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Fine-scale hunting strategies in Australian fur seals

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Introduction: Knowledge of the hunting strategies of top predators can provide insights into the cost-benefit trade-offs of their foraging activities. Air-breathing marine predators are constrained in their foraging activities due to their metabolic expenditure at depth being supported by limited body oxygen stores. Understanding how these species adapt their behaviours to maximise foraging success is of importance in view of the anticipated alterations to marine ecosystems in response to global change. The Australian fur seal (*Arctocephalus pusillus doriferus*), the largest fur seal species, has a distribution restricted to south-eastern Australia, which is one of the fastest warming oceanic regions and where the abundance, distribution and diversity of prey species is expected to change in coming decades.

Methods: In the present study, combined IMU (acceleration, magnetometer, gyroscope), depth and GPS data logger information was used to reconstruct 3-dimensional tracks during diving, assess energy expenditure and quantify prey capture events in adult female Australian fur seals during benthic foraging.

Results: The results revealed that individuals ascended at steeper pitches (to reduce transit time), remained for shorter durations and travelled shorter distances at the surface, and then descended at steeper pitches on subsequent dives after predatory events on the seafloor. Higher travel speeds and more directional changes during searching for prey along the seafloor, while requiring greater energy expenditure, were associated with more prey captures. Interestingly, individuals did not display conventional Area Restricted Search, with the heading between dives not influenced by prey encounters.

Discussion: Together, these results suggest Australian fur seals undertake rapid searching along the seafloor to surprise cryptic prey and, if prey is encountered, undertake rapid surfacing (to reload body oxygen stores) and return to nearby seafloor habitat with a similar but undisturbed prey field.

KEYWORDS

foraging ecology, *Arctocephalus pusillus doriferus*, hunting strategies, GPS tracking, 3D models

1 Introduction

Individual survival and fitness are linked to the success of foraging activities (Morse and Fritz, 1987), with long-term impacts on foraging success affecting population growth and survival of the species (Pyke, 1984). Foraging activities are the result of interactions between functional performance, ecological features, and energetic needs (Toscano et al., 2016). Optimization of foraging behaviours by individuals is based on evaluating the costs (time and energy expended) and benefits (energy and nutrients gained) of engaging in a particular strategy (Mobbs et al., 2018). Over the long-term, the energy gained must be higher than the energy expended in searching, capturing and handling prey (MacArthur and Pianka, 1966) in order to balance the energy expenditure of living (Stephens et al., 2007).

The foraging behaviours of air-breathing marine predators are constrained by their oxygen stores limiting the time they can spend submerged in search of prey (Andrews and Enstipp, 2016). Two primary foraging strategies (pelagic and benthic) have been described in these species, with differences in the duration of the bottom phase of the dive (Arnould and Costa, 2006) and distribution of prey items (Doniol-Valcroze et al., 2011). Pelagic foragers use the entirety of the dive in search of prey (Arnould and Costa, 2006), exploiting high-density patches of small schooling species (fish, crustacea and cephalopods) which can be distributed throughout the water column (Chimienti et al., 2017). In contrast, benthic foragers search for larger, cryptic prey on the seafloor (Meyers et al., 2021). The high energetic costs of diving to the sea floor (Costa, 1991) are balanced by the profitability of spatial and temporal predictability of benthic prey abundance and distribution (Arnould and Costa, 2006).

Pelagic environments are characterised by spatially variable patches of food resources in high marine productivity areas (Harcourt et al., 2002). Correspondingly, once profitable habitats have been encountered, pelagic predators have been observed to undertake Area Restricted Search (ARS) (Paiva et al., 2010) to maximise the rate of prey encounter (Pinaud, 2008). This behaviour involves a series of slow and sinuous movements scanning the area for prey (Weimerskirch, 2007), increasing residence time in productive resource areas (Fauchald and Tveraa, 2003). It has been shown to be prevalent in areas of high prey abundance and low competition (Salton et al., 2022). In addition, during ARS, effective prey detection is greater than direct detection distance (Tinbergen et al., 1967) and, therefore, such a strategy is assumed to decrease energy expenditure while searching for prey (Regular et al., 2013). However, some studies have shown that ARS does not necessarily reflect foraging success and that straight line searching can be more profitable in some instances (Weimerskirch et al., 2007; Hoskins et al., 2015b). In contrast, benthic environments are characterized by more spatially consistent but lower prey abundance (Snelgrove, 2001). Relatively little is known about which strategies air-breathing marine predators use for optimizing search patterns in benthic habitats (Takahashi et al., 2003; Maxwell et al., 2012; Blakeway et al., 2021).

The Australian fur seal (*Arctocephalus pusillus doriferus*, hereafter referred to as AUFS) is the largest fur seal species, with mean adult female and male body mass of 76 kg and 270 kg, respectively (Kirkwood and Arnould, 2008). The breeding distribution of AUFS is mostly restricted to Bass Strait, a shallow (60-80 m) continental shelf area of low marine primary productivity between the Australian mainland and Tasmania (Kirkman and Arnould, 2018) influenced by numerous oceanographic currents (Fandry, 1981). While its population is still recovering from the over-exploitation of the commercial sealing era (18th-19th centuries), the AUFS represents the largest resident marine predator biomass in the region (Kirkwood and Arnould, 2012).

The foraging range of AUFS is restricted to the continental shelf where diving is almost exclusively benthic (Arnould and Hindell, 2001; Arnould and Kirkwood, 2007; Hoskins et al., 2017). The species is considered a generalist predator, foraging on > 60 taxa, including elasmobranchs, bony fish, and cephalopods (Deagle et al., 2009; Kernaléguen et al., 2016). Its broad-scale foraging behaviour and habitat-use, as well as the environmental factors influencing these characteristics, have been extensively investigated (e.g (Hoskins et al., 2015a, b; Speakman et al., 2020)). However, little is known of the hunting strategies the species employs or the factors influencing their energetic consequences (Foo et al., 2016).

The Bass Strait region is one of the world's fastest-warming oceanic areas (Hobday and Pecl, 2014), with projected climate change impacts expected to lead to significant shifts in the diversity, abundance and distribution of species (Hobday and Lough, 2011). Such alterations are likely to affect the prey field of the region's marine predators (Fulton, 2011). Knowledge of the hunting strategies they employ, and the factors influencing their success and efficiency, is crucial for understanding the behavioural, energetic and, ultimately, population trajectory responses of these species to the anticipated ecosystem modifications (Niella et al., 2022). The aims of the present study, therefore, were to determine the: 1) fine-scale dive behaviour movements; 2) prey capture and energy expenditure consequences of these movements; and 3) factors influencing hunting search strategies of AUFS.

2 Materials and methods

2.1 Study site and data collection

The study was conducted on Kanowna Island (39° 9.1' S, 146° 18.5' E) in northern Bass Strait, south-eastern Australia, during the winters of 2015-19. The island hosts the third largest breeding colony of AUFS, with an annual production of ca. 2500 pups (Geeson et al., 2022). Adult females suckling pups were selected at random and captured using a modified hoop net (Fuhrman Diversified, Seabrook, Texas, U.S.A.). Individuals were then anaesthetised with isoflurane delivered via a portable gas vaporiser (StringerTM, Advanced Anaesthesia Specialists, Gladesville, NSW, Australia) for the duration of handling procedures.

A combined video/depth/IMU (Inertial Measurement Unit) data logger (CD v6, Customized Animal Tracking Solutions, Moffat Beach, Australia) was glued to the fur along the dorsal midline just posterior to the scapula using quick-setting epoxy (RS Components, Corby, UK; Figure 1). The video data logger was programmed to record for 1 h at 10:00 and 14:00 (AEST) each day. The IMU recorded depth (m), video/depth/IMU data logger and ambient temperature (°C) and three axes of acceleration (m·s^{-2}), magnetic field intensity (µT), and angular velocity (°·s^{-1}) at 20 Hz. A GPS/dive behaviour data logger (Mk10F, Wildlife Computers, Redmond, E.A., U.S.A.) and a VHF transmitter (Sirtrack Ltd, Havelock North, NZ) were also attached in series posterior to the first device. The GPS/dive behaviour logger was programmed to record location and depth at 15 min and 5 s intervals, respectively. The VHF transmitter was used to relocate the individual at the colony to facilitate recapture. Together, the devices represented <2% body mass and <1% cross-sectional surface area and, therefore, are likely to have had a negligible impact on hydrodynamic drag (McMahon et al., 2008; Field et al., 2011).

Following the attachment of data loggers, standard length and body mass data were determined using a tape measure (± 0.5 cm) and a digital suspension scale (± 0.1 kg), respectively. Uniquely numbered plastic tags (Super Tags, Dalton, Woolgoolga, Australia) were then inserted in the trailing edge of each fore-flipper for identification before the animal was left to recover from anaesthesia and resume normal behaviours. Individuals were recaptured at the colony after at least one complete foraging trip at sea following the above procedures and the data loggers removed. Data were downloaded onto portable computers in the field.

2.2 Dive behaviour, prey captures and index of energy expenditure

All dive behaviour data were determined from the depth measurements of the combined GPS/dive behaviour data logger. Due to the potential for pressure-transducer drift, depth data was first zero-offset corrected (ZOC) using the diveMove package (Luque, 2007) in R statistical environment version 4.0.3 (R Core Team, 2023). Assuming a minimum depth of 5 m for foraging dives, summary statistics were then extracted for each dive to determine dive depth (m) and durations (s) of the descent, bottom, ascent and post-dive phases. All dives which occurred below a 40 m threshold (Volpov et al., 2015) at ± 10% of the maximum depth of the preceding dive were considered benthic (Tremblay and Cherel, 2000). Since benthic dives were the focus of the present study, all non-benthic dives were excluded from further analyses. In addition, to exclude post-dive periods not associated with foraging (e.g. resting at the surface and/or commuting), all dives with a post-dive duration > 10 min (Speakman et al., 2020) were excluded from further analyses.

FIGURE 1
Adult female Australian fur seal (*Arctocephalus pusillus doriferus*) with (from right to left) a combined video/depth/IMU (accelerometer, magnetometer, gyroscope) datalogger, GPS/dive behaviour data logger, and VHF transmitter glued to the dorsal midline fur.

IMU signals were transformed from the tag reference frame to the seal reference frame following procedures described elsewhere (e.g (Johnson and Tyack, 2003; Johnson, 2011)). Peaks in the sway (Y; lateral) axis accelerometer data were used to estimate potential prey captures (PPC) using the Ethographer package (Sakamoto et al., 2009) in IgorPro (Version 6.34, Wavemetrics, USA) following the methods of Foo et al. (2016). Briefly, a 3 Hz high-pass filter was used to remove small movement noise (Viviant et al., 2010). The standard deviation (SD) of the filtered data over a 1.5 s moving window was then calculated for the whole record. Peaks over a pre-determined threshold were considered to reflect PPC (Foo et al., 2016).

To identify the optimal threshold for each individual, the frequency distribution of PPC determined with Y-acceleration SD ranging from 0.5 to 3.0 were visually inspected for discontinuity following the methods of Foo et al. (2016), the optimal threshold was the one before the discontinuity. To avoid double-counting multiple peaks from a single PPC event, a minimum interval of 3.5 s was applied between successive peaks (Volpov et al., 2015). Finally, as the minimum depth for all benthic dives recorded was 40 m, only peaks in Y-acceleration SD occurring at greater depths were considered to remove movement associated with prey handling during ascent or at the surface. The dimensions of the combined video/depth/IMU data logger precluded its attachment to the head. In addition, for the reconstruction of 3-dimensional tracks, the IMU sensor needs to be near the centre of gravity and, therefore data logger was placed on the dorsal midline just posterior to the scapula. While the majority of previous otariid seal studies using accelerometers to document PPC have involved data loggers placed on the head (Volpov et al., 2015; Foo et al., 2016), accelerometers mounted on the dorsal surface have been shown to detect PPC in northern fur seals (*Callorhinus ursinus*) and Antarctic fur seals (*A. gazella*) (Jeanniard-Du-Dot et al., 2017). In the present study, the PPC detection was validated by comparing accelerometer-derived data with the available video data.

To investigate the relationships between hunting strategies and foraging effort, Vectorial Dynamic Body Acceleration (VeDBA) was used as an index of energy expenditure. Previous studies have demonstrated VeDBA to be strongly correlated to energy expenditure in various taxa, including fur seals (Jeanniard-Du-Dot et al., 2017). VeDBA was calculated from the tri-axial accelerometer data, using the following equation:

$$\mathrm{VeDBA} \quad = \sqrt{(A_x - S_x)^2 + (A_y - S_y)^2 + (A_z - S_z)^2}$$

where S is the static acceleration and A is the acceleration. A 2 s running mean of S (reflecting the positioning of the animal in space in relation to gravity) was subtracted from A to calculate dynamic acceleration related to movement (Jeanniard-Du-Dot et al., 2017). The mean VeDBA (*g*) was determined for the four different dive phases (descent, bottom, ascent and post-dive).

2.3 Reconstruction of 3-dimensional dive profiles

Preliminary analyses indicated that the magnetometer, gyroscope and accelerometer sensors in the video/depth/IMU data logger were strongly influenced by temperature and that the internal temperature of the device increased at a rate of 5°C·h^{-1} and 10°C·h^{-1} in water and air, respectively, when the video data logger was recording. To account for these biases in each sensor, two video/depth/IMU data loggers (representing the device models used in deployment data collection) were subjected to a range of in-air and in-water temperatures experienced by AUFS at sea both with, and without, the video data logger recording. A low-pass filter was applied to each axis and the filtered data was fitted to a simple linear regression with temperature. The resulting equation was then used to determine the unbiased sensor information in the deployment data according to the experienced temperature.

The position on the horizontal plane at sea surface was provided by GPS data, from which the position estimates of the start and end of the dives were extrapolated. Depth profiles were used to extrapolate the position on the vertical dimension. The position of individuals on the horizontal plane was estimated via dead-reckoning (Davis et al., 2001); i.e. by integrating the IMU signals on the seal reference frame, albeit disregarding the vertical position solution. Acceleration signals were low-pass filtered and scaled to match realistic pinniped velocities (Sato et al., 2003) and corresponding to the GPS surface track. Euler angles from the x, y, and z axes were calculated to assess roll, heading (yaw) and pitch, respectively.

Speed of descent, bottom, and ascent phases were calculated using the following formulae:

$$D = \sqrt{(X_{pos2} - X_{pos1})^2 + (Y_{pos2} - Y_{pos1})^2 + (Z_{pos2} - Z_{pos1})^2}$$

$$TD = \sum D$$

$$Sp = {}^{TD}/_{T}$$

where $(X_{pos2} - X_{pos1})$, $(Y_{pos2} - Y_{pos1})$, $(Z_{pos2} - Z_{pos1})$ are the differences in position between two consecutive points, D is the distance (m) travelled over consecutive points, TD is the total distance travelled (m), T is the time during the dive phase (s), and Sp is the speed (m·s^{-1}). In addition, information on the longitude and latitude of the start of the descent phase and the end of the ascent phase was provided by the GPS data loggers. Through the raster (Hijmans et al., 2015) package, the distance travelled along the bottom phase, and between two dives at the surface, were calculated using the position of individuals on the horizontal plane during the dives and the coordinates of the descent and ascent phase, respectively.

To investigate the influence of sea-floor hunting activity on dive behaviour and energy expenditure, the number of substantial directional changes made by individuals was determined. Heading (yaw) values during the bottom phase of the dive were smoothed with a 3 s running mean, to remove small movements, and sampled every 3 s to document apparent changes in direction. The difference between consecutive values was determined to calculate the angular deflection of the movement and transformed into radians. The frequency distribution of directional changes was investigated in each individual to assess for discontinuities from which significant movements could be detected. Directional changes greater than this threshold were considered as intentional movements (Miller et al., 2019) related to hunting behaviour.

Mean heading during the descent phase and ascent phase were calculated. To exclude the potential influence of surface or bottom phase behaviour (e.g. prey handling) on heading during descent/ascent, only data > 5 m below the surface and > 5 m above the bottom phase were included. The difference in the mean heading during the descent phase between successive dives was then investigated to assess changes in travelling direction between subsequent dives.

2.4 Data analysis

All statistical analyses were conducted in the R statistical environment (Version 4.0.3 (R Core Team, 2023)). Linear mixed-effect models (LME) and Generalized mixed-effect models (GLME), within the nlme (Pinheiro et al., 2007) and lme4 (Bates et al., 2011) packages. To assess the factors influencing fine-scale movements, maximum depth, mean speed, mean pitch and duration of the different dive phases were used as predictor variables. Similarly, these variables were investigated as influences on energy expenditure and prey capture rates (Supplementary Table 1). In all models, the individual was considered a random factor to account for repetitive sampling. Correlation matrices were constructed to assess for collinearity between continuous factors. When correlation coefficients were $r > 0.7$, one of the two parameters was excluded from further analyses (Schober et al., 2018). Model comparison was conducted with AIC selection using the ‘dredge’ function in the MuMIn package (Barton and Barton, 2015). Where numerous candidate models with ΔAICc < 4 existed, model averaging was conducted and the 95% confidence intervals for the predictive variables inspected. Unless otherwise specified, data are presented as Mean ± SE and results considered significant at $P < 0.05$.

3 Results

3.1 Foraging trip metrics and fine-scale behaviours

Due to camera malfunction, animal-borne video data were available for only 3 individuals, for a duration of 4.5 h (2.7 ± 1.1 h) per individual during which benthic dives were made. Although available video data enabled the validation of prey captures from back-mounted accelerometers, it was insufficient to investigate relationships with seafloor habitat. Complete data sets of matching GPS, dive behaviour and IMU information were obtained from a total of 5 individuals with mean body mass of 70.5 ± 6.6 kg and standard length of 152 ± 3.8 cm (Table 1). Mean foraging trip duration was 4.6 ± 0.5 d, during which individuals travelled 234.9 ± 32.4 km within central Bass Strait. Throughout these foraging trips, individuals made 404.8 ± 57.3 benthic dives showing modes of maximum depths ranging from 75.0 - 82.9 m, with dive durations modes ranging from 2.89 - 4.56 min (Table 1).

The reconstructed 3 dimensional dive profiles typically revealed individuals descending to the sea floor at a steep angle (high pitch), swimming rapidly along the sea floor in a mostly constant direction, then ascending to the surface at a shallower angle (lower pitch; Figure 2). However, there was substantial variation in dive parameters between dive phases, between dives and between individuals (Table 2). During descent, the mode of mean downward pitch (from the horizontal) of individuals ranged from 34 – 75.1° while the mode of mean descent speed ranged from 0.37 – 0.50 $m \cdot s^{-1}$, resulting in the mode of mean VeDBA ranging from 0.51 – 0.92 *g* (Table 2).

During ascent, the mode of mean upward pitch (from the horizontal) of individuals ranged from 62.9 – 72.4° while the mode of mean ascent speed ranged from 0.35 – 0.53 $m \cdot s^{-1}$, resulting in the mode of mean VeDBA ranging from 0.59 – 1.13 *g* (Table 2). During the bottom phase of dives, where duration had a mode ranging from of 1.46 - 2.08 min, the distribution of directional changes suggested turns of > 45° indicated intentional movement changes. The number of such directional changes during bottom phases ranged from 0 - 45 with the mode for individuals ranging from 5 - 9. The mode of mean speed during the bottom phase ranged from 0.41 - 0.46 $m \cdot s^{-1}$, resulting in the mode of mean VeDBA ranging from 1.18 – 1.75 *g* (Table 2).

To investigate factors influencing potential foraging time within a dive (i.e. time along the sea floor), LMEs were constructed with the fine-scale diving behaviour variables. As time in the bottom phase of a dive has been shown to be influenced by dive depth (due to body oxygen store limitations (Thompson and Fedak, 1993), the bottom phase duration was converted to a proportion of total dive duration and arcsine-transformed before modelling. Since there were numerous candidate models with a $\Delta AICc < 4$, model averaging was conducted and revealed all predictor variables to have a consistent influence (95% CI not crossing 0; Table 3). Descent pitch and maximum depth were included in all candidate models with positive influences, indicating they are the most important parameters in explaining bottom time (%) (Figures 3B, D). Mean speed during descent also positively influenced bottom phase (%) duration whereas mean speed during the bottom phase had a negative influence (Figures 3C, A).

Factors influencing VeDBA during different dive phases were investigated with LMEs (Table 3). Individuals had a reduced VeDBA during the descent phase of dives with increasing (steeper) pitch and deeper maximum depths. Similarly, VeDBA was reduced during the ascent phase with increasing (steeper) pitch. During the bottom phase of dives, VeDBA was found to be positively influenced by the number of directional changes initiated and with greater depths (Table 3).

3.2 Factors influencing prey captures and inter-dive foraging strategies

A total of 150 benthic prey encounter events were recorded in the video data collection (50 ± 9 per individual). All were detected as PPC in the analysis of the back-mounted accelerometer data, while no false-positive events were recorded, validating the technique for quantifying potential prey captures. A total of 3524 PPC were recorded in 1559 dives (77% of the total benthic dives), with the number of PPC ranging from 0 - 10 per dive. Mean prey capture rate varied between individuals from 1.4 ± 0.1 $PPC \cdot dive^{-1}$ to 2.3 ± 0.1 $PPC \cdot dive^{-1}$ (Table 1).

Parameters influencing prey capture rate were investigated using GLME with the number of directional changes, mean bottom speed, proportion of bottom phase duration, and maximum depth as predictor variables. The full model was the most parsimonious (Table 3), showing that all measured variables positively influence prey capture rate (Figure 4).

The hunting success experienced by individuals during the bottom phase of dives was found to influence numerous aspects of subsequent fine-scale behaviours (Table 3). LME model selection revealed that individuals ascended to the surface at a steeper pitch and faster swim speed with increasing prey captures during the bottom phase (Figures 5A, B). In addition, post-dive duration and the distance travelled before the next dive were both negatively influenced by the number of prey captures during the bottom phase of the previous dive (Figures 5C, D). Furthermore, the descent pitch and speed during a dive were positively influenced by the number of prey captures in the preceding dive (Figures 5E, F).

TABLE 1 Summary information on adult female Australian fur seals (*Arctocephalus pusillus doriferus*) from Kanowna Island instrumented with combined GPS/dive behaviour/IMU data loggers.

Seal	Mass (kg)	SLEN (cm)	Trip duration (d)	Total distance travelled (km)	Dive duration (min)	Dive depth (m)	Benthic dives (n)(%)	Successful dives (%)	Prey Capture Rate ($PPC \cdot dive^{-1}$)
1	89	166	3.63	164.6	4.56	82.9	405 (90)	84	2.26 ± 0.08
2	67.5	143	5.58	210.6	4.05	75.0	325 (87)	80	2.01 ± 0.09
3	71	150	5.71	247.5	4.09	79.9	236 (47)	72	1.82 ± 0.12
4	76.5	153	3.77	198.3	3.89	72.8	528 (96)	73	1.48 ± 0.06
5	48.5	148	4.24	353.3	2.89	76.7	530 (81)	76	1.41 ± 0.05

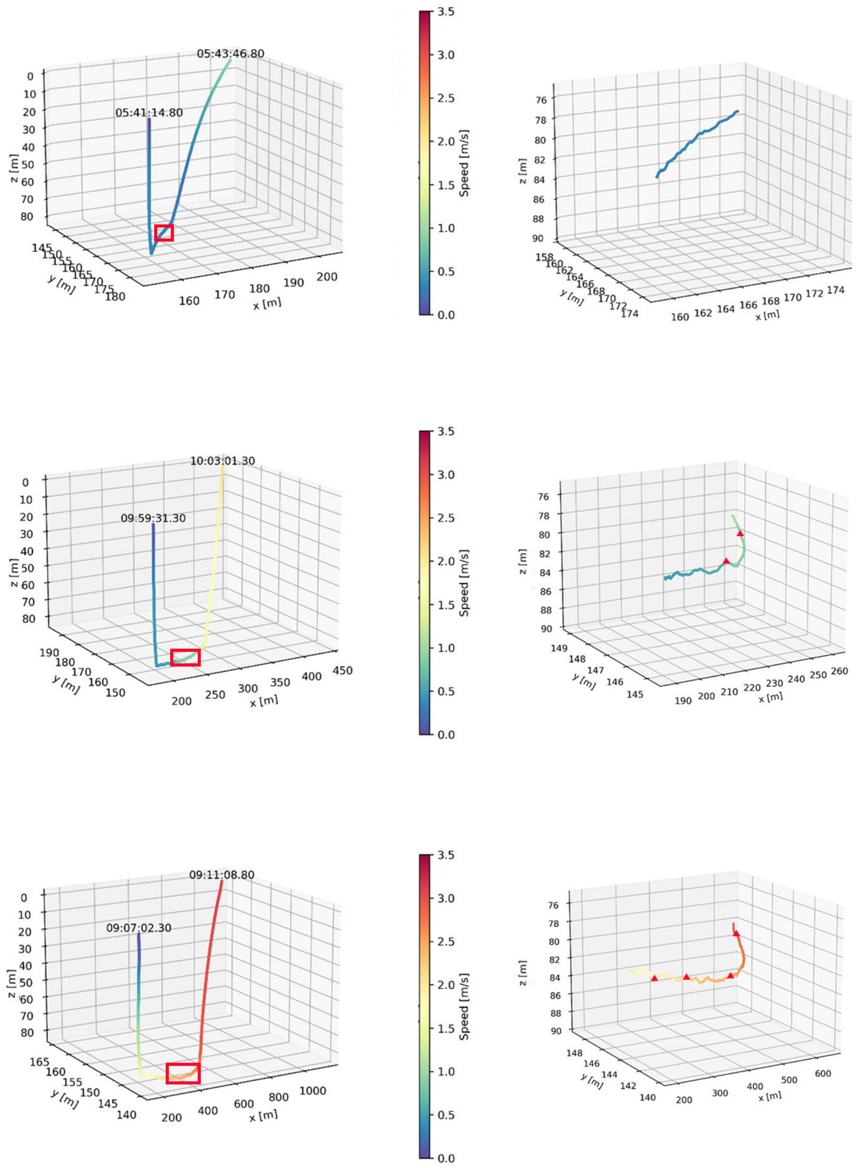

FIGURE 2
Representative 3-dimensional reconstructions of three foraging dives by adult female Australian fur seal (*Arctocephalus pusillus doriferus*) individuals from Kanowna Island in northern Bass Strait, south-eastern Australia. Swim speed along the track is indicated by the colour ramp. Right panels represent a zoomed in part of the track (indicated by red box in left panel). Red triangles denote recorded prey capturess events.

Directional heading during the descent and ascent phases of dives were generally consistent. In addition, while individuals on some dives made numerous directional changes during the bottom phase, travel throughout dives was in a relatively constant direction. To investigate whether individuals altered travel direction between dives, potentially as part of a prey searching strategy, the difference between the mean heading of descent during sequential dives was analysed. The change in heading varied considerably throughout trips and between individuals (mode: 35.0°, range: 0.02 - 179°). There was no significant influence of prey capture rate on change of direction (LME: t = -1.421; $P > 0.1$), indicating individuals did not alter their spatial search pattern in response to the success experienced in the preceding dive.

4 Discussion

Animals must adjust their behaviour in response to their prey field in order to optimise foraging success (Dylda and Wang, 2022). For benthic foraging air-breathing vertebrates, there is a need to maximise their time along the sea floor. The results of the present study suggest adult female AUFS optimise search time along the sea floor during benthic dives by travelling at high speeds to increase prey encounters. In addition, they alter pitch and swim speed during ascent and then subsequent descent phases in response to the success on the sea floor. Furthermore, the findings suggest AUFS do not adopt conventional Area Restricted Search (ARS) behaviour (i.e. increased track tortuosity) in response to

TABLE 2 Summary table showing modes of fine-scale behaviours for adult female Australian fur seal (*Arctocephalus pusillus doriferus*) individuals from Kanowna Island, in northern Bass Strait, south-eastern Australia, during the three dive phases: descent; bottom: and ascent.

Seal	Descent Phase				Bottom Phase				Ascent Phase			
	Duration (min)	Pitch (°)	Speed ($m \cdot s^{-1}$)	VeDBA (*g*)	Duration (min)	Directional turns (n)	Speed ($m \cdot s^{-1}$)	VeDBA (*g*)	Duration (min)	Pitch (°)	Speed ($m \cdot s^{-1}$)	VeDBA (*g*)
1	1.00	68.8	0.38	0.60	1.88	8	0.41	1.18	1.03	62.9	0.35	0.59
2	1.01	59.5	0.37	0.55	1.75	8	0.46	1.75	0.84	69.3	0.46	1.04
3	0.97	34.0	0.43	0.70	2.08	5	0.44	1.28	0.96	72.4	0.45	1.01
4	0.89	75.1	0.44	0.51	1.58	9	0.45	1.25	0.83	68.9	0.53	0.86
5	0.79	73.2	0.50	0.92	1.46	5	0.43	1.43	0.81	64.5	0.45	1.13

encountering successful foraging areas. Rather, in response to successful dives, individuals reduce the time away from the sea floor, reduce the horizontal distance travelled at the surface, and maintain heading, potentially to maximise searching in similarly profitable but undisturbed habitats of cryptic benthic prey. However, the present study was limited to 5 individuals and, therefore, the interpretation of the results should be viewed within this constraint.

4.1 Within-dive behaviour to optimise benthic foraging success

Since the foraging zone for benthic foragers is on the sea floor, transit periods to/from the sea floor are non-profitable areas and should be minimised in favour of longer bottom durations (Wilson and Wilson, 1988). A smaller proportion of the dive duration spent at the bottom might be expected in deep dives due to the greater travel distance consuming more energy/oxygen. However, consistent with previous findings in penguins (Zimmer et al., 2010) and other pinniped species (Schreer et al., 2001), the proportion of the dive duration spent on the sea floor (foraging zone) was positively influenced by dive depth in the present study. In addition, mean speed and pitch during descent was positively correlated with the proportion of the dive's bottom phase, indicating individuals prioritised rapid transit to the sea floor in order to maximise time in the foraging zone. Similar findings have been observed in rockhopper penguins (*Eudyptes chrysocome*), where greater descent rates and lower descent times were observed during benthic dives than pelagic ones, leading to greater bottom phase durations (Tremblay and Cherel, 2000).

The proportion of the dive duration spent on the sea floor by female AUFS was negatively influenced by swim speed in this dive phase. This is consistent with increased swim speeds being associated with higher metabolic costs (Feldkamp, 1987) and, thus, a greater use of available body oxygen stores (Hvas et al., 2017). However, the results of the present study suggest an apparent benefit of greater swimming speeds along the sea floor is increased prey encounter rates. Indeed, as AUFS prey mostly on cryptic benthic prey (e.g. numerous species of octopus (*Octopus*), gurnards (*Triglidae*) and leatherjackets (*Monacanthidae*)) (Kernaléguen et al., 2016), it may be advantageous to travel at high speeds to detect and capture unsuspecting prey before they disperse/hide (Zhang and Richardson, 2007). This is in contrast to harbour seals (*Phoca vitulina*) which were observed to swim at slower speeds when hunting cryptic prey in comparison to when hunting conspicuous species (Bowen et al., 2002).

Interestingly, in the present study, prey capture rate on benthic dives was found to increase with increasing sea floor depth. Foraging by female AUFS from Kanowna Island is almost exclusively restricted to central Bass Strait (Arnould and Kirkwood, 2007; Kirkwood and Arnould, 2012) where maximum depths range 60-80 m (Baird and Ridgway, 2012). Previous studies have shown an increase in benthic species diversity with depth in Bass Strait (Coleman et al., 1997). Consequently, foraging at these greater depths may provide AUFS greater prey diversity and, thus, better foraging opportunities.

TABLE 3 Best models of Linear mixed-effect (LME) and Generalized mixed-effect (GLME) models predicting factors influencing inter-dive and intra-dive behaviour, and VeDBA in adult female Australian fur seals (*Arctocephalus pusillus doriferus*) from Kanowna Island.

Response variable	Parameters	R^2	95% CI	*t-value*	*P*
Bottom phase duration	Descent pitch	0.317	0.30,0.40	11.78	**<0.001**
	Maximum depth		0.17,0.33	6.07	**<0.001**
	Mean descent speed		6.75,29.73	3.11	**0.002**
	Mean bottom speed		-12.50,-1.68	-2.57	**0.010**
Descent VeDBA	Descent pitch	0.187	-0.01,0.00	-7.01	**<0.001**
	Maximum depth		-0.01,-0.01	-9.70	**<0.001**
Bottom VeDBA	Number of directional movement changes	0.245	0.01,0.02	10.91	**<0.001**
	Maximum depth		0.00,0.01	2.50	**0.012**
Ascent VeDBA	Mean pitch	0.201	-0.02,-0.01	-9.67	**<0.001**
Ascent pitch	Prey capture rate	0.221	2.18,2.73	17.37	**<0.001**
	Mean ascent speed		14.75,26.12	7.05	**<0.001**
Ascent speed	Prey capture rate	0.526	0.02,0.02	17.05	**<0.001**
Post dive duration	Previous prey capture	0.123	-5.74,-3.56	-8.36	**<0.001**
Post Dive Distance travelled	Previous prey capture	0.141	-11.73,-8.11	-10.74	**<0.001**
Descent pitch	Previous prey capture rate	0.505	1.69,2.25	13.83	**<0.001**
	Mean descent speed		-3.39,13.39	1.17	> 0.1
Descent speed	Previous prey capture	0.579	0.00,0.01	7.43	**<0.001**
Response variable	Parameters	R^2	95% CI	*z-value*	*P*
Prey capture rate	Number of directional movement changes	0.437	0.01,0.02	5.25	**<0.001**
	Mean bottom speed		2.87,3.31	27.15	**<0.001**
	Maximum depth		0.02,0.03	6.88	**<0.001**
	Bottom phase duration		1.25,2.10	7.77	**<0.001**

Bold values indicate significant parameters.

The present study also found prey capture rate was positively related to the number of directional changes along the sea floor. While this could reflect an increase in prey encounters due to changes in search direction (Bell, 2012), the directional changes may reflect intentional movements towards detected prey (Bianco et al., 2011). Indeed, previous studies of AUFS instrumented with animal-borne video cameras have revealed individuals often make sharp turns upon detecting prey with a high degree of capture success (73%) (Meyers et al., 2021). However, without additional video data, it is not possible to disentangle the observed relationship between prey capture rate and directional changes during sea floor searches by AUFS. Nonetheless, such angular directional changes are likely to incur energetic costs and are likely undertaken only when foraging outcomes are more favourable than proceeding in a straight line (Wilson et al., 2013). This is supported by the observed greater mean VeDBA during the bottom phase of dives when more directional changes were made.

Individuals in the present study were found to have lower VeDBA when descending or ascending with greater (steeper) pitches. These findings may reflect the influence of buoyancy on mechanical power and the cost of transportation (Williams et al., 2000; Wilson et al., 2010). When buoyancy forces are taken into consideration, locomotion costs are lower when maintaining a vertical dive pitch (Thompson et al., 1993). For example, northern elephant seals (*Mirounga angustirostris*) had a higher cost of transport when a non-vertical pitch was adopted while diving compared to a vertical one (Miller et al., 2012). Hence, the most optimal technique to reach the seafloor foraging zone faster and with less energy or the sea surface for oxygen replenishment is to have higher (steeper) pitches.

4.2 Inter-dive foraging behaviour strategies

Optimal diving models propose individuals should maximise the bottom phase of dives to enhance prey encounter opportunities (Boyd et al., 1997). Indeed, the results of the present study suggest benthic diving AUFS maximise search time on the sea floor by minimising oxygen consumption (i.e. energy expenditure) during the descent and ascent phases. However, knowing where to dive for encountering productive habitats leads to optimal foraging (Humphries et al., 2010). Air-breathing pelagic marine predators

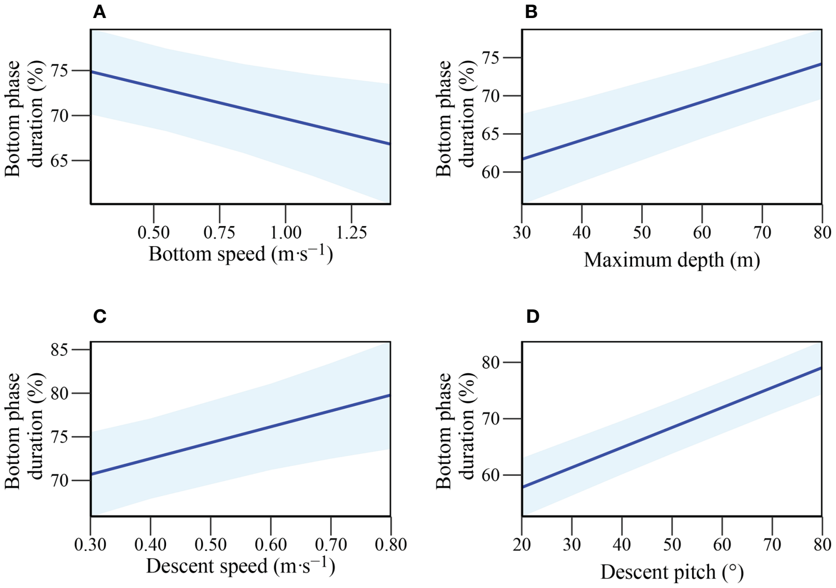

FIGURE 3
Relationship of Bottom phase duration (%) with: **(A)** Mean bottom speed (m·s^{-1}); **(B)** Maximum depth (m); **(C)** Mean descent speed (m·s^{-1}); **(D)** Descent pitch (°) in adult female Australian fur seals (*Arctocephalus pusillus doriferus*).

foraging in the water column have been shown to employ ARS at the surface to optimise foraging success (Fauchald, 2009; Weimerskirch et al., 2009). Since pelagic prey species form transitory and unpredictable aggregations (Weber et al., 2021), a strategy of increasing sinuosity, decreasing speed, and focusing search in small areas has been shown to lead to increases in energy intake in pelagic predators (Corbeau et al., 2019).

In contrast, relatively little is known of the search patterns of benthic foragers (Blakeway et al., 2021). Unlike pelagic foragers, benthic divers do not appear to have clearly defined bouts of diving related to patch quality (Shoji et al., 2015). In addition, previous studies suggest benthic foragers spend a large portion of their time at sea diving (Costa et al., 2004) while in a constant travel direction (i.e. commuting along the

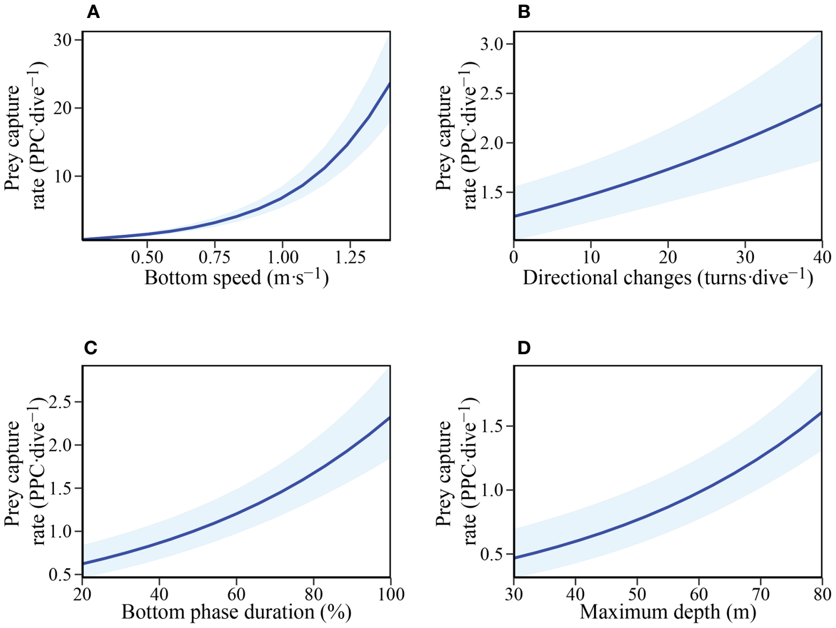

FIGURE 4
Relationship between Prey capture rate (Potential prey capture (PPC) ·dive^{-1}) and: **(A)** Mean bottom phase speed (m·s^{-1}); **(B)** Number of directional changes (turns·dive^{-1}); **(C)** Bottom phase duration (%); and **(D)** Maximum depth (m) in adult female Australian fur seals (*Arctocephalus pusillus doriferus*).

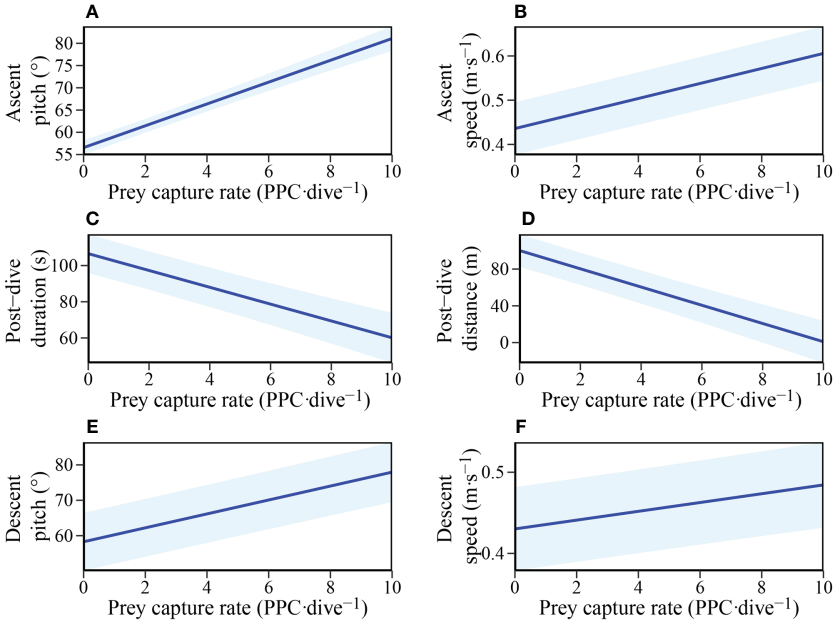

FIGURE 5
The influence of Prey capture rate (PPC·dive^{-1}) within a dive on: **(A)** Ascent pitch (°); **(B)** Mean ascent speed (m·s^{-1}); **(C)** Post-dive duration (s); **(D)** Post-dive surface travel distance (m); **(E)** Next dive descent pitch (°); and **(F)** Next dive mean descent speed (m·s^{-1}) in adult female Australian fur seals (*Arctocephalus pusillus doriferus*).

sea floor) (Ramasco et al., 2015). While this could be a mechanism for avoiding predation at the surface (Brown et al., 2010), it may also be a strategy for optimising search time (Mattern et al., 2007).

Australian fur seals primarily feed on benthic prey, as their large body size makes chasing small, highly agile pelagic species inefficient when in low abundance (Arnould and Hindell, 2001; Arnould and Costa, 2006; Hoskins and Arnould, 2014). Correspondingly, individuals should maximise search time along the seafloor. In the present study, following prey captures during the bottom phase of a dive, individuals increased both the pitch and the speed of ascent (Figure 5). This strategy could potentially be undertaken to minimise the transit time to the surface for oxygen replenishment once a profitable foraging habitat has been found. The increase in ascent pitch would also result in less horizontal distance being travelled from the productive habitat. In addition, the horizontal distance individuals travelled at the surface decreased with increasing prey capture rate on previous dives. Furthermore, a decrease in post-dive duration after successful dives was also recorded, suggesting individuals may remain at the surface only to replenish body oxygen stores before returning to profitable seafloor habitats as rapidly as possible (Cook et al., 2008). Lastly,

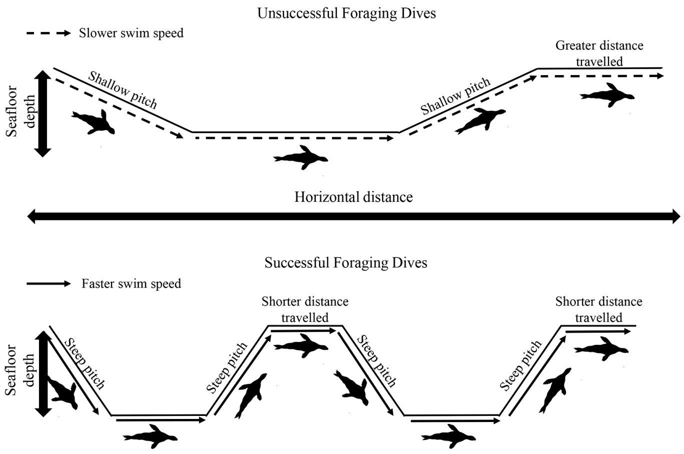

FIGURE 6
Graphical representation of diving behaviour in adult female Australian fur seals (*Arctocephalus pusillus doriferus*) associated with unsuccessful and successful foraging dives.

prey capture rate of the previous dive elicited an increase descent pitch, again potentially minimising the horizontal distance travelled from the previously exploited productive habitat, and descent swim speed, minimising transit time to the seafloor. Together, these findings suggest that central place foraging adult female AUFS individuals provisioning pups on land adopt fine-scale movement strategies at sea to maximise hunting opportunities in profitable seafloor habitats (Foo et al., 2016). Furthermore, the results of the present study suggest that benthic foraging adult female AUFS do not display conventional ARS behaviour. This is consistent with a previous study of the species which highlighted that areas of apparent ARS did not coincide with diving activity (Hoskins et al., 2015b). Indeed, the directional change for subsequent dives was not related to prey capture rate, suggesting that individuals do not focus searching activity in already exploited successful areas and, instead, move to new areas. This is in contrast to what has been observed in numerous pelagic marine predators where individuals adopt high sinuosity in search patterns once productive foraging areas are encountered (Freitas et al., 2018). One potential reason for the strategy observed in AUFS could be the prey type encountered by benthic foragers. Prey density is known to be the key factor for the adjustment of predator foraging behaviour (Mori et al., 2007). For example, the number of feeding lunges during dives by blue whales (*Balaenoptera musculus*) was proportional to krill density (Hazen et al., 2015). In the presence of predators, cryptic prey reduce movements and activity (Stein and Magnuson, 1976; Dill and Fraser, 1984) and/or move to and hide in protective habitats (Werner et al., 1983; Power et al., 1985). Once a predator has been detected, cryptic prey may hide for a very long time (Edmunds, 1974). In addition, prey have been found to reduce and randomize their movements to improve survivorship (Mitchell and Lima, 2002). As a counter-move, predators have been shown to delay their follow-up attacks (Mitchell, 2009) and expand their hunting activity over several areas (Brown et al., 1999; Lima, 2002). For example, sharp-shinned hawks (*Accipiter striatus*) have been found to use their foraging area unpredictably on a spatial and temporal degree, avoiding prey hotspots where prey vigilance is higher (Roth and Lima, 2007). Hence, for AUFS hunting cryptic benthic prey such as octopus, gurnards and leatherjackets (Kernaléguen et al., 2016), the best option may be to search in similar, nearby habitats rather than going over the same area again. Indeed, while successful dives did not elicit a change in heading, the horizontal distance travelled was reduced, potentially increasing the probability of covering similar productive but undisturbed habitats. In contrast, after unsuccessful dives, individuals had shallower pitch in ascent, travelled further at the surface and descended on the next dive at a shallower pitch, increasing the distance from an unproductive foraging zone to potentially increase the probability of encountering prey in a different habitat (Figure 6). A similar strategy of consistent heading in successful foraging routes has been suggested for benthic-foraging yellow-eyed penguins (Mattern et al., 2007). Studies of fine-scale hunting movement in other benthic-foraging marine predators are needed to determine whether this is a wide-spread strategy. In summary, the present study revealed adult female AUFS individuals adjust their fine-scale movements in relation to their prey field. The proportion of dive time spent in the bottom phase (foraging zone) was increased by travelling to and from the surface at steeper pitches and faster swim speeds following successful dives. An increase in the number of directional changes along the seafloor resulted in greater energetic costs during the bottom phase but this was compensated by an increase in prey capture rate. In addition, individuals did not adopt conventionally-described ARS, as successful dives were not associated with increased path tortuosity. Rather, individuals appear to adopt a strategy of hunting in similar but undisturbed seafloor habitats by maintaining a relatively constant heading and reducing the horizontal distance travelled after successful dives. These findings reveal important new insights into how air-breathing marine benthic predators exploit their foraging habits and provide a basis for future understanding of how animals could respond to environmental changes.

Data availability statement

The datasets presented in this study can be found in online repositories. The names of the repository/repositories and accession number(s) can be found below:Zenodo repository [10.5281/zenodo.10467539] https://zenodo.org/records/10467540?token=eyJhbGciOiJIUzUxMiJ9.eyJpZCI6IjAwODE2NTYyLTM5ZTItNGQ0Ni05NWE3LTY5NWNmMTBmYThlNSIsImRhdGEiOnt9LCJyYW5kb20iOiIzMmM5ZTljNmFlMTFjNWFiZjkxOTE4NTgxYzUzZDEwZiJ9.vsulFZILi0cLE56suJG06oh-d4mcQpermvojoGRFTsJxtPvKrYZVJr7yVlec0NAFTkooAz8OOOIEWHvieMH4jw.

Ethics statement

All research procedures were approved by the Deakin University Animal Ethics Committee (A16-2008, A14-2011, B16-2014) and conducted under a Department of Land, Water Environment and Planning (Victoria, Australia) Wildlife Research Permits (10005484, 10007153, 1000826).

Author contributions

PS: Data curation, Formal analysis, Methodology, Writing – original draft, Writing – review & editing, Conceptualization, Investigation. SL: Data curation, Formal analysis, Writing – original draft, Writing – review & editing, Conceptualization, Methodology. JA: Conceptualization, Data curation, Funding acquisition, Methodology, Project administration, Resources, Supervision, Writing – original draft, Writing – review & editing, Investigation.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2024.1368756/full#supplementary-material

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