of other species might require anaesthesia to minimize stress and facilitate capture and handling in general and, therefore, also for the application of the method presented herein. In Galapagos sea lions and species of similar size and docility, however, the use of anaesthetics does not seem necessary. Also, a much smaller number of predictors (one to three in male and three to five in female juveniles, respectively) than

the 12 originally measured variables were needed for accurate age estimation. Therefore, handling time can be reduced substantially in future applications of the method, further decreasing potential discomfort for the study animals.

Measurement error of teeth was smaller than the smallest difference between age groups (0.15 and 0.17 cm for females and males, respectively). Comparing coefficients of variation, teeth measurements were very precisely performed, while the coefficient of variation was highest for FW. However, FW did not play an important role in any of the best models. A model with a combination of body and teeth measurements estimated age most accurately in males and females. CL was an important predictor in both sexes, but more so in male juveniles: two models using only CL or CL² as a single predictor estimated age with sufficient precision. The canines of adult male otariids are

much longer than those of females (Lowry & Folk, 1990; Molina-Schiller & Pinedo, 2004), and our data show that this difference is developing already at an early stage. In contrast, the growth of the incisors slows down at an earlier age in both sexes. In 1-y-old juveniles, incisors were as long as or longer than upper canines, while 2-y-old animals had substantially longer canines. These two predictors (IL and IW) were discarded from models due to their low explanatory value.

Our results suggest that tooth growth has lower developmental plasticity than body growth and, thus, that tooth measurements are better predictors of age than body measurements (King et al., 2007). Linear models of tooth length and body measurements support these findings (best models: LCL~SL, $R^2 = 0.3858$, $p < 0.01$ and LCL~FL, $R^2 = 0.4527$, $p < 0.01$, male and female data, respectively). In contrast to recent findings in harbour seals (Blundell & Pendleton, 2008), age estimation models for Galapagos sea lion juveniles containing only SL, mass, and girth did not result in reliable age estimates. Mass and girth in relation to body length are commonly used to estimate condition rather than age (e.g., Antarctic fur seals [*Arctocephalus gazella*] and New Zealand fur seals [*Arctocephalus forsteri*] (Arnould, 1995; Bradshaw et al., 2000a), and our results suggest that these variables should not be used for age estimation for Galapagos sea lions and possibly closely related species. The models that provided accurate age estimates were more complex than those published for Steller sea lion juveniles (King et al., 2007), which indicates higher variation in growth for Galapagos sea lions. Galapagos sea lions live in a highly unstable environment with seasonally fluctuating sea surface temperatures and nutrient supplies (Palacios, 2004). Additionally, irregularly occurring El Niño events cause unpredictable major declines in food abundance (Barber & Chavez, 1983; Cane, 1983), which, in turn, strongly affects the growth and survival of juveniles (Trillmich & Limberger, 1985). The variation in size and in growth rates in Galapagos sea lion juveniles is, therefore, higher than in Steller sea lions, resulting in less uniform relationships between age and body or teeth measurements (Mueller et al., in press). Also, models in King et al. (2007) and Blundell & Pendleton (2008) contained a larger number of 1 y old and younger animals than this study, which improved the quality of the models due to near linear growth in young age classes. However, otariid pups are easy to distinguish from older juveniles because of their longer and differently coloured pup fur before they moult; thus, a modelling approach is not necessary to distinguish this age class from older juveniles.

Similar to the findings of King et al. (2007) and Blundell & Pendleton (2008), models containing 3-y-old animals did not produce reliable age estimates. This is in line with the slow decrease in growth rate of juvenile pinnipeds between the ages of 2 and 3 y (Mueller et al., in press). Their growth rate reaches asymptotic values at these ages and is sufficiently variable to blur distinctions between age classes > 2 y. In Galapagos sea lion juveniles, growth is particularly strongly correlated with environmental conditions and varies considerably between years (Mueller et al., in press). The application of our technique is, therefore, limited to juveniles up to 2 y of age. However, when applying our method to other pinniped and mammal species with less variable growth patterns, it might be possible to include older cohorts of juveniles.

Even so, major life history changes occur between the ages of 11 and 27 mo. Galapagos sea lion juveniles can be self-sufficient foragers, in the process of being weaned, still dependent, or even sharing their mothers' milk with a younger sibling of a trio (Trillmich & Wolf, 2008). Accurate age estimation, therefore, assists greatly in the detection of individual and age-specific ecological and behavioural differences in an otherwise non-differentiable group of young animals.

We consider this a practicable and reliable method that requires only brief periods of physical restraint of the study animals. We encourage the development of similar models in other species.

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Literature Cited

- Arnbom, T. A., Lunn, N. J., Boyd, I. L., & Barton, T. (1992). Aging live Antarctic fur seals and southern elephant seals. *Marine Mammal Science*, 8(1), 37-43.
- Arnould, J. P. (1995). Indices of body condition and body composition in female Antarctic fur seals (*Arctocephalus gazella*). *Marine Mammal Science*, 11, 301-313. doi: 10.1111/j.1748-7692.1995.tb00286.x
- Barber, R. T., & Chavez, F. P. (1983). Biological consequences of El Niño. *Science*, 222(4629), 1203-1210.
- Beauplet, G., Barbraud, C., Chambellant, M., & Guinet, C. (2005). Interannual variation in the post-weaning and juvenile survival of subantarctic fur seals: Influence of pup sex, growth rate and oceanographic conditions.

- Journal of Animal Ecology*, 74, 1160-1172. doi: 10.1111/j.1365-2656.2005.01016.x
- Bernt, K. E., Hammill, M. O., & Kovacs, K. M. (1996). Age estimation of grey seals (*Halichoerus grypus*) using incisors. *Marine Mammal Science*, 12(3), 476-482.
- Blundell, G. M., & Pendleton, G. W. (2008). Estimating age of harbor seals (*Phoca vitulina*) with incisor teeth and morphometrics. *Marine Mammal Science*, 24(3), 577-590. doi: 10.1111/j.1748-7692.2008.00194.x
- Boltnev, A. I., York, A. E., & Antonelis, G. A. (1998). Northern fur seal young: Interrelationship between birth size, growth and survival. *Canadian Journal of Zoology*, 76, 843-854.
- Bozdogan, H. (1987). Model selection and Akaike's information criterion (AIC): The general theory and its analytical extensions. *Psychometrika*, 52(3), 345-370.
- Bradshaw, C. J., Barker, R. J., & Davis, L. S. (2000a). Modeling tag loss in New Zealand fur seal pups. *Journal of Agricultural, Biological and Environmental Statistics*, 5(4), 475-485.
- Bradshaw, C. A., Davis, L. S., Lalas, C., & Harcourt, R. G. (2000b). Geographic and temporal variation in the condition of pups of the New Zealand fur seal (*Arctocephalus forsteri*): Evidence for density dependence and differences in the marine environment. *Journal of Zoology London*, 252, 41-51.
- Cane, M. A. (1983). Oceanographic events during El Niño. *Science*, 222, 1189-1195.
- Chabot, D., & Stenson, G. B. (2002). Growth and seasonal fluctuations in size and condition of male Northwest Atlantic harp seals *Phoca groenlandica*: An analysis using sequential growth curves. *Marine Ecology Progress Series*, 227, 25-42.
- Crawley, M. J. (2007). *The R book*. Chichester, UK: John Wiley & Sons Ltd.
- Engelhard, G. H., Brasseur, S. M., Hall, A. J., Burton, H. R., & Reijnders, P. J. (2002). Adrenocortical responsiveness in southern elephant seal mothers and pups during lactation and the effect of scientific handling. *Journal of Comparative Physiology B*, 172, 315-328. doi: 10.1007/s00360-002-0257-0
- Fowler, S. L., Costa, D. P., Arnould, J. P., Gales, N. J., & Burns, J. (2007). Ontogeny of oxygen stores and physiological diving capability in Australian sea lions. *Functional Ecology*, 21, 922-935. doi: 10.1111/j.1365-2435.2007.01295.x
- Fowler, S. L., Costa, D. P., Arnould, J. P., Gales, N. J., & Kuhn, C. E. (2006). Ontogeny of diving behaviour in the Australian sea lion: Trials of adolescence in a late bloomer. *Journal of Animal Ecology*, 75, 358-367. doi: 10.1111/j.1365-2656.2006.01055.x
- Gales, N. J., & Mattlin, R. H. (1998). Fast, safe, field-portable gas anesthesia for otariids. *Marine Mammal Science*, 14(2), 355-361.
- Gales, N. J., Barnes, J., Chittick, B., Gray, M., Robinson, S., Burns, J., et al. (2005). Effective, field-based inhalation anesthesia for ice seals. *Marine Mammal Science*, 21(4), 717-727. doi: 10.1111/j.1748-7692.2005.tb01261.x
- Gentry, R. L., & Kooyman, G. L. (1986). Methods of dive analysis. In R. L. Gentry & G. L. Kooyman (Eds.), *Fur seals: Maternal behaviour on land and at sea* (pp. 29-40). Princeton, NJ: Princeton University Press.
- Guinet, C., Servera, N., Deville, T., & Beauflet, G. (2005). Changes in subantarctic fur seal pups' activity budget and diving behaviours throughout the rearing period. *Canadian Journal of Zoology*, 83, 962-970. doi: 10.1139/Z05-087
- Heath, R. B., DeLong, R. L., Jameson, V., Bradley, D., & Spraker, T. (1997). Isoflurane anesthesia in free ranging sea lion pups. *Journal of Wildlife Diseases*, 33(2), 206-210.
- Horning, M., & Trillmich, F. (1997). Ontogeny of diving behaviour in the Galapagos fur seal. *Behaviour*, 134, 1211-1257.
- Jørgensen, C., Lydersen, C., Brix, O., & Kovacs, K. M. (2001). Diving development in nursing harbour seal pups. *Journal of Experimental Biology*, 204, 3993-4004.
- King, J. C., Gelatt, T. S., Pitcher, K. W., & Pendleton, G. W. (2007). A field-based method for estimating age in free-ranging Steller sea lions (*Eumetopias jubatus*) less than twenty-four months of age. *Marine Mammal Science*, 23(2), 262-271. doi: 10.1111/j.1748-7692.2007.00108.x
- Lawson, J. W., Harrison, D. D., & Bowen, W. D. (1992). Factors affecting accuracy of age determination in the harp seal, *Phoca groenlandica*. *Marine Mammal Science*, 8(2), 169-171.
- Lowry, M. S., & Folk, R. L. (1990). Sex determination of the California sea lion (*Zalophus californianus californianus*) from canine teeth. *Marine Mammal Science*, 6(1), 25-31.
- Lynch, M. J., Tahmindjis, M. A., & Gardner, H. (1999). Immobilisation of pinniped species. *Australian Veterinary Journal*, 77(3), 181-185.
- Mansfield, A. W. (1991). Accuracy of age determination in the grey seal, *Halichoerus grypus* of eastern Canada. *Marine Mammal Science*, 7(1), 44-49.
- Mansfield, A. W., & Fisher, H. D. (1960). Age determination in the harbour seal, *Phoca vitulina* L. *Nature*, 186, 92-93.
- McLaren, I. A. (1993). Growth in pinnipeds. *Biological Reviews*, 68, 1-79.
- McMahon, C. R., Burton, H. R., & Bester, M. N. (1999). First-year survival of southern elephant seals, *Mirounga leonina*, at sub-Antarctic Macquarie Island. *Polar Biology*, 21, 279-284.
- Molina-Schiller, D., & Pinedo, M. C. (2004). Using canine teeth for sex determination of the South American fur seal, *Arctocephalus australis*. *Latin American Journal of Aquatic Mammals*, 3(1), 19-24.
- Mueller, B., Pörschmann, U., Wolf, J. B. W., & Trillmich, F. (in press). Growth under uncertainty: The influence of marine variability on early development of Galapagos sea lions. *Marine Mammal Science*.

- Oosthuizen, W. H. (1997). Evaluation of an effective method to estimate age of Cape fur seals using ground tooth sections. *Marine Mammal Science*, 13(4), 683-693.
- Palacios, D. M. (2004). Seasonal patterns of sea-surface temperature and ocean colour around the Galapagos: Regional and local influences. *Deep Sea Research Part II: Topical Studies in Oceanography*, 51(1-3), 43-57.
- R Development Core Team. (2005). *R: A language and environment for statistical computing*. Vienna: R Foundation for Statistical Computing. Retrieved 24 August 2010 from www.r-project.org.
- Raum-Suryan, K. L., Rehberg, J., Pendleton, G. W., Pitcher, K. W., & Gelatt, T. S. (2004). Development of dispersal, movement patterns, and haul-out use by pup and juvenile Steller sea lions (*Eumetopias jubatus*) in Alaska. *Marine Mammal Science*, 20(4), 823-850.
- Trillmich, F. (1990). The behavioural ecology of maternal effort in fur seals and sea lions. *Behavioral Ecology and Sociobiology*, 114(1-4), 3-20.
- Trillmich, F., & Dellinger, T. (1991). The effects of El Niño on Galapagos pinnipeds. In F. Trillmich & K. Ono (Eds.), *Pinnipeds and El Niño* (pp. 66-74). Berlin: Springer-Verlag.
- Trillmich, F., & Limberger, D. (1985). Drastic effects of El Niño on Galapagos pinnipeds. *Oecologia*, 67, 19-22.
- Trillmich, F., & Wolf, J. B. W. (2008). Parent-offspring and sibling conflict in Galápagos fur seals and sea lions. *Behavioral Ecology and Sociobiology*, 62, 363-375. doi: 10.1007/s00265-007-0423-1
- Trillmich, F., Rea, L., Castellini, M. A., & Wolf, J. B. W. (2008). Age-related changes in hematocrit in the Galapagos sea lion (*Zalophus wollebaeki*) and the Weddell seal (*Leptonychotes weddelli*). *Marine Mammal Science*, 24(2), 303-314. doi: 10.1111/j.1748-7692.2007.00177.x
- Villegas-Amtmann, S., Costa, D. P., Tremblay, Y., Salazar, S., & Aurióles-Gamboa, D. (2008). Multiple foraging strategies in a marine apex predator, the Galapagos sea lion *Zalophus wollebaeki*. *Marine Ecology Progress Series*, 363, 299-309. doi: 10.3354/meps07457
- Wilson, S. (1974). Juvenile play of the common seal *Phoca vitulina* with comparative notes on the grey seal *Halichoerus grypus*. *Behaviour*, 48, 37-60.
- Wolf, J. B. W., Kauerman, G., & Trillmich, F. (2005). Males in the shade: Habitat use and sexual segregation in the Galapagos sea lion (*Zalophus californianus wollebaeki*). *Behavioral Ecology and Sociobiology*, 59, 293-302. doi: 10.1007/s00265-005-0042-7
- Wolf, J. B. W., Mawdsley, D., Trillmich, F., & James, R. (2007). Social structure in a colonial mammal: Unravelling hidden structural layers and their foundations by network analysis. *Animal Behaviour*, 74, 1293-1302. doi: 10.1016/j.anbehav.2007.02.024