Animal Behaviour 222 (2025) 123108

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav

Animal-borne video highlights diverse prey capture tactics and habitat use in the Australian sea lion

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ARTICLE INFO

Article history:
Received 11 June 2024
Initial acceptance 21 August 2024
Final acceptance 20 November 2024
Available online 27 February 2025
MS. number: 24-00352R

Keywords:
animal-borne video
Australian sea lion
benthic habitats
biologging
endangered species
foraging
Neophoca cinerea
pinniped
predation
specialization

Understanding the foraging ecology of predators is critical to identifying the resources and habitats that maintain their populations and is essential for their conservation and management. For marine predators that spend extended periods at sea and underwater, the use of animal-borne video provides a novel method of observing individuals in their environment and the foraging behaviours they employ. The endemic Australian sea lion, *Neophoca cinerea,* is listed as endangered, with its populations declining by more than 60% over the last 40 years. Due to the highly subdivided genetic structure of Australian sea lion populations, an intimate understanding of their foraging behaviour, throughout their distribution, is needed to support targeted management at the breeding site level. Here, we use animal-borne video collected from 10 adult female Australian sea lions from five colonies in South Australia to identify the prey capture tactics they use across different benthic habitats. We identified a variety of prey capture tactics (probing, chasing, pelagic ambushing of schooling fish, flipping rocks/substrate and sit-and-wait predation), exploiting a range of benthic habitats, including seagrass meadows, bare sand plains and macroalgae reefs, while hunting diverse prey, such as benthic/epibenthic fishes, cephalopods and elasmobranchs. The prey capture tactics most frequently observed were probing and chasing, which were used by all individuals, whereas flipping rocks, sit-and-wait predation and pelagic ambush were less frequent. Using specialist prey capture tactics, such as sit-and-wait predation, may increase the capacity of sea lions to exploit a greater diversity of prey and benthic habitats, which could increase their overall success and fitness. This study underscores the significance of animal-borne video as a crucial tool for identifying and mapping the critical habitats and resources essential for Australian sea lions.

Understanding the foraging ecology of species is central to determining critical habitats and resources for their populations (Bailey et al., 2012; Raine et al., 2021; Schofield et al., 2013). For predators in the marine environment that dive and spend extended periods of time both at sea and underwater, improving our understanding of key foraging behaviours, habitats and prey is challenging. Since the 1960s, data collected from animal-borne instruments (or biologgers) have been fundamental for understanding the foraging behaviours of marine predators (Hart & Hyrenbach, 2009; Hooker et al., 2007; Kooyman, 1965), considering the challenges involved in studying their ecology. Instruments, such as satellite transmitters, time-depth recorders, accelerometers and stomach-temperature and heart rate monitors, have elucidated critical information on movement (Hart & Hyrenbach, 2009; Lowther et al., 2011, 2013), diving behaviours (Bailleul et al., 2010; Kooyman, 1965; Mitani et al., 2010) and physiology (Gallon et al., 2013; Horsburgh et al., 2008; Ponganis et al., 2000). Collecting detailed information on the foraging behaviour of marine predators allows us to better understand broader ecological relationships and important factors that may impact their fitness.

In the past 30 years, technological advancements have led to an increased use of animal-borne cameras, offering deeper insights into the foraging behaviours and habitats of marine predators by providing direct visual observations of animals in their

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https://doi.org/10.1016/j.anbehav.2025.123108

environment. Originally developed in the late 1980s (Marshall, 1990, 1998), animal-borne cameras have expanded our understanding of the foraging behaviours of a wide range of both marine and terrestrial species. Examples include studies into the behaviour of sea turtles (Fukuoka et al., 2016; Heaslip et al., 2012; Hounslow et al., 2021), manta rays (Pelletier et al., 2023; Stewart et al., 2019), eastern grey kangaroos, *Macropus giganteus,* (Herbert et al., 2020) and Hawaiian monk seals, *Monachus schauinslandi* (Parrish et al., 2000, 2002).

The insights gained from animal-borne cameras have provided useful information for improving the management of populations and species. Some notable examples include deployments that revealed the impacts of domestic cats, *Felis catus*, on native mammals, birds, amphibians and reptiles (Loyd et al., 2013; McGregor et al., 2015) and northern gannet, *Morus bassanus* and Cape gannet, *Morus capensis*, interactions with trawl fishery vessels (Tremblay et al., 2014; Votier et al., 2013). Animal-borne cameras have captured the use of human seafloor infrastructure (pipelines, cables, wells and shipwrecks) as foraging habitat for Australian fur seals, *Arctocephalus pusillus doriferus* (Arnould et al., 2015) and marine pollution effects on black-footed albatrosses, *Phoebastria nigripes*, loggerhead turtles, *Caretta caretta* and green sea turtles, *Chelonia mydas* (Fukuoka et al., 2016; Nishizawa et al., 2021). Additionally, this technology has been extended to identify key habitats and foraging behaviours for endangered species. For example, such studies on Hawaiian monk seals, *M. schauinslandi* (Parrish et al., 2000, 2002) highlighted shifts in their foraging and diving behaviour across different benthic habitats (e.g. sand, coral beds and talus), which helped identify important foraging areas for the species.

In this study, we use animal-borne video to highlight the diversity of prey capture tactics employed and their use across different benthic habitats by 10 adult female Australian sea lions, *Neophoca cinerea*, from five colonies in South Australia. The Australian sea lion breeds at 80 sites across South and Western Australia, with South Australia accounting for 82% of the total population and Western Australia accounting for 18% (Goldsworthy et al., 2021). Diving studies have revealed that Australian sea lions are benthic predators that maximize bottom time when diving at sea (Costa & Gales, 2003; Fowler et al., 2006, 2007). Recent animal-borne video data have also highlighted that Australian sea lions forage across a diversity of benthic habitats (including sponge gardens, bare sand plains and macroalgae reefs; Angelakis et al., 2024). Dietary analyses indicate that Australian sea lions have a broad diet (more than 200 species), mostly consuming benthic fish, cephalopods, crustaceans and elasmobranchs (Berry et al., 2017; Goldsworthy et al., 2019; McIntosh et al., 2006; Peters et al., 2015). Previous studies have also identified marked individual, intracolony and intercolony foraging specialization in Australian sea lions, with adult females maintaining long-term fidelity to foraging locations (e.g. inshore and offshore areas; Lowther et al., 2011; Lowther & Goldsworthy, 2011a). Additionally, animal-borne video has provided evidence that Australian sea lion mothers use social learning to pass on foraging skills to pups, which is another potential factor driving their foraging specialization and long-term philopatry (Angelakis, unpublished data). However, little is known about the tactics Australian sea lions use to capture prey and how they use different benthic habitats throughout their distribution in southern Australia. Australian sea lions are an endangered species (International Union for Conservation of Nature Red List of Threatened Species and the Australian *Environmental Protection and Biodiversity Conservation Act* of 1999; Goldsworthy, 2015), whose populations have declined by more than 60% over the last 40 years (Goldsworthy et al., 2021). As adult female Australian sea lions show long-term fidelity to foraging locations, the genetic structure of their populations is highly subdivided, with half of the sampled breeding sites having unique mitochondrial DNA (mtDNA) lineages (Ahonen et al., 2016; Campbell et al., 2008; Lowther et al., 2011, 2012). As a result, effective conservation and management of the species must be focused on individual breeding sites.

Our study uses animal-borne video to gain insight into the foraging behaviours, benthic habitats and prey capture tactics used by adult female Australian sea lions. Specifically, we seek to (1) identify the diversity of prey capture tactics employed, (2) determine the variety of benthic habitats used during foraging trips, and (3) investigate potential relationships between the use of different prey capture tactics across different benthic habitats. By addressing these objectives, we aimed to enhance our understanding of the foraging ecology of Australian sea lions and contribute valuable insight into their conservation and management.

METHODS

Study Sites and Deployment of Animal-Borne Cameras

Data were collected from 10 adult female Australian sea lions from five colonies in South Australia (Fig. 1). Sea lions were selected from Lilliput Island (LI; 32.434°S, 133.692°E; $N = 3$) in the Nuyts Archipelago, Olive Island (OI; 32.721°S, 133.968°E; $N = 2$) on the western Eyre Peninsula, Lewis Island (LW; 34.955°S, 136.031°E; $N = 2$) and Dangerous Reef (DR; 34.815°S, 136.212°E; $N = 2$) in the southern Spencer Gulf and Seal Bay (SB; 35.994°S, 137.317°E; $N = 1$) on Kangaroo Island. Data were collected over four years, in September 2009 (LW), February 2010 (DR), March 2012 (LI), February 2022 (SB) and December 2022 (OI). Together, these colonies account for ~30% of species-wide pup production (Goldsworthy et al., 2021).

Sea lions were initially sedated with Zoletil (~1.3 mg/kg, Virbac, Australia), administered intramuscularly using a syringe dart (Paxarms, New Zealand, 3.0 ml syringe body with a 14 gauge 25 mm barbed needle), delivered by a dart gun (MK24c Projector, Paxarms, New Zealand), following the methods of McKenzie et al. (2013). After initial sedation (~10–15 min), sea lions could be approached, allowing the application of an anaesthetic mask over the muzzle, administering isoflurane (5% induction, 2.0%–3.0% maintenance) for ~20 min while cameras were attached. Isoflurane was administered through a purpose-built closed-loop gas anaesthetic machine using a Cyprane Tec III vapouriser (The Stinger Backpack anaesthetic machine, Advanced Anaesthesia Specialists, Australia).

Sea lions were instrumented with either National Geographic Crittercams (310 × 100 mm, 750 g), Zoolog Solutions cameras (116 × 60 × 43 mm, 312 g) or Customized Animal Tracking Solutions (CATS) cameras (96 × 35 × 40 mm, 400 g). Cameras were preadhered to neoprene patches that were subsequently glued to the pelage (fur) on the dorsal midline, at the base of the scapula, using a two-part quick-setting epoxy (RS Components Quick Set Epoxy or Selleys Araldite 5 Minute Epoxy Adhesive). Sea lions were recaptured after a single foraging trip (~2–6 days). The cameras were removed by cutting them from their neoprene patches to avoid damage to the pelage (the neoprene patches were shed during the subsequent moult).

Collection and Analysis of Animal-Borne Video

Animal-borne cameras collected high-definition video (forward-facing) when animals were at sea, triggered by depth or saltwater sensors, recording for either 1 h every 2 h (Dangerous Reef and Lewis Island), 1 h every 3 h (Lilliput Island) or continuously (Seal Bay and Olive Island) during daylight hours (between 0700 and 1800 hours local time).

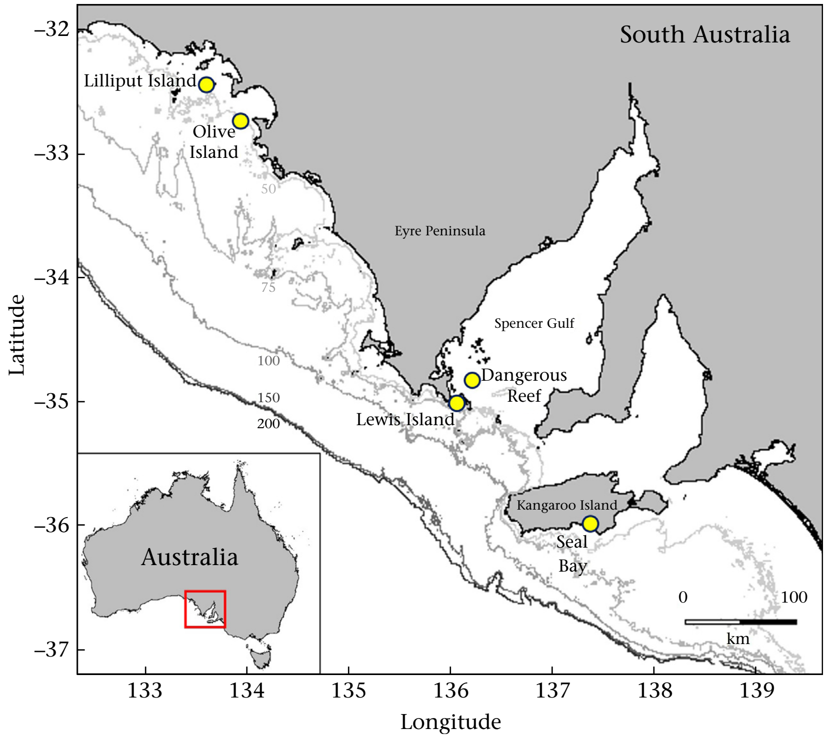

Figure 1. Locations of colonies for deployment of animal-borne cameras on 10 adult female Australian sea lions in South Australia (yellow circles), at (from west to east) Lilliput Island (32.434°S, 133.692°E) in the Nuyts Archipelago, Olive Island (32.721°S, 133.968°E) on the western Eyre Peninsula, Lewis Island (34.955°S, 136.031°E) and Dangerous Reef (34.815°S, 136.212°E) in the southern Spencer Gulf and Seal Bay (35.994°S, 137.317°E) on Kangaroo Island. Isobaths represent depth contours at 50, 75, 100, 150 and 200 m (light to dark grey).

Foraging and benthic habitat analyses of animal-borne video were performed using the open-source Behavioral Observation Research Interactive Software (BORIS, version 7.12.2). The duration of all predation events (captures and attempts) and bottom time spent in benthic habitats were recorded. Predation events were defined as commencing when an individual began pursuit of a prey item and ending either upon successful capture of the prey or when the individual ceased its effort, indicating an unsuccessful pursuit. Bottom time was defined as the observed time between an animal reaching and leaving the benthos. All animal-borne video analyses were performed manually by a single observer.

An ethogram (Table 1) and benthic habitat key (Fig. 2) were created in BORIS to classify predation events/prey capture tactics and benthic habitats. All predation events were recorded and prey species were identified to the lowest possible taxonomic level (as described in Gomon et al., 2008; Reid, 2016). Benthic habitats were classified following the methods of Angelakis et al. (2024), using the Collaborative and Annotation Tools for Analysis of Marine Imagery and Video (CATAMI) classification scheme, which provides a national (Australian) framework for classifying marine biota and substrata (Althaus et al., 2013).

Identifying the Use of Different Tactics and Benthic Habitats

To assess the use of different prey capture tactics and benthic habitats, we performed a permutational multivariate analysis of variance (PERMANOVA) using the vegan package (version 2.6−4) in *R* (version 4.3.1; Dixon, 2003; permutations = 999). First, we calculated (1) the percentage of time from all predation events allocated to different prey capture tactics and (2) the percentage of bottom time from all dives allocated to different benthic habitats by each sea lion. These percentages were used to calculate two dissimilarity matrices (using the Bray−Curtis distance), one to compare the use of prey capture tactics by each sea lion and one to compare the use of different benthic habitats by each sea lion. These two separate matrices were then hierarchically clustered to identify groups of sea lions, which shared similar use of prey capture tactics (distance threshold = 0.5) and benthic habitats (distance threshold = 0.5). A PERMANOVA was then used to determine whether these clusters differed significantly from each other. Similarly, a PERMANOVA was used to assess the relationship between the use of prey capture tactics in different benthic habitats. This PERMANOVA was performed on a separate dissimilarity

Table 1
Ethogram characterizing the prey capture tactics used by Australian sea lions

Prey capture tactic	Description of behaviour
Chasing	Quick, prolonged pursuit of prey above benthos
Flipping	Flipping of benthic rocks and/or substrate to capture prey
Pelagic ambush	Brief pause in swimming effort to hide from prey and then quick pursuit
Probing	Close contact of the muzzle with benthos to pin prey
Sit-and-wait	Prolonged stationary position on benthos, waiting for prey to appear

Predation events were identified from animal-borne video from 10 adult females from Dangerous Reef, Lewis Island, Lilliput Island, Olive Island and Seal Bay in South Australia. Predation events were either marked as successful or unsuccessful.

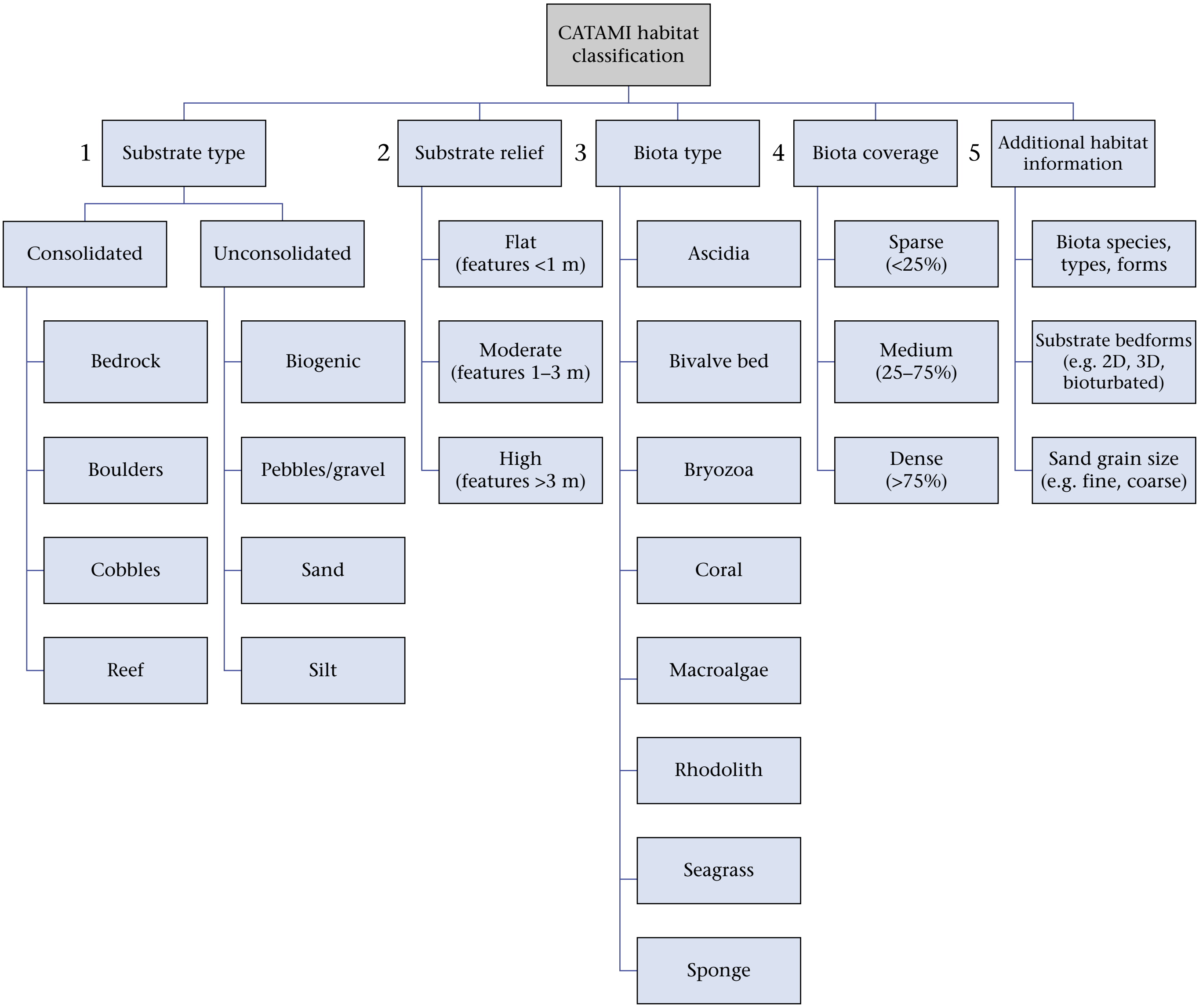

Figure 2. Habitat key used to classify benthic habitats identified from animal-borne video from 10 adult female Australian sea lions. Numbers highlight the order of stages for habitat classification. Benthic habitats were classified following the CATAMI (Collaborative and Automated Tools for Analysis of Marine Imagery) scheme.

matrix (using the Bray–Curtis distance), calculated from the percentage of time allocated to different prey capture tactics across different benthic habitats.

Ethical Note

Research for this manuscript was reviewed and approved by The University of Adelaide Animal Ethics Committee, PIRSA Animal Ethics Committee and the Department for Environment and Water (DEW; Permit/Licence to Undertake Scientific Research and Marine Parks Permit to Undertake Scientific Research). To minimize our impact on the sea lions sampled and maximize the benefits derived from the data we collected, there were several ethical considerations when designing and conducting our research. First, we chose sea lions from a range of colonies across their South Australian distribution to maximize the potential diversity of prey capture tactics, benthic habitats and foraging behaviours we captured. Additionally, we focused on adult females, as they take sole care of raising pups (Lowther & Goldsworthy, 2011b; McIntosh & Pitcher, 2021) and are thus vital for population viability. Where available, we opted for light, small, low-profile cameras that were <1% of the animal's weight to reduce drag impacts. Initial sedation with Zoletil also minimized sea lion disturbances associated with capture and anaesthetic procedures. During anaesthesia, vital signs (e.g. respiratory rate, gum refill, palpebral reflex) of sea lions were continuously monitored; where available, a pulse oximeter was clipped to the tongue to monitor heart rate and blood oxygen levels. Furthermore, adhering the cameras to neoprene patches allowed easier and less invasive recovery upon recapture.

RESULTS

Diversity of Prey Capture Tactics

From the 10 adult female Australian sea lions in this study, a total of 56 h and 36 mins of animal-borne video was available for analysis. A summary of the data available for each sea lion is provided (Table 2).

Animal-borne video highlighted that for the 10 adult female Australian sea lions, five different tactics were employed to capture

Table 2
Summary of animal-borne video data

Animal ID	Video duration (hh:mm)	Date of deployment	Camera type
DR1	07:27	February 2010	Crittercam
DR2	07:41	February 2010	Crittercam
LI1	02:00	March 2012	Crittercam
LI2	00:52	March 2012	Crittercam
LI3	03:59	March 2012	Crittercam
LW1	05:24	September 2009	Crittercam
LW2	04:06	September 2009	Crittercam
OI1	12:32	December 2022	CATS
OI2	11:42	December 2022	CATS
SB1	00:53	February 2022	Zoolog Solutions

Animal-borne video data were collected from 10 adult female Australian sea lions from Dangerous Reef (DR1, DR2), Lilliput Island (LI1, LI2, LI3), Lewis Island (LW1, LW2), Olive Island (OI1, OI2) and Seal Bay (SB1) in South Australia.

prey (Fig. 3 and Fig. A1), with individual sea lions using two or three different tactics (Fig. 3a). Comparing the use of prey capture tactics, hierarchical clustering resulted in three significantly distinct groups (PERMANOVA: $F_{427} = 33.533$, $P = 0.013$) for sea lions that mainly used probing (DR1, DR2, LI1, LI2, SB1, OI2), chasing (OI1, LW2, LI3) and one individual (LW1), which mainly used a combination of sit-and-wait predation and probing tactics (Fig. 4a). Prey capture rates varied between sea lions, from 0.4 successful captures/h to 10.9 successful captures/h (Fig. 3a).

Use of Tactics for Different Habitats and Prey

Differences in the use of prey capture tactics in different benthic habitats were apparent (PERMANOVA, $F_{427} = 11.092$, $P = 0.002$). For macroalgae and seagrass meadows and invertebrate reefs, prey were primarily pursued by probing, while for bare sand and sponge/sand habitats, prey were mainly pursued by chasing (Fig. 3b). Some tactics were only recorded in a particular benthic habitat (Fig. 3b). Sit-and-wait predation and pelagic ambushes, which were used by single individuals (Fig. 3a), were observed exclusively on macroalgae reefs (Fig. 3b).

The use of prey capture tactics also varied by prey taxa. Benthic and epibenthic fishes were mainly pursued by chasing (61% of all predation events) and probing tactics (34%); sea lions also used pelagic ambush (2%), sit-and-wait (2%) and flipping tactics (1%) to pursue fish. Cephalopods were mainly pursued by probing (89%); the rest were pursued by chasing (9%) and flipping tactics (2%), and elasmobranchs were pursued by a combination of probing (51%) and chasing tactics (49%).

Use of Benthic Habitats

Seven benthic habitats were identified (Fig. 5): macroalgae reef, macroalgae/seagrass meadow, macroalgae meadow, seagrass meadow, bare sand, sponge/sand and invertebrate reef habitats (Fig. 5 and Fig. A2). Comparing the use of benthic habitats, hierarchical clustering resulted in five significantly distinct groups (PERMANOVA, $F_{1631} = 142.49$, $P = 0.001$), for sea lions that mainly used bare sand habitats (OI1), macroalgae reefs (LI2, LI3, LW1, OI2), invertebrate reefs (SB1), macroalgae and seagrass meadows (DR1, DR2) and macroalgae meadows (LI1, LW2; Fig. 4b). Of the reef habitats used by sea lions, bottom time was mainly on moderate relief reefs (features 1–3 m high) and high relief reefs (features > 3 m high), 56% and 34% of total bottom time, respectively. Flat relief reefs (features < 1 m high) were used for 10% of total bottom time.

Prey Selection

Animal-borne video identified 41 prey taxa for Australian sea lions (Table 3). A total of 428 predation events were observed, 60% (255) of which resulted in prey captures. Prey taxa could be identified for 78% (200) of the 255 predation events and 18% (32) of the

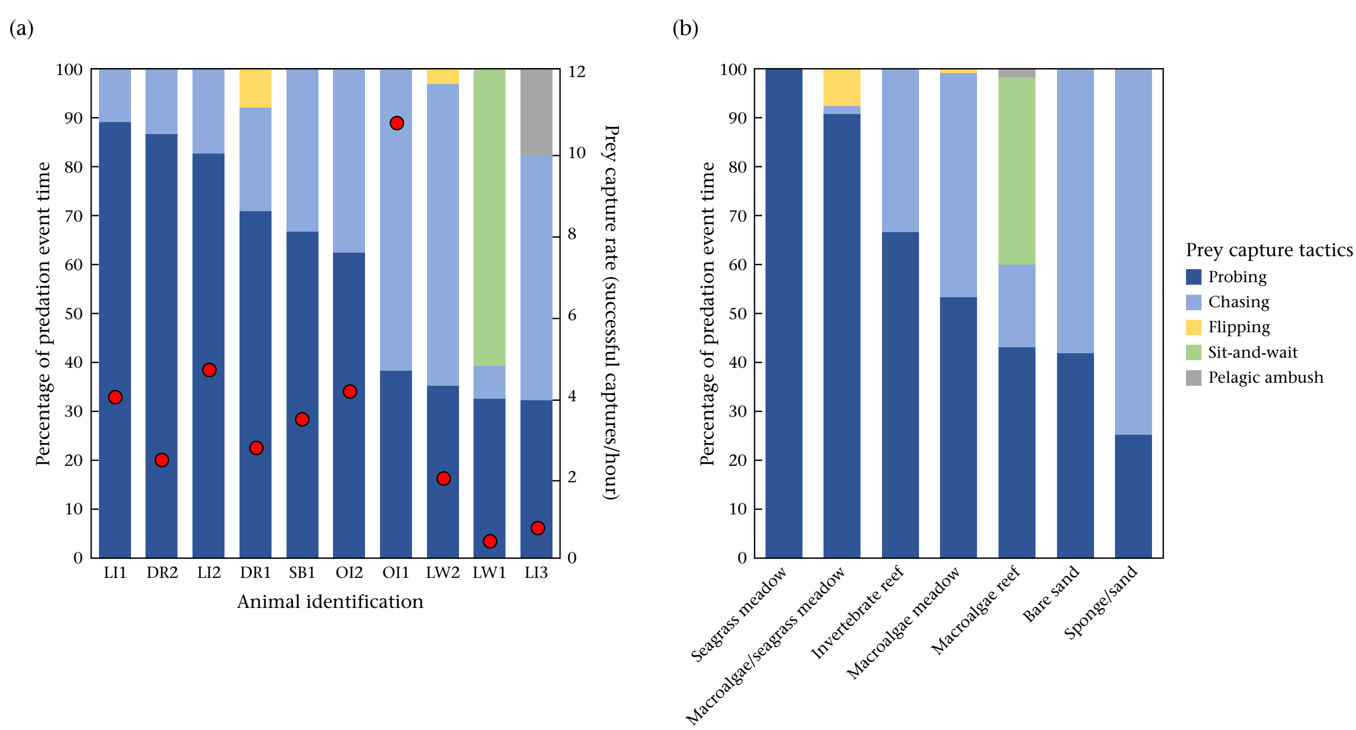

Figure 3. Prey capture tactics were identified from animal-borne video, from (a) 10 adult female Australian sea lions from Dangerous Reef (DR1, DR2), Lilliput Island (LI1, LI2, LI3), Lewis Island (LW1, LW2), Olive Island (OI1, OI2) and Seal Bay (SB1) in South Australia and (b) across different benthic habitats. Stacked columns represent the percentage of total predation event time allocated to different prey capture tactics. Prey capture rates (number of successful captures per hour) for each sea lion (a) are indicated (red circles).

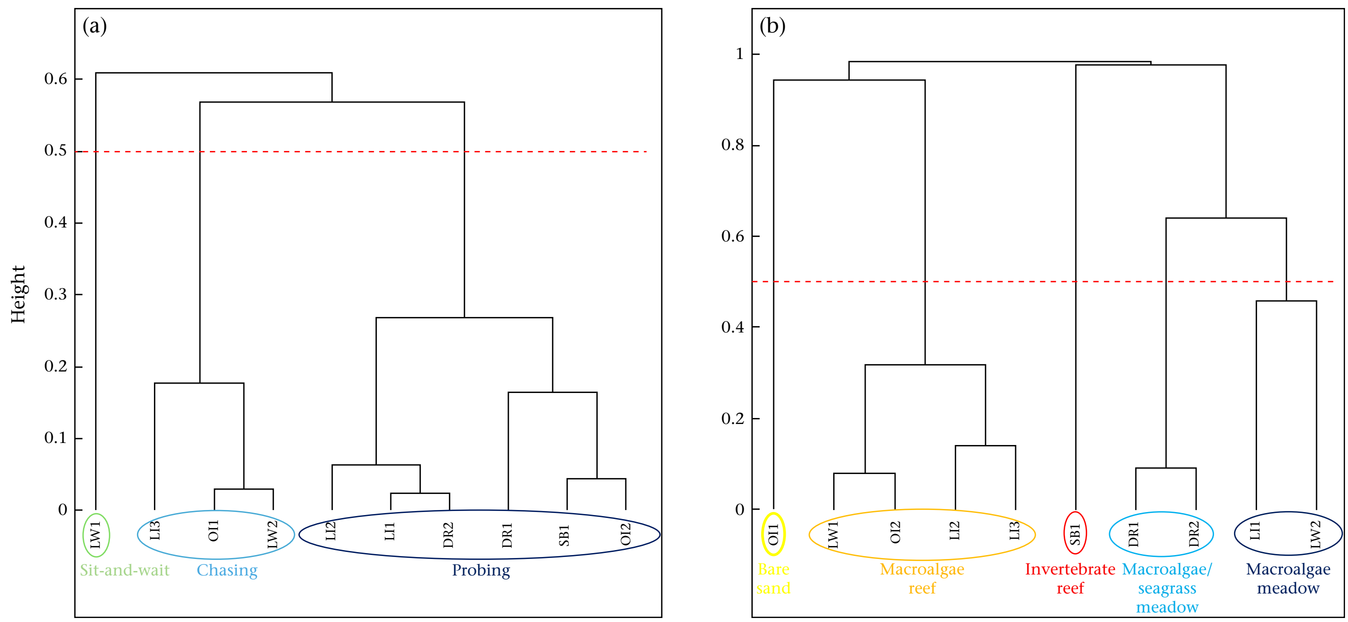

Figure 4. Dendrograms of hierarchical clustering comparing the use of (a) prey capture tactics and (b) benthic habitats by 10 adult female Australian sea lions from Dangerous Reef (DR1, DR2), Lilliput Island (LI1, LI2, LI3), Lewis Island (LW1, LW2), Olive Island (OI1, OI2) and Seal Bay (SB1) in South Australia. Dendrograms represent the allocation of predation event time to (a) different prey capture tactics and (b) bottom time across different benthic habitats. Distance thresholds (0.5) used to cluster groups are indicated (red dashed line).

173 unsuccessful events. For 3 of the 10 sea lions (LI1, LW1, SB1), fish represented all their identified prey. Other sea lions (LI2, LI3) also mainly predated on different species of fish. Several sea lions (DR1, OI1, OI2) predated on a combination of cephalopods, fish and elasmobranchs, while one (DR2) predated mostly on cephalopods, and another (LW2) predated both cephalopods and fish (Table 3). Prey were consumed at the benthos (68% of captures) or taken to the surface to process (32% of captures; Fig. A3).

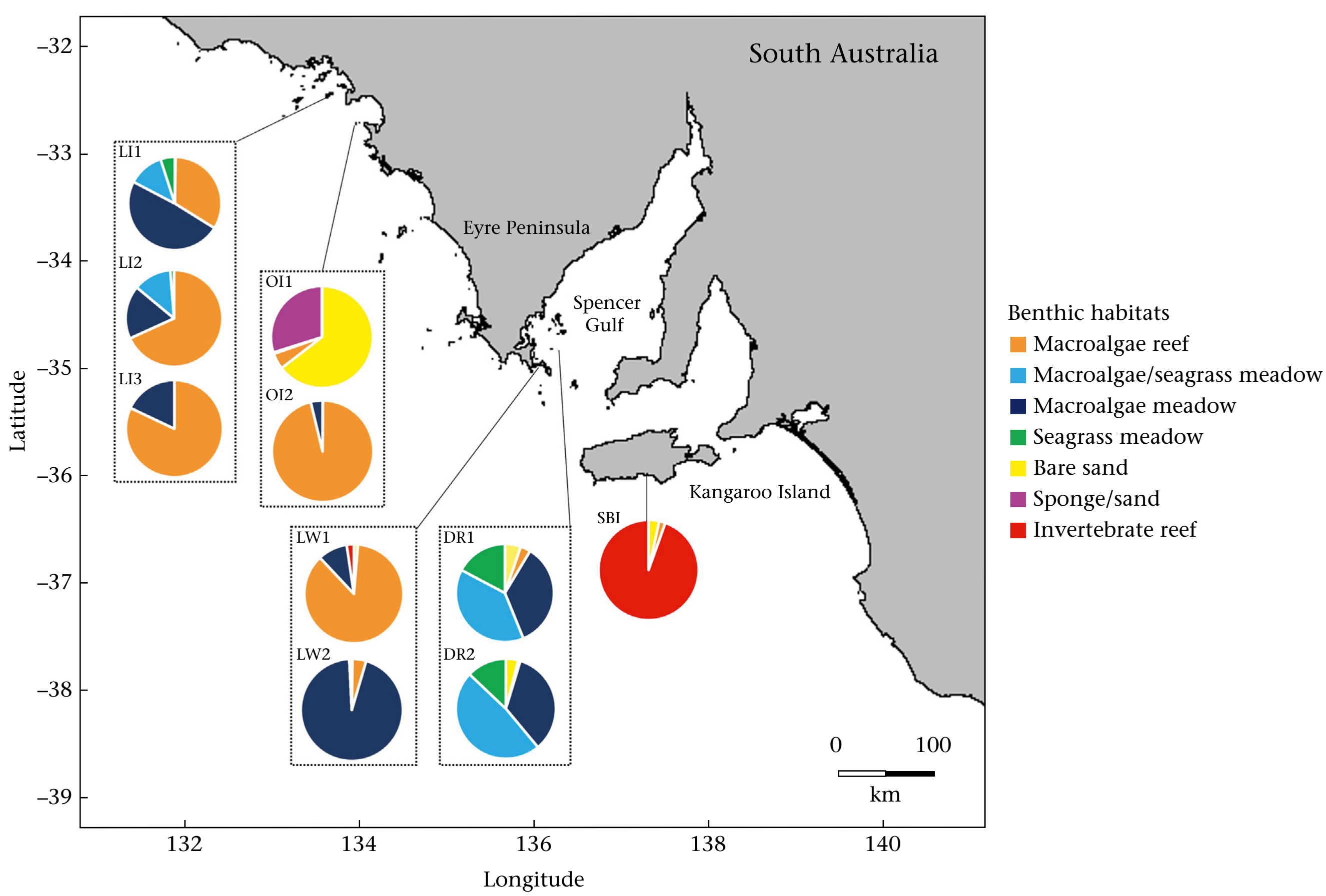

Figure 5. Benthic habitats identified from animal-borne video from 10 adult female Australian sea lions from Lilliput Island (LI1, LI2, LI3), Olive Island (OI1, OI2), Lewis Island (LW1, LW2), Dangerous Reef (DR1, DR2) and Seal Bay (SB1) in South Australia. Pie charts represent the percentage of bottom time across different benthic habitats.

Table 3
Prey targeted by adult female Australian sea lions

	DR1	DR2	LI1	LI2	LI3	LW1	LW2	OI1	OI2	SB1
Actinopterygii	20%	7%	100%	75%	93%	100%	60%	51%	70%	100%
Ray-finned fish *sp.*, Actinopterygii *sp.*	–	–	–	–	2	–	–	20 (6)	10 (3)	–
Spinytail leatherjacket, *Acanthaluteres brownii*	–	–	–	–	–	–	–	–	1	–
Australian herring, *Arripis georgianus*	–	–	–	–	2 (4)	–	(1)	–	–	–
Australian salmon, *Arripis trutta*	–	–	–	–	2	–	–	–	–	–
Western foxfish, *Bodianus frenchii*	–	–	–	–	1	–	–	–	–	–
Trevally *sp.*, Carangidae *sp.*	–	–	–	–	–	–	–	3	–	–
Estuary cobbler, *Cnidoglanis macrocephalus*	–	–	–	–	–	1 (1)	–	–	–	–
Globefish, *Diodon nicthemerus*	1	–	–	–	–	–	–	–	–	–
Dusky morwong, *Dactylophora nigricans*	–	–	–	–	–	–	1	1	–	–
Black reef leatherjacket, *Eubalichthys bucephalus*	–	–	–	–	–	–	–	–	1 (2)	–
Rock ling, *Genypterus tigerinus*	–	–	–	–	–	3	–	–	–	–
Red velvetfish, *Gnathanacanthus goetzeei*	–	–	–	–	2	–	–	–	–	–
Sea trumpeter, *Helotes octolineatus*	–	–	(2)	(3)	–	–	–	–	–	–
Wrasse *sp.*, Labridae *sp.*	–	–	–	–	–	–	–	–	1	–
Brownstriped leatherjacket, *Meuschenia australis*	–	–	–	–	–	–	–	–	1	–
Yellowstriped leatherjacket, *Meuschenia flavolineata*	–	–	–	–	–	–	–	–	(1)	–
Sixspine leatherjacket, *Meuschenia freycineti*	–	–	–	–	–	–	–	–	2	–
Leatherjacket *sp.*, Monacanthidae *sp.*	3	–	–	–	–	1	–	2	6 (3)	(1)
Gurnard perch *sp.*, Neosebastidae *sp.*	–	–	–	–	–	–	–	2	–	–
Blue-throated wrasse, *Notolabrus tetricus*	–	–	–	–	–	–	–	–	1	–
Boarfish *sp.*, Pentacerotidae *sp.*	–	–	–	–	–	1	–	–	–	–
Southern sand flathead, *Platycephalus bassensis*	–	–	–	–	–	–	(1)	6	–	–
Flathead *sp.*, *Platycephalus sp.*	–	1	–	–	–	–	–	1	–	–
Silver trevally, *Pseudocaranx georgianus*	–	–	–	–	–	–	–	3	–	–
Magpie perch, *Pseudogoniistius nigripes*	–	–	–	–	–	–	–	–	–	3
Latchet, *Pterygotrigla polyommata*	–	–	–	–	–	–	–	1	–	–
Whiting *sp.*, *Sillaginodes sp.*	–	–	–	–	–	–	–	2	–	–
Gurnard *sp.*,Triglidae *sp.*	–	–	–	–	–	1	–	–	–	–
Red mullet, *Upeneichthys vlamingii*	–	–	–	–	–	–	–	5 (4)	–	–
Cephalopoda	75%	93%	–	–	7%	–	40%	12%	15%	–
Cephalopod *sp.*, Cephalopoda *sp.*	5	6	–	–	–	–	1	6	1	–
Southern sand octopus, *Octopus kaurna*	6	2	–	–	–	–	–	–	–	–
Maori ocotpus, *Macroctopus maorum*	4	1	–	–	–	–	–	–	–	–
Octopus *sp.*, *Octopus sp.*	–	5	–	–	1	–	1	1	–	–
Giant cuttlefish, *Sepia apama*	–	–	–	–	–	–	–	4	6	–
Southern calamari, *Sepioteuthis australis*	–	–	–	–	–	–	–	2	–	–
Chondrichthyes	5%	–	–	–	–	–	–	37%	15%	–
Gulf catshark, *Asymbolus vincenti*	–	–	–	–	–	–	–	–	3	–
Gummy shark, *Mustelus antarcticus*	–	–	–	–	–	–	–	2	–	–
Varied carpetshark, *Parasycllium variolatum*	–	–	–	–	–	–	–	–	4	–
Western shovelnose stingaree, *Trygonoptera mucosa*	–	–	–	–	–	–	–	39	–	–
Stingaree *sp.*, *Urolophus sp.*	1	–	–	–	–	–	–	–	–	–
Gastropoda	–	–	–	25%	–	–	–	–	–	–
Greenlip abalone, *Haliotis laevigata*	–	–	–	1	–	–	–	–	–	–
Unidentified species	- (6)	3 (3)	3 (6)	8 (15)	1 (5)	- (48)	- (19)	34 (10)	9 (22)	- (7)
Total prey attempts	20 (6)	18 (3)	3 (8)	9 (18)	11 (9)	8 (49)	3 (21)	134 (20)	46 (31)	3 (8)

Prey identified from animal-borne video from 10 adult female Australian sea lions from Dangerous Reef (DR1, DR2), Lilliput Island (LI1, LI2, LI3), Lewis Island (LW1, LW2), Olive Island (OI1, OI2) and Seal Bay (SB1) in South Australia. Prey is listed to the lowest identified taxonomic level (as described in Gomon et al., 2008; Reid, 2016). For each sea lion, the number of captures and unsuccessful attempts (in brackets) is listed, both for each taxon and in total. For each sea lion, the percentage that each taxon accounts for in all of their identified prey is also provided.

DISCUSSION

Developing a Suite of Prey Capture Tactics

This study employed animal-borne video to gain deeper insight into critical foraging behaviours and benthic habitats used by Australian sea lions. Our data highlight that Australian sea lions use a variety of prey capture tactics and benthic habitats and vary these tactics for different benthic habitats and prey.

Some sea lions pursued most of their prey by probing the benthos, some predominantly chased prey above the benthos, and some used specialized tactics, such as sit-and-wait predation, flipping rocks/substrate and pelagic ambushing of schooling fish. Australian sea lions used these diverse prey capture tactics to pursue a range of benthic/epibenthic fishes, cephalopods, elasmobranchs and gastropods. These prey constitute a portion of those known to be predated by Australian sea lions. Analyses of DNA, stomach contents and regurgitates indicate that Australian sea lions have a broad diet, consisting of over 200 species, including primarily benthic fish, cephalopods, crustaceans and elasmobranchs (Berry et al., 2017; Goldsworthy et al., 2019; McIntosh et al., 2006; Peters et al., 2015). Similarly, other species that have broad diets, such as orcas, *Orcinus orca* and chimpanzees, *Pan troglodytes*, show diversification in their prey capture tactics (Ford, 2019; Ford & Ellis, 2006; Lonsdorf, 2006; Watts et al., 2012). Therefore, the variety in prey capture tactics used by Australian sea lions in this study may highlight flexibility and adaptation in their behaviour (Araújo et al., 2011; Bolnick et al., 2002), which increases their ability to successfully exploit the wide diversity of prey the species uses (Berry et al., 2017; Goldsworthy et al., 2019; McIntosh et al., 2006; Peters et al., 2015).

When pursuing mobile benthic and epibenthic fish, sea lions used several tactics, and fish were mainly chased above the benthos. Furthermore, some tactics, such as sit-and-wait predation and pelagic ambush, were only observed when pursuing different species of fish. This diversity in prey capture tactics may reflect behavioural development towards multiple tactics for pursuing prey that are challenging to catch. Several marine and terrestrial mammals have developed prey-specific tactics. Bottlenose dolphins, *Tursiops truncatus,* use mud plume feeding to hunt mullet, *Mugil sp.,* (Torres & Read, 2009); orcas, *O. orca,* intentionally strand themselves to capture seals (Guinet & Bouvier, 1995; Lopez & Lopez, 1985); and chimpanzees, *P. troglodytes,* use sticks to 'fish' for termites inside wooden branches and trunks (Bogart & Pruetz, 2008; Lonsdorf, 2006). In many marine and terrestrial mammals, including sea otters, *Enhydra lutris*, bottlenose dolphins, *T. truncatus* and chimpanzees, *P. troglodytes*, these specialized and prey-specific tactics correspond to increases in foraging efficiency and overall fitness (McGrew & Marchant, 1999; Tinker et al., 2008; Torres & Read, 2009). While some caution is required with the interpretation of our results, as the sample size of 10 adult females is limited, these specialized behaviours observed in Australian sea lions could represent prey-specific tactics. However, for Australian sea lions, any relationship between the use of these different tactics and an individual's foraging success (e.g. prey capture rate) and overall fitness is unclear.

From these 10 adult female Australian sea lions, five different prey capture tactics were observed, with individual sea lions employing two or three different tactics. This diverse behavioural repertoire of Australian sea lions may also reflect the specific ecological niches that different sea lions exploit. Stable isotope analyses have indicated that adult female Australian sea lions have long-term fidelity to foraging locations, with marked differences in behaviour that occur at the individual, intracolony and intercolony levels, for example, between sea lions that show 'inshore' or 'offshore' foraging ecotypes (Lowther et al., 2011; Lowther & Goldsworthy, 2011a). Australian sea lions could then conceivably have some long-term fidelity to prey capture tactics as well. Furthermore, long-term foraging specialization is thought to be more likely to occur when a population has access to a wide variety of habitats and prey, providing more opportunity for niche partitioning (Araújo et al., 2011; Polito et al., 2015; Pyke, 1984). In this study, some tactics, such as probing and chasing, were observed across all individuals/colonies, while other tactics, such as flipping, sit-and-wait and pelagic ambush, were less common. This may be further evidence of specialization in Australian sea lion foraging behaviour, with differences in the use of prey capture tactics existing at both the individual and colony levels. Therefore, these contrasts in the use of prey capture tactics could reflect behavioural adaptation by Australian sea lions in response to differences in prey availability and habitat structure across their distribution in southern Australia.

Using a Variety of Benthic Habitats

In this study, some sea lions used macroalgae reefs, some mainly used macroalgae and seagrass meadows, one sea lion mainly foraged on bare sand plains and one sea lion used invertebrate reefs. In these habitats that Australian sea lions used, a range of different macroalgae, seagrass and macroinvertebrate assemblages were observed (e.g. *Ecklonia radiata*-dominated reefs, *Posidonia sp.* seagrass meadows and mixed sponge, ascidian, bryozoan and soft coral reefs; Fig. A2). When foraging across reefs, sea lions also used high and moderate relief reefs, as opposed to flat relief reefs. The benthic habitats identified here only represent data collected from 10 Australian sea lions, and these benthic habitats comprise those used on a single foraging trip. However, since adult female Australian sea lions have long-term fidelity to foraging locations (Lowther et al., 2011, 2012; Lowther & Goldsworthy, 2011a), the benthic habitats identified in this study could reflect some individual long-term habitat preferences. The degree to which the habitats identified here are a consequence of individual preferences by sea lions or are influenced by the accessibility/availability of different habitats for different populations is unclear.

Disentangling these drivers of habitat preference is further complicated by our poor overall understanding of the distribution and structure of benthic habitats off the South Australian coast (Currie et al., 2009; Edyvane, 1999; James et al., 2001; Ward et al., 2006). Resolving this relationship would require comparing fine-scale habitat data collected from animal-borne video with habitat data collected at a coarser spatial scale, for example, from towed cameras, autonomous underwater vehicles or swath mapping. Recently, animal-borne video from Australian sea lions has been used to build machine learning models to develop benthic habitat maps for large areas of the continental shelf in southern Australia (Angelakis et al., 2024). Our data complements these past studies by providing detailed information on foraging behaviours and habitat use, which could be integrated with such data in the future to investigate relationships in the ecological value of different benthic habitats, prey resources and foraging areas for Australian sea lions. Future animal-borne video that expands the spatial extent and detail of available habitat data will contribute much-needed information on the fine-scale biotic structure of benthic habitats used by Australian sea lions and more broadly, the distribution of different benthic habitats across southern Australia.

Habitat-Specific Prey Capture Tactics

Australian sea lions used different prey capture tactics in different benthic habitats, suggesting that there is some habitat context to these behaviours. Similarly, other marine species, like bottlenose dolphins, *T. truncatus*, Australasian gannets, *Morus serrator* and basking sharks, *Cetorhinus maximus,* use habitat-specific foraging tactics (Sims et al., 2005; Torres & Read, 2009; Wells et al., 2016). In this study, a single individual (LW1) used sit-and-wait predation, exclusively on high relief macroalgae reefs. Although our dataset is limited, it is conceivable how this tactic may be more useful on high relief reefs, as opposed to more open habitats, like seagrass or macroalgae meadows. If there is sufficient availability of benthic and epibenthic prey, sea lions could better hide using prominent features and cover in reef habitats to then ambush their prey. Similar prey capture tactics are seen in leopard seals, *Hydrurga leptonyx*, where seals exploit cover to hide themselves to then ambush penguins (Mader, 1998; Krause et al., 2015). Interestingly, for the sea lion in this study (LW1), only 2 of its 35 sit-and-wait predation attempts resulted in prey captures. Sit-and-wait predation is relatively common among marine and terrestrial predators and can be a highly rewarding, low-energy tactic (Blamires, 2020; Nadjafzadeh et al., 2016; Nilsson et al., 2010; Olive, 1982). Therefore, the energetic tradeoffs of different prey capture tactics for Australian sea lions are of interest for future research.

Intuitively, the capture of highly mobile prey across open benthic habitats like bare sand and sponge/sand habitats would necessitate a more chase-orientated predation, as shown in our study. Presumably, tactics such as chasing incur a greater energetic cost on sea lions than probing or sit-and-wait predation. Therefore, it would be expected that the use of more energy-intensive tactics by sea lions should necessitate more frequent prey captures or the capture of larger or more energy-dense prey, to balance the energetic requirements of the individual (Bowen et al., 2002; Pyke, 1984).

Conclusions

This study presents novel information on the variety of prey capture tactics and benthic habitats used by Australian sea lions, improving our understanding of important resources for the species. Since the sample in this study is derived from a single foraging trip of 10 adult female Australian sea lions from five colonies (Supplementary Material), it is likely that this study only captured a portion of the prey capture tactics and benthic habitats used, not just by individual sea lions but also by the species as a whole. Future animal-borne videos from Australian sea lions will improve our understanding of the variety of prey capture tactics and benthic habitats used by the species. Repeated deployments on individual sea lions would better resolve any long-term fidelity that Australian sea lions have to prey capture tactics and their preferences for particular benthic habitats and prey. Furthermore, determining the relationship between different tactics and foraging success, and the extent to which these tactics are specific to prey and/or habitat, will provide a considerable improvement to our foundational understanding of Australian sea lion foraging behaviour in the future.

Author Contributions

Nathan Angelakis: Writing – review & editing, Writing – original draft, Visualization, Validation, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Sean D. Connell:** Writing – review & editing, Visualization, Validation, Supervision, Project administration, Methodology, Conceptualization. **Simon D. Goldsworthy:** Writing – review & editing, Visualization, Validation, Supervision, Resources, Project administration, Methodology, Funding acquisition, Data curation, Conceptualization. **Andrew D. Lowther:** Writing – review & editing, Visualization, Validation, Project administration, Methodology, Funding acquisition, Data curation. **Brad Page:** Writing – review & editing, Visualization, Validation, Project administration, Methodology, Funding acquisition, Data curation.

Data Availability

The data sets used and analysed in this study can be found in the supplementary material.

Declaration of Interest

The authors have no conflicts of interest to declare.

Acknowledgments

We acknowledge Greg Marshall, Kyler Abernathy, Mark Thorpe and the Exploration Technology Lab of the National Geographic Society for their support and collaboration in the collection of the National Geographic Crittercam data. We also acknowledge Roger Kirkwood (SARDI Aquatic Sciences), Dirk Holman (Department for Environment and Water DEW), Mel Stonnill and the staff at Seal Bay Conservation Park (DEW), as well as Dale Furley (deceased) and the staff of the Far West Coast Aboriginal Corporation (FWCAC). We also thank Carey Kuhn (National Oceanic and Atmospheric Administration NOAA) and Niko Liebsch (Customized Animal Tracking Solutions CATS). We also acknowledge Tobin Woolford (Eyrewoolf Abalone), Henry Basedow and Bec Souter. We also thank SARDI Aquatic Sciences and The University of Adelaide for their continued support. Research for this study was supported with funding from the Australian Marine Mammal Centre, Nature Foundation (and Australian Geographic) and Australian Government under the National Environmental Science Program (NESP), Marine and Coastal Hub (Project 2.6, Mapping critical Australian sea lion habitat to assess ecological value and risks to population recovery). Additional operating costs were funded by the Ecological Society of Australia under the Holsworth Wildlife Research Endowment, awarded to Nathan Angelakis (006010901).

Supplementary Material

Supplementary material associated with this article is available at https://doi.org/10.1016/j.anbehav.2025.123108.

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Appendix

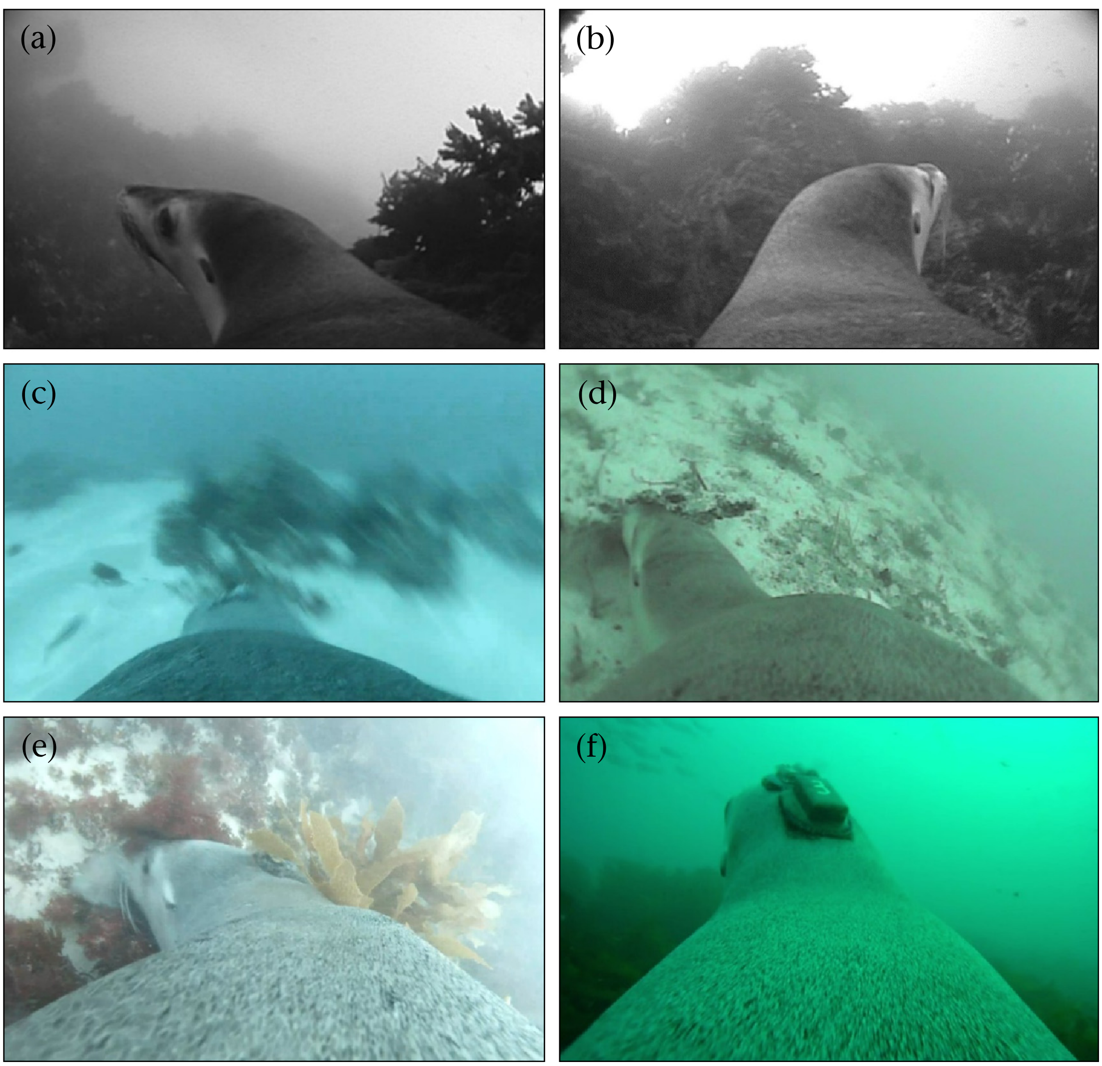

Figure A1. Prey capture tactics identified from animal-borne video from 10 adult female Australian sea lions in South Australia. Still images highlight examples of (a) and (b) sit-and-wait predation, (c) chasing, (d) flipping rocks/substrate, (e) probing and (f) pelagic ambush tactics.

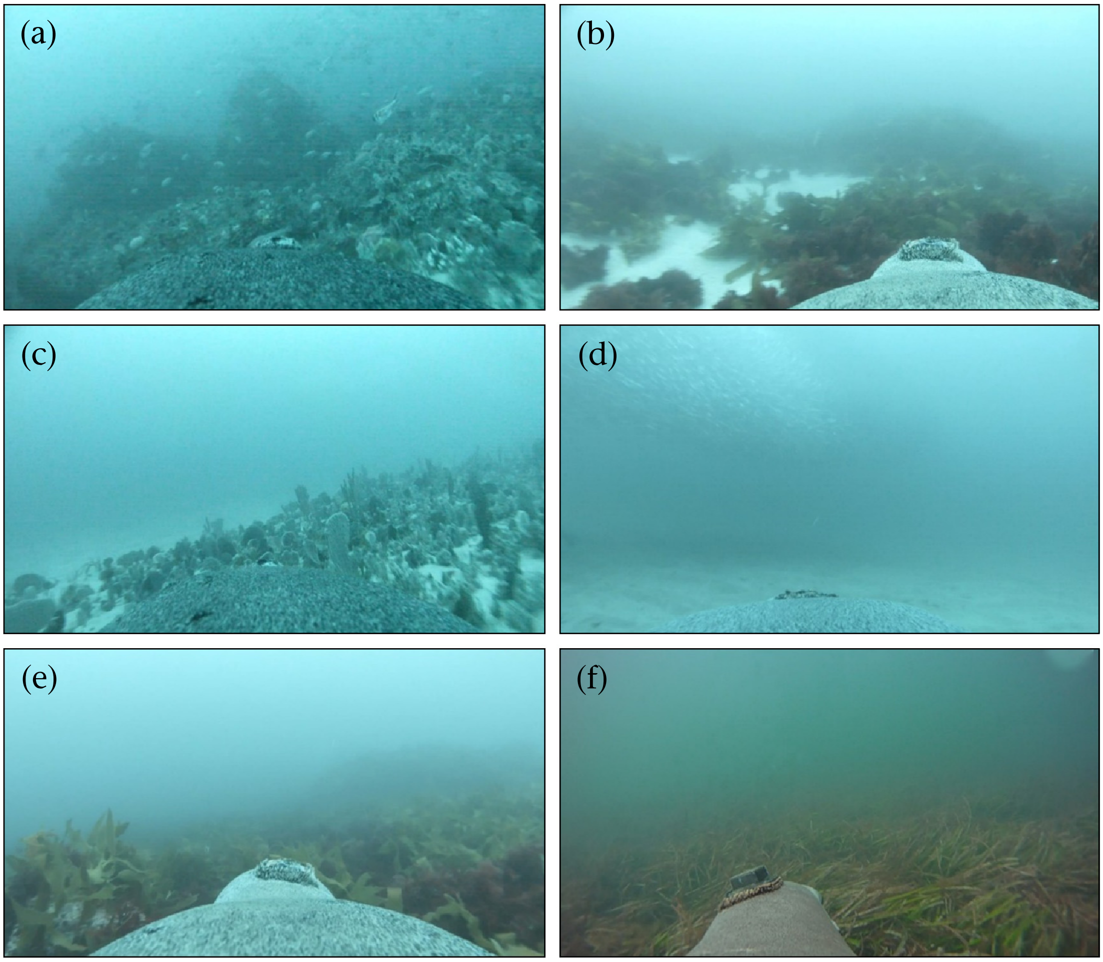

Figure A2. Benthic habitats identified from animal-borne video from 10 adult female Australian sea lions in South Australia. Still images highlight examples of (a) invertebrate reef, (b) macroalgae meadow, (c) sponge garden, (d) bare sand, (e) macroalgae reef and (f) seagrass meadow habitats.

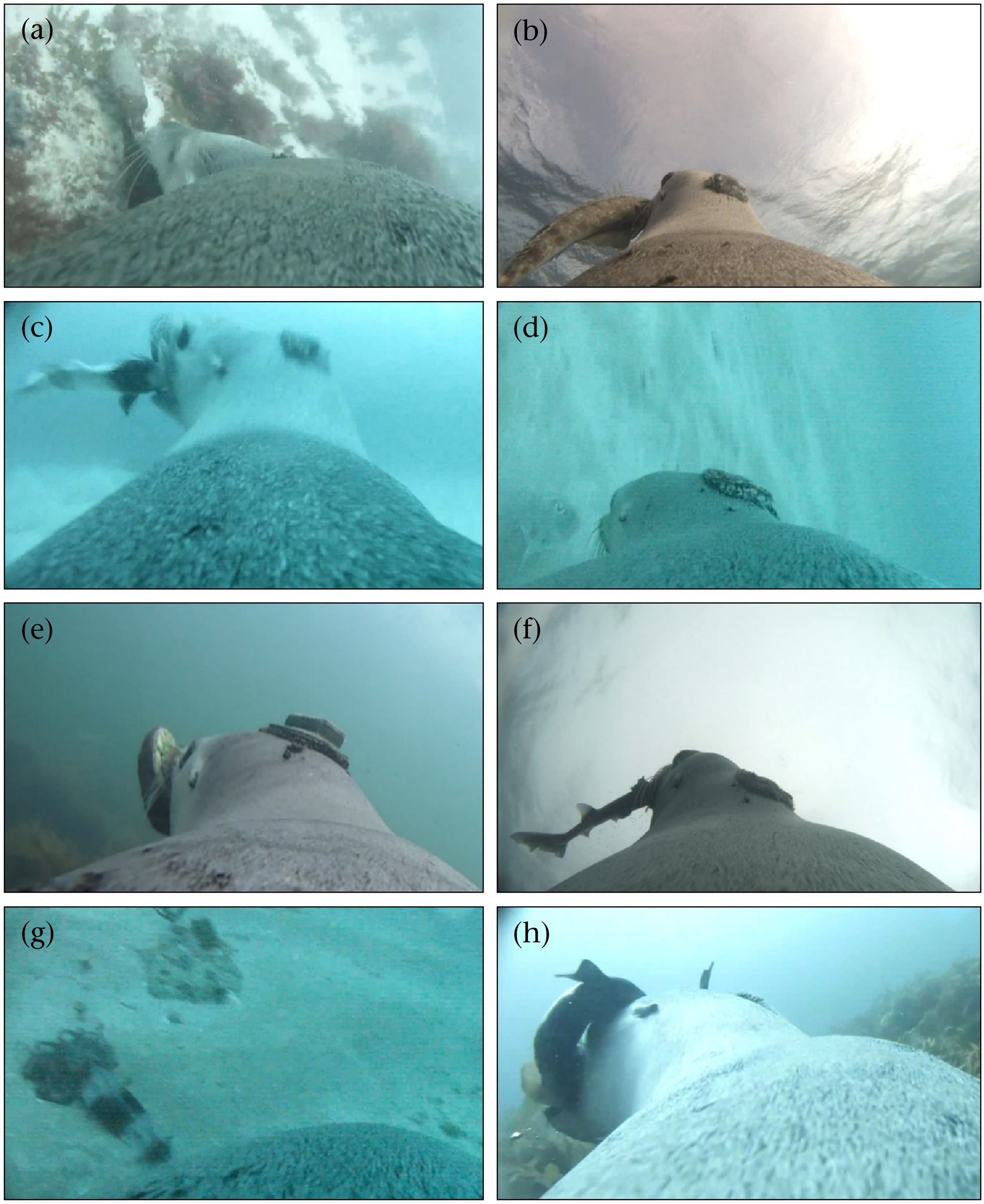

Figure A3. Predation events identified from animal-borne video from 10 adult female Australian sea lions in South Australia. Still images show captures of (a) a giant cuttlefish, *Sepia apama*, (b) a southern sand flathead, *Platycephalus bassensis*, (c) a magpie perch, *Pseudogoniistius nigripes*, (d) a western shovelnose stingaree, *Trygonoptera mucosa*, (e) a greenlip abalone, *Haliotis laevigata*, (f) a gummy shark, *Mustelus antarcticus*, (g) a southern calamari, *Sepioteuthis australis* and (h) a varied carpetshark, *Parascyllium variolatum*.