

NOTE

Enhanced pelagic biomass around coral atolls

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ABSTRACT: Understanding the processes driving the distribution of mid-water prey such as euphausiids and lanternfish is important for effective management and conservation. In the vicinity of abrupt topographic features such as banks, seamounts and shelf-breaks, mid-water faunal biomass is often elevated, making these sites candidates for special protection. We investigated the spatial distribution of water column acoustic backscatter—a proxy for macrozooplankton and fish biomass—in the 9 km transition zone between the pelagos and coral atolls in the Chagos Archipelago (6° N, 72° E). The purpose was to determine the magnitude and distance over which bathymetry may enhance biomass in the mid-water, and thereby identify the scale over which static topographic features could influence the open ocean. Two distinct sound scattering layers were identified, from the surface to 180 m and from 300 to 600 m, during daytime. Both layers exhibited significant increases in backscatter near features. Close to features, the shallow layer backscatter was ca. 100 times higher and was driven partly by increasing numbers of larger individuals, evident as single target echoes. We determine the regional scale of influence of features on pelagic biomass enhancement to be ca. 1.8 km in the Chagos Archipelago, and suggest possible ecological explanations that may support it. Our approach determining the scale of influence of bathymetry should be applied during the process of marine reserve design, in order to improve protection of mid-water fauna associated with topographical features, such as seamounts and coral reefs.

KEY WORDS: Oceanic · Acoustic scatterers · Seamount · Tuna · Reserve · Coral reefs

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INTRODUCTION

The interaction between physical features and the distribution and abundance of mid-water organisms has important implications for spatial management and conservation. Abrupt topography such as seamounts and shelf breaks is known to attract free-ranging/mobile animals such as tunas and oceanic

sharks (Morato et al. 2010), making knowledge of prey and predator concentration around such features an important guide for conservation measures, including marine reserves. Ecological coupling between static features and the pelagic realm is a facet of the 'topographic enhancement' hypothesis, which posits that pelagic prey is subsidising demersal (or pelagic) predators residing on seamounts. For

topographic enhancement to occur, 2 conditions are required: (1) topographic blockage, where mid-water organisms are constricted against bathymetric features (Genin 2004); and (2) trophic enhancement, whereby resident or demersal predators capture blocked prey (McClain 2007). Coupling may further occur because the features are themselves sources of local prey, thereby attracting roving predators. For example, in the vicinity of a coral reef, yellowfin tuna *Thunnus albacares* feed predominantly on reef fish and larvae (Fernandez & Allain 2011).

In proximity to bathymetric features, the timing of predation is influenced by diel vertical migration (DVM), undertaken by a substantial proportion of the mid-water community. This daily migration between the surface and meso- and bathypelagic depths (200 to 1500 m, Brierley 2014) may result in trapping of organisms on the summits of features (McClain 2007), thereby resulting in prey-provision for resident predators. Topographic enhancement on seamounts is moderated by the punctuated vertical distribution of mid-water organisms residing in discrete but horizontally extensive layers (Boersch-Supan et al. 2015) that, when viewed on echograms, are described as sound scattering layers (herein referred to as 'layers'). Organisms within layers belong to a multitude of taxa, ranging in size from below that of mesozooplankton (ca. 1 mm) to large micronekton (ca. 20 cm), and belong to ecological guilds from grazers to piscivores (Brierley 2014). Organisms residing in layers represent a substantial part of the available prey for large mobile predators such as tuna (Potier et al. 2007). The acoustic intensity of layers has been used as proxy for prey biomass (Irigoiien et al. 2014), while their vertical structure—the depth and thickness of individual layers—affects the accessibility of these prey to foraging predators (Boersch-Supan et al. 2012).

In the present study, scientific echosounders were used to observe layers in depths ranging from 5 to 1000 m, as part of a multi-disciplinary study of the Chagos Marine Reserve (CMR, 640 000 km², British Indian Ocean Territory). We investigated the transition zone between mid-water and coral atolls, as well as a seamount, in order to determine the range over which there was an interaction, and hence the range over which conserved topographic features could influence the open ocean. The CMR harbours exceptionally high levels of coral reef fish biomass (6500 kg ha⁻¹, MacNeil et al. 2015) and its reefs are largely undisturbed; yet its efficiency in protected pelagic species has been called into question (Dunne et al. 2014). Characterising drivers of pelagic processes is

therefore a necessary step in assessing the efficacy of the CMR.

By overcoming the depth limitation of SCUBA observations, echosounders enabled us to probe the under-sampled twilight margins between the epi/mesopelagic and neritic zone down to 1000 m and explore potential coupling mechanisms between the mid-water and the seabed. Our purpose was to document patterns in layers in order to (1) describe the vertical distribution of pelagic prey around coral reef atolls and seamounts in the CMR; (2) predict mid-water biomass distribution as a function of distance from a feature, in order to determine the distance over which there was an interaction between bathymetry and the mid-water, and hence the minimum scale over which static topographic features could influence species in the open ocean.

MATERIALS AND METHODS

Line-transect acoustic backscatter data were collected from 08:00 to 17:00 h local time from 22 November to 8 December 2012 in the CMR. The surveys targeted island slopes near Petite Ile Coquillage on the Peros Banhos atoll, with a reef crest of 6 m, the slopes of Speakers Bank, a submerged atoll with reef crests at 10 m, Sandes Seamount, a shallow seamount with a summit plateau at 70 m, and deep water (>750 m) areas near Speakers Bank and Blenheim Reef (Fig. 1). Survey transects were between 1.5 and 9 km long and oriented perpendicular to the topographic features' slope. A calibrated split-beam echosounder (EK60, Simrad) was deployed from a 6.5 m rigid hulled inflatable boat using an over-the-side mount. The echosounder operated at 38 kHz with ping interval 4 s, pulse duration 1.024 ms, transducer depth 1 m, and beam width 12°.

Acoustic data were processed using Echoview (v4.9, Myriax) to remove background and intermittent noise. Sea-surface noise, seabed returns, and false-bottom echoes were also removed. Mean volume backscattering strength (MVBS, MacLennan et al. 2002) was integrated into 10 m vertical by 250 m horizontal bins. Acoustic single targets were detected with a minimum threshold of -60 dB re 1 m², and exported as individual observations of beam-geometry-compensated target strength. Although there are some uncertainties, notably in the presence of resonant scattering, MVBS in general can be interpreted as a relative measure of layer biomass, and target strength can be interpreted as a relative measure of animal size.

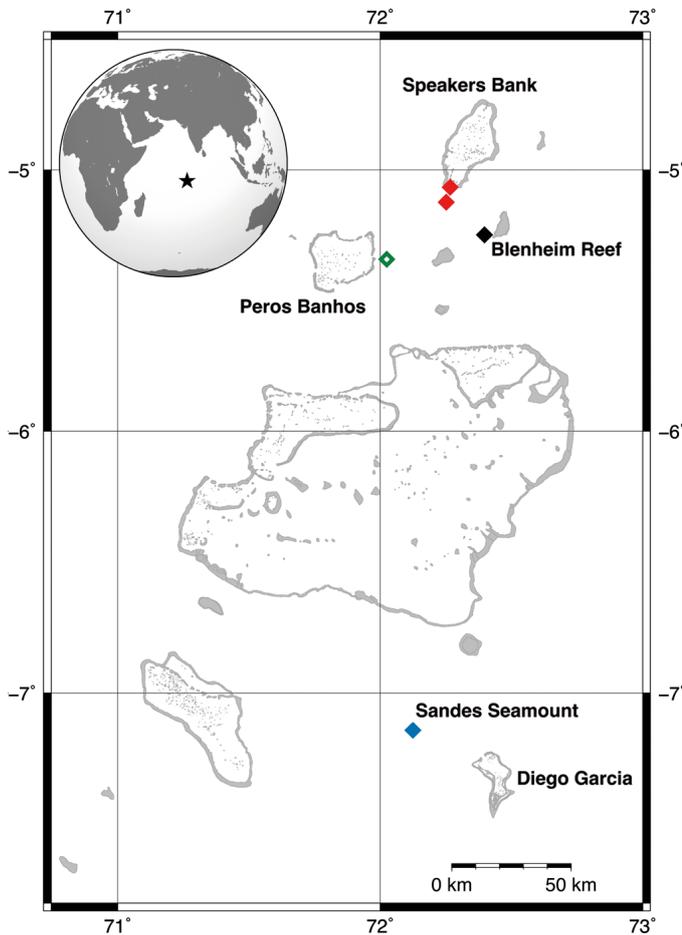


Fig. 1. The Chagos Marine Reserve study area and sampling locations. The star marks the location of Chagos Archipelago in the Indian Ocean (inset). Locations and features of acoustic surveys within the archipelago are indicated by diamonds. The open diamond marks the transect shown in Fig. 2A. Diamond colour corresponds to the feature-specific models shown in Fig. 3A. Shading indicates coral reef cover, most of which is permanently submerged

Great circle distances from each sampling unit to the nearest topographic feature were calculated using GRASS GIS 7 (<http://grass.osgeo.org/grass7>) and the `sp` package in R (<http://cran.r-project.org/package=sp>) as the minimum great circle distance to either Sandes Seamount or the shallow coral reefs as mapped by the Millennium Coral Reef Mapping Project (<http://imars.marine.usf.edu/millennium-coral>). Non-linear regressions were used to investigate the relationship between MVBS of individual layers and distance to nearest topographic features. The regression models were based on previous observations that, within a given water mass and on the scale of 10–100 km, oceanic scattering layers tend to be relatively homogenous in backscattering strength and structure (Irigoiien et al. 2014, Boersch-Supan et al.

2015). Topographic features were modelled as exerting an effect on layers that decreased exponentially with distance to a feature. In the absence of detailed knowledge of the mechanisms by which topography affects scattering layers, we chose a simple exponential decay model. Models were fitted for each feature individually (with the exception of Blenheim Reef due to lack of data to justify a model at that location), and for all features combined using the pooled data in a regional model. The models took the form:

$$S_v(r) = (S_{v0} - S_{v\infty})e^{-\lambda r} + S_{v\infty} \quad (1)$$

where $S_v(r)$ is the backscatter at distance r from the topographic feature, S_{v0} is the backscatter at $r = 0$ (summed across bins within the layer in question, Fig. 2), $S_{v\infty}$ is an asymptote representing the mean volume backscattering strength in the oceanic state (i.e. in the absence of the topographic effect) and λ is the rate constant of an exponential process used to model any topographic effect. Confidence intervals were obtained by bootstrapping, using 10000 replicates. Residuals of ordinary least squares models showed significant spatial autocorrelation (Moran's I , $p < 0.001$), so we used the R `nlme` package (<http://cran.r-project.org/package=nlme>) to fit generalised least squares models with spherical spatial correlation structures. The sill range of the spherical variogram (the range of the spatial autocorrelation) was estimated to be between 1.4 and 1.6 km, across all transects. Spatial patterns in layer composition were explored further using a 2-sample Kolmogorov-Smirnov test. We compared the beam-compensated target strength distributions of acoustically detected single targets that fell in the zone of elevated MVBS with observations that fell beyond the boundary region of feature influence. The feature effect range (r_{eff}) was defined as the distance at which the predicted SSL MVBS declined to within 1% of its asymptotic value ($S_{v\infty}$, Eq. 1).

RESULTS AND DISCUSSION

Two distinct layers were observed throughout the CMR (Fig. 2), comprised of a collection of shallow scattering layers (SSLs) from the surface to 180 m, and a deep scattering layer (DSL) from 300 to 600 m. The lower extent of the SSL corresponded with the 14°C isotherm (Fig. 2). The vertical structure of these layers was similar to that observed in 1964 with a 30 kHz sonar between the Seychelles and Maldives, which from net samples were shown to contain over 150 species of fish and invertebrates (Bradbury et al. 1970).

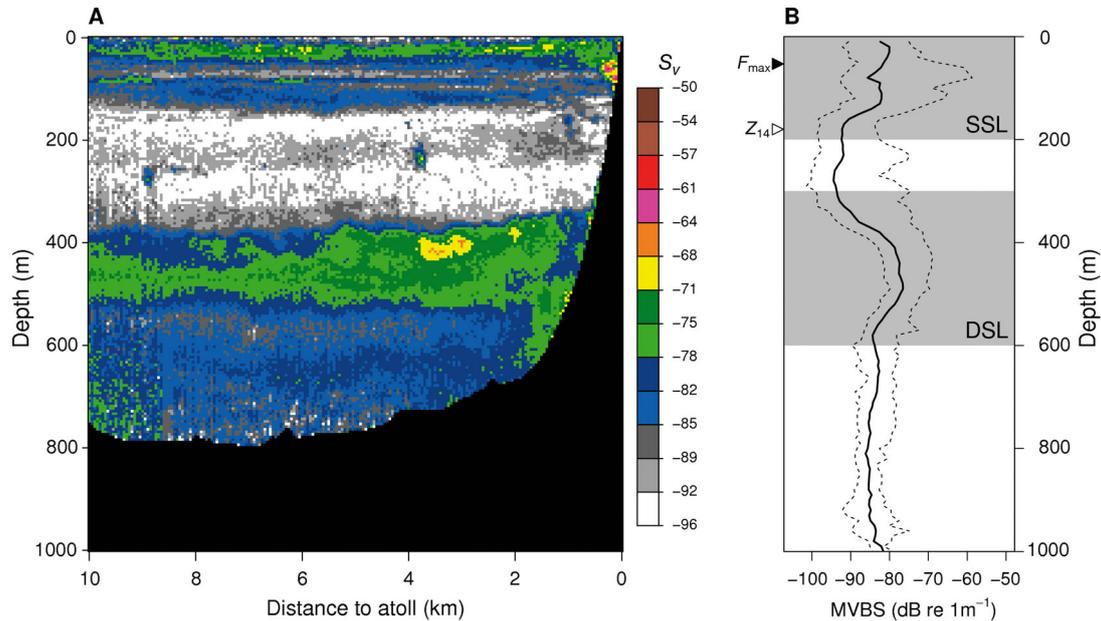


Fig. 2. Vertical and horizontal patterns in layer mean volume backscattering strength (MVBS). (A) An echogram of a transect running from offshore onto Peros Banhos atoll (cf. Fig. 1). Colour scale is logarithmic, units dB re 1 m⁻¹. (B) The vertical profile of MVBS (median, 2.5th and 97.5th percentiles) for the entire survey. Shaded depth intervals highlight the shallow (SSL) and deep scattering layer (DSL) modelled (Fig. 3). The filled and open arrowheads indicate the mean depth of the fluorescence maximum (F_{max}) and the 14°C isotherm (Z_{14}), respectively

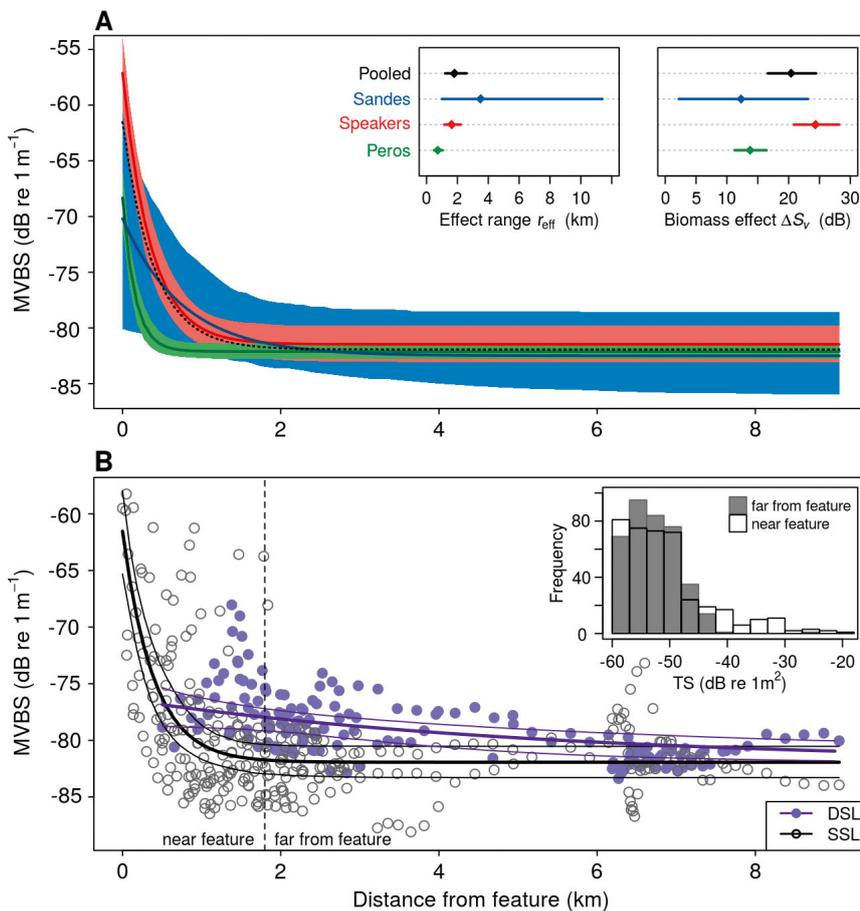


Fig. 3. Non-linear regression models (lines, with 95% confidence intervals), of scattering layers in the Chagos Archipelago. (A) Feature-specific models (as illustrated in Fig. 2B) for the shallow scattering layer (SSL), with effect range and biomass effect shown as insets. (B) Regional regression model and MVBS observations and of the SSL and deep scattering layer (DSL) across all features for the archipelago. Each data point represents MVBS for 10 m vertical and 250 horizontal bins. Vertical dashed line indicates the range of horizontal influence of the topographic effect (1.8 km). The inset shows target strength histograms for single targets in the SSL within and beyond the range of the topographic effect

Both layers displayed an increase in MVBS ($\Delta S_v = S_{v0} - S_{v\infty}$) as the seabed shallowed near atolls and Sandes Seamount (Fig. 3A). MVBS in the SSL increased dramatically towards topographic features. Biomass effect in terms of ΔS_v differed between features (Fig. 3A), but the estimated spatial effect ranges (r_{eff}) were consistent between models and the regional model (Fig. 3). Confidence intervals (CIs) for the Peros Banhos model did not overlap with those for the pooled data (lower S_v effect, lower range than pooled data), although the narrow CIs probably arise because the model is based on a single transect, i.e. CIs reflect model uncertainty but not spatial variability of the SSL. Sandes Seamount and Speakers Bank had multiple transects each, so the spatial variability is captured more reliably. Exponential models are very sensitive to data points close to 0 distance, resulting in very large CIs on the parameter estimates.

The regional SSL model expressed a doubling of MVBS intensity for every 100 m from its asymptotic value ($S_{v\infty}$, Eq. 1), which occurred at a range of 1.8 km from a feature. MVBS in the immediate vicinity, i.e. within 50 m, of a feature was over 100 times higher ($\Delta S_v = 20.4$ dB re 1 m^{-1} , 95% CI [16.5, 24.4]) than MVBS beyond the 1.8 km feature boundary (Fig. 3B). Moreover, target strength distributions of acoustically detected single targets within the SSL differed significantly (2-sample Kolmogorov-Smirnov test, $D = 0.1417$, $p < 0.001$) between the zone of elevated MVBS and compensated target strength observations beyond the 1.8 km boundary region (open bars in Fig. 3B inset). The difference was driven in part by the presence of strong acoustic targets (target strength ≥ -40 dB re 1 m^2) near features (<50 m) which, if assumed to be tunas, would correspond to individuals larger than 40 cm (Bertrand & Josse 2000).

The increase in SSL backscatter near features is indicative of enhanced biomass and demonstrates ecological associations between scattering layers and coral reef atolls and seamounts. The features of the Chagos Archipelago are thus hotspots of mid-water biomass in the tropical Indian Ocean, with a range of ca. 1.8 km, in addition to holding record levels of conspicuous reef fish biomass that reside on the shallow reef (MacNeil et al. 2015).

Several examples of mechanisms sustaining benthopelagic connectivity have been reported previously in the context of coral reefs. For example, reef fish zooplanktivory of pelagic prey has been observed on windward sides of shallow coral reefs, such as the 'wall of mouths' of Hamner et al. (1988), where the reef is being subsidised by pelagic plankton.

Alternatively, tuna routinely feed on small fish and meroplankton produced on and exported from the reef (Fernandez & Allain 2011). Both these mechanisms are consistent with our single target observations, which under a uniform species assemblage distribution suggest that near-feature organisms are larger than those further away. Moreover, both mechanisms would explain observation of a net increase in biomass near features, and could conceivably operate at the same time and to various degrees.

In our survey a substantial part of the SSL enhancement was observed to occur around mesophotic reef depths (>30 m, Fig. 2). Although knowledge of trophic pathways at these depths is limited (Kahng et al. 2010), many mesophotic reef community characteristics may be related to pronounced energy input from SSL prey subsidies, and to a reduction in autotrophic input due to low light levels. For example, mesophotic reefs typically harbour higher ratios of zooplanktivorous to herbivorous fish (Kahng et al. 2010) and of heterotrophic to autotrophic coral (Feitoza et al. 2005), compared with shallow reefs.

The DSL exhibited a less pronounced increase in backscatter intensity, with MVBS in the vicinity of features up to 4 times higher ($\Delta S_v = 5.7$ dB re 1 m^{-1} , 95% CI [3.4, 7.9]). Previously studied DSLs associated with island slopes in Hawaii, and seamounts elsewhere, have been found to harbour a distinct mesopelagic-boundary community of macrozooplankton, characterised by elevated densities and species richness (Reid et al. 1991, Letessier et al. 2015), which may explain observations of backscatter increase.

Our results offer a view of oceanic atolls and seamounts as hotspots of mid-water biomass at epi- and mesopelagic depth. Acoustic surveys are routinely used to infer ecological interactions (e.g. Boersch-Supan et al. 2012) but we are unable to determine the true nature of the enhancement in either layer, in the absence of direct sampling. An important ecological link is thereby lacking from the current picture of coral reef energy pathways, which could render reefs either net sources (Fernandez & Allain 2011), or sinks (Hamner et al. 1988), of pelagic energy. We have determined the boundary of influence of atolls and other features on mid-water biomass, and thus provide a blueprint for assessing spatial management strategies. Future reserve design can be informed by the knowledge that a minimum range is necessary for robust mid-water faunal protection around atolls (although protection for mobile species will obviously require larger radii, such as that offered by the CMR). In the same vein, existing reserves that do not allow sufficient buffer areas may offer imperfect pro-

tection of the wildlife residing on the feature they are intended to protect. Since the scale that we identify is applicable at the regional level, it may be possible to estimate the minimum size of an effective reserve (in the sense of protecting mid-water fauna). Here, reserves with an area less than 12 km² would be inappropriate for a seamount with a summit with a 300 m diameter. We stress that since ecological processes vary due in part to geographical differences in production regimes and oceanography patterns, similar surveys should be undertaken at the regional level to ascertain the range of influence rather than assume a constant. This would ensure that important ecological processes linked to topography remain adequately considered during the design phase of reserve implementation.

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