

Size and experience matter: diving behaviour of juvenile New Zealand sea lions (*Phocarctos hookeri*)

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Abstract The diving ability of juvenile animals is constrained by their physiology, morphology and lack of experience, compared to adults. We studied the influences of age and mass on the diving behaviour of juvenile (2–3-year-old females, $n = 12$; 3–5-year-old males, $n = 7$) New Zealand (NZ) sea lions (*Phocarctos hookeri*) using time-depth recorders (TDRs) from 2008 to 2010 in the NZ subantarctic Auckland Islands. Diving ability (e.g. dive depth, duration and bottom time per dive) improved with age and mass. However, the percentage of each dive spent at the bottom, along with percentage time at sea spent diving, was comparable between younger and lighter juveniles and older and heavier juveniles. These suggest that younger and older juveniles expend similar foraging effort in terms of the amount of time spent underwater. Only, 5-year-old male juveniles dove to adult female depths and durations and had the highest foraging efficiency at depths >250 m. It appears that juvenile NZ sea lions attain adult female diving ability at around 5 years of age (at least in males), but prior to this, their performance is limited. Overall, the restricted diving capabilities of juvenile NZ sea lions may limit their available foraging habitat and ability to acquire food at deeper depths. The lower diving ability of juvenile NZ sea lions compared to adults, along with juvenile-specific constraints, should be taken into consideration for the effective management of this declining, nationally critical species.

Keywords Age · Mass · Size · Sex differences · Lower diving ability · Conservation management

Introduction

The foraging ability of juvenile diving animals is limited compared to adults, due to physiological and morphological constraints that ultimately affect their fitness and survival (Daunt et al. 2007). Combined with inexperience, these limitations for young animals can lead to lower foraging success that needs to be compensated for with an energetically costly increase in foraging effort (Weathers and Sullivan 1989; Daunt et al. 2007). These constraints have important implications for population dynamics because restricted foraging skills can result in reduced juvenile survival (Craig and Ragen 1999; Irvine et al. 2000; Daunt et al. 2007). Although juvenile survival is usually lower than adult survival across numerous mammalian taxa (Caughley 1966), population declines of various mammal and bird species have been attributed to particularly low levels of juvenile survival (Craig and Ragen 1999; Jenkins and Barten 2005; Finkelstein et al. 2010). Consequently, investigating factors that affect juvenile foraging ability can lead to an understanding of how these factors influence the dynamics of a population (Raum-Suryan et al. 2004).

Air-breathing marine predators must deal with the additional constraint of the separation between air at the surface and prey at depth (Fowler et al. 2006). Reduced diving performance can influence the ability to forage successfully (Daunt et al. 2007), but the ability for juvenile diving animals to effectively acquire food is limited by physiological and morphological constraints (Burns 1999). When taking into consideration the basic differences in physiological and morphological constraints between

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smaller and larger individuals (without accounting for differences in energetic requirements, e.g. breeding status), smaller animals have higher mass-specific metabolic rates and consequently utilize more oxygen stores (Schreer and Kovacs 1997). Mass-specific metabolic rates decrease with body mass, while oxygen stores increase with mass (Schreer and Kovacs 1997). Furthermore, smaller animals have lower aerobic dive capacity, which restricts their ability to stay submerged for long durations (Halsey et al. 2006). Smaller individuals also experience more drag per unit mass (Schreer and Kovacs 1997). Combined, these factors allow larger animals to dive deeper and longer than smaller animals (Halsey et al. 2006).

In addition to these physiological and morphological constraints, younger animals can lack foraging experience. Experience-based development of foraging abilities has been observed in a variety of taxa, including pinnipeds (sea lions, seals and walrus) (Le Boeuf et al. 1996; Horning and Trillmich 1997), birds (Kohlmann and Risenhoover 1998) and fish (Wildhaber and Crowder 1991). Predators rely on experience to find and travel to prey patches (Fauchald et al. 2000). However, as inexperienced foragers, juveniles may not be able to increase their foraging effort as much as adults through changes in behaviour during periods of low prey availability (Merrick and Loughlin 1997). For example, juveniles are limited in their ability to forage deeper or farther offshore, compared to adults. Additionally, juveniles that have not completed physical growth may be limited in prey selection due to the inability to handle larger prey (Brito 2004; La Croix et al. 2011). Juveniles are more sensitive to decreases in prey distribution/availability than adults as these declines can amplify the negative effects of juvenile-specific constraints, which impact on juvenile growth, and ultimately result in higher juvenile mortality (Owen-Smith 1990; Horning and Trillmich 1997; Jeglinski et al. 2012).

Diving behaviour has been studied in various juvenile pinniped species, and the diving ability of these animals increased with age (Horning and Trillmich 1997; McCafferty et al. 1998; Baker and Donohue 2000; Loughlin et al. 2003; Baylis et al. 2005; Fowler et al. 2006). However, few studies have examined juvenile pinniped diving behaviour beyond 2 years of age (Fowler et al. 2006; Rehberg and Burns 2008). Juvenile (17–30 months old) Steller sea lions (*Eumetopias jubatus*) (Merrick and Loughlin 1997; Rehberg and Burns 2008) were capable of diving to the same depths and durations as adults. However, juvenile (up to 3 years old) Australian sea lions (*Neophoca cinerea*) did not reach adult depths or durations (Fowler et al. 2006). This indicates that in some otariids (sea lion and fur seal) species, diving performance continues to develop prior to physical maturity, but with juvenile diving ability still limited compared to adults

(Fowler et al. 2006). Such limitations on juvenile diving ability can lead to increased susceptibility to human and environmental impacts that change prey abundance or distribution (Fowler et al. 2006). Indeed, high mortality rates of juvenile Galapagos fur seals (*Arctocephalus galapagoensis*) during periods of resource limitation (e.g. El Niño) are thought to result from their reduced diving ability, and consequently low foraging efficiency, compared with adults (Horning and Trillmich 1997).

The New Zealand (NZ) sea lion (*Phocarctos hookeri*) provides a unique system to study diving behaviour in a marine top predator. Adult female NZ sea lions at the subantarctic Auckland Islands are one of the deepest, longest diving otariids (Gales and Mattlin 1997), operating close to their physiological maximum in a marginal foraging habitat (Chilvers et al. 2006). Because a species functioning close to its physiological limits is more vulnerable to human and environmental changes that decrease prey availability (Costa et al. 2001), it is essential to investigate the factors influencing the diving ability of juveniles. Diving behaviour differs between age–sex classes before physical maturity due to varying body sizes and experience; these differences have significant ecological implications, as individuals with differing diving capabilities may respond differently to changes in prey abundance and availability (Rehberg and Burns 2008). Furthermore, examining juvenile NZ sea lion diving behaviour is important for conservation because the NZ sea lion is a declining species of management concern. The endemic NZ sea lion is one of the rarest otariids in the world (Chilvers et al. 2006) and is listed as “vulnerable” by the International Union for Conservation of Nature (IUCN 2011) and as “nationally critical” under the NZ threat classification system (Baker et al. 2010). The main anthropogenic threats to the NZ sea lion are mortality as bycatch and potential resource competition with a commercial arrow squid (*Nototodarus sloanii*) trawl fishery at the Auckland Islands, where 71 % of the NZ sea lion population is based (Robertson and Chilvers 2011).

The effective conservation management of NZ sea lions requires the knowledge of the foraging patterns and habitat use of all life stages, including juveniles, which have lower survival rates than adults (Chilvers and Mackenzie 2010). Female NZ sea lions sexually mature at 4 years of age and males at 6 years of age (Gales 1995). In this study, individuals younger than the age at sexual maturity are considered juveniles (i.e. females <4 years old and males <6 years old) and sexually mature-aged individuals are considered adults. This is the first study on the diving behaviour of juvenile NZ sea lions at the Auckland Islands and serves as a starting point to investigate an important demographic group for which no previous data exist. Our study aimed to examine: how does the diving behaviour of

juvenile NZ sea lions vary with age and mass? Related to our main aim, given the extreme diving behaviour of adult female NZ sea lions, we also wanted to answer: are juveniles capable of adult diving? In the sexually size-dimorphic NZ sea lion, males are larger than females from birth (Chilvers et al. 2007). As larger animals have disproportionately greater diving abilities (Schreer and Kovacs 1997), we hypothesize that older juveniles and males (predominantly larger-sized animals) will dive deeper, for longer durations, and have greater foraging efficiency than younger juveniles and females. We also hypothesize that in order to compensate for their limited diving capabilities, younger juveniles and females would increase their frequency of diving in order to maximize the amount of time in the foraging zone (e.g. Burns et al. 1997).

Materials and methods

Capture and deployment

We collected data over three austral summers from January to February, 2008–2010 (Table 1) at Sandy Bay, Enderby

Island, in the NZ subantarctic Auckland Islands (50°30'S, 166°17'E; Fig. 1). Study animals were chosen based on flipper tags that identified their age. Known-aged juvenile (2–3-year-old female and 2–5-year-old male) NZ sea lions were captured using a specially designed hoop net and physically restrained them with two handlers (Chilvers et al. 2006). The juveniles were anaesthetized using isoflurane delivered with oxygen to a mask via a field-portable vaporizer (Gales and Mattlin 1998) and then strapped into a custom-designed restraint frame and weighed using a 200-kg capacity scale (± 0.5 kg, Salter Housewares) suspended from an aluminium tripod.

Sea lions were instrumented using time–depth recorders (TDRs; Mk9, 65 mm \times 18 mm \times 18 mm, 25 g or Splash, 100 mm \times 35 mm \times 35 mm, 150 g, Wildlife Computers, Redmond, WA, USA) and also very high frequency (VHF; 3 cm \times 5 cm \times 2 cm, 15 g, Sirtrack, Havelock North, NZ) transmitters to facilitate recaptures. We attached the instruments to the dorsal pelage of the animal below the shoulder blades on the back midline using two-part epoxy resin (Devcon 5 Minute Epoxy). Once the instruments were securely attached, we stopped the flow of anaesthetic and the sea lion was allowed to recover. We observed each

Table 1 Instrument deployment data for 19 female and male juvenile New Zealand sea lions

Year	Animal Identity	Sex	Age	Mass (kg)	Tag	No. of days deployed	No. of foraging trips
2009	7445	F	2	53.0	Splash	8.6	4
2009	7610	F	2	54.0	Splash	22.3	7
2009	8023	F	2	54.0	Splash	14.7	6
	Mean \pm SE			53.7 \pm 0.3		15.2 \pm 4.0	5.7 \pm 0.9
2008	5857	F	3	71.0	Splash	13.0	8
2008	5863	F	3	68.0	Mk9	2.0	1
2008	5913	F	3	68.0	Mk9	11.1	3
2008	6059	F	3	84.5	Mk9	3.9	1
2008	6130	F	3	68.0	Splash	17.5	6
2009	6363	F	3	79.0	Splash	10.3	4
2009	6536	F	3	70.0	Splash	18.7	8
2010	7199	F	3	78.5	Splash	15.5	13
2010	7584	F	3	68.0	Splash	7.6	3
	Mean \pm SE			72.8 \pm 2.1		11.1 \pm 1.9	5.2 \pm 1.3
2009	6214	M	3	81.0	Mk9	12.5	2
2010	7260	M	3	89.0	Splash	11.1	3
2008	5093	M	4	83.0	Mk9	12.2	3
	Mean \pm SE			84.3 \pm 2.4			
2008	3727	M	5	102.0	Mk9	17.4	4
2008	4121	M	5	103.5	Splash	13.8	2
2009	4907	M	5	117.0	Mk9	12.9	4
	Mean \pm SE			107.5 \pm 4.8		14.7 \pm 1.4	3.3 \pm 0.7
2010	5752	M	5	150.0	Mk9	27.8	13

SE standard error

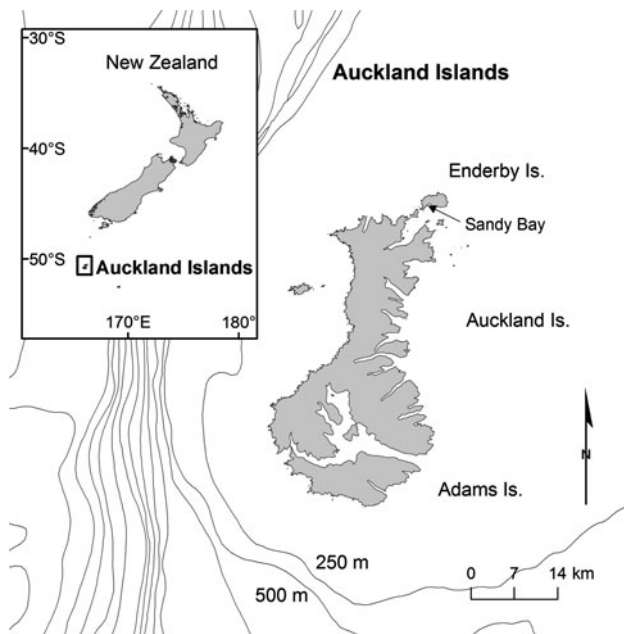


Fig. 1 Sandy Bay study site, Enderby Island, Auckland Islands, New Zealand (50°30'S, 166°17'E)

animal until it was fully conscious and had returned to the location of capture. Where possible, we recaptured each animal before the end of the field season (February 18) to retrieve instruments.

Dive analysis

TDRs sampled dive depth (± 0.5 m) every 5 s when wet. Depth readings were corrected for shifts in the pressure transducer at the surface of the time–depth recorders before analyses. We analysed diving data by producing summary statistics for each dive using the package *diveMove* (Luque 2007) in R software version 2.11.1 (R Development Core Team 2010). The dive summary file for each individual included the date, time, maximum depth, duration, and bottom time for each dive, along with the time spent at the surface after each dive (surface interval). Bottom time was defined as the time the sea lion spent at depths $>85\%$ of the maximum depth for that dive (Gales and Mattlin 1997). Foraging efficiency was calculated by dividing bottom time by total dive cycle time (dive duration + post-dive surface interval) (Ydenberg and Clark 1989), and we calculated mean foraging efficiency for 25 m depth bins for different age–sex classes. We analysed the dives separately using two different depth thresholds (≥ 4 m and ≥ 6 m in depth). There were no significant differences in dive parameters (e.g. depth, duration, bottom time and surface interval) between the 4 and 6 m datasets (E. Leung, unpublished data). However, because very shallow dives could be misidentified due to error in surface correction or in wave

action, we only used dives ≥ 6 m in depth for statistical analysis. Furthermore, dives <6 m were considered to be non-foraging dives primarily associated with travel (Gales and Mattlin 1997) and using dives ≥ 6 m in depth enabled comparison with previously published dive data on adult female NZ sea lions (Chilvers et al. 2006). A period ashore began after the tag was dry for 20 min and ended after the tag was wet for 30 s. Foraging trips were identified if continuous wet activity (i.e. continuous depth readings) were available for at least 1 h. This limit was chosen to exclude trips to sea that were for non-foraging activities. Summary statistics (dives per hour at sea, percentage time at sea spent diving and percentage time at sea) were calculated for each foraging trip.

Statistical analysis

Although interannual variation may influence the diving behaviour observed, small sample sizes each year precluded the differentiation between annual and individual differences. Due to limited sample size, we pooled the data by age–sex classes across all years. The largest tagged individual (5-year-old male, animal id 5752) travelled almost 500 km to the NZ mainland shortly after instrument deployment. This male's data are provided in the summary table (Table 1), but were not included in the data analysis as this animal was foraging in a completely different habitat, and thus, his diving behaviour was not comparable to the other study animals. We assessed the relationship between juvenile NZ sea lion age and mass with linear models. Values reported are mean \pm standard errors.

Diving behaviour was analysed at the scale of individual dives and foraging trips. For individual dives, diving behaviour was characterized by the mean depth, duration, bottom time, percentage of dive that was spent at the bottom and foraging efficiency. At the scale of foraging trips, diving behaviour was characterized by the maximum dive depth, duration and bottom time; and by dives per hour, percentage time at sea spent diving and percentage time at sea. We ran multiple linear mixed-effects models using diving behaviour characteristics as response variables and individual animal as the random effect on repeated-measures data, using the R package *nlme* (Pinheiro et al. 2010). Due to the lack of overlap in the age range of male and female study animals, we assessed age differences in males and females separately using linear mixed-effects models with age as the predictor variable. Since there was only one 4-year-old male for which dive data were available, we grouped this male with the 3-year-old males to compare the diving behaviour of younger (3–4 years old) versus older (5 years old) males. We did not expect this to be an issue as the mass and dive characteristics of the 4-year-old male were within the range of the 3-year-old

males (Table 1). Due to the strong collinearity between age and mass of juvenile NZ sea lions (see results), we assessed mass effects in separate linear mixed-effects models, with mass as the predictor variable and diving behaviour characteristics as response variables, in males and females separately. To improve the interpretability of regression coefficients, we centred and standardized the age and mass predictor variables (Schielzeth 2010). We also qualitatively compared the diving behaviour of juvenile NZ sea lions with previously collected data on adult females (Chilvers et al. 2006).

We assessed sex differences in diving behaviour within an age class between 3-year-old females and 3-year-old males, because the 3-year-old age class was the only age class with study animals of both sexes. We used multiple linear mixed-effects models to examine sex and mass (predictor variables) effects on diving behaviour (response variables: mean and maximum dive depth and duration, dive frequency and percentage time at sea diving). To identify the influence of the predictor variables (sex and mass) across the different dive parameters, we used a model-averaging approach based on the Akaike's information criterion correction for small sample size (AICc) scores (Burnham and Anderson 2002). We fitted a global model in R using the maximum-likelihood method. A full submodel set was generated from the global model using the R package MuMIn (Bartoń 2010). Models were ranked by their AICc scores, and models with $\Delta < 2$ were included in the confidence model set (Burnham and Anderson 2002); AICc weights (wAICc), as proportional weight of evidence in support of the particular models, were calculated for additional support.

Results

Between January and February, 2008–2010, a total of 26 TDRs were deployed and 19 were recovered (Table 1). The remaining seven TDRs fell off the study animals and were lost during the deployment period. Dive duration ($F_{1,27781} = 86,266.64$, $p < 0.001$) and bottom time ($F_{1,27781} = 14,743.44$, $p < 0.001$) were positively related to dive depth for all juveniles. Age and mass were also positively related for female ($F_{1,10} = 26.36$, $p < 0.001$) and male ($F_{1,5} = 6.41$, $p = 0.05$) juvenile NZ sea lions (Table 1).

Dive depth

Older and heavier animals dove deeper than younger and lighter animals of the same sex (Figs. 2a, 3a; Tables 2, 3). The 3-year-old females had over five times more dives >180 m than the 2-year-old females (Fig. 4), but did not

dive to significantly deeper mean and maximum depths. Older and heavier males dove significantly deeper (Tables 2, 3) than younger and lighter males (Fig. 2a). Overall, the 5-year-old males dove the deepest (79 % of dives >100 m and 5 % of dives >300 m; Fig. 4) and were the only age–sex class of juveniles that dove to adult female depths (Fig. 2a).

Male dives had deeper maximum depths than female juveniles (maximum depth range 170–530 m for males versus 143–313 m for females; Fig. 2a), with 3-year-old males diving to significantly deeper maximum depths than 3-year-old females ($t_{9,41} = 3.19$, $p = 0.01$). However, on average, 3-year-old females dove significantly deeper than 3-year-old males ($t_{9,16298} = -2.86$, $p = 0.02$; Fig. 2a). More than 60 % of 3-year-old female dives were to depths >100 m, compared to only 37 % for the 3-year-old males (Fig. 4). Variations in mean and maximum dive depth were best explained by a model containing only sex (Table 4). Mass had little influence on mean and maximum dive depth as the next best model, sex + mass, fitted the data less than half as well as the best model (wAICc = 0.26 and 0.28, respectively; Table 4).

Dive duration and bottom time

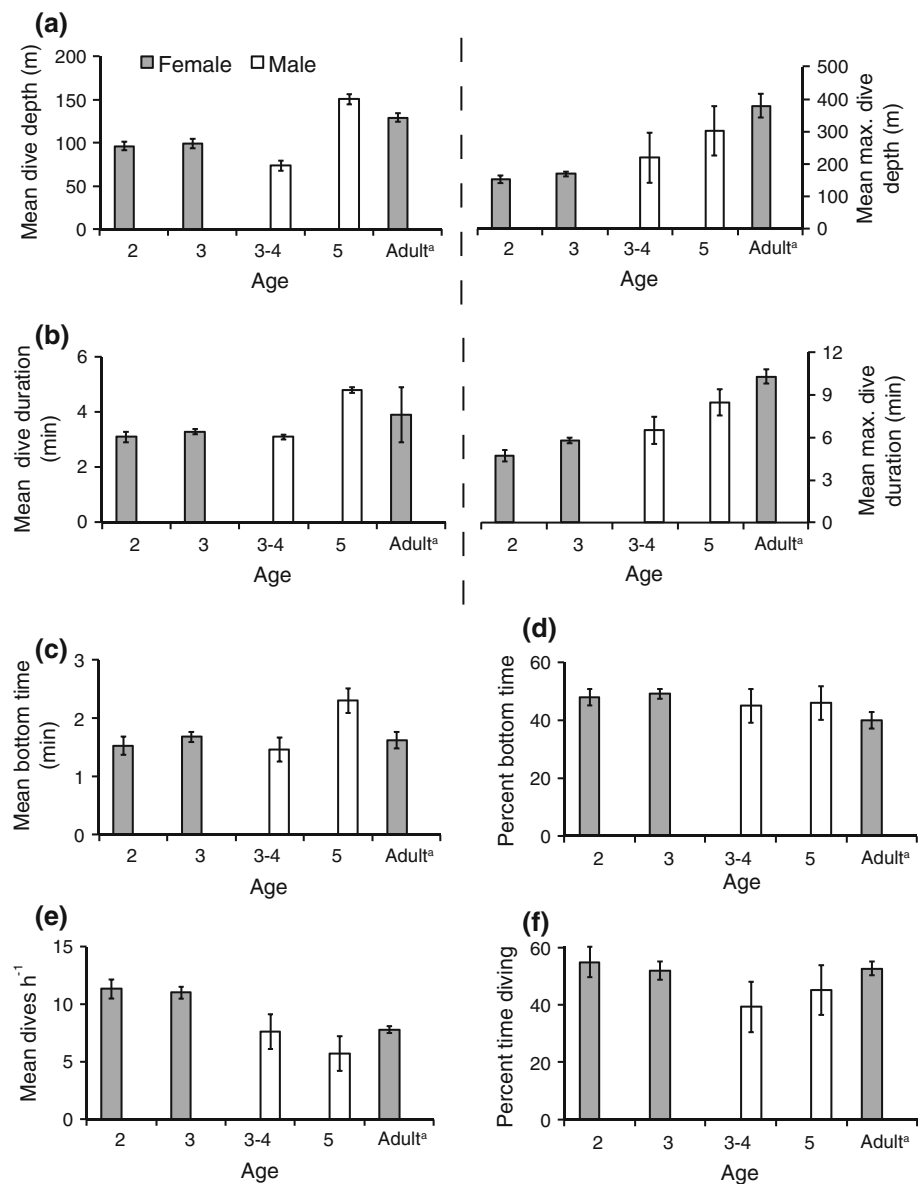
Mean and maximum dive durations and bottom times increased with age and mass within the same sex (Figs. 2b, c, 3b, c; Tables 2, 3). However, the percentage of the dive spent at the bottom was similar between older and heavier individuals and younger and lighter individuals (Tables 2, 3), with approximately 50 % of the dive spent at the bottom across all age–sex classes (Fig. 2d). Older juvenile females dove for significantly longer maximum durations than younger females (Table 2). Older and heavier males also dove significantly longer than younger juvenile males (Tables 2, 3). The 5-year-old males dove the longest on average (81 % of dives >4 min) and had the longest mean and maximum dive durations and bottom times of all the juveniles. Only, 4-year-old males dove to adult female durations (Fig. 2b).

Males dove for longer maximum durations than female juveniles (maximum duration range 6.4–11 min for males vs. 4.6–7.8 min for females; Fig. 2b). However, sex and mass were poor explanatory variables for variations in mean and maximum dive duration, with the null model having the highest weight for both mean and maximum dive durations (wAICc = 0.47 and 0.35, respectively; Table 4) and models containing sex and/or mass having low weights (wAICc ≤ 0.30 ; Table 4).

Foraging efficiency

With all dives averaged, foraging efficiency ranged from 0.32 to 0.35 across all age–sex classes and did not differ

Fig. 2 Mean and maximum (\pm standard error) of **a** dive depth, **b** dive duration, **c** bottom time, **d** percentage of dive spent at bottom, **e** dive frequency and **f** percentage time at sea spent diving for different age–sex classes of juvenile and adult female New Zealand sea lions (*Phocarctos hookeri*)



between older and heavier juveniles and younger and lighter juveniles (Tables 2, 3). When dive depth was taken into consideration, foraging efficiency was the highest for all age–sex classes between 75 and 150 m depth and ranged from 0.37 to 0.43 (Fig. 5). With the exception of 5-year-old males, foraging efficiency generally dropped steeply for all age–sex classes beyond 225 m depths (Fig. 5).

Dives per hour

Younger juvenile females dove at slightly higher frequencies than older females, and on average, juvenile females dove 60 % more frequently than adult females (Fig. 2e). Younger and lighter juvenile males dove over 30 % more frequently than older and heavier males, though the

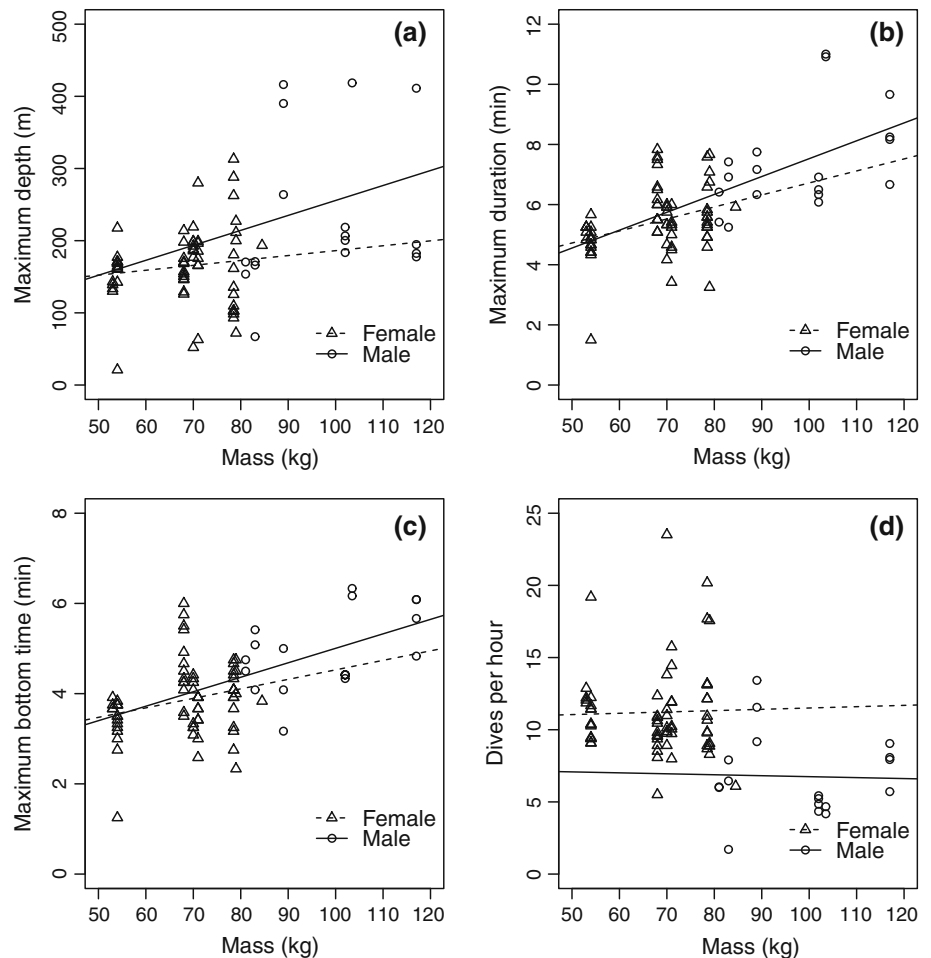
difference was not significant, and at similar frequencies as adult females (Figs. 2e, 3d; Tables 2, 3).

Three-year-old females dove 20 % more frequently than 3-year-old males (Fig. 2e). However, sex and mass had little influence on dive frequency, with the null model having the highest weight ($wAICc = 0.38$; Table 4) and models containing sex and/or mass having low weights ($wAICc \leq 0.27$).

Time spent diving and at sea

There were no significant age or mass differences in the percentage of time at sea spent diving and the percentage of time at sea per foraging trip within each sex (Fig. 2f; Tables 2, 3). Three-year-old females spent 50 % of their time at sea diving in contrast to 37 % for 3-year-old males

Fig. 3 Maximum **a** dive depth, **b** dive duration, **c** bottom time and **d** dive frequency per foraging trip in relation to mass for juvenile New Zealand sea lions (*Phocarctos hookeri*)



(Fig. 2f). Again, sex and mass had little influence on time at sea diving, with the null model having the highest weight ($wAICc = 0.48$; Table 4) and models containing sex and/or mass fitting the data only half as well as the null model ($wAICc \leq 0.23$; Table 4).

Discussion

We provide evidence that age, mass and sex are important influences on the diving behaviour of juvenile NZ sea lions, with sex and age effects likely mediated by mass. Within each sex, dive depth, duration and bottom time increased with age (Fig. 2) and mass, indicating that older and heavier juvenile NZ sea lions have greater diving performance than younger and lighter animals. However, only 5-year-old males dove to adult female depths and durations (Fig. 2), indicating that prior to 5 years of age (at least in males), juvenile NZ sea lions do not have the diving capabilities of adults and are limited in their ability to successfully forage at the same depths as adults. Five-year-old males also had the highest foraging efficiency at depths

>250 m, further suggesting the lower ability of younger and smaller juveniles to exploit prey at deeper depths. The logistical difficulties of deploying and recovering instruments on juveniles should be noted, a rarely seen age group (e.g. <4 and 6 % of known-aged individuals seen over the 3-year study period at Sandy Bay were juvenile females and males, respectively; B.L. Chilvers, unpublished data), restricted our sample sizes. Although the findings of this study should be interpreted conservatively due to low sample size, no other diving behaviour data on juvenile NZ sea lions at the Auckland Islands exist; as such, this study provides the best available information to inform population management plans for this declining, nationally critical species.

Age- and mass-related changes in diving behaviour

Older and heavier juvenile NZ sea lions dove to deeper depths for longer durations and less frequently than younger and lighter individuals of the same sex (Fig. 2). Dependent yearling NZ sea lions tagged in a separate study dove to one-third of the depths and half of the durations of

Table 2 Linear mixed-effects models assessing age effects for dive parameters of juvenile female and male New Zealand sea lions (*Phocarctos hookeri*)

Dive parameter	Females ($n = 12$)	Males ($n = 6$)
Dive depth (m)	$t_{10,19493} = -0.51$, $p = 0.62$	$t_{4,8289} = -10.95$, $p < 0.001$
Maximum dive depth (m)	$t_{10,52} = -1.10$, $p = 0.30$	$t_{4,12} = -0.86$, $p = 0.44$
Dive duration (min)	$t_{10,19493} = -1.22$, $p = 0.25$	$t_{4,8289} = -17.94$, $p < 0.001$
Maximum dive duration (min)	$t_{10,52} = -2.44$, $p = 0.04$	$t_{4,12} = -1.67$, $p = 0.17$
Bottom time (min)	$t_{10,19493} = -0.88$, $p = 0.40$	$t_{4,8289} = -3.43$, $p = 0.03$
Maximum bottom time (min)	$t_{10,52} = -1.90$, $p = 0.09$	$t_{4,12} = -1.65$, $p = 0.17$
Percentage bottom time (of dive)	$t_{10,19493} = -0.35$, $p = 0.73$	$t_{4,8289} = -0.14$, $p = 0.89$
Foraging efficiency	$t_{10,18639} = 0.005$, $p = 0.99$	$t_{4,7615} = 0.23$, $p = 0.83$
Dives per hour	$t_{10,52} = 0.21$, $p = 0.84$	$t_{4,12} = 0.99$, $p = 0.37$
Percentage time at sea	$t_{10,52} = -0.38$, $p = 0.71$	$t_{4,12} = 1.39$, $p = 0.24$
Percentage time at sea diving	$t_{10,52} = 0.52$, $p = 0.62$	$t_{4,12} = -0.54$, $p = 0.62$

Bolded values indicate dive parameter significantly differs with age

juvenile females (Leung et al. 2013). Combined, these demonstrate the greater diving ability of older individuals over younger juveniles. This is in concurrence with many other pinniped species (Le Boeuf et al. 1996; Horning and Trillmich 1997) and is likely associated with older animals having a combination of more foraging experience and more advanced physiological and morphological development, along with the benefits linked with larger body size. The greater diving ability of heavier animals is expected because larger size confers physiological and morphological advantages, such as lower mass-specific metabolic rates, higher oxygen stores and lower drag per unit mass (Schreer and Kovacs 1997). Older juvenile NZ sea lions were heavier than younger individuals (Table 1), and mass has also been documented to be positively related to dive depth and duration in various bird and mammal species (Halsey et al. 2006). Although younger sea lions dove at higher frequencies, the percentage of time at sea spent diving was similar between older and younger juveniles of the same sex (Fig. 2f). Thus, younger individuals may be able to dive at higher frequencies due to targeting shallower depths, but older juveniles dive for longer durations, and thus overall, older and younger juveniles expend similar foraging effort in terms of the amount of time spent diving.

Table 3 Linear mixed-effects models assessing mass effects for dive parameters of juvenile female and male New Zealand sea lions (*Phocarctos hookeri*)

Dive parameter	Females ($n = 12$)	Males ($n = 6$)
Dive depth (m)	$t_{10,19493} = -0.36$, $p = 0.72$	$t_{4,8289} = 4.90$, $p = 0.01$
Maximum dive depth (m)	$t_{10,52} = 1.44$, $p = 0.18$	$t_{4,12} = 0.85$, $p = 0.44$
Dive duration (min)	$t_{10,19493} = 0.95$, $p = 0.37$	$t_{4,8289} = 4.62$, $p = 0.01$
Maximum dive duration (min)	$t_{10,52} = 2.00$, $p = 0.07$	$t_{4,12} = 1.58$, $p = 0.19$
Bottom time (min)	$t_{10,19493} = 0.32$, $p = 0.76$	$t_{4,8289} = 2.06$, $p = 0.11$
Maximum bottom time (min)	$t_{10,52} = 1.18$, $p = 0.27$	$t_{4,12} = 1.67$, $p = 0.17$
Percentage bottom time (of dive)	$t_{10,19493} = -0.17$, $p = 0.86$	$t_{4,8289} = -0.28$, $p = 0.79$
Foraging efficiency	$t_{10,18639} = -0.34$, $p = 0.74$	$t_{4,7615} = -0.54$, $p = 0.62$
Dives per hour	$t_{10,52} = 0.09$, $p = 0.93$	$t_{4,12} = -0.14$, $p = 0.90$
Percentage time at sea	$t_{10,52} = -0.55$, $p = 0.60$	$t_{4,12} = -2.15$, $p = 0.10$
Percentage time at sea diving	$t_{10,52} = -0.86$, $p = 0.41$	$t_{4,12} = 1.58$, $p = 0.19$

Bolded values indicate dive parameter significantly differs with mass

Implications of lower juvenile diving ability

Only, 5-year-old male juvenile NZ sea lions (which are similar in mass to adult females; 113.8 ± 2.9 kg, $n = 18$; Chilvers et al. 2006) dove to adult female depths and durations (Fig. 2a, b). Juvenile females reached maximum depths and durations that were approximately 50 % of adult female maximum depths and durations. Additionally, the aerobic dive limit of juvenile female NZ sea lions is 19 % lower than that of adult females (Costa et al. 1998), further indicating their reduced physiological diving capability. Juvenile male NZ sea lions (3–4 years old) achieved maximum depths and durations that were only approximately 60 % of adult female levels. These indicate that although diving behaviour improved with age, most juvenile NZ sea lions do not have the diving capabilities of adults. Reduced diving capacity would restrict the available foraging habitat to juveniles (by limiting the depth ranges at which juveniles can efficiently exploit prey), which, in turn, affects the type of prey they can target. Juvenile NZ sea lions feed on the same prey species as adults, but targeted smaller opal fish (*Hemerocoetes* spp.) and rattail (*Coelorinchus* spp.) (Meynier et al. 2009). This suggests that juvenile NZ sea lions are restricted to foraging at depths where prey is smaller than at the deeper depths that adults exploit.

Fig. 4 Frequency plots of dive depth for different age–sex classes of juvenile New Zealand sea lions (*Phocarctos hookeri*) **a** 2-year-old females, **b** 3-year-old females, **c** 3–4 year-old males and **d** 5-year-old males. Axes are identical for all groups

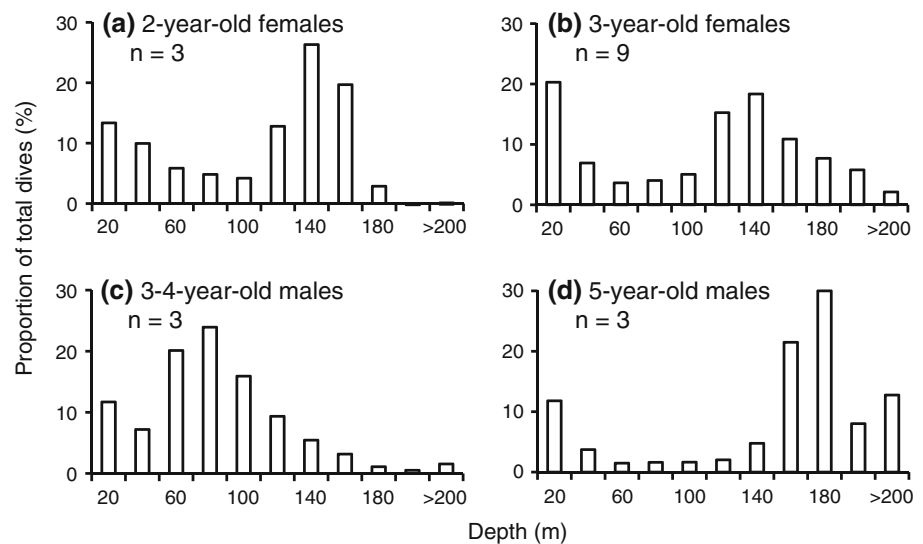


Table 4 Linear mixed-effects model selection results within $\Delta < 2$ for dive behaviour of 3-year-old juvenile female and male New Zealand sea lions (*Phocarctos hookeri*)

Dive parameter	Predictor variable	k	AICc	Δ AICc	wAICc
Mean dive depth (m)	Sex	4	178,824.25	0.00	0.66
	Sex + mass	5	178,826.15	1.90	0.26
Max. dive depth (m)	Sex	4	585.42	0.00	0.54
	Sex + mass	5	586.69	1.28	0.28
Mean dive duration (min)	Null	3	57,643.67	0.00	0.47
	Sex	4	57,645.15	1.48	0.23
	Mass	4	57,645.25	1.58	0.22
Max. dive duration (min)	Null	3	148.50	0.00	0.35
	Sex	4	148.80	0.30	0.30
	Mass	4	149.35	0.85	0.23
Dives per hour	Null	3	278.68	0.00	0.38
	Sex	4	279.39	0.72	0.27
	Sex + mass	5	279.86	1.18	0.21
	Mass	4	280.68	2.00	0.14
Percentage time at sea diving	Null	3	-115.50	0.00	0.48
	Sex	4	-113.99	1.51	0.23
	Mass	4	-113.84	1.67	0.21

Models related different dive parameters of 3-year-old juveniles to sex and mass. Values are the number of parameters in the model (*k*), Akaike’s information criterion corrected for small sample sizes (AICc), the difference between model AICcs and minimum (best model) AICc (Δ AICc) and the Akaike weights (wAICc). Models are ranked in the order of their corrected Akaike weights

Given the reduced diving capabilities of juveniles, younger sea lions may be restricted in their ability to increase dive depth or duration in response to reductions in prey (Fowler et al. 2006). The lower diving ability of juvenile NZ sea lions compared to adults is in concurrence with studies on the development of diving ability in

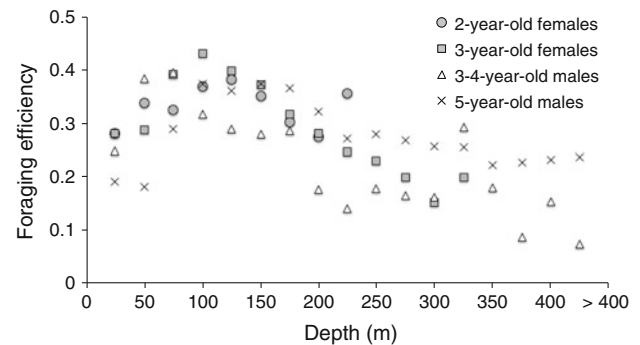


Fig. 5 Foraging efficiency in relation to dive depth for different age–sex classes of juvenile New Zealand sea lions (*Phocarctos hookeri*). Mean foraging efficiency was calculated for 25 m depth bins for different age–sex classes

Australian sea lions (Fowler et al. 2006) and Galapagos fur seals (Horning and Trillmich 1997). Restricted juvenile foraging ability has important implications for population dynamics since inadequate diving skills were the proximate cause of low juvenile survival for various marine predators (e.g. Hawaiian monk seals, *Monachus schauinslandi*, Craig and Ragen 1999; southern elephant seals, *Mirounga leonina*, Irvine et al. 2000; European shags, *Phalacrocorax aristotelis*, Daunt et al. 2007). Furthermore, predators rely on experience to find and travel to prey patches (Fauchald et al. 2000), but limitations in dive capacity combined with lack of experience may limit the ability of juvenile sea lions to forage successfully (Raum-Suryan et al. 2004).

It is important to note that juveniles may be able to dive deeper or longer than observed in this study, but they simply chose not to or did not need to. Because juvenile otariids do not have as high energetic requirements as lactating females (Winship et al. 2002), it is possible that juveniles exploit sufficient prey to meet energetic demands at shallower depths, and accordingly, it is unnecessary for

them to dive deeper or longer. Thus, although juveniles face age- and size-related constraints, juvenile NZ sea lions are not under the same energetic constraints and pressures as lactating females and may cope sufficiently in habitat that is considered marginal for adult females. However, juveniles are sensitive to human and environmental impacts that decrease prey abundance since these declines intensify the negative effects of juvenile-specific physiological, morphological and behavioural constraints (Owen-Smith 1990; Horning and Trillmich 1997; Jeglinski et al. 2012). Additionally, juveniles have lower tolerance than adults for food limitation due to their smaller size (Millar and Hickling 1990). Therefore, juveniles, along with lactating females, are likely the most susceptible life history stages to human and environmental impacts that decrease prey abundance/distribution. This potential increased vulnerability to external impacts, along with differences in juvenile and adult NZ sea lion foraging behaviour, suggests that juvenile-specific constraints and resultant foraging adaptations should be considered when modelling foraging habitat and trophic interactions, and devising conservation strategies (Jeglinski et al. 2012).

Intersexual differences

Because juvenile male NZ sea lions are larger than females of the same age (Chilvers et al. 2007), we expected males to have greater diving ability as quantified by diving deeper and longer. While individuals may not always dive to the maximum levels they are capable of, recorded maximum dive depths and durations likely provide the best measures of diving abilities of animals (Fowler et al. 2006). Although males were indeed capable of diving to deeper maximum depths for longer maximum durations (Fig. 2), we were surprised to find that, on average, 3-year-old females dove 30 % deeper and spent more time diving (larger proportion of time at sea diving and higher dive frequency) than 3-year-old males (Fig. 2). The low importance of mass indicates sex differences in the dive depths, and foraging ranges (Leung et al. 2012) of juvenile NZ sea lions is mainly influenced by sex-intrinsic factors, as opposed to size-related effects associated with sexual size dimorphism. Similarly, sex, instead of body size, accounted for the sex differences in diving behaviour of sexually dimorphic grey seals (*Halichoerus grypus*) (Beck et al. 2003). Furthermore, it is possible that sex differences in dive depths are attributed to the bathymetry of different foraging areas dictating possible dive depths, as has been observed with yearling NZ sea lions (Leung et al. 2013). Unfortunately, we did not have access to high-resolution bathymetry data that enabled us to discern whether female and male juvenile NZ sea lions forage in areas of differing depths or whether individuals employ benthic or pelagic foraging strategies.

When taking their smaller size (and associated physiological and morphological constraints) into consideration, the observed sex differences in diving behaviour suggest that 3-year-old female NZ sea lions appear to expend more effort foraging than 3-year-old juvenile males. As such, juvenile female NZ sea lions would be more susceptible to external impacts that change prey availability/distribution due to their smaller size, reduced diving ability and greater foraging effort. This has important implications for population dynamics, especially if female survival is negatively impacted (Wearmouth and Sims 2008). Indeed, 3-year-old juvenile female NZ sea lion survival is lower than 3-year-old males (Chilvers and Mackenzie 2010) and this may be a consequence of various factors, including their lower diving ability. Although the observed sex differences in juvenile NZ sea lion diving behaviour should be interpreted cautiously due to low sample size, similar observations of higher foraging effort by females have been reported in various taxa (Ruckstuhl and Neuhaus 2005), including pinnipeds (e.g. Steller sea lions, Pitcher et al. 2005; California sea lions, *Zalophus californianus*, Weise 2006). Females may be more selective of prey and thus spend more time searching, or males may be more efficient predators (Ruckstuhl and Neuhaus 2005). Alternatively, these sex differences may be associated with various causes, including different body sizes or tactics to reduce intra-specific competition (Ruckstuhl and Neuhaus 2005). As female juvenile NZ sea lions utilize different foraging space horizontally (Leung et al. 2012) and also vertically (i.e. different depth ranges) from male juveniles, this would result in niche specialization that likely minimizes intra-specific competition for prey resources.

Conclusions

Diving behaviour improved with age and mass in juvenile NZ sea lions. The greater diving ability of older juvenile NZ sea lions is likely attributed to the advantages associated with larger body size along with more advanced physiological and morphological development. However, only 5-year-old males dove to adult female depths and durations, indicating that prior to 5 years of age (at least in males), juvenile NZ sea lions have lower diving capacity than adults. Lower diving capacity would restrict the available foraging habitat to juveniles, by limiting the depth ranges at which they can successfully exploit prey. Although it is possible that juveniles can acquire sufficient prey at shallower depths due to lower energetic requirements than lactating females, juveniles are sensitive to environmental and human impacts that decrease prey availability. This is because decreases in prey distribution augment the negative effects of juvenile-specific physiological and morphological

constraints, which impact on juvenile growth, survival and recruitment, and, ultimately, has important implications for population dynamics. Furthermore, juveniles, along with lactating females, are likely the most vulnerable life history stages to human and environmental impacts that alter prey distribution. Thus, effective conservation and management strategies should consider this increased susceptibility to external impacts, along with juvenile-specific constraints and differences in juvenile and adult NZ sea lion diving behaviour.

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