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Dynamic foraging by Risso's dolphins revealed in four dimensions

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ABSTRACT: Quantifying details of an animal's foraging strategy can provide insight into its energetic requirements, environmental constraints, and other pressures it must balance in behavioral decision-making. Data from ship-based echosounders provided 4888 observations of Risso's dolphins *Grampus griseus* in the context of heterogeneous prey fields, while an autonomous underwater vehicle carrying similar instruments was used to describe 519 discrete prey patches containing dolphins. We integrated these data with prey net tows, dolphin surface observations, and results from a parallel tagging study that quantified detailed aspects of behavior of 3 individuals. These data provide complementary perspectives on the foraging strategies of Risso's dolphins at a range of time scales from individual prey patch selection to diel cycles. Rather than being solely nocturnal teuthivores as previously suggested, we found that Risso's dolphins dove to depths exceeding 500 m both day and night. Risso's dolphins switched many times daily from being more generalist predators near the surface to specializing on larger squid at depth, commonly within the course of a single 5–10 min dive. Simple energy calculations suggest that shallow prey comprise relatively small contributions to individual energy gains, yet these prey played a strong role in determining the spatio-temporal habitat use of Risso's dolphins. This underscores the importance of examining strategic foraging behavior in light of requirements to access both prey resources and oxygen. The novel integration of multiple complementary sensing methods employed simultaneously on Risso's dolphins provide remarkable insights into the behavioral ecology of individuals and the population.

KEY WORDS: Foraging strategy · Pelagic · Odontocete · *Grampus griseus* · Acoustics

1. INTRODUCTION

Efficient foraging is critical to individual fitness (MacArthur & Pianka 1966, Charnov 1976a). The collection of decisions and actions used by an individual to best obtain food resources is often described as a foraging strategy. Aspects of an animal's strategy include prey selection, dietary breadth, and movement between resources. Measuring these behaviors can reveal much about the energy needs, environmental constraints, and other pressures that must be balanced when making foraging decisions (Charnov 1976b). Species-specific foraging strategies also reveal how a species may influence the ecosystem (Huey & Pianka 1981, Dell et al. 2014), its ability to respond to change (Robinson et al. 2007), and its interactions with humans (Monk et al. 2018).

One key aspect of an animal's foraging strategy is prey choice. This behavior falls on a continuum where 'generalist' predators at one extreme forage on a wide range of prey types. Conversely, 'specialists' predominantly or exclusively use a single prey

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type. Sometimes prey specialization is dynamic; the predator shifts from its preferred prey type to an alternative when the main prey is scarce or hard to acquire, a process referred to as 'prey switching' (Murdoch 1969). Prey switching has been documented in a wide range of taxa (e.g. Ostfeld 1982, Kiørboe et al. 1996, Suryan et al. 2000, Kjellander & Nordström 2003). Most commonly, prey switching has been described seasonally or interannually, mainly because of the challenges of measuring fine-scale dynamics of prey and predator behavior over shorter intervals (Paiva et al. 2010). However, animals live in a dynamic landscape and must develop tactics in response to multi-scale spatio-temporal changes in prey distribution, potentially on very fine scales. This is particularly true of pelagic marine ecosystems where the constantly moving medium drives dynamic spatial patterns much more rapidly than is typical in many other ecosystems (Steele 1991, Steele et al. 1994). Pelagic predators must assess and respond to those changes over a wide range of spatial scales to meet their foraging needs (Hazen et al. 2015).

The heterogeneity of resources in the ocean led us to hypothesize that prey switching may be more prevalent and frequent in marine predators. The dynamics of difficult-to-access marine habitats have made understanding the tradeoffs in prey selection in pelagic systems a challenge. Provisioning seabirds, which are particularly amenable to foraging studies because of their frequent returns to land, sometimes rapidly alter their foraging strategy; they alternate between one type of prey acquired far from their nest for themselves and a different, often less profitable prey, for their offspring acquired closer to the nest (Chaurand & Weimerskirch 1994, Paredes et al. 2014). Underwater, an additional dimension is added to the prey landscape. For air-breathing predators, including seabirds and marine mammals, the pelagic also partitions 2 key resources: food at depth and oxygen at the surface. Along with vertical heterogeneity in prey availability (Benoit-Bird et al. 2013), the costs of foraging for these breath-hold divers increase dramatically with depth, setting up conditions amenable to prey switching.

A variety of techniques including bio-logging, passive acoustics, active acoustics, imaging, and direct sampling are now making it possible to observe the dynamics of prey and predator behaviors beneath the ocean's surface. Unfortunately, disparate techniques are often used to assess predator and prey, resulting in data that are mismatched in resolution and scale (reviewed by Rose & Leggett 1990, Benoit-Bird & Au 2003). Active acoustic techniques, primarily echosounders, have proven successful in synoptically describing the distribution and behavior of predators and prey (e.g. Nøttestad et al. 2002, Benoit-Bird & Au 2003). These techniques have been used most successfully to quantify the foraging ecology of air-breathing predators, including seabirds and dolphins (Axelsen et al. 2001, Nøttestad & Similä 2001, Benoit-Bird et al. 2011), taking advantage of the significant differences in acoustic properties of the air-filled predator and their much smaller prey (reviewed by Benoit-Bird et al. 2009).

To explore how air-breathing predators may change their prey selectivity in a 4-dimensional ecosystem, we sought to examine the foraging ecology of a top marine predator with an apparently dynamic foraging strategy and whose main prey is sometimes difficult to access. The moderate-depth (~500 m) diving Risso's dolphin *Grampus griseus* meets both of these criteria. Risso's dolphins, the fifth largest members of the family Delphinidae, are found in shelf and slope waters of tropical to temperate zones throughout the world (Baird 2002). Their habitat includes the entirety of the US west coast, a region which contains a single distinct population (Carretta et al. 2010). Stomach contents from stranded and bycaught Risso's dolphins around the world indicate that their diet is nearly exclusively cephalopods, particularly muscular mesopelagic squid species (Baird 2002). Limited behavioral (Shane 1995) and passive acoustic research suggests that Risso's dolphins feed primarily at night (Soldevilla et al. 2010, Au et al. 2013), presumably exploiting prey that exhibit diel vertical migration which makes them more accessible to air-breathing predators at night. However, recent work has indicated that under some circumstances Risso's dolphins may also forage hundreds of meters deep during the day (Benoit-Bird et al. 2017, Arranz et al. 2018), as well as over shallow water (Arranz et al. 2019), revealing the potential for plasticity that makes this species an excellent subject for examining the environmental pressures affecting its approach to energy acquisition.

These recent efforts have also resulted in the development of new tools that allow the *in situ* observation of presumed prey selection through hydroacoustic measurements (Benoit-Bird et al. 2017). In this study, we deployed these acoustic tools from an autonomous underwater platform to simultaneously measure predator and prey at the scale of the individual. This high-resolution view was complemented by the rapid coverage and larger sampling volume of more traditional ship-based acoustic sensing in the first application of this approach for Risso's dolphins. Finally, visual surveys and net tows provided species identification of both predator and prey. These carefully integrated sampling approaches afford a population-level perspective on foraging ecology, complementing the detailed individual measurements made on a small number of animals in a concomitant tagging study. We applied simple energetic analysis to integrate results from all of these tools to estimate the relative value of various components of Risso's dolphins' foraging strategy to evaluate their behavioral selectivity within the context of foraging specialization.

2. MATERIALS AND METHODS

In the Southern California Bight, off the eastern coast of Santa Catalina Island, California (USA), we used a suite of sampling tools to describe the behavior of Risso's dolphins and the small pelagic squid, fish, and crustaceans that are their potential prey. Sampling occurred in an area of about 30 km^2 over 10 d and nights in September 2013 over the San Pedro Basin, a semi-enclosed channel averaging depths of ~850 m and bordered to the east by the coast of California near Los Angeles, the west by Santa Catalina Island, and to the north and south by shoals ~300 m deep. The area around Santa Catalina Island is an important area for Risso's dolphins year-round, although it is particularly well-used in the fall (Soldevilla et al. 2010), overlapping the time period of the field sampling here. Acoustic data were collected from 2 different platforms. We conducted ship-based echosounder surveys using split-beam EK 60 echosounders to characterize the time-space distribution of scattering features and individual diving dolphins throughout the water column (maximum seafloor depth in sampled areas was ~925 m). We also employed a novel, autonomous echosounder system (downward-looking, split-beam Simrad EK60s at 38 and 120 kHz) integrated into an advanced autonomous underwater vehicle (AUV: 'REMUS 600') capable of sampling within scattering layers at depths down to 600 m (Moline et al. 2015). The AUV allowed us to resolve the distribution of individual animals within scattering layers, attribute them to scattering classes, measure their length, and observe the relationship between these features and dolphins to infer prey selection. Midwater trawls were used to identify and measure the constituents of scattering features, while visual observations from the ship were used to quantify marine mammal species.

2.1. Acoustic data

The research vessel acoustic data provided a full water column view of scattering layers that may serve as food for Risso's dolphins as well as a population-scale view of the habitat use of diving dolphins. On the RV 'New Horizon,' the transducers for a 4-frequency EK60 system (38 kHz with a 12° conical beam, and 70, 120, and 200 kHz each with a 7° conical beam) were mounted on a pole 1 m beneath the surface. Data were collected continuously throughout the expedition. During the acoustic surveys presented here, the vessel traveled at about 2.5 m s^{-1}. Each calibrated echosounder used a 512 µs long pulse at a rate of 1 Hz and a source level <180 dB re 1 µPa (rms).

The AUV acoustic measurements allowed us to resolve the individual targets inside scattering layers and examine the relationship between these animals and Risso's dolphins detected simultaneously (Benoit-Bird et al. 2017). The AUV carried 2 split-beam echosounders, 38 and 120 kHz, both with 7° conical beams. The AUV traveled at a speed of ~1.5 m s^{-1} at pre-determined depths between 50 and 500 m, depending on the locations of layers identified from the ship-based echosounders. Each calibrated echosounder used a 512 µs long pulse at a rate of 1 Hz and a source level <180 dB re 1 µPa (rms). For a more detailed description of the sensors and platform, see Moline et al. (2015).

Acoustic scattering data from both platforms were processed using Echoview software. Before analysis, the data were preprocessed to remove the seafloor and noise. A number of individual Risso's dolphins were visually observed swimming directly beneath the ship-based echosounders. The echoes from these dolphins were consistent with those from previous studies of marine mammals which allow them to be isolated and identified (Figs. 1 & 2). These characteristics include a flat frequency response, consistent, high-intensity scattering from the center of each animal (likely from its air-filled lungs), surrounded by lower intensity scattering from well impedance-matched blubber (Au 1996), along with overall size and shape (Benoit-Bird et al. 2009). Targets that exhibited a flat (±1.5 dB) frequency response in volume scattering and had at least 1 target strength measurement about −15 dB or an equivalent volume scattering strength were automatically flagged for assessment by an experienced analyst who confirmed that the echo's morphological characteristics (length, vertical dimension, and vertical and horizontal position of the lung echo) were consistent with

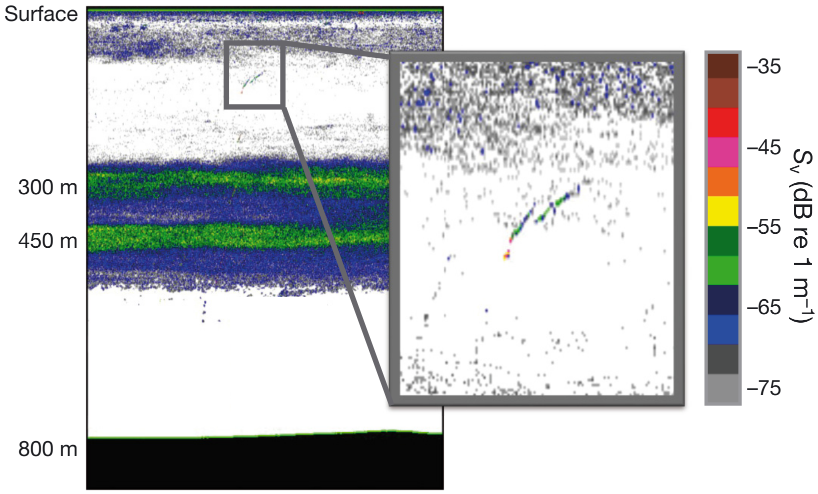

Fig. 1. Echogram showing the 3 scattering layers (surface, 300 m, and 450 m depth) identified in the Catalina Basin along with echoes from 2 Risso's dolphins (inset) diving downwards after surfacing next to the research vessel

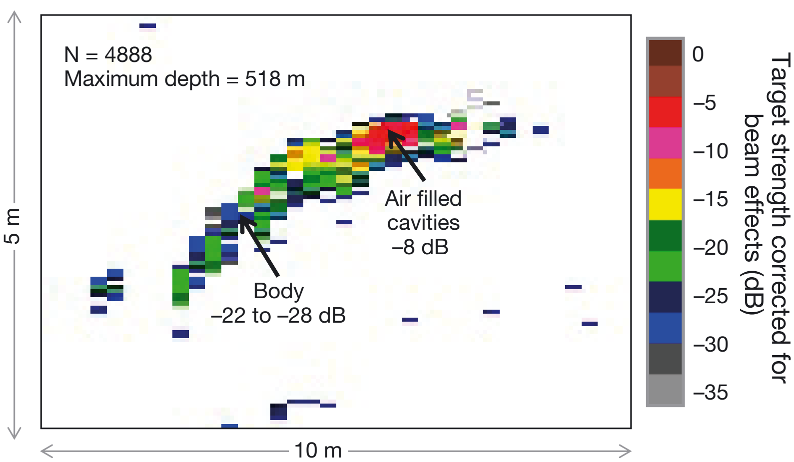

Fig. 2. Detailed echogram of a Risso's dolphin just before it ascended next to the research vessel, showing the key characteristics used to identify these targets. A total of 4888 echoes consistent with Risso's dolphins were identified during the study down to a maximum depth of 518 m

expectations for a dolphin target. The 4-dimensional location of each dolphin echo was noted and masked for further analyses of the scattering features.

We identified 4 spatially distinct scattering features (Fig. 3) of the foraging habitat within which dolphins were diving. These included: a shallow scattering layer centered around 50 m depth, a midwater scattering layer near 300 m that migrated to the surface at night, a region of scattered patches that was intermittently present between these 2 layers, and a scattering layer near 425 m that remained at depth at night. We delineated the upper and lower edges of each layer using a scattering threshold of –60 dB for the 2 deep layers during the day and all layers at night and a threshold of –65 dB for the shallow daytime layer. These thresholds were determined empirically as those which contained at least 95% of the total acoustic energy within each feature while allowing contiguous boundaries to be delineated and linked using a particle tracking approach (Cade & Benoit-Bird 2014). Within each layer, we calculated the mean volume scattering strength in 5 km intervals to describe changes in their intensity over space and time.

Ship-based echosounder detections of dolphins were used to describe their overall distribution at a population level. Each detection was attributed to the scattering feature it was within or when not clearly surrounded by a scattering feature on at least 3 sides, a value of none. For calculation of dolphin detection rates, the depth of each dolphin detection was corrected for search area differences as a function of depth by dividing by the diameter of the beam at that depth (Benoit-Bird & Au 2003). The rate of dolphin detections was calculated for 5 km segments of surveys during the day, defined as 1 h after sunrise to 1 h before sunset, and at night, defined as 1 h after sunset to 1 h before sunrise. These calculations were conducted as a function of depth within the water column and, separately, as a function of scattering feature. A 2-sample Kolmogorov-Smirnov test was used to compare the vertical distribution of dolphin echoes during the day and at night. A paired-samples *t*-test was used to compare the daytime and nighttime detection rates of each scattering feature. The dolphin detection rate throughout the water column was separately calculated as a function of the mean volume scattering strength of each of the 3 scattering layers during the day and 2 at night in each 5 km segment of ship-based echosounder surveys to observe the effects of variation in each layer in the overall habitat use by dolphins.

Acoustic data from the AUV were analyzed for single targets; target strength and frequency response of these targets was reduced to a single metric of similarity; discrete patches within scattering layers

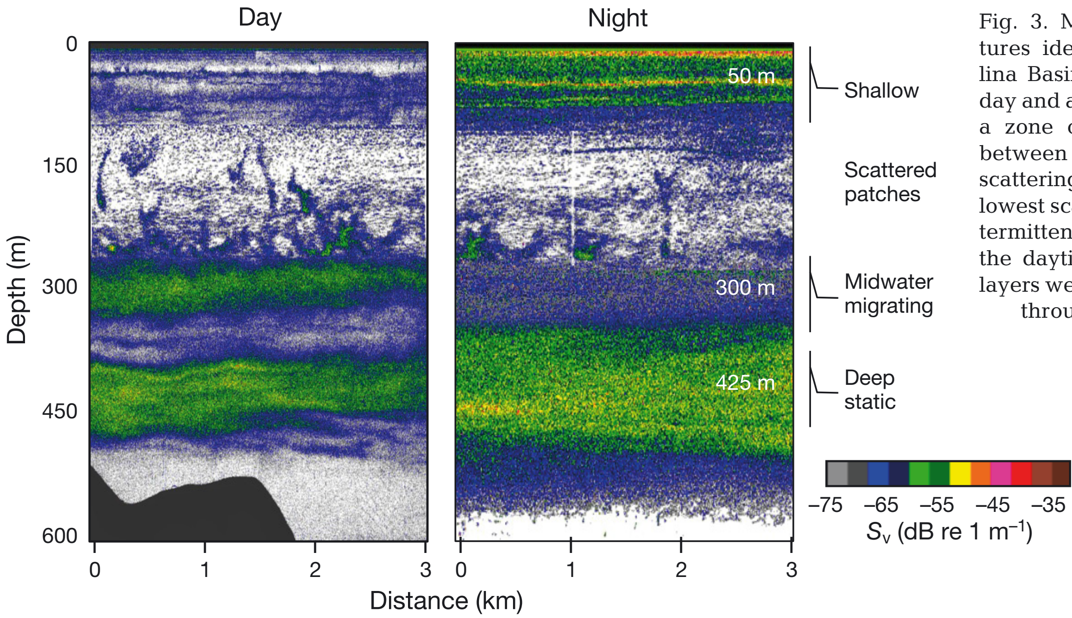

Fig. 3. Major scattering features identified in the Catalina Basin, shown during the day and at night. We observed a zone of scattered patches between 50 and 200 m and 3 scattering layers. The shallowest scattering layer was intermittently present during the daytime, but the other 2 layers were found consistently throughout the region

were identified; the frequency response and mean target strength of animals in each patch were characterized (as in Benoit-Bird et al. 2017). The characteristics of patches containing dolphins were compared to those that did not contain dolphins as a function of scattering layer both day and night. The interpretation of the results was aided by classification of acoustic targets. Targets measured from the AUV were identified as (1) consistent with squid if their target strength at 38 kHz was 3.1–10 dB higher than their 120 kHz target strength, as (2) fish if target strength values between the 2 frequencies were no more than 3 dB different, and as (3) crustaceans if the differences was >–3 dB. Target strength can be interpreted as a proxy of length within each taxonomic class ('squid,' 'fish,' and 'crustacean'). Conversions to estimated metric length to support the interpretation of the results were made following Benoit-Bird et al. (2017). A chi-squared test was used to determine if the composition of patches was independent of the presence or absence of dolphin echoes. A multivariate ANOVA (MANOVA) was used to determine if there was a significant effect of layer and dolphin presence on the mean target strength measured for each patch.

2.2. Direct samples and observations

As reported by Benoit-Bird et al. (2017), we conducted net tows from the ship with a 4 m^2 mouth-opening Isaacs-Kidd midwater trawl with a 3.2 mm mesh net equipped with a real-time pressure sensor (Simrad PI-32) to validate the relative composition data obtained from the AUV-based acoustic data. The net was towed for a total duration of 20 min within the same layer targeted by the AUV during each mission and then hauled back. Deployment and recovery were achieved using a rate of 20 m of wire min^{-1} which reduced the mouth opening to near 0. The net, which was dark in color, towed at relatively high speeds of 1–2.2 m s^{-1}, and with minimal hardware to create a head wake, captured mobile organisms with body lengths between 1 and 35 cm (outliers excluded). Net samples were immediately preserved in 4% buffered formalin in seawater. In the laboratory, individuals were measured and identified to species. From each tow, the dominant classes (by taxon and size group) of organisms were identified as those that together accounted for at least half of the catch. To compare to acoustic data, catch data were grouped into 3 major groups: fishes, shrimp, and squids. The relative proportions of these groups were compared against those obtained from AUV-based acoustic data at the same time in the same location using a Bray-Curtis test followed by a permutational ANOVA (Goslee & Urban 2007).

To identify the presence of air-breathing predators and estimate their relative abundance, a visual observer on the bridge identified all marine mammals observed to species, estimated the number of individuals, their abundance, behavioral state (Baird & Dill 1995), and position relative to the boat. These observations were made during all daytime underway surveys, matching the time windows for approximately half of all of the dolphin detections with the ship-based echosounder. The times that any individuals were visually observed to swim beneath the vessel was specifically noted for comparisons with the ship-based echosounder data.

2.3. Estimation of relative foraging gains

To provide insights into the benefits of the various prey layers exploited by Risso's dolphins, we integrated our data to estimate the relative energetic value of each prey layer to the dolphins. While a simplified proxy of gross energy gains, this relativistic approach (following Benoit-Bird 2004, Southall et al. 2019) provides an important understanding of how foraging choices integrate into an overall strategy. We interpreted the relative proportion of animal detections in each layer from ship-based echosounders as the average time dolphins spent foraging in each layer. This interpretation is reasonable based on concomitant tagging of individual Risso's dolphins, which showed that when these animals were diving, they were actively foraging (Arranz et al. 2018, 2019). From the AUV measurements, we obtained the proportion of each prey type and the average size of prey selected by Risso's dolphins. The caloric value of the average size of each prey type in each layer was calculated following previous work (Benoit-Bird & Au 2002, Benoit-Bird 2004). We assumed a constant rate of prey capture to estimate the potential gross energy gains in each layer per unit time. This rate of energy gain was combined with the proportion of time spent by the population in each prey layer to develop a coarse estimate of the energy gains possible from each distinct prey layer.

2.4. Sampling effects

Any time that we sample, it is important to consider whether our presence or sampling may have affected the outcome measured. This question is particularly salient when sound, a key sense for marine mammals, is used to examine their environment (Frisk et al. 2003). While strong effects of military sonars on some species of marine mammals are well-documented (Bernaldo de Quirós et al. 2019), studies of the effects of scientific echosounders on marine mammal species are limited (Quick et al. 2017). No controlled echosounder exposure studies exist for Risso's dolphins. Controlled echosounder exposure studies in other odontocete species have shown modest effects on some behaviors (Cholewiak et al. 2017, Quick et al. 2017), although Quick et al. (2017) noted no evidence for a change in the foraging behavior of pilot whales, a species that is a moderately deep-diving, teuthivorous delphinid cetacean, like Risso's dolphins. Field studies of foraging marine mammals have documented few, if any, observed effects of echo sounder-type active acoustic studies on the behavior of marine mammals (Nøttestad et al. 2002, Benoit-Bird & Au 2003). Like other field studies of foraging behavior and ecology, ours was not explicitly designed to measure the behavioral responses of Risso's dolphins to echosounder sampling.

While our study did not include a controlled exposure design, we did have high-resolution animal-borne tag measurements from the same area and sampling period. The acoustic recorders on the tags of all 3 animals recorded echosounder signals from the ship, and in 2 animals, from the autonomous platform. All 3 of these tags and those from a number of other Risso's dolphins in the area at other time periods (Arranz et al. 2019) recorded sounds from other echosounder sources as well, suggesting that narrow-band signals of short-duration and relatively high-frequency are a regular feature of the habitat. Examining the time periods when our echosounder signals were recorded on the tags in detail and comparing them to similar time periods before and after revealed no significant effects of echosounder pings from either the vessel or the AUV on dive pattern, orientation, degree of turning angle, incidence of acoustic behavior, or other metrics (Arranz et al. 2018). This, combined with the large number of detections of dolphins by our echosounders (some made in very close proximity to the source), suggests a limited effect of our sampling on the animals' gross behavior.

Other potential reasons for modifications of animal behavior cannot be ruled out. Tracks of epipelagic and mesopelagic animals measured near the AUV showed no bias in their direction of movement, suggesting limited avoidance or attraction to the vehicle (Benoit-Bird et al. 2017). We also observed no obvious behavioral responses from our visual sampling: dolphins were not seen bow-riding or changing swimming direction as the surface vessel passed. Our visual surveys did not strictly follow the form of a line-transect for density estimation of marine mammals because of the relatively small sampling region. A qualitative comparison, however, between our daytime visual observations and acoustic detections within the upper 50 m of the water column were similar, while overall acoustic detection rates were higher than the visual surveys, perhaps not unexpectedly given the larger sampling volume. It should be noted that our sampling design involved pre-planned, relatively long, linear transects through the area with the ship and the autonomous platform and thus Risso's dolphins would likely have been able to avoid the platforms and the narrow echosounder beams below them if they chose to. In addition, the power levels on the echosounders were carefully chosen to limit the source levels of the echosounders while maintaining an appropriate signal-to-noise ratio, particularly for the 38 and 70 kHz systems that would have been most audible to this species.

3. RESULTS

3.1. The context: prey layers

Using the ship-based echosounders, 4 biological scattering features were identified throughout the study area (Fig. 3). Between 100 and 250 m, we observed scattered patches 10–100 m in horizontal extent with a flat frequency response ($S_{v120kHz} - S_{v38kHz} = -2.6$ to 2.2 dB), consistent with fish. No net tows were carried out within these patches. Three scattering layers were observed. As reported by Benoit-Bird et al. (2017), the relative composition of net tows from within each of these 3 layers matched the relative composition of acoustically classified individuals in the AUV data set when sampling effort was accounted for (Bray-Curtis test values 0.01–0.08, $p > 0.05$ for all comparisons). Centered around 50 m, the shallowest layer was intermittently present. Observed above our typical echo integration threshold about 50% of the time, this shallow layer could change presence on repeat sampling of the same transect line. Net tows targeted at this layer were dominated by larval fish and a diverse array of small crustaceans. A midwater layer, centered around 300 m during the day but less than 100 m at night, was observed throughout the study area. Net tows from within this layer were numerically dominated by myctophids and krill, which together made up >90% of the total catch. The deepest layer was observed around 450 m both day and night throughout the study area, although the vertical extent of the layer expanded from approximately 50–75 m during the day to approximately 100–125 m at night. Net catches were made up primarily of dragonfish, squid, shrimp species, and large krill. The catch within each layer was similar throughout the study region (PERMANOVA $F = 1.17$, $p > 0.35$).

3.2. Regional-scale observations of Risso's dolphins and prey

Echoes consistent with dolphins (Benoit-Bird et al. 2009) were detected frequently throughout the study area. A total of 4888 individual detections were made from the ship-based echosounders (Figs. 1 & 2), with a maximum observed depth of 518 m. In 3 individual animals tagged at the same time and place, the maximum recorded dive depth was 560 m (Arranz et al. 2018). During the duration of our experiment, ship-based visual observations revealed that more than 95% of the marine mammals and nearly all of the cetaceans observed were *Grampus griseus*. Because of the abundance of sightings, we interpreted all dolphin echoes as Risso's dolphins in the remainder of the results.

Echoes from Risso's dolphins were detected throughout the water column using the ship-based echosounders to look for their unique echo signatures. However, the distribution of these snapshots of individual location changed at night (Kolmogorov-Smirnov test, $D = 0.47$, $p < 0.05$, Fig. 4). During the

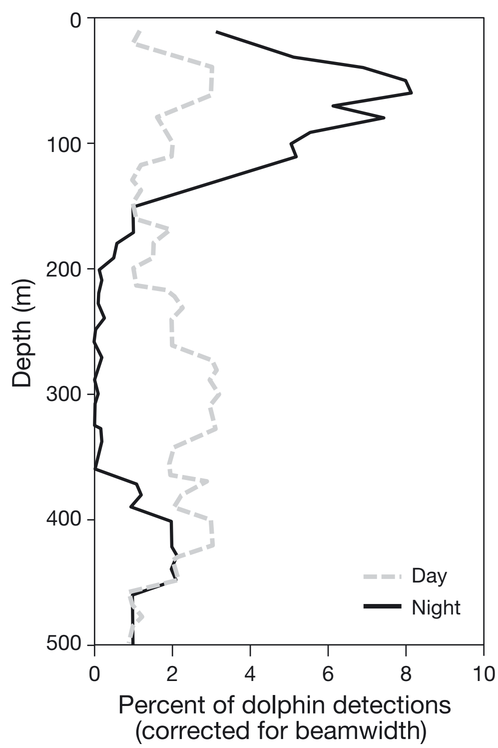

Fig. 4. Distribution of dolphin targets measured from ship-based echosounders throughout the water column during the day and night, showing that dolphins forage down to depths of 500 m throughout the day and night but are found more often near the surface at night when some of their potential prey migrates to the surface. Dolphin detections are corrected for depth-dependent changes in sampling due to the beamwidth of the acoustic transducers

daytime, dolphin echoes were relatively evenly distributed from the surface to 500 m, while at night, when the midwater scattering layer migrated upwards, very few dolphins were detected between 175 and 350 m. However, Risso's dolphins were detected between 350 and 500 m both day and night.

The overall vertical distribution of Risso's dolphin echoes throughout the water column as shown in Fig. 4 masks patterns of potential prey use because of spatial and temporal variation in the vertical distribution of discrete prey features. Categorizing each dolphin echo by the scattering feature in which it was collocated shows that, during the day, dolphin echoes were found most frequently in the midwater layer (Fig. 5). Migration of the midwater layer at night (Fig. 3) was coupled with a change in the vertical distribution of dolphin echoes. Dolphins were found most commonly in the combined shallow/midwater layer at night (Fig. 5). There were no significant differences in dolphin detection rates day and night for the scattered patches or deep layer (scattered patches: $t = 0.86$, deep layer $t = 0.51$; $p > 0.05$ for both comparisons). There was a significant difference between day and night for the shallow layer ($t = 3.96$, $p < 0.001$) and for echoes found outside distinct scattering features ($t = 1.97$, $p < 0.05$). Variation in mean scattering strength in the combined shallow/midwater layer and the daytime midwater and deep layers was quite low. The scattering strength in these features showed no significant correlations with the detection rate of dolphins. Despite the relatively low frequency of detections of dolphins during the day within the shallowest scattering layer at 50 m, this layer had a large impact on the detection rate of dolphin echoes throughout the water column (Fig. 6). As the daytime scattering strength of the shallowest scattering layer increased, so did the rate of dolphin detections throughout the water column.

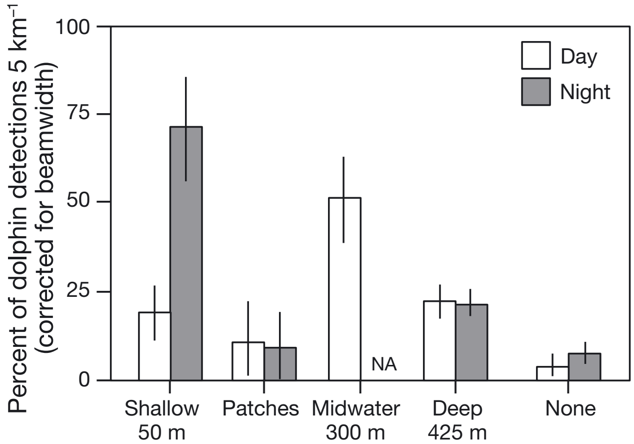

Fig. 5. Dolphin target detection rates, corrected for beam width, in 5 km survey sections from the ship-based echosounders shown for day and night as a function of scattering feature surrounding each detection. Error bars indicate 95 % confidence intervals

3.3. Patch scale observations of Risso's dolphin prey selection

The echosounder-equipped AUV was used to make observations within scattering layers, providing the resolution necessary to observe individual fish, crustaceans, and squid. In all 3 layers observed, these animals were arranged in monospecific groups or patches within the layer (Benoit-Bird et al. 2017). As reported by Benoit-Bird et al. (2017), the relative composition of net tows matched the relative composition of acoustically classified individuals in the AUV data set when sampling effort was accounted for. Echoes consistent with dolphins were found in a total of 519 monospecific patches within scattering layers (Fig. 7). The relative composition of patches found to contain dolphins was compared with the composition of patches in which no dolphin echoes were detected (Fig. 8). A chi-squared test showed that these were independent ($\chi^2 = 11.21$, $p < 0.01$, df = 2); patches containing dolphins were signif-

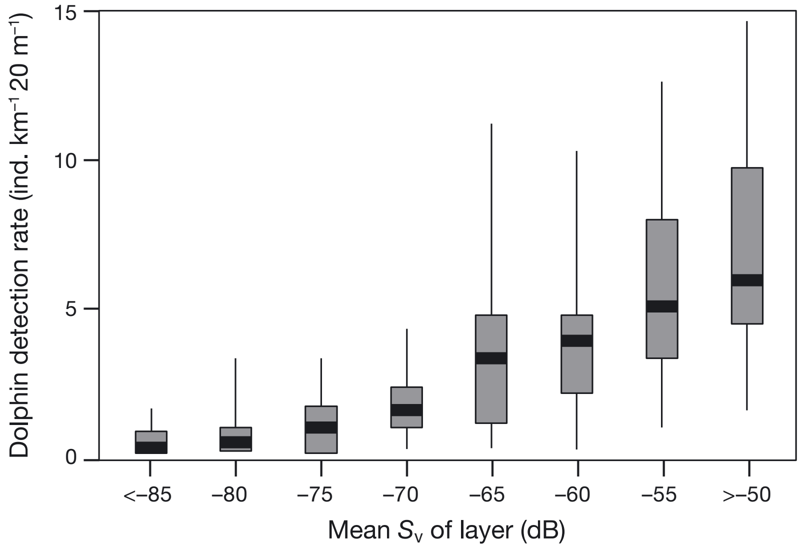

Fig. 6. Daytime dolphin target detection rates (ind. km^{-1} 20 m depth^{-1}) shown as a function of the mean volume scattering of the shallow scattering layer centered near 50 m. The black line indicates the mean, gray boxes represent the interquartile range, and the whiskers indicate the full extent of the data

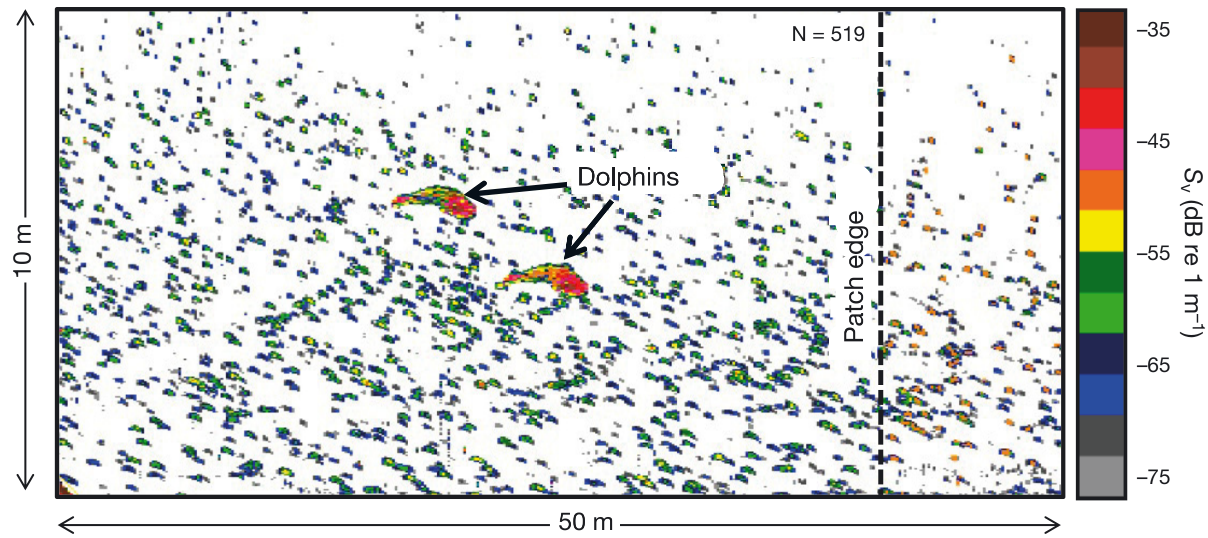

Fig. 7. Dolphin targets were detected within scattering features from the autonomous vehicle as shown here at 38 kHz. Potential prey were grouped within the layer by size and taxonomic group into 'schools' (Benoit-Bird et al. 2017). Even in this single-frequency echogram, a change in target characteristics is visually identifiable, labeled here as the edge of the patch. The grouping of prey allowed comparison of the schools in which dolphins were found to those in which they were not found to examine prey selection by these predators

icantly different taxonomically from those that did not contain dolphins. A MANOVA showed that there were significant effects of both layer ($F_{2,1138}$ = 13.15, p < 0.01) and dolphin presence ($F_{1,1138}$ = 10.88, p < 0.01) on the mean target strength of the animals in each patch (Fig. 9).

3.4. Relative foraging gains

Estimating the potential gross energetic gains from each foraging layer provided a mechanism to combine our data with tagging data to develop biologically meaningful evaluations of relative layer importance. For these estimates, we interpret co-occurrence of Risso's dolphins and their prey as a relativistic yet reasonable metric of foraging success, a linkage supported by the tagging observations during the daytime. The shallow layer accounted for about 5%, the midwater 34%, and the deep layer 61% of the population's gross energy gain during daytime in our study. At nighttime, the shallow and midwater layers merged at shallow depths and dolphins increased the time they spent in shallow water proportionately. Consistent dive behavior by Risso's dolphins to the deep layer means that these deepest prey continue to account for ~60% of the gross energy gain at night. Both day and night, squid accounted for 90% of the dolphins' gross energy gain, while fish accounted for about 10% of the gross calories gained.

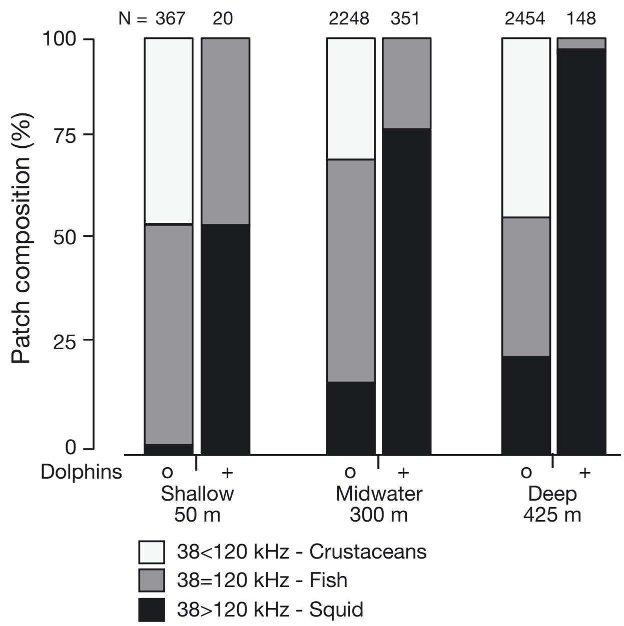

Fig. 8. Relative composition of patches that did not contain dolphins (o) versus those that did (+) as a function of scattering layer. A multivariate ANOVA showed there was a significant effect of dolphin presence on the relative composition of patches

4. DISCUSSION

We developed a unique integration of synoptically applied technologies to describe the foraging ecology of Risso's dolphins over various space and time scales ranging from the selection of individual

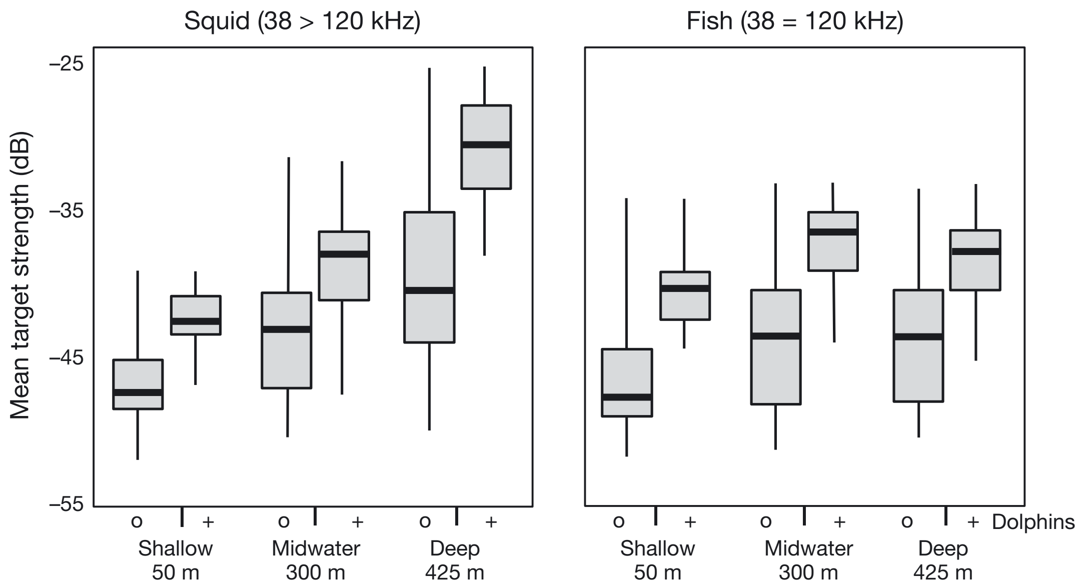

Fig. 9. Per patch mean target strength of targets with a frequency response consistent with squid (left) and fish (right) is shown for patches that did not contain dolphins (o) versus those that did (+) as a function of scattering layer. Black lines indicate the median, the gray boxes represent the interquartile range, and the whiskers show the full range of the observations. A multivariate ANOVA revealed that there were significant effects of layer and dolphin presence on the mean target strength of individual prey in each patch

patches by individual Risso's dolphins, a short-time scale, ~100 m physical scale process, to the basin scale (tens of km^2), documenting day–night differences covering ~500 m in the vertical dimension. We observed a large number of Risso's dolphins using active acoustics — nearly 5000 discrete detections from the ship-based echosounders and at least 1 dolphin in more than 500 patches from the AUV. Importantly, we were able to simultaneously measure the distribution, abundance, type, and size of prey synoptically, enabling us to consider foraging behavior within a relevant ecological context. By using this large-scale dataset with various complementary measures of behavior and ecology, we found that the foraging strategies of the local population of Risso's dolphins during our study were highly dynamic. Dolphins foraged within patches of fish and squid in all 4 scattering features identified. Daytime records from tags borne by individual Risso's dolphins at the same time showed that each tagged animal foraged within all 4 scattering features present (3 layers and a region of scattered patches), often within a single dive, in ways that suggest anticipatory behavior tuned to the spatial heterogeneity in the immediate vicinity (Arranz et al. 2018). These results suggest that each individual was also flexible in its foraging. While we lacked tag data from dolphins foraging at night, using the ship-based echosounder data, we found no significant diel differences in the overall detection rates of diving dolphins, suggesting that Risso's dolphins were foraging both during the day and at night. Our observations that individuals were apparently foraging within a variety of prey types around the clock is in contrast to previous studies which concluded that Risso's dolphins are primarily nocturnal teuthivores (summarized by Baird 2002).

Using the ship-based echosounder data, we observed that 2 of the scattering layers identified, the shallowest and deepest, remained at the same depth throughout the day and night. We documented the diel vertical migration of the midwater layer which moved from a depth of about 300 m during the day to less than 50 m at night. The vertical distribution of Risso's dolphins changed along with the vertical distribution of their prey from day to night. However, despite large decreases in time, energy, and oxygen costs to access the midwater layer at night, the use of this feature did not increase at night. Similarly, Risso's dolphins used the deep scattering layer at 425 m equally throughout the day and night, although animals had to approach their observed dive limits (Wells et al. 2009, Arranz et al. 2018) to do so. This use of the deepest layer was particularly interesting at night as foraging opportunities in midwater were decreased, yet dolphins continued to dive through an extended range of water largely devoid of potential prey to access the deep layer, suggesting that this layer contains important prey. This deep layer had the largest proportion of squid, the previously assumed primary prey of Risso's dolphins, in nets and the AUV-based echosounder data compared to the other scattering layers. These squid were substantially larger than those found in shallower features (also see Benoit-Bird et al. 2017).

To quantify the potential selectivity and degree of foraging specialization of Risso's dolphins, we used the AUV-based echosounders to observe the relationship between individual diving Risso's dolphins and the prey around them and compared those patches to potential prey (e.g. patches in which no dolphins were detected) in the same region. The foraging efforts of Risso's dolphins did not reflect the relative abundance of prey in the environment. Risso's dolphins were found preferentially in patches of squid in each layer relative to the overall abundance of these patches. In all 3 layers, Risso's dolphins were found in patches of both fish and squid that had a significantly higher target strength (i.e. larger individual animals) than generally available. Risso's dolphins were selective, found preferentially within patches of the largest available squid in each layer, with estimated mantle length modes at 10, 17, and 34 cm in the shallow, midwater, and deep layers, respectively. The 34 cm estimated mode length of squid near Risso's dolphins in deep water compares reasonably with the estimates of maximum mantle length of 35 cm estimated from gut contents (Clarke & Young 1998). However, Risso's dolphins here were nowhere near as selective in potential prey type as has been generally assumed (Baird 2002), although some studies have documented low abundances of fish and crustaceans in gut contents (Blanco et al. 2006, D'Amico & Rivilla 2006). If we combine our observations of the time spent by the population in each layer and the proportion of squid targeted in each layer, we estimate that about 65–70% of the time Risso's dolphins were diving they were associated with squid, with the remainder of the time accounted for within schools of fish. This number was consistent both day and night.

Risso's dolphins switched dynamically and seamlessly from being more generalist predators to specialists, frequently over the course of a single 5–10 min dive. Risso's dolphins were never found in patches of crustaceans, which have the lowest energy density of the available prey groups (Benoit-Bird 2004, Schaafsma et al. 2018), although they were equally abundant as fish patches. Risso's dolphins' relative prey selectivity between squid and fish changed with depth. In shallow and midwater layers, Risso's dolphins were frequently found in patches of fish. In the deepest layer, they were found almost exclusively in squid patches. In this habitat, Risso's dolphins appear to be squid specialists near their maximum dive depths, but they had a broader diet nearer the surface. As observed in foraging copepods (Kiørboe et al. 1996), once the preferred prey reach a certain density (here, >1 squid patch km^{-1}), predators can focus exclusively on the preferred prey, leading to a monospecific diet within the deep layer. However, unlike copepods, because dolphins need to surface to breathe, they cannot choose to remain in this preferred prey layer indefinitely or to forage exclusively at great depths because of the oxygen implications. As shown by Arranz et al. (2018), while some individual dives focus exclusively on shallower prey layers, up to half of prey capture attempts occur on descent/ascent to/from dives to deeper prey layers. During these dives to presumably more preferred prey, opportunistic descent or ascent feeding on a more diverse prey assemblage may help mitigate the costs of longer transits. Quantifying foraging strategies for air-breathing pelagic predators provides insights into the tradeoffs individuals experience as they seek to balance the need to obtain oxygen at the surface with food obtained at depth (Ydenberg & Clark 1989, Hazen et al. 2015) which include not only the time and energy to transit between these 2 locations but also critical physiological constraints (Ydenberg & Clark 1989, Friedlaender et al. 2016). Risso's dolphins make these switches in foraging tactics regularly, moving between near-surface generalist to mesopelagic specialist many times per day.

Both echosounder and parallel tagging data provided valuable new insights into the foraging tactics of a midwater pelagic predator. Integrating these data can provide further insights into the morphological, behavioral, and ecological constraints faced by these animals and the benefits of their overall strategy. The utilization of various prey layers by the population of Risso's dolphins present during sampling is indicated by the proportion of animal detections in each layer. These relative use estimates for the population were consistent with relative time of use for the 3 scattering layers measured in a tagging study of individual animals in the same area at the same time (Arranz et al. 2018). We incorporated our relative use estimates with the prey type and size selection information from the autonomous vehicle measurements to estimate the relative energetic value of each layer to the dolphins. While not a formal energetic model given the lack of critical data with which to derive more precise absolute values, these simple and reasonable calculations suggest that the deep layer, despite representing only about 15% of dolphin detections, accounted for most of the population's gross energy gain, about 61% during our study. The shallow layer, despite driving the overall distribution of Risso's dolphins, made only a small estimated contribution to the animals' total energy acquisition (shallow: 5%, midwater 34%, deep 61%). These calculations also suggest that squid, which accounted for about 75% of the patches in which Risso's dolphins were found, accounted for an outsized proportion of the animals' energy gain, about 90%, while fish, which made up 25% of dolphin-populated patches, accounted for only 10% of the gross calories gained. Tagging studies during daylight hours suggest different rates of prey capture attempts in the various prey features (Arranz et al. 2018), violating a simplifying assumption of our calculation. Using the rates of the buzz sounds that are indicative of prey capture attempts for these tagged individuals instead of ship-based echosounder dolphin detection rates, however, had little effect on the estimates of relative contributions of the layers and prey types to energy gains, indicating that these estimates are relatively robust.

Despite the apparent limited energetic value of prey in the shallowest scattering layer, Risso's dolphins were detected as frequently in this layer during the day as they were in the deep layer. This layer was intermittent in intensity. As the intensity of scattering from this layer was reduced, the rate of dolphin detections throughout the water column decreased, suggesting that the presence of this layer was important for overall foraging success and was controlling the small-scale horizontal distribution of Risso's dolphins in this area. These presumably 'inexpensive' dives, in terms of time, energy, and oxygen along with feeding during the ascent from and descent to more valuable prey may play a larger role in the success of these animals than our estimates of gross energy gain from these features alone would suggest. We hypothesize that the need to return to the surface may be responsible for Risso's dolphins' layer and prey switching. In other words, the currency of foraging in these mid-depth diving mammals is more than the energy or time alone as diving mammals balance multiple competing currencies (Ydenberg & Clark 1989, Hazen et al. 2015). During our sampling period, the energy Risso's dolphins could acquire from their preferred prey, larger squid, within their diving constraints did not appear to be adequate and animals complemented that prey with smaller squid and fish in shallower features, both on the way up from deep dives and in dives planned to these shallower prey features (Arranz et al. 2018). The use of food that appears to make a relatively small contribution in energy gains suggests that these predators may be working near the edge of their energy needs where small gains may be most important to the individual's overall success.

Alternative explanations for why Risso's dolphins forage on apparently low-gain prey include their assessment of uncertainty and risk (Kagel et al. 1986) and individuals' incomplete knowledge of the habitat (Stephens & Krebs 1986).

Detailed aspects of Risso's dolphins' foraging strategies, including prey selection, breadth of prey choices, and movement between distinct prey features, reveal much about the energy needs and the environmental and physiological constraints that these predators must balance when making foraging decisions. Due to their abundance in the study region, at least for this study period, and their amenability to tagging and echosounder sampling, Risso's dolphins are a good focal species for studies of foraging ecology. This species serves as a reasonable proxy for understanding predator–prey dynamics in other odontocetes and air-breathing predators, particularly moderate and deep-diving species foraging in spatially heterogeneous environments (Benoit-Bird et al. 2017, Southall et al. 2019). Our results highlight the rapid time scale over which predators make decisions in pelagic environments as their prey field rapidly evolves in 3 dimensions. Prey switching has been observed between years (Ostfeld 1982, Kjellander & Nordström 2003), seasons (Lehikoinen 2005, Latham et al. 2013), and even feeding trips (Chaurand & Weimerskirch 1994, Paredes et al. 2014) in other predators. Despite the potential reductions in efficiency that can result from prey switching, combining parallel tagging results (Arranz et al. 2018) with our regional population study revealed that Risso's dolphins switch prey rapidly, both between and within dives. For an air-breathing predator, the challenge of foraging in a 4-dimensional prey field is amplified by the spatial separation of 2 critical resources, oxygen and food. Prey switching was likely not driven directly by the availability of food (Lack 1954, Murdoch 1969, Kiørboe et al. 1996, Reif et al. 2001), changing accessibility (Gawlik 2002), or predation risk (Siddon & Witman 2004), but rather by the physiological and time limitations of accessing food and oxygen alternately. Prey specialization in these predators is dynamic and context-dependent. That small, less preferred prey played a strong role in determining the spatial distribution and overall habitat use of Risso's dolphins emphasizes the need for us to examine their behavior in light of their complete strategy for foraging rather than the average rate of gain or net gain approach often employed in foraging models (Stephens & Krebs 1986, Ydenberg 1998). However, doing so in pelagic environments remains challenging. The integration of various unique methods employed synoptically on Risso's dolphins and their prey provides remarkable insights into the behavioral ecology of individuals and local populations. This new view that the precise integration of multi-scale measurements in the pelagic provides reveals not only the complexity of Risso's dolphins' foraging behavior, it also highlights the selective pressures faced by pelagic species in general.

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