

Deakin University  
Faculty of Science Engineering & Built Environment  
School of Life and Environmental Sciences



# THE COST OF A MEAL: FORAGING ECOLOGY OF FEMALE AUSTRALIAN FUR SEALS

Nelle Meyers – 01204891

Promotor: Prof. John P. Y. Arnould

Co-promotor: Prof. John P. Y. Arnould

Supervisor: Prof. John P. Y. Arnould



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## Executive summary

To maximise survival and reproduction, a species' foraging strategies must balance the costs and benefits of time and energy needed to search, chase, capture, manipulate and consume prey with the nutritional reward obtained. While such information is vital for understanding how prey assemblage changes may affect predator species, determining these components is inherently difficult in cryptic predators such as marine mammals. Using animal-borne cameras, this study investigated the costs and benefits of foraging on different prey types and the factors influencing this in female central-place foraging Australian fur seals (*Arctocephalus pusillus doriferus*) from Kanowna Island, south-eastern Australia. A total of 2022 prey events were observed in 63.5h of video from 23 individuals. The gross energy content of consumed prey was calculated from the estimated length/mass of prey items and the energy expended during prey encounters was estimated from the number of flipper strokes (during chase and capture) and published values for resting metabolic rate in water (prey handling and consumption). Baitfish encountered in the pelagic and demersal zones had the lowest capture successes, whereas elasmobranchs, benthic cephalopods and both benthic and pelagic solitary fish were encountered with the highest capture successes. Fast-swimming baitfish in both foraging zones required much greater chase times than other prey types but short handling durations. In contrast, chase times were short but handling times much higher for cephalopods and elasmobranchs. Benthic solitary fish showed intermediate chase and handling times. Morphological traits known to influence a seal's manoeuvrability and dive durations during foraging trips did not affect capture success nor chase and handling time. Gross energy gain of the prey types differed because of size and nutritional differences. Although chase and handling times, capture success, energy gain and energy expenditure

varied between prey types, their profitability did not differ. However, search time influences prey profitability profoundly but could not be considered in this study. The low marine productivity in Bass Strait and its effect on prey availability may have an influence on the foraging mode of the Australian fur seal. They are predominantly benthic foragers, therefore the abundance of nutritional baitfish in Bass Strait is assumed to be low. The results reflected that profitability of benthic prey outweighed search costs associated with pelagic baitfish. Anthropogenic-induced changes in the marine environment may however cause increases in baitfish abundance and make it a more reliable food source, which may facilitate the switch towards a more epipelagic foraging mode.

## Abstract

Knowledge of the factors shaping a species' foraging behaviour is central to understanding its ecosystem role and predicting its response to environmental variability. To maximise survival and reproduction, foraging strategies must balance the costs and benefits related to time and energy needed to search, chase, capture, manipulate and consume prey with the nutritional reward obtained. While such information is vital for understanding how changes in prey assemblages may affect predator species, determining these components is inherently difficult in cryptic predators such as marine mammals. This study used animal-borne cameras to study costs and benefits related to different prey types in female Australian fur seals (*Arctocephalus pusillus doriferus*) and found that although chase and handling times, captures successes, energy gain and energy expenditure varied between prey types, prey profitability did not differ. The low marine productivity in Bass Strait and its effect on prey availability may influence the foraging mode of the Australian fur seal, they are known to be predominantly benthic foragers as profitability of benthic prey outweighs searching costs associated with nutritious, pelagic baitfish prey. Anthropogenic-induced changes in the marine environment may however cause increases in baitfish abundance, which may facilitate the switch towards a more epipelagic foraging mode.

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## Introduction

Foraging success is one of the basic components of individual fitness, with direct impacts on individual reproductive success, population growth and, ultimately, survival of a species (Schoener, 1971). Understanding the factors shaping foraging behaviour of animals has been an important aim in behaviour studies for a long time (Pyke, 1984) as it is central to understanding an animal's role in an ecosystem and to predicting its response to environmental variability.

The Optimal Foraging Theory (Schoener, 1971) states that a foraging animal's fitness depends on its foraging efficiency. Behaviours which minimise energy expenditure and maximise energy gain will increase an animal's lifetime fitness and will consequently be selected for over time (Krebs & Davies, 2009; Pyke, 1984). Animals need to apply foraging strategies and tactics that maximise their survival and reproduction (Sinervo, 1997) as any prey resource has a cost and benefit to it. A classical version of this theory, the Optimal Diet Model (Pyke, 1984), uses profitability of prey (defined as net energy intake per unit handling time) as a currency which has been shown to strongly correlate with fitness (Schoener, 1971). According to this model, animals will select the most nutritional prey that can be obtained in the most economical way and will ignore prey types of lower profitability unless the more profitable prey are limited in availability (Goss-Custard, 1977).

An important factor influencing optimal diet choice involves the time needed to process the food item. Handling time is defined as the time needed to chase, capture, manipulate and consume a prey (Cohen & Tang, 1997). It may vary with prey type, size and abundance and can also be influenced by the presence of other animals and the individual's degree of satiation (Bindoo & Aravindan, 1992; Cohen & Tang, 1997; Lima et al., 1985; Werner,

1985). Correspondingly, it determines the time left to search for more prey (Wolf et al., 1975) and, therefore, plays an essential role in prey selection. Optimal diet choice also involves energetic constraints such as the metabolic cost of the different foraging activities (searching, chasing, catching, manipulating and processing) (Sinervo, 1997). Ultimately, the nutritional reward per unit time spent handling an animal receives from a prey will influence its optimal diet choice. Quantification of energy expenditure in terms of chase and handling duration and intensity of prey, and of energy gain related to size, morphology and nutritional content of prey, allows to estimate prey profitabilities which can be used to make further predictions on the foraging strategies of animals living in dynamic ecosystems.

Marine mammals inhabit ecosystems that are highly spatially and temporally variable (Harris et al., 1988; Perry et al., 2005). Several studies suggest that anthropogenic climate change is having an unfavorable impact on the marine environment and their biological communities (Hays et al., 2005; Hoegh-Guldberg & Bruno, 2010; Hughes, 2000). Foraging patterns of species have evolved to long-term patterns in timing, geographic distribution and availability of their prey resources in a particular habitat, climate driven mechanisms (Murphy et al., 1998; Palacios, 2004) can however modify these patterns of prey distribution and availability, forcing predators to alter their foraging strategies and tactics.

The majority of marine mammals forage at considerable depths, and often in remote locations (Bowen et al., 2002), making observations of their foraging behaviour is logistically difficult. Early studies on marine mammal foraging ecology involved indirect methods such as stomach content, fecal or stable isotope analyses to infer diet (Arnould et al., 2011; Littnan et al., 2007; Pierce & Boyle, 1991). These techniques, however, were limited in their ability to reveal foraging strategies and the factors influencing them. Consequently, fine-scale aspects of their feeding ecology have remained largely unknown.



Technological advances for monitoring of wild animals over the past decades have enabled the ability to study animal behaviour more into depth (Davis et al., 1999; Marshall, 1998). Animal-borne cameras allow to integrate video footage of animal activity from the perspective of the animal into behaviour research, which is crucial for the study of foraging strategies of elusive marine mammal species in inaccessible environments at a fine scale (Moll et al., 2007). Many studies have been performed on animal movements at sea and on search time for prey (Austin et al., 2006; Sims et al., 2008), yet little is known about animal energetics due to the difficulty of simultaneously measuring energy gains and energy expenditure of cryptic marine foragers. By using animal-borne cameras researchers can quantify energetic requirements of marine mammals and prey profitability in terms of nutritional content, information that is essential to predict consequences of changes in prey abundance and distribution due to environmental variability.

The Australian fur seal (*Arctocephalus pusillus doriferus*), the largest of the fur seal species with adult females and males weighing on average 76 kg and 279 kg, respectively (Shaughnessy & Warneke, 1987), has a breeding distribution largely restricted to the shallow continental shelf region of Bass Strait in south-eastern Australia (Arnould & Hindell, 2001; Kirkwood & Arnould, 2011). While the Australian fur seal population is still recovering from the severe over-exploitation of the commercial sealing era (1798-1825), at an estimated 120,000 individuals (ca 60% of pre-sealing levels), it represents the greatest marine predator biomass in the region (Arnould & Kirkwood, 2007; Kirkwood et al., 2010). The species is a generalist predator that forages on and near the seafloor at depths of 60-80 m on a wide range of prey types like cephalopods, elasmobranchs and bony fish (Arnould & Hindell, 2001; Arnould & Kirkwood, 2007; Deagle et al., 2009; Hume et al., 2004).

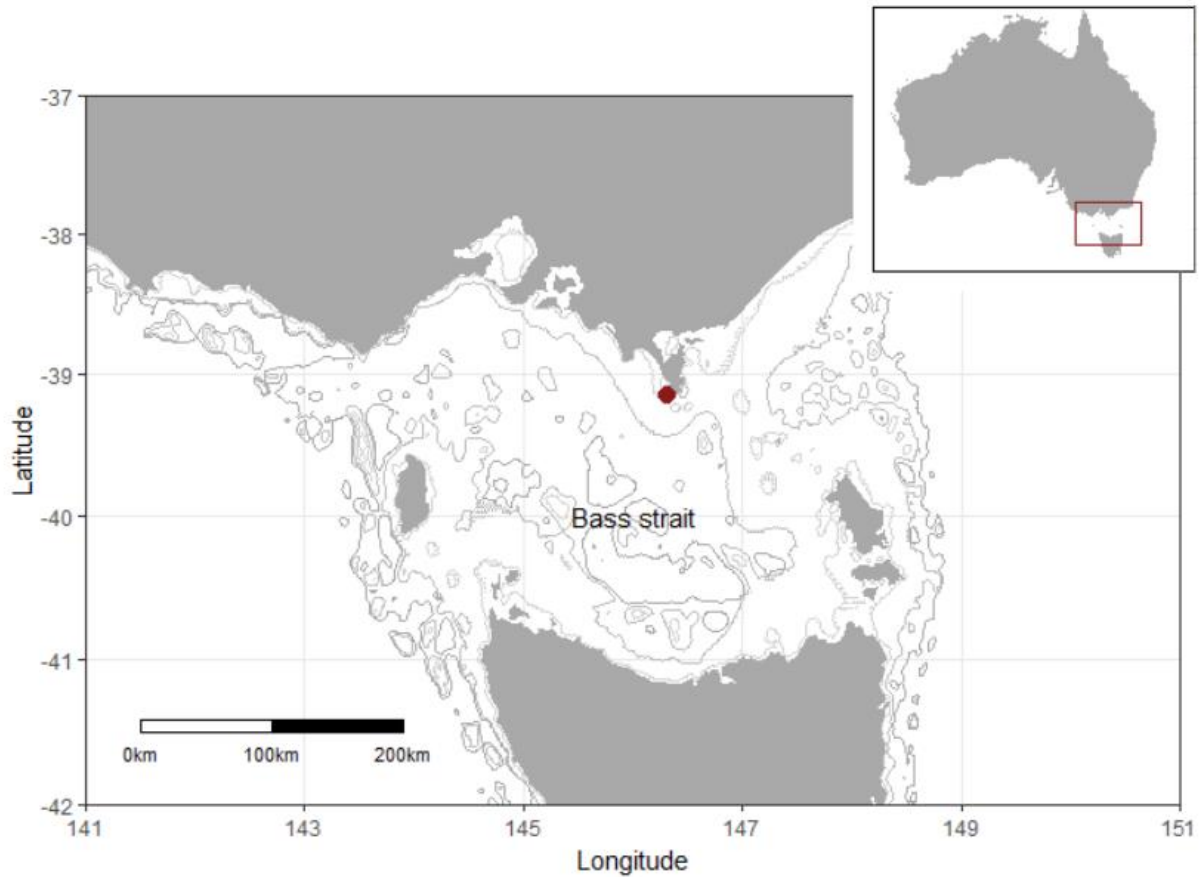
While Bass Strait is recognized as an area of low primary oceanic productivity, oceanographic features like the Bonney Upwelling and the South Australia Current feed the area with secondary productivity (Gibbs et al., 1986; Kampf, 2015; Sandery & Kampf, 2007). Australian fur seal females forage exclusively within the shallow waters over the continental shelf of Bass Strait during the 10 month lactation period (Arnould & Hindell, 2001). The region is one of the fastest warming oceanic areas in the Southern Hemisphere, with rates of warming over the past decades approximating 3-4 times the global average (Holbrook & Bindoff, 1997; Ridgway, 2007) as a result of intensification of the East Australian Current. The increased incursions of warm, nutrient poor water is reflected in changes in many marine ecosystem communities (Hobday et al., 2006; McLeod et al., 2012).

The ability of Australian fur seals in Bass Strait to respond to environmental changes that are likely to affect their prey abundance, distribution and diversity will determine their fitness, reproductive success and, ultimately, their population trajectory. However, the behavioural responses of the species to these changes remain largely unknown. Knowledge of how changes in the diversity, distribution and abundance of prey will impact the foraging behaviour of the species is crucial for understanding its role within a changing ecosystem. In particular, information on the factors which influence prey choice and foraging efficiency is necessary for making predictions on the response of the species towards future environmental changes (Costa et al., 2010; Littnan & Arnould, 2002). The aims of the present study, therefore, were to: 1) determine time and energetic costs related to prey chase and handling by Australian fur seals; 2) estimate profitability of the different prey types; and 3) investigate factors influencing these parameters.

## Materials and methods

### *Animal handling and instrumentation*

The study was conducted at Kanowna Island, northern Bass Strait ( $39^{\circ} 10'S$ ,  $146^{\circ} 18'E$ ) in southeastern Australia (Fig. 1). All research procedures were approved by the Deakin University Animal Ethics Committee (A16-2008, A14-2011, B16-2014) and under a Department of Sustainability and Environment (Victoria, Australia) Wildlife Research Permits (10005484, 100071531000826).



**Fig 1. :** A map of Bass Strait with location of the breeding colony of Australian fur seals at Kanowna Island indicated in red.

Between May-August during 2008-2017, adult females provisioning pups were selected at random, captured with a modified hoop net (Fuhrman Diversified, Seabrook, Texas, U.S.A.) and anaesthetised using isoflurane ( $1.5 \pm 0.4\%$ ) delivered via a portable gas anaesthetic machine (Stinger<sup>TM</sup>, Advanced Anaesthesia Specialists) (Gales & Mattlin, 1998) to facilitate handling during procedures. Once anaesthetised, individuals were weighed on a platform using a digital suspension scale ( $\pm 0.5$  kg) and morphometric measurements (standard length, flipper length, axillary girth, axis length and head width) were obtained using a tape measure ( $\pm 0.5$  cm).

A digital video data logger was then attached to the dorsal fur between the scapula using quick-setting epoxy (Accumix 268, Huntsmen, Texas, U.S.A.). Various video data logger models were used during the study: Crittercam<sup>®</sup> (Gen 5.7, 25 cm length  $\times$  5.7 cm diameter; National Geographic Society, Washington, U.S.A.); CATS-DC (v6-5.7.0, Customized Animal Tracking Solutions, Moffat Beach, Australia; 8.0 x 11.0 x 4.5 cm; 180 g) and custom built cameras (BBC v1, Mr ROV, Bristol, UK; 13.0 x 5.0 x 4.5 cm, 240 g) (Fig. 2). The cameras were positioned so that the seal's head was visible in the field of view. The distance between the top of the seal's head (between the pinnae) and snout to the lens of the video camera was determined using a tape measure ( $\pm 0.5$  cm) for prey size estimation.



**Fig 2:** Photographs of an Australian fur seal equipped with data loggers (left) and of a video data logger, dive behaviour data logger, GPS data logger and VHF transmitter, glued to the dorsal fur (right).

A dive behaviour data logger ( $5.2 \times 5.3 \times 2.4$  cm, MK10, Wildlife Computers, Washington, USA) and a GPS data logger (2 cm x 4 cm x 10 cm, F1G, Sirtrack, Havelock North, NZ) were also glued to the dorsal fur in series with the video data logger (data not presented here) as well as a VHF transmitter (1 x 2 x 3 cm, Sirtrack, Havelock North, NZ) to facilitate relocation for recapture. Individually-numbered plastic tags were then inserted into the trailing edge of the fore-flippers before the animal was allowed to recover from anaesthesia and resume normal behaviours. Animals were recaptured after one or more foraging trips to sea upon which the data loggers were removed by cutting the fur beneath them and the data were downloaded to a portable computer.

The Crittercams were programmed to record video data on a duty cycle of 1 hour on: 3 hours off starting at 6 am (local time) after the animal entered the water. To conserve battery life and to maximise the number of recorded dives, the video data logger started recording only when seals were submerged below 40 m and stopped recording once the seal ascended again above 40 m. Night recordings were possible through near-infra red LED beams that illuminated the field of view up to 5 m in front of the seal. The CATS Cams and BBC Cams

were programmed on a recording schedule of 1 h and 2 h, respectively, starting at 10:00 and 14:00 (local time) daily until the battery power expired.

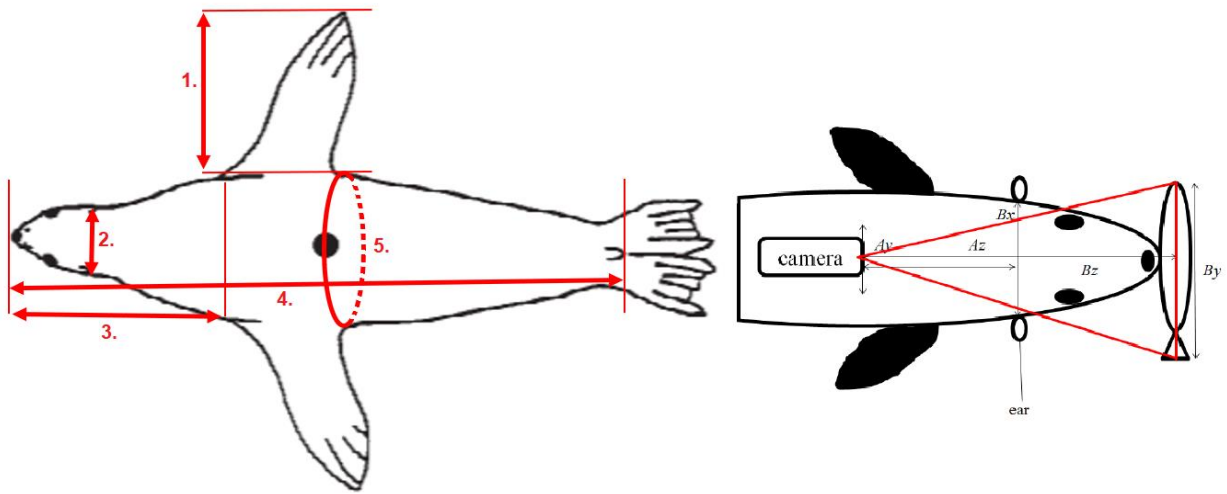
### *Data processing*

Information from the video data loggers were processed frame-by-frame using the Solomon Coder Software version Beta 17.03.22 (Eötvös Loránd University, Budapest, Hungary). Information was categorized for where in the water column the animal was (surface, descending, transiting at the seafloor and ascending), foraging behavior (chasing prey, handling prey), what prey were present and prey abundance (solitary or schooling). Prey were identified to the lowest taxonomic level possible using a field guide (Kuitert, 1997). Subsequently, prey items were categorized into broader more general groups: 'Benthic – Cephalopods', 'Benthic - Elasmobranchs', 'Demersal – Baitfish', 'Benthic - Solitary fish', 'Pelagic – Baitfish' and 'Pelagic - Solitary fish'.

A prey chase was defined as starting when the seal made intentioned movements towards a prey and ended once the prey was captured, if successful chases, or when the seal terminated the chase. The handling duration was defined as from the time the seal captured the prey until the seal consumed the prey or left any remaining portion of the prey.

Fork length of a selected number of fish prey, total length of all captured stingrays (tip of the anterior part of the head to the tip of the tail) and mantle length of all captured cephalopods (tip of the mantle to the bottom of the mantle) were measured from digital still images obtained from the video data. If a prey item was right in front of the camera lens, actual prey size  $A_y$  was estimated using the formula  $A_y = \frac{B_x}{B_m} * A_m$  where  $B_x$  is the actual width of the seal's head,  $B_m$  the seal head width in the digital image and  $A_m$  the length of

the prey in the photograph (Fig. 3). If prey capture was obscured in the video data, it was measured at the closest distance to the seal's snout, the distance between both was estimated and actual prey size  $B_y$  was estimated using the previously mentioned formula and the new formula  $B_y = A_y * \frac{B_z}{A_z}$  where  $B_z$  is the subject distance and  $A_z$  is the distance between the camera and the crown of the seal its head.



**Fig. 3:** A Schematic diagram illustrating the following morphological measurements taken for each seal (left): 1. flipper length, 2. head width, 3. axis length, 4. standard length and 5. axillary girth. The other diagram is a perspective projection transformation showing how a prey's true size was determined in the still images when the prey was viewed from a central view point (camera lens). The known seal's head width  $B_x$  was used as a reference for prey size estimation (right, figure adapted from Dorville (2013)).

For a random selection of representative items from all prey groups, estimated prey lengths were converted to estimates of body mass using published length-mass relationships for the observed, or a closely related, species (Table 1) (Alejo-Plata & Mendez, 2014; Lteif et al., 2016; Smallwood et al., 2017; Vallisneri et al., 2010). The gross energy content (J) of prey consumed ( $GE_{\text{gained}}$ ) was estimated from published prey-specific energy densities ( $J \cdot g^{-1}$ ) (Pehrsson et al., 2015; Sidwell, 1981) and their estimated mass. An index of the rate of energy gain from each prey was then calculated as GE consumed per unit of chasing and handling time (s).

**Table 1:** Length-mass relationship parameters a and b (mass =  $a \cdot \text{length}^b$ ) and energetic values of representative prey types of each group used to estimate their nutritional content.

Prey type	Relationship parameters		Energetic value ( $\text{J} \cdot \text{g}^{-1}$ )	References
	a	b		
Benthic - cephalopods (octopus sp.)	0.001600	2,7175	3431	(Alejo-Plata & Mendez, 2014); (Pehrsson et al., 2015)
Benthic - elasmobranchs (stingray sp.)	0.002970	3,2030	3766	(Lteif et al., 2016); (Sidwell, 1981)
Demersal/Pelagic - baitfish (mackerel sp.)	0.000189	2,4705	6627	(Smallwood et al., 2017); (Sidwell, 1981)
Benthic/Pelagic - solitary fish (leatherjacket sp.)	0.000439	2,4006	3500	(Smallwood et al., 2017) (Sidwell, 1981)
Benthic - solitary fish (Scorpaeniformes)	0.007000	3,2400	4184	(Vallisneri et al., 2010); (Pehrsson et al., 2015)

The amount of energy expended ( $\text{GE}_{\text{expended}}$ ) by the seals during prey chase and handling durations was estimated where possible for representatives of each of the broad prey categories using two different approaches. The first approach was based on the number of fore-flipper strokes observed during this period. Flipper strokes could be counted in the video data from the distinctive dorso-ventral head movement associated with each cycle. A value of  $3.79 \pm 0.39 \text{ J} \cdot \text{kg}^{-1}$  per stroke, previously determined in northern and Antarctic fur seals (*Callorhinus ursinus* and *A. gazella*, respectively) (Jeanniard-du-Dot et al., 2016), was then assigned to the total number of flipper strokes and adjusted for the individual's body mass. For prey chases without flipper strokes, a value of 0.5 strokes was assumed to account for any prior forward propulsion used to capture the prey. During prey handling, where no flipper strokes or forward movement was observed, a mass-specific resting metabolic rate previously estimated for female Antarctic fur seals ( $1.45 \text{ J} \cdot \text{s}^{-1} \cdot \text{kg}^{-1}$ ) (Boyd & Duck, 1991) was assigned to this period. The second approach used the diving metabolic rate of captive Steller sea lions (*Eumetopias jubatus*) recorded by respirometry ( $11\text{-}16 \text{ mL O}_2 \cdot \text{kg}^{-1} \cdot \text{min}^{-1}$ , Volpov et al.



(2016)), a standard method for measuring energy expenditure, combined with chase and handling durations of different prey types obtained in this study for the seal individuals.

The profitability of various prey types was determined by the foraging efficiency with which they were consumed using the equation (Schoener, 1971):

$$\text{Prey profitability (J}\cdot\text{s}^{-1}) = \frac{\text{GEgained (J)} - \text{GEexpended (J)}}{\text{chase+handling time (s)}}$$

### *Statistical analyses*

All statistical analyses were performed in the R statistical environment (version 3.4.0, R Core Team 2017). ANOVAs were used to identify possible differences in size of conspecifics in the pelagic and demersal/benthic zone. Box plots were created using the *ggplot2* package (Wickham, 2005) to explore the distribution of variables related to energy gained and expended in prey capture attempts. Scaled Linear Mixed-Effects-Models and Scaled Binomial Generalized Mixed-Effects-Models were used (*lme4* package) (Bates et al., 2015) to identify factors influencing prey chase and handling time and capture success based on the maximum-likelihood method. The full model included the following fixed effects: prey type and the morphometric measurements mass, flipper length, flipper length/standard length, axis length and axillary girth (Fig. 3). Additional morphometric measurements were obtained from the seals but after collinearity was assessed using a Pearson correlation matrix, one variable of a highly correlated pair of variables (Pearson correlation,  $r \geq 0.7$  or  $\leq -0.7$ ) was each time removed so that only the biologically most relevant variables were kept in the model. Seal identity was used as a random factor to account for repeated measurements. The

dredge function of the *MuMIn* package (Bartoń, 2016) was used for model comparison and averaging. Candidate models were selected using the Akaike Information criterion (AIC), an estimator of the relative quality of statistical models relative to each of the other for a given set of data and done so by balancing the level of fit (in terms of log-likelihood) with model complexity. Eventually the best model was obtained through averaging models which had  $\Delta AICc$  values lower than 4. Weighted Linear Mixed-Effects-Models with seal identity as random factor were used (*nlme* package) (Pinheiro et al., 2013) to identify the effect of prey type on (rates of) GE gain, (rates of) total energy expenditure and prey profitability based on the maximum-likelihood method. All results are reported as median [interquartile range] unless stated otherwise, statistical significance was set at  $\alpha = 0.05$  for all results.

## Results

### *Prey types and capture successes*

Video data were obtained from a total of 23 individuals (Fig. 4, table 2), for a total 63.5 h. A total of 2027 prey encounter events were observed in the video data, with 2022 leading to prey chases (99.7%) and 1263 observed prey captures (62.3%). The main prey types observed were Scorpaeniformes (gurnards, gurnard perches and occasionally flatheads, 28.85%), Perciformes (mainly jack mackerel and occasionally red bait and trevally, 15.34%) and Tetraodontiformes (leatherjackets, 12.17%; Table 3). Occasionally encountered prey types included Cephalopoda (octopuses, squids and a single giant cuttlefish, 1.78%), Zeiformes (silver dories, 1.19%), Myliobatiformes (stingrays, 0.40%) and Gadiformes (codlings, 0.30%). Prey types contributing negligibly to the seal's diet included Scombriformes

(Barracoutas, 0.5%), Ophidiiformes (Pink lings, 0.15%); other Elasmobranchii (catsharks, dogsharks and necklace carpetsharks), Beloniformes (Garfish), Centrarchiformes (knifejaws) and Decapoda (Spiny rock lobster) were all observed only once. Of all prey items 17.27% were classified as unknown benthic fish and 21.97% was not visible on video footage and was therefore classified as unknown benthic prey.

Various models including morphometric measurements had  $\Delta AICc$  values ( $< 4$ ), but only prey type seemed to significantly influence capture success ( $F_{6,931} = 85.191$ ,  $P < 0.001$ ). Prey capture success was therefore not influenced by the morphology of individuals but was affected by prey type (Table 4).



**Fig. 4:** Representative images from animal-borne cameras showing prey captures of Australian fur seals. From left to right, upper to lower row: Schooling jack mackerel (*Trachurus* sp.), an octopus (*Octopus* sp.), a dogfish (Squaliformes), a stingray (Myliobatiformes), a leatherjacket (Tetraodontiformes) and a gurnard (Scorpaeniformes).

The highest capture rates were observed for cephalopods and pelagic solitary fish like leatherjackets (both 100%) (Fig. 5). Benthic solitary fish (e.g. gurnards and gurnard perches) and elasmobranchs (stingrays and sharks) showed slightly lower but still high capture

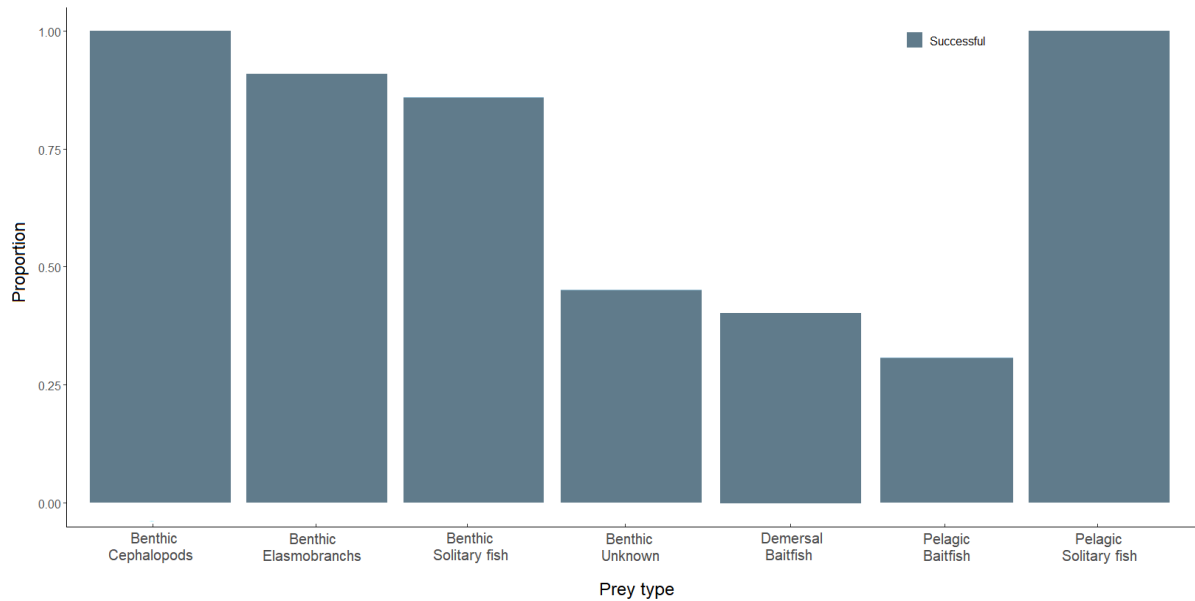
successes (85.8% and 90.9%, respectively). Baitfish encountered in both pelagic and demersal zones (e.g. jack mackerels and red bait) showed the lowest capture successes (30.6% and 40.3%, respectively). Unknown benthic prey items (including benthic fish) had capture successes of 45.02%, which is comparable to but slightly higher than capture successes of demersal baitfish.

**Table 2:** Summary of video camera deployments and morphometric measurements of all 23 instrumented Australian fur seal females in Bass Strait, south-eastern Australia.

Seal	Date	Head	Mass	Standard	Flipper	AXG	Axis
		width		length	length		
		[cm]	[kg]	[cm]	[cm]	[cm]	[cm]
1	17/05/2008	15.0	98.0	171.0	45.5	108.0	69.0
2	19/05/2008	15.0	90.0	160.0	43.5	106.5	66.5
3	23/05/2008	15.0	85.5	157.0	45.5	101.0	65.5
4	28/05/2008	15.0	91.0	160.5	41.0	112.5	64.5
5	05/06/2009	15.0	80.0	150.0	41.5	106.0	72.5
6	05/06/2009	15.0	63.5	146.5	40.5	98.5	64.5
7	07/06/2009	15.0	81.5	156.5	43.5	112.0	66.5
8	23/07/2010	14.5	63.5	145.0	42.0	92.0	61.0
9	25/07/2010	17.0	84.5	158.0	45.0	103.0	64.5
10	25/07/2010	15.5	75.5	141.5	41.5	110.0	58.0
11	14/05/2011	15.5	88.5	166.0	48.0	100.0	66.0
12	14/05/2011	13.5	50.5	132.0	40.0	82.0	51.0
13	15/05/2011	14.5	54.5	136.0	40.5	85.0	52.0
14	15/05/2011	15.5	90.5	158.5	46.0	103.0	66.0
15	25/05/2011	15.0	88.0	161.5	47.5	103.0	69.5
16	11/06/2011	14.0	87.5	142.0	39.0	95.5	58.5
17	14/06/2011	14.5	55.5	159.0	42.5	104.5	66.5
18	17/05/2012	14.0	78.0	134.0	39.0	85.5	50.0
19	09/06/2017	/	79.5	157.5	43.5	104.0	60.0
20	03/07/2015	/	66.5	144.0	42.0	99.0	63.0
21	13/08/2018	/	89.0	166.0	45.5	104.0	70.0
22	13/08/2018	/	76.5	153.0	42.0	101.0	61.0
23	02/06/2017	/	76.5	161.5	45.0	93.0	70.0

**Table 3:** Number of prey events recorded through animal borne cameras attached to 23 Australian fur seal females in Bass Strait, south-eastern Australia.

Prey type	Encountered [n]	Captured [n]
<b>Invertebrates</b>		
Spiny rock lobster <i>Jasus edwardsii</i>	1	1
Octopoda ( <i>Octopus</i> spp.)	30	30
Giant cuttlefish <i>Sepia apama</i>	1	1
Tethida (Squids)	5	5
<b>Elasmobranchs</b>		
Necklace carpetshark <i>Parascyllium variolatum</i>	1	0
Carcharciniformes (Catsharks)	1	0
Squaliformes (Dogfish)	1	0
Myliobatiformes (Stingrays)	8	8
<b>Teleosts</b>		
Garfish ( <i>Hyporhamphus</i> spp.)	2	2
Pink Ling <i>Genypterus blacodes</i>	3	3
Silver dory <i>Cyttus australis</i>	24	18
Codling (Moridae)	6	4
Barracouta <i>Thyrsites atun</i>	3	3
Jack Mackerel ( <i>Trachurus</i> spp.)	280	85
Knifejaw ( <i>Oplegnathus</i> spp.)	1	1
Slender-spined porcupine fish <i>Diodon nichthemerus</i>	3	3
Redbait <i>Emmelichthys nitidus</i>	4	3
Trevalley ( <i>Pseudocaranx</i> spp.)	5	3
Carangidae	21	11
Platycephalidae (Flatheads)	6	5
Triglidae (Gurnards)	334	301
Neosebastidae (Gurnard perches)	83	75
Monacanthidae (Leatherjackets)	246	225
Scorpaeniformes (mail-cheeked fish)	160	119
<b>Unidentified</b>		
Unknown benthic fish	349	230
Unknown benthic species	444	127
<b>Total</b>	<b>2022</b>	<b>1263</b>



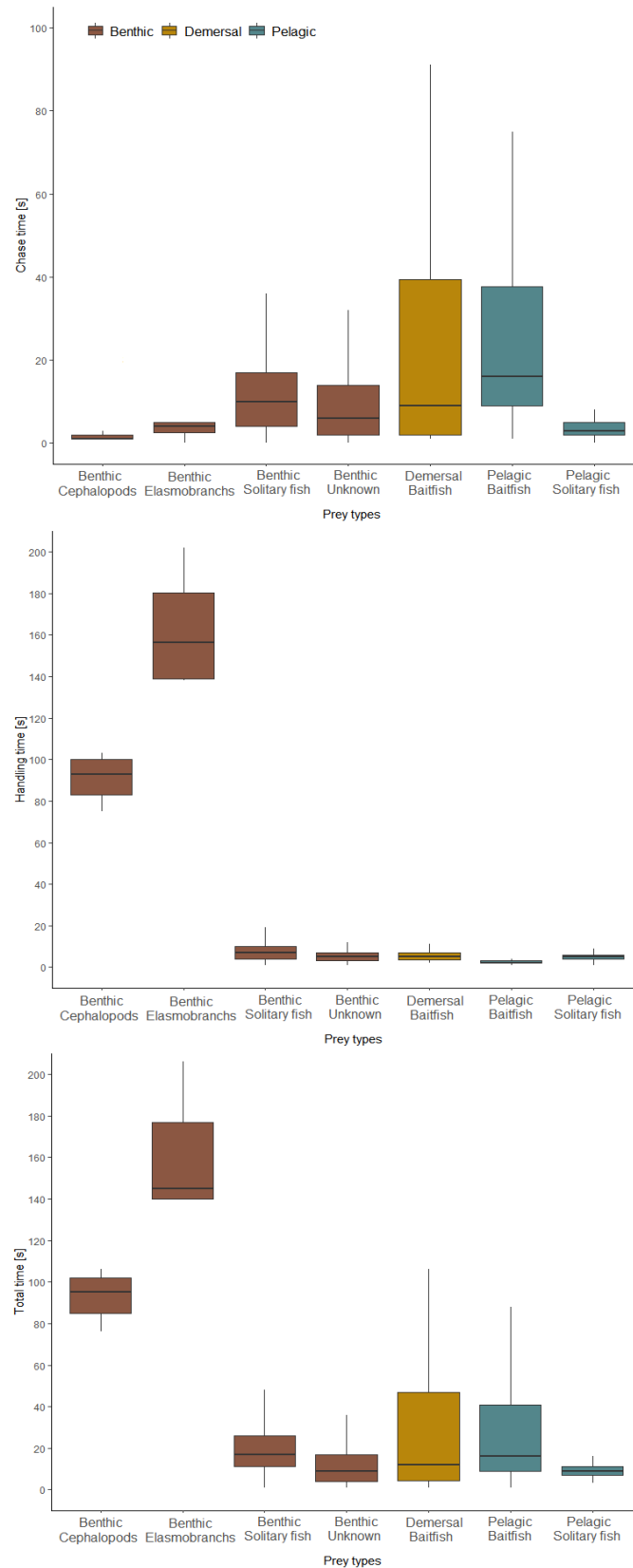
**Fig. 5:** Capture success of the different prey types, determined from animal-borne video data loggers, by Australian fur seal females in Bass Strait, south-eastern Australia.

#### *Prey chase and handling times, energy gain and profitability*

Several models with low  $\Delta AICc$  values ( $< 4$ ) included combinations of the morphometric measurements, however only the effects of prey type were significant ( $F_{6,994} = 31.351$ ,  $P < 0.001$  (chase time) and  $F_{6,964} = 28.396$ ,  $P < 0.001$  (handling time)). The modelling results indicated that chase and handling durations were not affected by any of the measured seal morphometric parameters, prey type however had a considerable effect (Table 4).

The shortest chase times were for cephalopods (1-2 s) and elasmobranchs (4 s) but their handling times were the highest of all prey types (90 s and 157 s respectively) (Fig. 6). In contrast, baitfish in both pelagic and benthic foraging zones required much longer chase times (respectively 32 s and 31 s) while their handling times were very short (respectively 3 s and 3 s). Intermediate chase times were observed for solitary fish in benthic waters (8 s), it took less time to catch solitary fish midwater (leatherjackets) (2 s). Solitary fish in both

foraging zones showed rather low handling times (5 s in pelagic waters and 7 s in benthic waters), similar to baitfish in both zones (3 s in pelagic waters and 3 s in benthic waters). In a few observations, larger benthic solitary fish took longer to be handled as they were brought to the surface to be consumed.



**Fig. 6:** Boxplots comparing a) chase time, b) handling time and c) total time spent by Australian fur seal females on different prey types in Bass Strait, south-eastern Australia. The bold solid line within each box represents the median, the bottom and top of each box represent the 25th and 75th percentiles and the whiskers represent the extreme values found within 1.5 times the length of the box



**Table 4:** Models with  $\Delta AICc < 4$ , listed in descending order, used for assessing the factors influencing prey capture success, chase time and handling time in Australian fur seal females in Bass Strait, south-eastern Australia. Seal individual was used as a random factor in all models to account for repeated measurements.

Model	AICc	$\Delta AICc$	Weight
capture success ~ prey	2240.9	0.00	0.203
capture success ~ flipper length/standard length + prey	2242.4	1.57	0.093
capture success ~ axis + prey	2242.8	1.89	0.079
capture success ~ mass + prey	2243.0	2.11	0.071
capture success ~ flipper length + prey	2243.0	2.13	0.070
capture success ~ axg + prey	2243.0	2.15	0.069
capture success ~ axg + flipper length/standard length + prey	2244.4	3.55	0.034
capture success ~ flipper length/standard length + mass + prey	2244.5	3.61	0.033
capture success ~ axis + flipper stroke + prey	2244.6	3.70	0.032
capture success ~ axis + flipper length/standard length + flipper stroke + prey	2244.6	3.76	0.031
capture success ~ flipper length/standard length + flipper length + prey	2244.7	3.79	0.030
capture success ~ axis + mass + prey	2244.7	3.84	0.030
capture success ~ axg + axis + prey	2244.8	3.94	0.028
chase ~ flipper length + prey	9990.9	0.00	0.143
chase ~ axg + flipper length + prey	9992.0	1.03	0.086
chase ~ prey	9992.0	1.08	0.083
chase ~ flipper length/standard length + flipper length + prey	9992.2	1.31	0.075
chase ~ axis + flipper length + prey	9992.4	1.45	0.070
chase ~ flipper length + mass + prey	9993.0	2.02	0.052
chase ~ flipper length/standard length + prey	9993.2	2.27	0.046
chase ~ mass + prey	9993.7	2.81	0.035
chase ~ axis + prey	9993.9	2.92	0.033
chase ~ axis + flipper length/standard length + prey	9994.0	3.04	0.031
chase ~ axg + prey	9994.1	3.18	0.029
chase ~ axg + flipper length/standard length + prey	9994.1	3.19	0.029
chase ~ axg + axis + flipper length + prey	9994.2	3.23	0.029
chase ~ axg + flipper length + mass + prey	9994.2	3.32	0.027
chase ~ axis + flipper length/standard length + flipper length + prey	9994.4	3.49	0.025
chase ~ flipper length/standard length + mass + prey	9994.4	3.50	0.025
chase ~ flipper length/standard length + flipper length + mass + prey	9994.5	3.59	0.024
chase ~ axis + flipper length + mass + prey	9994.6	3.67	0.023
handling ~ prey	12789.0	0.00	0.188
handling ~ flipper length/standard length + prey	12790.1	1.03	0.112
handling ~ axg + prey	12791.1	2.02	0.068
handling ~ flipper length + prey	12791.1	2.11	0.066
handling ~ mass + prey	12791.2	2.11	0.065
handling ~ axis + prey	12791.2	2.12	0.065
handling ~ axis + flipper length/standard length + prey	12792.0	2.92	0.044
handling ~ axg + flipper length/standard length + prey	12792.2	3.11	0.040
handling ~ flipper length/standard length + mass + prey	12792.2	3.18	0.038
handling ~ flipper length/standard length + flipper length + prey	12792.2	3.21	0.038

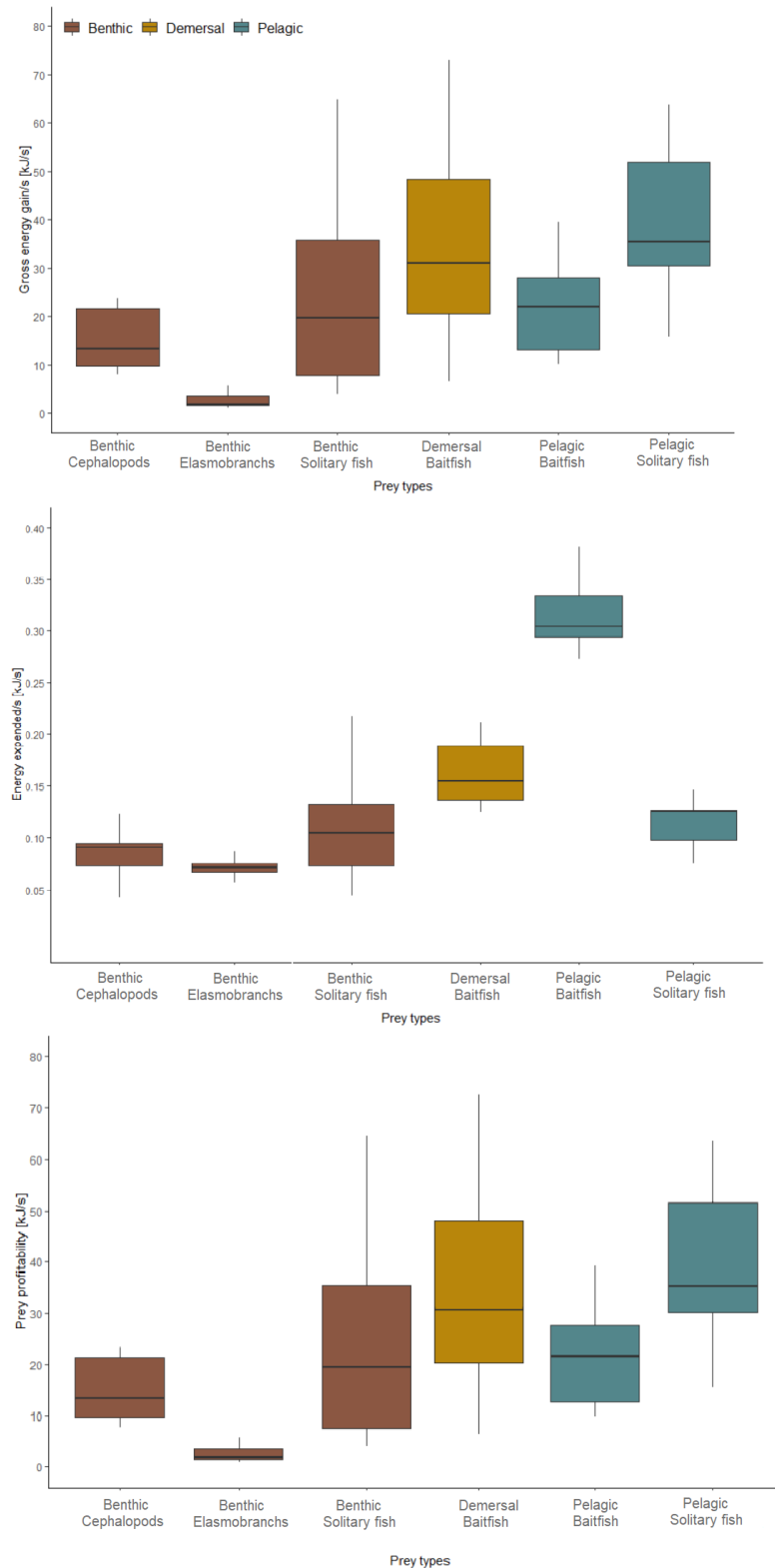
The ranges in prey length and mass estimates can be found in Table 5 (expressed as median [interquartile range]). Baitfish in both the pelagic and demersal foraging zone did not differ significantly in size ( $F_{1, 27} = 0.909$ ,  $P = 0.349$ ) although leatherjackets chased in the benthic zone were larger than midwater congeners ( $F_{1, 35} = 8.786$ ,  $P = 0.005$ ). Estimated gross energy intake increased rapidly with prey length and mass. Correspondingly, gross energy gain differed significantly between prey groups ( $F_{5, 87} = 12.353$ ,  $P < 0.001$ ). Consumption of cephalopods provided the highest GE gain as octopuses were considerably larger than other prey types (1,492,890 J) (see Table 5 for interquartile range). Consuming baitfish and benthic solitary fish also resulted in high GE gain (respectively 670,610 J (pelagic), 863,210 J (benthic) and 437,390 J). While octopuses captured weighed approximately 5 times more than baitfish and solitary fish captured in the demersal/benthic zone, their nutritional value ( $3,431 \text{ J} \cdot \text{g}^{-1}$ ) was much lower compared to that of baitfish like jack mackerel ( $6,627 \text{ J} \cdot \text{g}^{-1}$ ) and benthic solitary fishes belonging to the Scorpaeniformes ( $4,184 \text{ J} \cdot \text{g}^{-1}$ ). Solitary leatherjackets captured in pelagic (and benthic) waters were of low nutritional value ( $3,500 \text{ J} \cdot \text{g}^{-1}$ ), similar to stingray prey ( $3,766 \text{ J} \cdot \text{g}^{-1}$ ). Because both prey types were of low mass, they represented low GE gain per item (respectively. 304,050 J and 287,400 J).

The relatively low rates of gross energy intake ( $\text{J} \cdot \text{s}^{-1}$ ) (Fig. 7) for cephalopod prey arose from their prolonged handling times ( $13,370 \text{ J} \cdot \text{s}^{-1}$ ). Stingrays had high handling times as well, combined with their rather low nutritional values GE gain/s was low ( $1,860 \text{ J} \cdot \text{s}^{-1}$ ). Consumption of pelagic baitfish resulted in higher rates of gross energy intake ( $21,990 \text{ J} \cdot \text{s}^{-1}$ ), comparable to that for benthic solitary fish ( $19,600 \text{ J} \cdot \text{s}^{-1}$ ). Demersal baitfish and pelagic solitary fish both led to high rates of gross energy intake ( $30,960 \text{ J} \cdot \text{s}^{-1}$  and  $21,990 \text{ J} \cdot \text{s}^{-1}$ ,

respectively). The highest rates of gross energy intake resulted from consumption of relatively slow-moving pelagic solitary fish which had very short chase and handling times ( $35,470 \text{ J} \cdot \text{s}^{-1}$ ). Substantial variability within and between prey types groups was found but no significant differences between groups were present ( $F_{5, 89} = 1.630$ ,  $P = 0.1604$ ).

**Table 5:** Estimates of prey length, mass, associated gross energy gain and total energy expenditure in capture and handling per prey type group for Australian fur seal females in Bass Strait, south-eastern Australia, expressed as median [interquartile range].

Prey type	n	Length [cm]	Mass [g]	Gross energy gain [J]	Total energy expended [J]
Benthic - cephalopods	10	11 [10-13]	622 [402-852]	1,492,890 [1,012,310-2,046,480]	8,854 [7,390-11,380]
Benthic - elasmobranchs	8	33 [29-37]	208 [143-319]	287,400 [197,640-440,920]	11,361 [9,300-13,890]
Demersal - baitfish	10	23 [22-27]	131 [111-187]	863 [73,092-123,883]	5,013 [1,930-8,950]
Benthic - solitary fish	40	19 [16-21]	116 [57-151]	437,390 [268,410-584,000]	2,464 [1,430-3,640]
Pelagic - baitfish	20	21 [20 - 24]	101 [78-145]	670,610 [516,660-96,181]	10,570 [350-14,310]
Pelagic - solitary fish	20	16 [16-17]	87 [81-93]	304,050 [284,020-325,140]	878 [760-1,060]



**Fig. 7:** Boxplots comparing a) rates of gross energy intake, b) rate of total energy expenditure and c) prey profitability of Australian fur seal females between the different prey type groups in Bass Strait, south-eastern Australia. The bold solid line within each box represents the median, the bottom and top of each box represent the 25<sup>th</sup> and 75<sup>th</sup> percentiles and the whiskers represent the extreme values found within 1.5 times the length of the box.

Total energy expenditure during capture and handling estimated with the different approaches was comparable for pelagic baitfish (11,850 J for approach 1 and 10,570 J for approach 2) (Table 6). Estimates for other prey species were higher for the first approach. Energy expenditure calculated in both ways varied with prey type in a similar way (Pearson correlation,  $r = 0.81$ ,  $R^2 = 0.65$ ,  $P < 0.001$ ). The 2<sup>nd</sup> approach was used for calculations of prey profitability for simplicity.

**Table 6:** Estimates of total energy expenditure per prey type group for Australian fur seal females in Bass Strait, south-eastern Australia. Estimates were calculated using 2 different methods and are expressed as median [interquartile range].

Prey type	n	Total energy expenditure [J] approach 1	Total energy expenditure [J] approach 2
Benthic - cephalopods	10	34,320 [29,990 – 42,010]	8,854 [7,390 – 11,380]
Benthic - elasmobranchs	8	56,430 [50,330- 65,190]	11,361 [9,290 – 13,890]
Demersal - baitfish	10	12,380 [4,160 – 17,340]	5,013 [1,930 – 8,940]
Benthic - solitary fish	40	7,430 [4,420 – 7,430]	2,464 [1,430 – 3,640]
Pelagic - baitfish	20	11,850 [8,490 – 16,010]	10,570 [7,170 – 14,310]
Pelagic - solitary fish	20	2,830 [2,120 – 3,360]	878 [760 – 1,060]

Total energy expended in chasing, handling and consuming prey differed significantly between prey groups ( $F_{5, 46} = 20.375$ ,  $P < 0.001$ ). The lowest was for pelagic solitary fish because the number of flipper strokes used during the chase and handling period was negligible compared to other prey types (878 J) (see Table 5 for interquartile range). Similarly, the capture of benthic solitary fish required relatively little effort (2,464 J). Total energy expended to capture baitfish was higher in the pelagic zone due to the longer period and effort needed to chase baitfish midwater than in the demersal zone (respectively 10,570 J (pelagic) and 5,013 J (demersal)). Variability in energy expenditure was large for baitfish in both foraging zones.

Benthic cephalopods and elasmobranchs were almost always brought to the surface during the handling period to facilitate consumption, which required a considerable amount of energy

(respectively 8,854 J and 1,1361 J). Rates of energy expenditure ( $\text{J}\cdot\text{s}^{-1}$ ) (Fig. 7) on the other hand were much higher for pelagic baitfish than for any other prey type ( $300 \text{ J}\cdot\text{s}^{-1}$ ). Demersal baitfish were also captured using high rates of energy expenditure ( $150 \text{ J}\cdot\text{s}^{-1}$ ). Capture of baitfish required short bursts of activity whereas the capture and consumption of cephalopods and elasmobranchs involved much lower energy expended over greater durations (respectively  $90 \text{ J}\cdot\text{s}^{-1}$  and  $70 \text{ J}\cdot\text{s}^{-1}$ ). Solitary fish in both foraging zones showed intermediate rates of energy expenditure ( $130 \text{ J}\cdot\text{s}^{-1}$ , pelagic and  $100 \text{ J}\cdot\text{s}^{-1}$ , benthic). Observed differences between prey types were significant ( $F_{5, 94} = 123.73$ ,  $P < 0.001$ ).

A profitable prey species for Australian fur seals to capture and consume seemed to be demersal baitfish (e.g. jack mackerel) ( $30,830 \text{ J}\cdot\text{s}^{-1}$ ) and pelagic solitary fish (e.g. leatherjackets) ( $35,370 \text{ J}\cdot\text{s}^{-1}$ ) (Fig. 7). Consumption of pelagic baitfish (e.g. jack mackerel) and benthic solitary fish (e.g. leatherjackets and Scorpaeniformes) seemingly led to intermediate rates of net energy gain (respectively  $21,670 \text{ J}\cdot\text{s}^{-1}$  and  $19,460 \text{ J}\cdot\text{s}^{-1}$ ). Cephalopods and elasmobranchs seemed to be prey types of slightly lower profitability (respectively  $13,290 \text{ J}\cdot\text{s}^{-1}$  and  $1,790 \text{ J}\cdot\text{s}^{-1}$ ). However, although large variabilities of prey profitability within and between groups were found, differences between groups were not significant ( $F_{5, 89} = 1.638$ ,  $P = 0.1582$ ).

## Discussion

Understanding how animals exploit food resources is essential to interpreting their foraging decisions in environments which are heterogenous in both space and time (Schoener, 1971). The present study investigated the time and energetic costs associated with

chase and handling of different prey types by Australian fur seal females to assess their profitability and the factors influencing it. The results indicated that while net energy intake varied profoundly between different prey types, prey profitability (rate of net energy intake) varied little. Surprisingly, intrinsic factors related to seal morphology had no effect on prey capture successes nor on foraging activities associated with prey profitability.

### *Observed prey*

There are many inherent challenges to studying fine-scale foraging behaviour in cryptic foragers feeding at considerable depths. The use of animal-borne cameras overcomes this obstacle by allowing researchers to conduct prolonged observations, to record their foraging behaviour and to obtain data that facilitates identification of prey items. Because cameras can be deployed on multiple individuals and each of them can record for a substantial amount of time during different periods of the day, large datasets can be collected allowing researchers to investigate spatial and temporal factors influencing diet which can aid towards a more comprehensive understanding of the foraging ecology of a species. The use of animal-borne cameras has its caveats however, the cameras could create drag which in turn may impact swimming speed, capture success and prey choice of the studied animal (Wilson et al., 1986).

Australian fur seals are generalistic and opportunistic feeders (Gales & Pemberton, 1994), their foraging decisions result from proactive decisions to increase energetic and nutritional requirements during the prevailing conditions. In this study video data of 23 individuals was obtained, for a total of 63,5h. A total of 2027 prey events were observed which led to 2022 (99.7%) prey chases and 1263 (62.3%) prey captures. Based on the video footage breeding

Australian fur seal females foraged mainly on benthic solitary fish belonging to the Scorpaeniformes (gurnards and gurnard perches), on baitfish belonging to the Perciformes (jack mackerels) and on Tetradontiformes (leatherjackets) which were encountered both in the pelagic and benthic zone. Octopuses were also consumed every now and then. Other prey types captures contributed only little to the Australian fur seals' diet.

Studies based on scat and regurgitate analysis and DNA-based techniques (Deagle et al., 2009; Kirkwood et al., 2008) showed some differences in diet composition compared to the findings in this study. Contrary to other studies, benthic fishes belonging to the Scorpaeniformes were identified as the prime diet component. Redbait (*Emmelichthys nitidus*), Goulds squid (*Nototodarus gouldi*) and cods (Gadiformes) were previously identified as main diet components (Gales & Pemberton, 1994; Gales et al., 1993; Littnan et al., 2007) while they were only occasional prey types in this study. Kernaleguen et al. (2016) showed that video data provides essential diet information but is not representative of the general Australian fur seal diet, which explains the observed differences in diet composition compared to other studies.

#### *Chase and handling times*

Prey type influenced chase and handling times in Australian fur seals as capturing different prey types required divergent foraging strategies, reflecting differences in prey behaviour, size and morphology. Overall time spent per prey item was high for elasmobranchs and cephalopods, intermediate for baitfish and relatively low for solitary fish. Time spent chasing was high for baitfish in both foraging zones (pelagic and benthic) and considerably lower for all other prey types. Baitfish like jack mackerels are often encountered



in baitballs in pelagic waters (Keenleyside, 1955). The schooling behaviour is known as an antipredator strategy, each individual benefits from a reduction in predation risk through mechanisms like dilution effects (Turner & Pitcher, 1986) where the chance of individual capture decreases as school size increases. Associated confusion effects (Krakauer, 1995) cause predators to experience difficulty targeting an individual prey because the large number of moving targets creates a sensory overload of the predator's visual channel. This is reflected in the present study with chase times for pelagic schooling baitfish being high and capture successes being low.

Furthermore, baitfish show higher manoeuvrability compared to Australian fur seals which causes increased chase times, impedes easy prey capture and consequently decreases capture success. Manoeuvrability of an animal is commonly expressed as the turning rate (measured in degrees per second) and the radius of curvature of its path (Combes et al., 2012). Studies have shown that turning rate tends to decline and turning radius generally increases with body size for fish and marine mammals (Blake & Chan, 2006). Consequently, small baitfish which require extensive escape patterns are often well adapted for high maneuverability. Moreover, highly maneuverable baitfish have more opportunities to escape their predators in a three-dimensional pelagic environment compared to a two-dimensional benthic environment.

Handling of prey by Australian fur seals took relatively long for elasmobranch and cephalopod prey, which both showed very high capture successes. Handling times were intermediate for benthic solitary fish prey and almost negligible for all other prey types. Certain prey types were more difficult to handle than others types, due to prey size or prey resistance. For example, unlike baitfish, captured octopuses and rays could not be consumed at depth and were brought to the surface for processing. Video footage showed that seals

violently shook these prey to break them up into smaller pieces for consumption. However, not all pieces of these prey were consumed, leading to a reduced energy gain.

Correspondingly, when prey become too large the predator will run into processing constraints causing handling time to increase considerably, which renders the prey less profitable (Sinervo, 1997). Benthic solitary fish were also frequently handled at the surface because of their size (e.g. certain leatherjackets) or to get rid of their inedible spines and pectoral fins (e.g. Scorpaeniformes). Gurnard and gurnard perches are no easy consumable prey types, separation of the heads from the body was observed during many prey captures. This likely caused the loss of otoliths which may explain why earlier scat studies, that are based on hard materials, showed an underrepresentation of these prey types.

Morphological traits which facilitate foraging efficiency will increase the fitness of an animal. The effects of the morphometric measurements mass, flipper length, flipper length/standard length, axis length and axillary girth on chase time, handling time and capture success of Australian fur seal females were assessed in this study. Turning rate, a measure of manoeuvrability, is dependent on an marine mammal's body mass (Fish et al., 2003). Furthermore bigger females, which can be measured in term of axillary girth, are expected to be better foragers as they can dive aerobically for longer (Kooyman, 2012). Additionally flipper length/standard length as well as flipper length and axis length are known to affect maneuverability in marine mammals too (Arnould et al., 2015; Segre et al., 2017). The fore-flippers of marine mammals act as biological hydroplanes (Fish et al., 2011) and provide hydrodynamic lift for manoeuvring (Fish et al., 2008). However, although many candidate models included these morphometric measurements, none of the measurements were found to influence chase time, handling time and capture success. The absence of effects of morphological features may be the result of a too small sample size.

### *Prey energy gain and profitability*

Estimates of GE gain were shown to be sensitive to size and energy content of the prey types, as was found in previous studies (e.g. Wanzenböck (1995)). Although only lengths of a few prey for certain prey type groups could be measured, several size classes were covered, which provided a reasonable foundation to draw initial conclusions from.

The video data in this study showed that individuals selected prey types with both high and low calorific values. Baitfish and benthic solitary fish species belonging to the Scorpaeniformes had much higher energy densities than cephalopods, elasmobranchs and pelagic solitary fish like leatherjackets, due to their extensive size however, gross energy gain was highest when cephalopod prey were consumed. Although gross energy gain for pelagic solitary fish was lower due to their small size and relatively low energy content, rate of gross energy gain was considerably higher than for other prey species due to the short chase and handling times associated with this prey type. This allowed fur seals to capture more prey in a short period of time, rendering this prey type much more profitable than expected. Although consumption of cephalopods led to an extensive gross energy gain, the estimated rate of energy gain was markedly lower compared to most other prey types because of processing constraints related to their large size, which made them energetically less profitable for fur seals. Baitfish provided vast energy gains and had high rates of energy gain, their low capture success however renders them less profitable than expected.

Capture of pelagic solitary fish required the least effort as total time spent on it was considerably lower than for any other prey type, rate of energy expenditure was consequently low too. Baitfish are fast-swimming and very manoeuvrable fish, the observed seals had to make big efforts in order to capture them. Consequently relatively large amounts of energy

were expended when foraging upon baitfish, rates of energy expenditure were the highest of all prey types. Energy expended during chase and handling of cephalopod and elasmobranch prey approximated energy expended on pelagic baitfish, rates were however much lower as the total time spent on the former was much higher and because the intensity of chasing pelagic baitfish in terms of fore-flipper stroke frequency was much higher than the intensity of handling cephalopods and elasmobranchs.

This study shows that foraging decisions of Australian fur seal females includes trade-off in terms of energy gain and total time spent per prey. Our video data showed that individuals foraged upon small prey of low energy content that had high capture successes and could quickly be captured and handled (pelagic solitary fish, e.g. leatherjackets), upon small prey of high energy content that had low capture successes and required extensive effort to be caught but were easily handled (baitfish, e.g. jack mackerel), upon medium-sized prey of intermediate energy content with intermediate capture successes, chase times and handling times (benthic solitary fish, e.g. scorpaeniformes) and large prey of low energy content that had very high capture successes, negligible chase times but required high handling efforts (e.g. benthic cephalopods).

Although prey types showed differences in chase and handling times, capture success, energy gain and energy expenditure, no differences in profitability could be observed in the present study.

### *Abundance, availability and distribution patterns of prey*

Other factors besides prey profitability in terms of rates of net energy gain affect an animal's foraging decisions. Long-term average rate of net energy intake will not necessarily be maximized when the most profitable prey in the present study is selected because search time between prey encounters needs to be taken into account too (Engen & Stenseth, 1984; Stephens et al., 1986) i.e. the prey encounter rate. Availability (e.g. due to seasonal variation, Hume et al. (2004)), abundance and distribution of a prey species affects search time which in turn affects profitability of a prey. Benthic prey types are usually more evenly distributed in the marine environment than patchily distributed schooling fish in pelagic waters, this was also observed in the results as many seal individuals encountered benthic prey while only few encountered baitballs of pelagic prey. Although capture successes were generally low and efforts were high, high rates of prey capture were present which made this prey type profitable when it was not actively searched for.

### *Consequences of anthropogenic ecosystem changes*

Changes in wind and wind-driven upwelling systems and warming of waters as a consequence of human-induced climate change affect pinnipeds like the Australian fur seal in various ways. Increases in wind activity may benefit Australian fur seals through fish prey being brought to surface waters by upwelling currents and flushed into Bass Strait (Kirkwood et al., 2008). Intensification of the oligotrophic, warm East Australian Current has made Bass Strait one of the fastest warming regions in the southern hemisphere (Holbrook & Bindoff,

1997; Ridgway, 2007) and has caused shifts in prey distribution and abundance of Australian fur seals (e.g. Last et al. (2011), Ramos et al. (2015)).

Patchily distributed schooling jack mackerel and redbait are commonly foraged upon by Australian fur seals, annual variability in their schooling behaviour in pelagic waters is known to be related to patterns of sea temperature and ENSO cycles along coastal Tasmania (Young et al., 1993). Primary production is reduced as a result of the incursions of warm, oligotrophic water (Harris et al., 1991) which lead to a cascade of trophic effects throughout the food chain as they reduce the abundance of key planktonic species like krill (*Nyctiphanes australis*), a primary prey source of baitfish like jack mackerel and redbait (Young et al., 1993).

McLeod et al. (2012) predicted a replacement of jack mackerel prey with redbait. Both fish species forage on krill, but due to its prey preferences redbait is expected to have an advantage over jack mackerel as the former are known to forage upon small, warm-water copepods.

Benthic fish are expected to shift their ranges south with warming waters (Hobday et al., 2006), which means new prey species from more northern latitudes may settle in Bass Strait and be foraged upon by Australian fur seals in the future. Populations of benthic fish species that are vulnerable to climate change and have ranges bounded to the south may show declines in size (Hobday et al., 2006), which may in turn change their abundance and availability as a prey species.

The size of cephalopods like the arrow squid (*Nototodarus gouldi*) may be influenced by sea temperature as well, Jackson et al. (2003) showed that squid generally grown faster and to a greater size when in warmer waters compared to being cooler waters. Moreover, a new prey

cephalopod prey species has emerged for Australian fur seals. Studies have shown a poleward range shift of the common Sydney octopus (*Octopus tetricus*) towards the coastal waters of south-eastern Australia, the shift is thought to be associated with the intensification of the East Australian Current (Ramos et al., 2015).

Jack mackerel, red bait and arrow squid, important components of the Australian fur seal's diet, are commercially targeted species. Climate change impacts may potentially combine with fishery impacts and intensify the depletion of prey species stocks, however temporal analysis of at-sea movements of Australian fur seal females showed no substantial overlap of their foraging grounds and areas targeted by commercial fisheries (Arnould & Kirkwood, 2007).

## **Conclusion**

In summary, some prey were harder to capture and hence had larger chase times but were easy to consume, while others were easy to capture but required a considerable amount of handling. This led to differences in total energy expenditure, there was also a large variety in gross energy gain due to the prey's size and nutritional value. However, prey profitability did not seem to differ between prey types.

The low marine productivity in Bass Strait and its effect on prey availability may have an influence on the foraging mode of the Australian fur seal (Arnould & Costa, 2006). Jack mackerel is a highly nutritious prey type compared to cephalopods, however, as Australian fur seals are predominantly benthic foragers, their abundance is assumed to be low. Because of their low abundance and patchily distribution in Bass Strait, search time of pelagic baitfish is too high and therefore foraging upon benthic prey is more advantageous. The data in this

study reflects that profitability of benthic prey outweighs the cost of searching for more nutritious pelagic prey.

Anthropogenic induced effects will seemingly continue to alter ecosystem structure, prey abundance, availability and distribution and population trends of Australian fur seals at Bass Strait (Kirkwood et al., 2008). Changes in the marine environment could influence cephalopod abundance positively and allow new benthic fish species to settle in Bass Strait, which is beneficial for benthic foragers such as the Australian fur seal. However, baitfish may also become a more reliable, stable prey type when their abundance in Bass Strait increases, which might facilitate the switch towards a more epipelagic foraging mode like the conspecific cape fur seal (*Arctocephalus pusillus pusillus*) along the southwest coast of South Africa.



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