Prey in oceanic sound scattering layers organize to get a little help from their friends

Kelly J. Benoit-Bird 1*, Mark A. Moline, 2 Brandon L. Southall 3

1Monterey Bay Aquarium Research Institute, Moss Landing, California
2College of Earth, Ocean, and Environment, University of Delaware, Lewes, Delaware
3Southall Environmental Associates, Inc, Aptos, California

Abstract

Group formation in animals is a widespread phenomenon driven by food acquisition, reproduction, and defense. Life in the ocean is characteristically aggregated into horizontally extensive layers as a result of strong vertical gradients in the environment. Each day, animals in high biomass aggregations called “deep scattering layers” migrate vertically, comprising the largest net animal movement on earth. This movement is commonly thought of as a predator avoidance tactic, however, the aggregation of animals into layers has been viewed as an incidental outcome of similar responses by many individuals to the risk of visual predation coupled with the location of resources including food and oxygen rather than active, socially mediated congregation for defense purposes. Here, using a newly adapted autonomous vehicle to measure individual characteristics, we provide the first measures of the internal layer structure, demonstrating that these features are made up of many topologically scaled, mono-specific aggregations, or “schools” rather than an indiscriminate mix of sizes and species. Schools responded to predators using behavior much like flash compression while neighboring aggregations increased their spacing to maintain coherent layers. Rather than simply an incidental outcome, the formation of layers of life in the sea is a highly organized process driven, at least in part, by biotic pressures for cohesion with broad adaptive significance for the myriad species that inhabit these ubiquitous features. These observations highlight the range of spatial scales we must examine in order to understand the strong impacts these high-biomass layers have on ecological and biogeochemical processes in the sea.

Group formation is widespread in the animal kingdom, resulting from pressures for food acquisition, reproduction, and defense (Hamilton 1971; Pulliam 1973; Partridge 1982). One of the most recognized examples of animal grouping is shoaling and schooling in fish. Schooling is a self-organized social behavior where animals coordinate their movements with neighbors, in part by careful maintenance of spacing among neighbors, to obtain benefits such as reduced predation and more efficient and effective resource acquisition (Pitcher 1986; Pitcher and Parrish 1993; Ritz et al. 2011).

The research attention on congregations in the sea including schools of fish and the socially mediated shoals of krill have produced considerable knowledge on the formation mechanisms and significant consequences of these discrete aggregations (reviewed in Ritz et al. 2011). However, with the exception of spawning aggregations, studies of formation mechanisms of the horizontally extensive but vertically compressed aggregations of biota that are characteristic of the sea have focused on the relationship between the environment and organisms (Cushing 1973; Stacey et al. 2007; Birch et al. 2008) rather than intra-specific interactions (but, see Parrish 1989; Benoit-Bird and Au 2003; Ritz et al. 2011). As gradients of physical and chemical properties in the ocean are typically much stronger vertically than horizontally (Robison 2004), matching the relative dimensions of these ubiquitous biotic features, the attention to environmental variability underlying layered aggregations ranging from phytoplankton to zooplankton to cephalopods and fish makes sense.

Layers comprised of a variety of invertebrate and vertebrate species in midwater, often referred to as deep scattering layers because of their propensity to strongly reflect sonar signals, are observed throughout all oceans (Marshall 1951). Each day, many of the animals in these high biomass aggregations (Irigoien et al. 2014) exhibit vertical migration,
comprising the “largest net animal movement on earth” (Hays 2003) and strongly affecting both ecological and biogeochemical processes (Robinson et al. 2010). While this vertical movement is commonly thought to be a predator avoidance tactic (Iwasa 1982; Lampert 1989), the grouping of animals into layers has been attributed most often to similar responses by many individuals to the risk of visual predation coupled with the location of resources including food and oxygen (Herdman 1953; Enright 1979; Ringelberg 1995; Bianchi et al. 2013) rather than a social response that directly serves a purpose like group defense. Some authors have even argued that diel vertical migration and social aggregation serve the same purpose and are thus redundant and unlikely to be observed together (Lampert 1989; Kaartvedt et al. 1998).

Here, using a newly adapted autonomous vehicle, we provide measures of the internal structure of mesopelagic layers while quantifying the constituents’ responses to the presence of predators. Our goal was to examine the role of biological cohesion on the formation of layers that are characteristic features in the sea. Understanding the underlying mechanistic details of aggregations is important because these details can profoundly influence fundamental processes including prey-detection, predator avoidance, reproduction, and mortality (Grünbaum and Okubo 1994).

**Methods**

**Acoustic measurements**

In the Catalina Basin, off the eastern coast of Catalina Island, California, we utilized a novel, autonomous echosounder system (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 up to 600 m (for a detailed description of the sensors and platform, see Moline et al. 2015) over 10 d and nights in September, 2013 for a total survey distance of 366 km. This approach provided the resolution necessary to make acoustic measurements of the individual animals that make up layers, approximately 10 cm in the vertical (range) and up to 15 cm horizontally near the AUV. The AUV travelled at a speed of ~1.5 m/s at pre-determined depths between 50 m and 500 m, depending on the locations of layers identified from the ship-based echosounders. At the same time, surveys of the entire water column were conducted using echosounders (split-beam Simrad EK60s at 38 kHz, 70 kHz, 120 kHz, and 200 kHz) mounted to the research vessel New Horizon were conducted at a speed between 1.5 m/s and 2.6 m/s. Each calibrated echosounder used a 512 microsecond long pulse at a rate of 1 Hz and a source level < 180 dB re 1 μPa (rms).

**Direct samples and observations**

In order to compare the descriptions of the scattering layer from acoustics with those from more traditional techniques, we also conducted net tows from the ship with a 4-m² mouth opening Isaacs-Kidd midwater trawl with a 3.2 mm mesh net equipped with a real-time pressure sensor (Simrad PI-32). 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 was achieved using a rate of 20 m of wire per minute which reduced the mouth opening to near zero. 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 cm 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 taxa and size group) of organisms were identified as those that together accounted for at least half of the catch. The relative composition of each tow and the counts/tow were compared using a Bray–Curtis test followed by a permutation analysis of variance (Goslee and 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 and Dill 1995), and position relative to the boat during all underway surveys during the daytime, covering approximately half of all of the dolphin detections with the echosounder. The time that any individuals were visually observed to swim beneath the vessel was specifically noted for later comparisons with the ship-based echosounder data. During the duration of our experiment, more than 95% of the marine mammals observed visually and nearly all of the cetaceans observed were *Grampus griseus*, commonly known as Risso’s dolphins.

**Analysis of acoustic data**

Acoustic scattering data from both platforms was processed using Echoview software. First, the seafloor and any noise artefacts were removed. Ship-based data were used here only to provide context for other measurements and were not analyzed further here. Acoustic data from 3 m to 13 m beneath the AUV, the region with the horizontal resolution necessary to separate individual echoes across the typical range of target densities observed in the measured scattering layers, were first analyzed for single targets, e.g., only one target per acoustic reverberation volume for each pulse (Sawada et al. 1993). Single targets were extracted from both the 38 kHz and 120 kHz data. Echoes consistent with marine mammals were identified based on their frequency response, intensity, and morphology (Benoit-Bird et al. 2009), their positions noted, and their echoes removed from the dataset for further analyses of the scattering layer (Fig. 1A). For other targets identified at both frequencies (> 85% of all single targets detected), the intensity of the echo at 120 kHz was subtracted from the 38 kHz intensity to provide a measure of
A 38 kHz echogram measured from shipboard sensors shows the scattering layers identified in the Catalina Basin. Each layer was identified with net tows to contain a distinct variety of species and size classes that remains consistent throughout the region. Panels (B–D) show data simultaneously measured from within one layer using sensors on an autonomous underwater vehicle (AUV), providing increased resolution that allows individual organisms close to the vehicle to be measured despite relatively high densities. Panels (B, C) show how each individual target measured from the AUV compares to its neighbors by examining an index of the dissimilarity in acoustic properties, scaled from 0 to 1. Panel (B) shows an interpolated map of the dissimilarity index over the 3 km transect while the inset in panel (C) shows the dissimilarity of each identified individual over 250 m, identifying three aggregations of individuals with distinct acoustic scattering characteristics. In panel (D), data from the 38 kHz echosounder shows parts of two distinct aggregations, one of which contains echoes from two marine mammals identified from surface observations as Risso's dolphins.

Fig. 1. (A) A 38 kHz echogram measured from shipboard sensors shows the scattering layers identified in the Catalina Basin. Each layer was identified with net tows to contain a distinct variety of species and size classes that remains consistent throughout the region. Panels (B–D) show data simultaneously measured from within one layer using sensors on an autonomous underwater vehicle (AUV), providing increased resolution that allows individual organisms close to the vehicle to be measured despite relatively high densities. Panels (B, C) show how each individual target measured from the AUV compares to its neighbors by examining an index of the dissimilarity in acoustic properties, scaled from 0 to 1. Panel (B) shows an interpolated map of the dissimilarity index over the 3 km transect while the inset in panel (C) shows the dissimilarity of each identified individual over 250 m, identifying three aggregations of individuals with distinct acoustic scattering characteristics. In panel (D), data from the 38 kHz echosounder shows parts of two distinct aggregations, one of which contains echoes from two marine mammals identified from surface observations as Risso's dolphins.
frequency response which is related to target identity. The target strength at each frequency and the frequency response of each target were each averaged over any detections that were determined to be of the same individual in subsequent pings (Blackman 1986) and those values were referenced to those of neighboring targets using spatial autocorrelation, a geostatistical approach that is used to describe clustering. To collapse the variables measured for each target into a single metric, a dissimilarity index, was calculated. This normalized distance metric in variable space (TS_{38kHz}, TS_{120kHz}, TS_{38-120kHz}) makes the effect of changes in each variable equivalent (e.g., it is standardized and Euclidian) and is scaled from 0 (identical for all parameters) to 1 (the most different in the data set) (Gower and Legendre 1986). This was computed by comparing the dissimilarity of each target to all targets within 0.5 m windows increasing in horizontal range from the focal target in 0.5 m steps out to a range of 500 m both forwards and backwards along the transect (approximately 700 pings). This calculation was repeated using one neighbor as the window size and the number of neighbors as the distance metric to a range of 300 neighbors in each direction. To identify the scales of clustering, a variogram was constructed for each analysis, the first with the geometric distance and the second with the neighbor number (topological) distance. The mathematical function that best fit each variogram was selected from linear, exponential, rational quadratic, power, spherical, and Gaussian using Akaike’s information criteria (Cressie 2015). Targets in the neighbor number classified groups were then assigned to a group if they were adjacent and had a dissimilarity index of less than 0.2 to allow group characteristics to be examined. This threshold corresponds to a total difference of about 20% of that observed in the entire data set, a relatively lenient value. Group membership based on neighbor number was insensitive to the choice of dissimilarity value between 0.1 and 0.9 with less than 5% of all individuals being differently classified across this entire range of values.

For additional analyses, interpretation of the results were aided by classification of acoustic targets. Targets measured from the AUV were identified as consistent with squid if their target strength at 38 kHz was 3.1–10 dB higher than their 120 kHz target strength (Benoit-Bird et al. 2008), as fish if target strength values between the two frequencies were no more than 3 dB different, and as crustaceans if the differences was >–3 dB. Target strength can be interpreted as a proxy of length (McClatchie et al. 2003) within each taxonomic class (“squid,” “fish,” and “crustacean”). Conversions to estimated metric length were made following Benoit-Bird (2009), assuming that the distribution of animals was generally orthogonal to the acoustic beam.

The nearest neighbor distance was measured for every target individually identified in the AUV data using the position of the target both within the beam and along the track. It is important to note that while this measurement was made in three dimensions, because of the shape of the acoustic beam, it emphasizes the direction of the vehicle’s travel. The nearest neighbor distance was averaged for all adjacent targets with a dissimilarity index of less than 0.2 to obtain an estimate of the mean spacing within each aggregation. From these data, the within group variability of nearest neighbor distance was calculated as the mean absolute deviation of inter-individual distance divided by the estimated length of the focal target, expressing distance as a percent of individual length to account for the pattern of increasing spacing observed as a function of animal length. We examined the effects of individual length within each taxa using regression analysis and between taxa using chi-squared statistics. The nearest neighbor distances in squid schools containing Risso’s dolphins detected with the echosounder (n = 425) were compared to squid schools lacking a Risso’s dolphin detection (n = 5069) and the nearest neighbor distances for schools made up of other taxa adjacent to these squid schools using chi-squared analyses. On seven occasions when the AUV was spiralling in order to ascend or descend (Moline et al. 2015), we observed schools of squid before and after the arrival of a Risso’s dolphin. We measured the time course of the mean inter-individual distance and compared the end points with the distributions observed during surveys.

Finally, to determine if effects of the AUV’s presence were observed, individual targets were tracked over multiple pings using an alpha-beta tracking algorithm (Blackman 1986). The direction of target travel after removal of the platform’s movement was tested in both the vertical and horizontal planes using chi-squared tests. Neither distribution was significantly different from uniform, suggesting there was no strong avoidance of or attraction to the vehicle. While the presence of other behavioral responses could not be measured, utilizing only data within a constant, fixed range from the vehicle holds these effects consistent across all samples and would be unlikely to affect comparative analyses.

Results and discussion

Using ship-based echosounders, we found coherent scattering layers throughout the Santa Catalina Basin at a variety of depths (Fig. 1A). All layers with the exception of the deepest layer observed underwent diel vertical migrations, moving up to 300 m upwards at night and down again at dawn. Net tow results were consistent with those from oceanic scattering layers throughout the world; these extensive layers were comprised of vertebrate and invertebrate organisms that appear to be mixed together relatively uniformly in the horizontal dimension given that composition measured with nets may vary significantly with depth but not with within region location. The shallowest layer, centered around 50 m was dominated by larval fish and a diverse array of small crustaceans. The midwater layer, centered around 300 m during the day but at less than 100 m at night was
numerically dominated by myctophids and krill. The deepest layer, centered around 450 m both day and night was made up primarily of dragonfish, squid, shrimp species, and large krill. Overall, 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.

We were afforded unique insight into the internal structure of these layers by collecting acoustic data using echosounders carried by an autonomous underwater vehicle (AUV) capable of diving directly into scattering layers at depths of up to 600 m (Moline et al. 2015). This provided the dramatic increase in spatial resolution necessary to acoustically distinguish the individual animals comprising these features rather than providing only measurements of their collective properties as in conventional ship-based measurements. Using a metric that integrates data from the two-frequency echosounder system to compare the characteristics of targets over horizontal space (Fig. 1B,C), it is clear in all layers examined that animals in these multi-species assemblages are not indiscriminately mixed or even stratified into monospecific sub-layers as has been assumed based on low horizontal spatial resolution data, but, are instead highly organized in small, horizontally bounded features throughout the day and night. The observed organization of these layers is in line with both theoretical predictions and observed phenomena for mass-migrating animal groups which at high relative densities exhibit cohesive, ordered group behaviors (Buhl et al. 2006).

We used spatial statistics to examine the potential spatial scales of the non-random pattern we observed in scatterer
characteristics. Spatial patterns in the dissimilarity index, a combined metric of the target strength and frequency characteristics of each identified target (Fig. 2A, B show examples), were quantified in both physical distance and in terms of the number of neighbors, a topological measure. The relationship between physical distance and the dissimilarity of animal characteristics show a generally increasing trend; animals are found near other animals like them and generally far from those of different taxonomic identity, size, and other features that could affect acoustic scattering like tilt angle. The wide variation in the dissimilarity index at a given distance indicates that there is no characteristic physical scale to organism grouping (Fig. 2C). Examining the same data with respect to the number of neighbors also shows an increasing trend. However, the best fit model for the topological measure is Gaussian, with a distinctive break between two plateaus (Fig. 2D), indicating that animals within a radius of approximately 50 individuals are nearly identical in terms of taxonomic identity and size but quite different in these characteristics from neighbors just outside of that radius. Looking within a single aggregation, variability in target strength was quite low; more than 95% of groups had a mean absolute deviation of less than 4 dB at each frequency and 99% of aggregations having a mean absolute deviation in the difference in target strengths for a single target of 1 dB or less (Fig. 3). Each of these aggregations had approximately the same topological extent, 100 individuals across, regardless of the taxonomic identity, size, depth, whether it was day or night, and regardless of whether the animals underwent migration or stayed in place, suggesting the generality of this phenomenon. The narrow range of individual sizes within a single group is consistent with observations of fish schools that are frequently segregated so that neighboring individuals are nearly identical (Breder 1951; Pitcher et al. 1985) reducing the individual risk of predation (Theodorakis 1989).

The constancy of topological dimension suggests a consistent group size, contrasting with observations of other species (Pitcher et al. 1996; Bonabeau et al. 1999), indicating that there is an optimal group size within these layers that is conserved across taxa. The basic mechanisms of aggregation in these features are likely constrained by the need to aggregate at two scales, the mono-specific group and the layer.

The spacing between individuals within each mono-specific aggregations was relatively uniform, with no individual distance within a group exceeding 15% of the mean spacing for the group, consistent with the coordination expected within a school, that is a socially mediated, coordinated group (Norris and Schilt 1988). The mean inter-individual spacing varied between aggregations, a feature that accounts for the variation in the physical scale of aggregations despite a constant topological scale. Inter-individual spacing varied with relative animal size within each taxonomic group (Fig. 4); as often observed in schooling and flocking (Partridge 1982; Reynolds 1987), animals generally increased their distance from neighbors as their individual length increased.

There was also a significant effect of putative predation risk on inter-individual spacing. Risso’s dolphins, *Grampus*...
**griseus**, a squid predator (Baird 2002), were detected frequently throughout the study area both visually and from the active acoustics. The unique echo characteristics of marine mammals (Benoit-Bird et al. 2009) make them easy to distinguish in echograms (Fig. 1D). We detected Risso’s dolphins from the AUV-based echosounders within the boundaries of 519 mono-specific schools, each about 20–150 m across, primarily those with an acoustic frequency response characteristic of squid ($n = 425$). At the depths of these scattering layers (50–500 m), it is highly likely that the observed dolphins are actively hunting (P. Arranz pers. comm.); interactions observed with these predators carry risk for potential prey. The average spacing between neighbors in squid schools that contained a dolphin was significantly smaller ($\sim 50$ cm) compared with those schools that did not contain a dolphin ($\sim 110$ cm, $n = 892$) (Fig. 5). The variability of within group inter-individual spacing was also affected by the presence of a dolphin within the school (Fig. 6) with a marked decrease in variability when dolphins were present, even when controlling for taxa, similar to the increase in organization observed in individual schools in experiments exposing the group to a predator, a process shown to improve collective responsiveness to risk (Rieucau et al. 2016). Note, however, that unlike observations on fish schools which respond more intensely at high densities (Rieucau et al. 2014), we observed very similar responses by squid over a range of packing densities (here measured as inter-individual distance), a measurement that was positively correlated with the target strength (e.g., length) of individual squid that made up each group in the absence of observed predation pressure.

On seven occasions, we were able to observe a squid school as a dolphin entered it as the AUV conducted a spiraling descent or ascent maneuver with a very small pitch angle, providing a short time-series of one location. In these cases, we were able to observe the in inter-individual spacing decrease by approximately half over 4–5 s while the variability in spacing decreased from a range of 3–5% to less than 1%. This sort of “flash” compression and increased coordination is commonly observed in schools under attack (Partridge 1982) and is sometimes used to distinguish schooling from other types of aggregations (Norris and Schilt 1988). Other behaviors like expansion, fragmentation, and diving which have also been observed in schools under predation (Handegard et al. 2012; Rieucau et al. 2014), may not be possible for these squid as they are surrounded on all sides by the other animals that make up the layer. These adjacent animals also responded when squid did. The

![Fig. 4. The between school variation in inter-individual distances is shown as a function of the estimated length for each taxa. Each heavy bar shows the median of the distribution while each box shows one inter-quartile range and the whiskers indicate the 95% confidence interval. For each taxa, spacing increases so that inter-individual distances average just over two times individual body length in aggregations in which no dolphin was observed.](image-url)
consolidation of squid in the presence of a predator was accompanied by compensatory movements of adjacent aggregations which increased their inter-individual distances from about 60 cm to 1 m (Fig. 5). Each aggregation adjacent to squid threatened by Risso’s dolphins made up about half of the spacing decrease of the squid, allowing the separate mono-specific aggregations to remain connected in a layer.

**Fig. 5.** The mean distance between individual targets within each aggregation is shown for squid and for aggregations of other taxa adjacent to squid aggregations in the presence and absence of Risso’s dolphins. Inter-individual distances within each group varied by no more than 15%. Squid aggregations show a decrease in the distance between individuals in the aggregation when dolphins are within the aggregation ($n = 425$) while the neighboring aggregations, which vary in taxonomy and individual length, increase their spacing, compensating for the compression of squid.

**Fig. 6.** The within school variation in inter-individual individual distance is shown for schools in which is dolphin was observed and those in which no predator was detected. Variability was calculated as a percent deviation to control for the effects of individual animal length.

**Conclusions**

Rather than resulting incidentally from similar responses to environmental cues coupled with density-dependent population dynamics, our results demonstrate layers of animals in the mesopelagic form, at least in part, due to biotic cohesion—a social response with adaptive value. The inferred collective reaction of both the squid and their neighbors to
predators indicates that horizontal extent of the response is larger than the entire mono-specific aggregation, making it difficult for a predator to divide the group into independent subparts and making the effective perception range of each individual as large as the entire group, allowing information to transfer to all animals from a point disruption (Cavagna et al. 2010). These aggregations appear to act as critical systems (Cavagna et al. 2010), poised to respond maximally to predation (Berdahl et al. 2013) which may overcome the negative effect of increased predator encounter rates for animals in layers. This grouping may also have additional benefits for these animals as they try to follow gradients including resources and light (Røstad et al. 2016) (taxis) in a noisy environment as outlined by Grünbaum (1998). The ability to maintain group cohesion both within and between mono-specific aggregations despite rapid changes in animal density during an external perturbation like predation may be augmented by the fact the aggregations are topological rather than metric in total dimension (Ballerini et al. 2008). It is important to recognize, however, that these group dimensions emerge as a result of collective movement (Deutsch et al. 2012) and the patterns we observed to do not tell us about the mechanisms of information transfer or movement that led to them. Discretely bounded, organized animal groups, 'schools', within oceanic scattering layers have not been previously discovered because they are nestled amidst a background of similar animal densities, unlike other swarms which are typically defined by a change in biomass on a neutral background. Their presence, however, highlights the importance of cohesive aggregation—at multiple scales—as a means to evade predation in a habitat without cover. The recognition that active social organization underlies observed patterns provides a fundamentally different paradigm for the adaptive significance of the ubiquitous layers of life in the sea (Fig. 7) and highlights the range of scales which we must study these extensive biotic features to understand their ecological and biogeochemical impacts.

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Fig. 7. A visual analogy that summarizes (A) how the multi-species scattering layers appeared from surface-based sampling, as a mixed assemblage of species and sizes. With finer resolution sampling from within the layers, we instead found (B) that the layer is made up of discrete aggregations of a single taxa with a narrow size distribution, or “schools.” These schools are adjacent to other discrete schools to form a larger layer. Squid schools respond to the presence of predators by decreasing their inter-individual spacing while adjacent groups increase their spacing to maintain the layered structure.
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Conflict of Interest

None declared.

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