

Enhanced pelagic biomass around coral atolls

Tom B. Letessier^{1,2}, Martin J. Cox³, Jessica J. Meeuwig^{1,4}, Philipp H. Boersch-Supan^{5,6,*}
Andrew S. Brierley⁵

[1] tom.letessier@uwa.edu.au, Centre for Marine Futures, The Oceans Institute, The University of Western Australia, (M470), 35 Stirling Highway, Crawley WA 6009

[2] Institute of Zoology, Zoological Society of London, Regent's Park, London NW1 4RY

[3] Australian Antarctic Division, Channel Highway, Kingston, Tasmania 7050, Australia

[4] School of Animal Biology, The University of Western Australia, (M470), 35 Stirling Highway, Crawley WA 6009

[5] Pelagic Ecology Research Group, Scottish Oceans Institute, University of St. Andrews, Fife KY16 8LB, UK

[6] Department of Zoology, University of Oxford, Oxford OX1 3PS, UK

* Current address: Department of Integrative Biology, University of South Florida, Tampa, FL 33620, USA

Abstract

Understanding processes driving the distribution of mid-water prey such as euphausiids and lanternfish is important for effective management and conservation of their predators. 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 c. 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 c. 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

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 are 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 important to guide conservation measures, including marine reserves. Ecological coupling between static features and the pelagic realm are 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, two 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 further 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 1,500 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 less than mesozooplankton (≈ 1 mm) to large micronekton (≈ 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 (Irigoien et al. 2014), while their vertical structure - the depth and thickness of individual layers - effects their accessibility to foraging predators (Boersch-Supan et al. 2012).

Here, scientific echosounders were used to observe layers in depths ranging from 5 m to 1,000 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, and 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 (6,500 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 are 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.

Material and Methods

Line-transect acoustic backscatter data were collected from 08:00 to 17:00 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 10m, 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 km and 9 km long and oriented perpendicular to the topographic features' slope gradient. A calibrated 38 kHz split-beam echosounder (EK60, Simrad, Horten, Norway) was deployed (transducer depth 1 m, beam width 12°) from a 6.5 m rigid hulled inflatable boat using an over the side mount. The echosounder operated at 38 kHz with a ping interval of 4 s and pulse duration of 1.024 ms.

Acoustic data were processed using Echoview (v4.9, Myriax, Hobart, Australia) to remove background and intermittent noise. Sea-surface noise, seabed returns, and false-bottom echo 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.

Great circle distances from each sampling unit to the nearest topographic feature were calculated using GRASS 7 (<http://grass.osgeo.org/>) and the sp package (<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. 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 10-100km - 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 r is the distance to 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. Residuals of ordinary least squares models showed significant spatial autocorrelation (Moran's I, $p < 0.001$), so we used the R nlme (<http://cran.r-project.org/package=nlme>) package 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 two-sample Kolmogorov-Smirnov test to compare 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 defined as a decline in predicted SSL MVBS to within 1% of its asymptotic value ($S_{v\infty}$, Equation 1). Confidence intervals were generated using bootstrapping, with 10000 replicates.

Results and discussion

Two distinct layers were observed throughout the CMR (Fig. 2), which included a collection of shallow scattering layers (SSLs) from the surface to 180m, and a deep scattering layer (DSL) from 300m to 600m. 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 showed to contain over 150 species of fish and invertebrates (Bradbury et al. 1970).

Both layers displayed an increase in MVBS as the seabed shallowed near atolls and Sandes Seamount (Fig. 3A). MVBS in the SSL increased dramatically towards topographic features. Effect sizes in terms of ΔS_v differed between feature (Fig. 3A), but the estimated spatial ranges were consistent between models and the regional model (Fig. 3A and B). **CI 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 CI probably arises because the model is based on a single transect, i.e. CI reflect model uncertainty but not spatial variability of the SSL. Sandes and Speakers have multiple transects each, so the spatial variability is captured more faithfully. Exponential models are very sensitive to data points close to 0 distance and thus we get very large CI on the parameter estimates.**

The regional SSL model expressed a doubling of MVBS intensity for every 100 m from its asymptotic value ($S_{v\infty}$, Equation 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 ($\Delta S_v = S_{v0} - S_{v\infty} = 20.4$ 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 (Two-sample Kolmogorov-Smirnov test, $D = 0.1417$, p -value < 0.001) between the zone of elevated MVBS and compensated target strength observations beyond the 1.8 km boundary region (unfilled bars, 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-feature (< 50 m) which, if assumed to be tunas, would correspond to individuals larger than 40 cm (Bertrand and 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 c. 1.8 km, in addition to holding record level 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), in which case 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 feature, could conceivably operate at the same time and to various degrees.

In our survey a substantial part of the SSL enhancement was observed occurring around mesophotic reef depths (> 30 m, Fig. 2). Although knowledge of trophic pathways at those depths are limited (Kahng et al, 2010), many mesophotic reef community

characteristics may be related to pronounced energy input from SSL prey subsidies, and by 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 reef.

The DSL exhibited a less pronounced increase in backscatter intensity, with MVBS in the vicinity of features up to 4 times higher ($\Delta S_v = S_{v0} - S_{v\infty} = 5.7 \text{ dB re } 1\text{m}^{-1}$, 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 in 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. For example, 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 required bigger radii, such as that offered by the CMR). In the same vein, existing reserves that do not allow sufficient buffer areas may offer imperfect protection 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 11 km^2 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, it is recommended that similar surveys 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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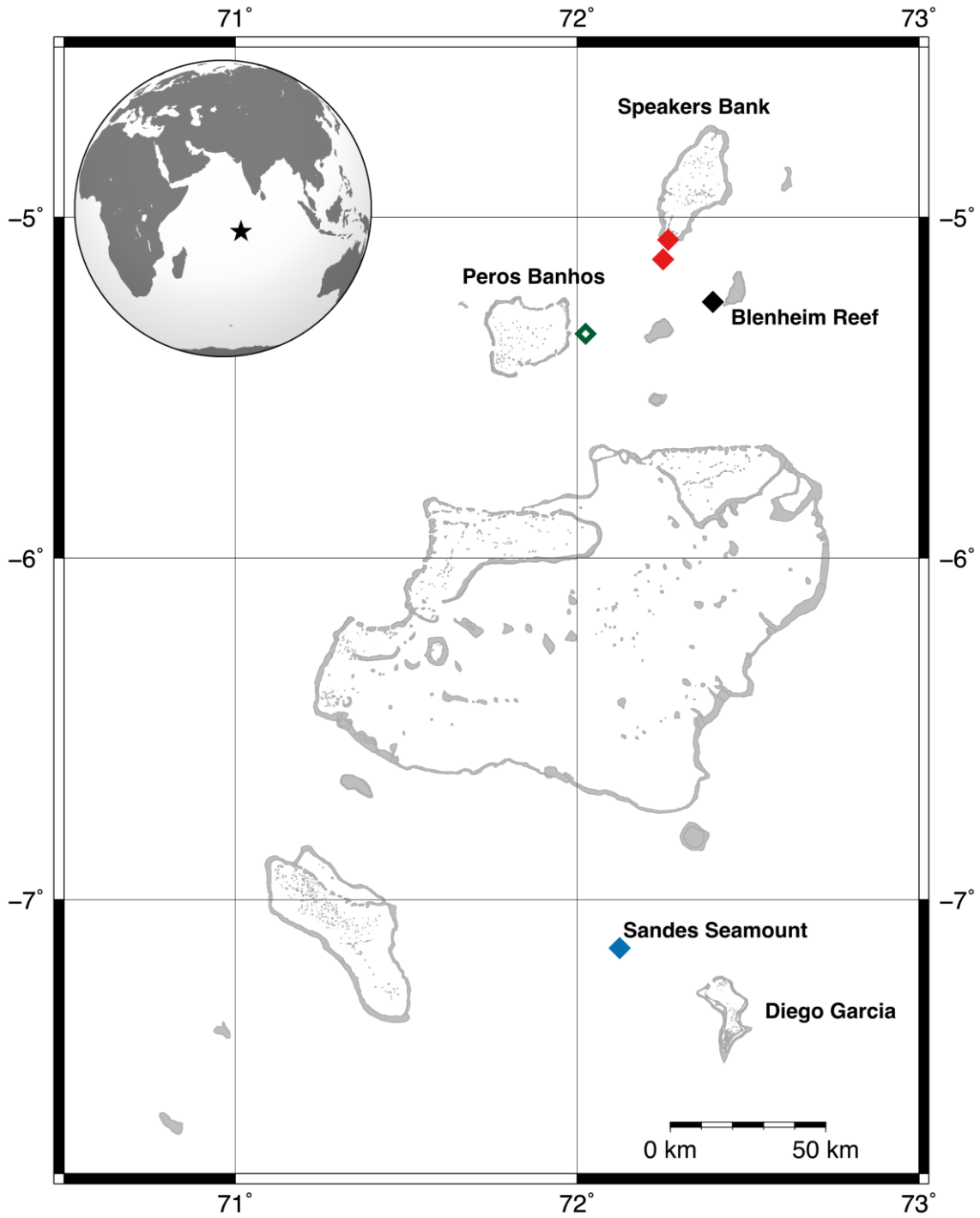


Figure 1. The Chagos study area and sampling locations. The star marks the location of Chagos in the Indian Ocean (inset). Locations and features of acoustic surveys within the archipelago are indicated by diamonds. The open diamond marks the transect shown in Fig 2A. Diamond colour corresponds to the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

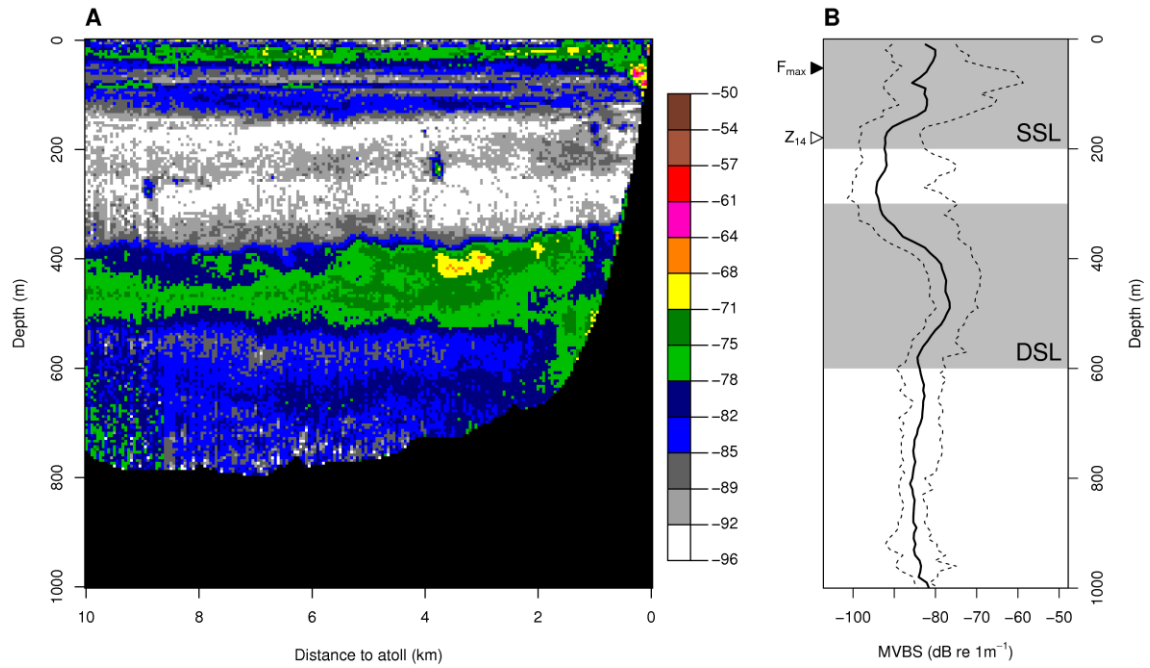


Figure 2. Vertical and horizontal patterns in layer mean volume backscattering strength [MVBS, $S_v = 10 \log_{10}(s_v)$]. (A) An echogram of a transect running from offshore onto Peros Banhos atoll (cf. Fig. 1). Colour scale is logarithmic, units dB re 1m⁻¹. (B) The vertical profile of MVBS (median, 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 arrows indicate the mean depth of the fluorescence maximum F_{max} and the 14°C isotherm Z_{14} , respectively.

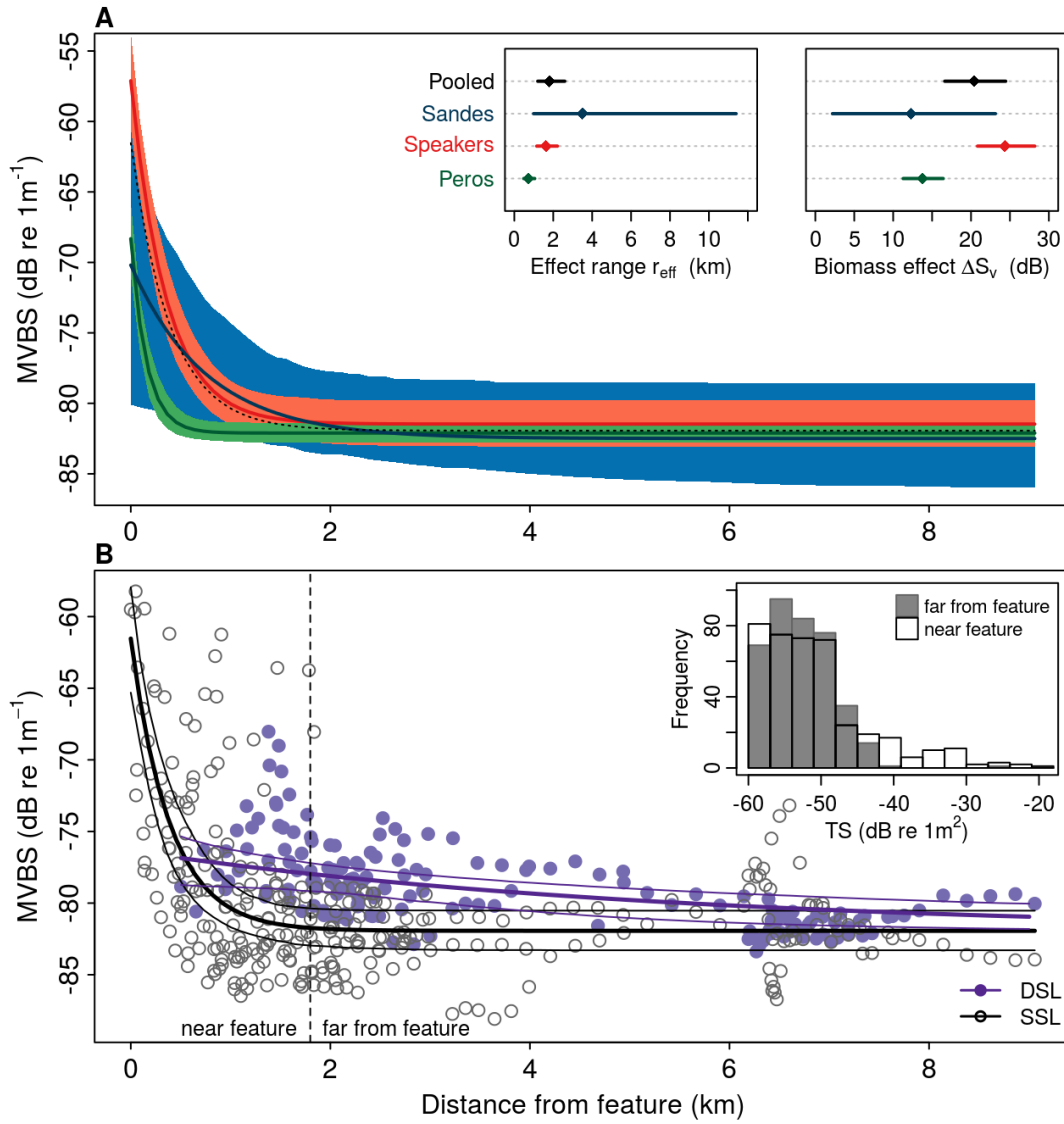


Figure 3. Non-linear regression models (lines, with 95% confidence intervals), of scattering layers in the Chagos Archipelago. A) Feature specific models (as illustrated in Fig 2B) for the shallow scattering layer (SSL), with effect range and biomass effect shown as insets. B) Regional regression model and MVBS observations and of the shallow (open points) and deep scattering layer (DSL, closed points, in purple) across all features for the archipelago. Each data point represent MVBS for 10 m vertical and 250 horizontal bins. The dotted lines on the plot indicate 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.

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