

1 ***Biogeography of the global ocean's***
2 ***mesopelagic zone***

3
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10
11 **Summary**

12
13 The global ocean's near-surface can be partitioned into distinct provinces on the basis of regional
14 primary productivity and oceanography [1]. This ecological geography provides a valuable
15 framework for understanding spatial variability in ecosystem function, but has relevance only part
16 way into the epipelagic zone (the top 200 m). The mesopelagic (200-1,000 m) makes up
17 approximately 20% of the global ocean volume, plays important roles in biogeochemical cycling [2],
18 and holds potentially huge fish resources [3–5]. It is, however, hidden from satellite observation, and
19 a lack of globally-consistent data has prevented development of a global-scale understanding.
20 Acoustic Deep Scattering Layers (DSLs) are prominent features of the mesopelagic. These vertically-
21 narrow (tens to hundreds of m) but horizontally-extensive layers (continuous for tens to thousands
22 of km) comprise communities of fish and zooplankton, and are readily detectable using
23 echosounders. We have compiled a database of DSL characteristics globally. We show that DSL and
24 acoustic backscattering intensity (a measure of biomass) can be modelled accurately using just
25 surface primary production, temperature and wind-stress. Spatial variability in these environmental
26 factors leads to a natural partition of the mesopelagic into ten distinct classes. These classes demark
27 a more complex biogeography than the latitudinally-banded schemes that have been proposed
28 before [6,7]. Knowledge of how environmental factors influence the mesopelagic enables future
29 change to be explored: we predict that by 2100 there will be widespread homogenisation of
30 mesopelagic communities, and that mesopelagic biomass could increase by c. 17%. The biomass
31 increase requires increased trophic efficiency, which could arise because of ocean warming and DSL
32 shallowing.

34 **Keywords:** pelagic ecology; ecological geography; environmental change; trophic efficiency; ocean
35 warming; marine acoustics; deep scattering layers; Longhurst; myctophid

36

37 **Results**

38 *Deep Scattering Layers and Acoustic Sampling*

39 Deep Scattering Layers (DSLs) are ubiquitous features of the global ocean that comprise biomass-rich
40 communities of zooplankton and fish. They are so dense (biomass per unit volume) that in early
41 acoustic surveys echoes from DSLs were mistaken for seabed echoes, hence the common name
42 ‘false bottom’. The mesopelagic is defined as the 200 to 1,000 m depth horizon (e.g. [8]). The physics
43 of sound propagation enables this zone to be sampled effectively from the surface with commonly-
44 employed 38-kHz echosounders. Previous studies from tropical to sub-polar seas suggest that DSLs
45 are rare beneath 1,000 m (e.g. [9,10]).

46

47 *General characteristics of regional-scale DSLs*

48 We used an automated, reproducible technique [11] to identify and characterise DSLs in 38-kHz
49 acoustic data collected from the top 1,000 m by numerous research and fishing vessels around the
50 world. We collated data from survey transects totalling 104,688 km in length (see Figure S1).

51 Together these contained 26,474 DSLs >10 km long.

52

53 Inspection of the global DSL dataset revealed pronounced geographic differences in DSL depth,
54 vertical extent (thickness) and acoustic backscattering intensity (quantified as area backscattering
55 coefficient [ABC], $\text{m}^2 \text{m}^{-2}$ [12]). ABC can be a linear proxy for biomass [3]. In this case, ABC is the total
56 acoustic backscatter per m^2 from DSLs in the mesopelagic zone: henceforth, we use the term
57 ‘backscatter’ for simplicity. Although it is tempting to convert backscatter to a measure of actual
58 biomass [3], we lack the data on species composition and size, and also on acoustic target strength,
59 to do this [13]. Our analysis henceforth is therefore relative rather than absolute.

60

61 Generally speaking, during the day-time the mesopelagic zone contained a principle DSL that was
62 vertically broad (extending over >200 m vertically), relatively dense (backscatter c. $1.59 \times 10^{-5} \text{m}^2 \text{m}^{-2}$
63 2), and commonly (>66% chance) centred at a depth of c. 525 m (Figure 1). There was also
64 sometimes (<20% chance) a secondary, less dense DSL (backscatter c. $1.26 \times 10^{-6} \text{m}^2 \text{m}^{-2}$)
65 approximately 300 m deeper.

66

67

68 *Environmental drivers of DSL variability*

69 Differences in DSL characteristics across oceanographic frontal boundaries have been reported
70 previously [15], but variability at the global scale has not been quantified. The spatial coverage of
71 our data spanned 14 of Longhurst's [1] 32 pelagic surface provinces (excluding his Coastal biome;
72 see Figure S1). We binned daytime DSL data by these surface provinces (there can be major
73 differences between day-time and nighttime depths of DSLs due to diel vertical migration [16], so
74 we separated daytime and nighttime data to avoid introducing temporal artefacts to our spatial
75 analysis). Variability in depth of the principle daytime DSL (Z_{PDSL} , m; see Figure 1) was explained well
76 at this spatial scale ($n = 14$, $R^2 = 0.68$, root-mean-square error [RMSE] = 28 m) by a simple multi-
77 linear model with mean annual primary production (PP, $\text{g C m}^{-2} \text{ day}^{-1}$, $p = 0.01$) and surface wind
78 stress (τ , N m^{-2} , $p = 0.001$) as explanatory variables (Figure 2A). The variability in backscatter from
79 DSLs was explained well ($n = 14$, $R^2 = 0.65$, $\text{RMSE} = 9.11 \times 10^{-6} \text{ m}^2 \text{ m}^{-2}$) by a simple multi-linear model
80 incorporating PP ($p = 0.017$) and the temperature at the depth of the principal DSL (T_{PDSL} , $^{\circ}\text{C}$, $p =$
81 0.0001 ; Figure 2B).

82

83 *Mesopelagic biogeography*

84 We used a clustering approach to explore the likely geographic distribution of distinct DSL types
85 across the global ocean (areas where total depth $\geq 1,000$ m). We gridded (at 300×300 km scale) PP
86 and T_{PDSL} (estimated from predicted values of Z_{PDSL} , which is a function of PP and τ ; see Figure 2A),
87 and used K-means clustering (see Supplemental Information) of the normalised variables to identify
88 coherent mesopelagic classes across a range of spatial scales (from $n = 3$ to 35 classes globally,
89 classes having characteristic backscatter, PP and T_{PDSL} values; see Supplemental Information, Figure
90 S3).

91

92 The ability to model regional variability in backscatter was best at the scale of 22 mesopelagic
93 classes ($n = 17$, $R^2 = 0.93$, $p < 0.0001$, $\text{RMSE} = 4.5 \times 10^{-6} \text{ m}^2 \text{ m}^{-2}$; Figure 2C). The best linear model
94 included just one explanatory variable, $\text{PP} \times T_{\text{PDSL}}$, which was positively correlated with backscatter.
95 Although the 22-class scale was optimal for modelling spatial variability in backscatter, several other
96 scales also enabled very good prediction ($R^2 > 0.83$, see Figures S2 and S3). As the number of classes
97 increased, finer scale features emerged in a progression from a simple polar and non-polar
98 dichotomy, to biomes, to ocean gyres, to frontal features (see Figure S3). We selected the ten-class
99 scale ($R^2 = 0.87$) to present mesopelagic biogeographic structure here (Figure 3; also see Table S1).
100 Projecting at the ten-class scale produced a map of 36 spatially-distinct mesopelagic provinces, a
101 number similar to the 32 surface provinces advocated by Longhurst [1] (see Supplemental

102 Information, Figure S2). By choosing to focus on this scale, we were able to compare Longhurst's
103 surface biogeography and our mesopelagic biogeography: they do not overlap directly (Figure 3A).

104

105 Our ten-class mesopelagic biogeographic structure is more complex and heterogeneous than the
106 simple latitudinal banding that pervades previous surface [6] and abyssal [7] schemes. Although the
107 Southern Ocean is latitudinally-banded in our scheme (reflecting the quasi-parallel oceanographic
108 frontal structure in that ocean [18]), a markedly different arrangement is evident elsewhere. For
109 example, the central tropical gyres of the north and south Pacific Ocean both cluster in to the same
110 class. Classes with high backscatter values (high mesopelagic biomass) are found across the north
111 Atlantic and within frontal zones at mid-latitudes, with the exception of the south Pacific sector of
112 the Southern Ocean. Classes with lower backscatter values (low mesopelagic biomass) include the
113 polar oceans and the south Atlantic.

114

115 *Present day backscatter and trophic efficiency*

116 We estimated total global backscatter by summing together the products of the predicted mean
117 backscatter value ($\text{m}^2 \text{m}^{-2}$) and surface area of each mesopelagic class. The present-day value was
118 $6.02 \times 10^9 \text{ m}^2 \pm 1.4 \times 10^9$ (error limits from regression model RMSE value; see Figure 2C).

119

120 Biological production (the increase in biomass per unit time) is a function of biomass, temperature
121 and trophic level [19]. The mesopelagic community is made up of organisms operating at a range of
122 trophic levels (TL) between 2 and 4. Myctophid fish (TL = 3.2; www.fishbase.org) are a major
123 component of mesopelagic biomass [20,21]. Zooplankton, squid and gelatinous predators operate at
124 TL = approximately 3, whilst herbivorous zooplankton reside at TL = 2. We used backscatter as a
125 proxy for biomass, the temperature at the depth of the principle DSL, and a nominal modal trophic
126 level of 3 to predict a value of DSL backscatter production (per m^2 per unit time) for each
127 mesopelagic class. For each class, we determined a ratio of backscatter production to primary
128 production (TL = 1) and quantified the total amount of wet-weight primary-producer biomass
129 required to generate 1 unit of backscatter (PP_{bs} , tonnes m^{-2} ; see Supplemental Information). PP_{bs}
130 serves as an inverse proxy for the trophic efficiency between TL 1 and TL 3, i.e. an increase in PP_{bs}
131 signifies a decrease in trophic efficiency. For the present day, we estimated a global mean PP_{bs} value
132 of 108 tonnes m^{-2} (error limits 62 to 195.6 tonnes m^{-2} from regression model RMSE values). To
133 enable regional comparisons of trophic efficiency to be made, mean PP_{bs} values were calculated for
134 each of Longhurst's [1] surface provinces. PP_{bs} , and hence trophic efficiency, was geographically
135 diverse (Figure 4A).

136

137 *Impacts of environmental change on DSL structure and distribution*

138 As the atmosphere warms the ocean will warm [22], its density structure will change [23]
139 (influencing stratification and near-surface nutrient supply [24]), surface wind intensity will change
140 (influencing vertical mixing, stratification and nutrient supply), and primary production will change
141 [25,26]. Our finding that the depth of, and backscatter from, present-day DSLs are influenced by PP,
142 temperature and wind stress, suggests that regional DSLs characteristics will change too in the
143 future as a result of expected environmental change. We used the coupled climate-ecosystem model
144 NEMO-MEDUSA-2.0 [27] (under the Representative Concentration Pathways (RCP) 8.5 climate
145 scenario, and with surface forcing as per the UK Meteorological Office's HadGEM2-ES model) to
146 obtain PP, τ and T_{PDSL} for the period 2090-2100. Values of PP and T_{PDSL} (estimated from predicted
147 values of Z_{PDSL} , which is a function of PP and τ) were gridded (300×300 km scale), and each grid cell
148 was attributed a DSL class using the K-means centroids (see Table S1) from the present-day (2005-
149 2008) ten-class scale mesopelagic biogeography (Figure 3B).

150

151 According to NEMO-MEDUSA-2.0, oceanic PP will remain fairly constant over the 21st century, with
152 mean values over the pelagic realm of 0.319 and 0.324 g C m⁻² day⁻¹ for the present and 2100
153 respectively. While there are differences between the predictions of various Earth system models,
154 predictions of future PP by NEMO-MEDUSA-2.0 are consistent with those from a number of other
155 models [28–31], and this ensemble agreement is mutually supportive. By 2100, the predicted mean
156 Z_{PDSL} will be shallower on average than present (shallowing from 545 m to 510 m, RMSE = 28 m; see
157 Figure 2A and 4B), the predicted T_{PDSL} will increase (from a mean of 7.2 +/- 0.28 to 8.5 +/- 0.37 °C,
158 error limits based on Z_{PDSL} regression model RMSE value), and wind stress will weaken (from 0.085 to
159 0.058 Nm⁻²).

160

161 *Future backscatter and trophic efficiency*

162 In light of the environmental changes predicted by NEMO-MEDUSA-2.0, we estimated that global
163 DSL backscatter will increase by 16.7% from a present-day value of 6.02×10^9 m² +/- 1.4×10^9 to 7.03
164 $\times 10^9$ m² +/- 1.4×10^9 in 2100 (error limits from regression model RMSE value; see Figure 2C). We
165 estimate that the global mean PP_{bs} will decrease from 108.0 tonnes m⁻² (error limits from 62.0 to
166 195.6) to 73.9 tonnes m⁻² (error limits from 53.6 to 145.7) by 2100 (error limits from regression
167 model RMSE values; Figure 4A), i.e. that 34.1 tonnes less primary producer biomass per m² will be
168 needed to generate 1 unit of DSL backscatter by 2100, equivalent to a factor increase in trophic
169 efficiency of 1.232 +/- 0.015 (error limits from regression model RMSE values, see Supplemental

170 Information). The predicted increase in global backscatter and decrease in the mean global value of
171 PP_{bs} is indicative of an overall future increase in mesopelagic biomass and trophic efficiency.

172

173 **Discussion**

174 The analysis reported here is the first to apply a consistent, automated technique to identify and
175 determine characteristics of DSLs from data collected on multiple acoustic surveys across the global
176 ocean. As such, it provides the first consistent view of DSL variability globally, and has enabled the
177 development, for the first time, of a DSL-based mesopelagic biogeography. Several site-specific DSL
178 studies have been published [32,33], but quantitative comparisons between studies have not usually
179 been possible because a consistent approach to DSL detection and parameterisation has not been
180 used. Longhurst's surface biogeography [1], defined in part using globally-consistent satellite remote
181 sensing data, has been extremely valuable for improving understanding of spatial variability in
182 ecosystem function in the visible and accessible ocean surface. We hope that the analysis presented
183 here will be of value for understanding operation on a global-scale of the ecosystem of the hidden
184 mesopelagic realm.

185

186 *Drivers of backscatter from DSLs*

187 *Primary production (PP)* – Foodweb theory holds that biomass at higher trophic levels (such as
188 zooplankton grazers at level 2 and myctophid fish predators at level 3.2) is constrained by PP [34].
189 Indeed PP-to-biomass relationships have already been reported for mesopelagic fish [3]. It is no
190 surprise, therefore, that PP is a significant factor in our model of DSL backscatter (a proxy for
191 biomass; $p = 0.01$). PP in turn is influenced by light intensity, nutrient availability, stratification and
192 mixing, and sea surface temperature (PP occurs in the illuminated, near-surface zone where
193 biological processes are strongly-influenced by sea surface temperature).

194

195 *Temperature at the depth of the* – Sea surface temperature was not a significant driver of
196 backscatter ($n = 14$, $R^2 = 0.07$, $p = 0.19$), but temperature at the depth of the DSL was. Mesopelagic
197 organisms live their lives away from the surface, which is one reason why the mesopelagic
198 biogeography revealed here does not map well on to Longhurst's [1] surface scheme (Figure 3).
199 Biomass, production, and production-to-biomass ratios for marine fish all vary with temperature [34]
200 (positively; temperature influences metabolic rates and therefore growth and reproduction), and
201 our finding of a highly significant positive linear relationship ($p = 0.0001$) between DSL backscatter
202 and temperature at the depth of the DSL is consistent with this. A consequence is that by 2100, the

203 majority of surface provinces where DSLs are predicted to shallow significantly (> 28 m) will have
204 increased biomasses because they will be warmer habitats (Figures 3 and 4B).

205

206 *Biogeographic change by 2100*

207 Using predicted values of PP, τ and T_{PDSL} for 2090 - 2100 (from NEMO-MEDUSA-2.0 [27]), and
208 mapping the ten present-day mesopelagic classes on to grid cells (300 x 300 km), it becomes
209 apparent that environmental change will lead to a marked change in global mesopelagic
210 biogeographic structure by the end of this century (Figure 3). Prominent changes by 2100 include:
211 the low biomass regions of the north and south Pacific gyres expanding to almost fill their respective
212 ocean basins (being separated by only a narrower, but more productive, east Equatorial Zone); the
213 south Indian Ocean gyre decreasing in biomass (Figure 3); southern mid-latitudinal frontal zones
214 increasing in area and biomass; the presently diverse south and central Atlantic Ocean coalescing to
215 a more homogeneous, and relatively productive (for an open-ocean gyre system) regime, and
216 increasing biomass in sub-polar regions. This latter change will be mediated strongly by DSL
217 shallowing (Figure 4B), and may indicate northward and southward range expansions of mesopelagic
218 fish. For the northern hemisphere, this in turn may be supportive of the view that the Atlantic and
219 Arctic food webs will merge [27], and will lead to increasing abundance and diversity of polar
220 mesopelagic fish.

221

222 *Trophic Efficiency now and by 2100*

223 The rule-of-thumb mean figure for trophic efficiency is approximately 10% per trophic level [35]. As
224 temperature increases (up to the point that it becomes physiologically challenging), for a given food
225 supply fish production will increase [19], yielding a higher trophic efficiency. This is because with
226 increased temperature more food can be metabolised per unit time, increasing growth and
227 reproduction rates (via shorter generation times). More rapid growth also leads to increased survival
228 and recruitment because, by growing, individuals more rapidly escape some predation risk in size-
229 structured food webs. We predict a mean increase in trophic efficiency between trophic level 1 and
230 3 by a factor of 1.232 +/- 0.015 by 2100. In the context of the rule-of-thumb 10% efficiency per
231 trophic level, this is an increase of 1.1% per level. The magnitude and direction of change will,
232 however, be geographically diverse because of geographic variation in temperature change and
233 primary production (food supply). At the ocean scale, the backscatter in the Atlantic as a whole is
234 predicted to change dramatically by 2100: substantial reductions in PP (-21% caused by stratification
235 and nutrient depletion [27]) will lead to reduced biomass (Figure 3) despite the Atlantic maintaining
236 some of the lowest values of PP_{bs} (i.e. highest values of trophic efficiency; Figure 4A). Estimated

237 values of PP_{bs} are presently highest in the polar regions but, by 2100, we predict substantially
238 greater trophic efficiency in those regions due to ocean warming and DSL shallowing (Figure 3 and
239 Figure 4A).

240

241 *Mesopelagic fish*

242 Although we do not know the extent to which mesopelagic fish contribute to DSL biomass [13], it is
243 not unreasonable to expect it to be high [3]. Consequently, in light of predictions here of an increase
244 in global backscatter by 2100 (of 16.7%), we predict an increase in the biomass of mesopelagic fish in
245 the future.

246

247 Mesopelagic fish are a key component of pelagic food webs [36], fuelling some commercially
248 important fisheries [21]. They also play a major role in the biological pump [2,37,38], the active
249 transport of carbon to the ocean interior that buffers atmospheric CO_2 , so provide an important
250 'ecosystem service'. In recognition of these roles, the US National Oceanic and Atmospheric
251 Administration's National Marine Fisheries Service prohibited in April 2016 commercial fisheries for
252 myctophids (Myctophidae, or 'Lantern fish' are major constituents of mesopelagic biomass) and
253 other small forage fish in the Pacific Ocean off the U.S. West Coast [39]. Our global-scale analysis can
254 contribute towards ecosystem-based management of the mesopelagic because it highlights regions
255 of relatively high (and low) biomass, and because present-day spatial variability (e.g. DSL
256 characteristics in the sub-tropics versus in temperate regions) can be used as a proxy for future
257 temporal change (e.g. regional warming). The ability to predict the redistribution of oceanic
258 mesopelagic production could aid conservation management by, for example, guiding placement of
259 open-ocean marine protected areas.

260

261 *Concluding remarks*

262 We have defined a global biogeography for the mesopelagic zone and used it to infer changes in
263 mesopelagic biomass and trophic efficiency in to the future. This has gone some way to fill the 'dark
264 hole' [4,5] in our understanding of the mesopelagic. Predictions based on output from NEMO-
265 MEDUSA-2.0 suggest that the mesopelagic will become more productive by 2100, but that this
266 production will be condensed into smaller regions (e.g. concentrated at fronts) and spread
267 polewards as DSLs shallow and the ocean warms. It has been suggested that constancy of light
268 regime under climate change will prevent myctophid fish invading the Arctic [40]. Our results bring
269 this in to question: ice loss will bring change to the Arctic surface and – we suggest – will presage
270 change to the deep sea there as well. These changes may bring new opportunities for fishing.

271

272 **Author Contributions**

273 A.S.B conceived the study. R.P, A.S.B and M.J.C conceived the method. R.P put the method in to
274 practise, collated the data and analysed the results. R.P and A.S.B wrote the manuscript. A.S.B, R.P
275 and M.J.C edited the manuscript.

276

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286

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377

378 **Figure Legends**

379 **Figure 1. Scattering Layer Daytime Vertical Distribution and Acoustic Backscattering Intensity.**

380 A typical day-time water-column acoustic profile (an echogram), showing a ‘surface’ scattering layer
381 in the epipelagic zone (0 – 200 m), a principal deep scattering layer (DSL) at around 525 m (the global
382 mean) and a secondary DSL at around 825 m, both in the mesopelagic (200 – 1,000 m). Data were
383 recorded using a 38 kHz echosounder from the fishing vessel *Will Watch* [14] on the 30th May 2012
384 in the south west Indian Ocean (28.8°S, 47.3°E). The colour bar is mean volume backscattering
385 strength (MVBS, dB re 1m⁻¹, [12]).

386

387 **Figure 2. Weighted linear regressions between Observed and Predicted Principal Depths of, and** 388 **Acoustics Backscattering Intensities from, DSLs.**

389 (A) Principal DSL depth (Z_{PDSL} , m; $n = 14$, $R^2 = 0.68$, $\text{RMSE} = 28$ m) predicted for 14 of Longhurst’s 32
390 surface provinces [1], using mean values of primary production (PP, g C m⁻² day⁻¹: data from
391 <http://www.science.oregonstate.edu/ocean.productivity/index.php>) and wind stress (τ : output from
392 SODA [17]) as explanatory variables ($\widehat{Z_{\text{PDSL}}} = 483.8 + 1272 \times \tau - 143 \times \text{PP}$);

393 (B) Backscatter (ABC, m² m⁻²; $n = 14$, $R^2 = 0.65$, $\text{RMSE} = 9.11 \times 10^{-6}$ m² m⁻²) predicted for 14 of the 32
394 surface provinces [1] using surface PP and the temperature at Z_{PDSL} (T_{PDSL} , °C: inferred from ocean
395 temperature output from SODA [17]) as explanatory variables

396 ($\widehat{\text{ABC}} = -1.18 \times 10^{-5} + 2.99 \times 10^{-5} \times \text{PP} + 3.38 \times 10^{-6} \times T_{\text{PDSL}}$);

397 (C) Backscatter (ABC, m² m⁻²; $n = 17$, $R^2 = 0.93$, $\text{RMSE} = 4.5 \times 10^{-6}$ m² m⁻²) predicted for 17 of the 22
398 mesopelagic classes (determined by K-means clustering of normalised gridded PP and T_{PDSL} values,
399 see Figure S3G) using $\text{PP} \times T_{\text{PDSL}}$ as an explanatory variable ($\widehat{\text{ABC}} = -1.34 \times 10^{-6} + 8.62 \times 10^{-6} \times (\text{PP} \times T_{\text{PDSL}})$).

400 Cross size represents the relative weighting of samples. Colours for (A) and (B) differentiate
401 between Longhurst Biomes: red = Trades; green = Westerlies, and blue = Polar. Grey regions indicate
402 the range of RMSE for each regression model. Z_{PDSL} is weighted by probability of observation, and
403 backscatter is weighted by sample size (spatial coverage within surface province or mesopelagic
404 class). See also Figure S1.

405

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407

408 **Figure 3. Present-Day Mesopelagic Biogeography Derived from Values of Surface Primary**
409 **Productivity and Temperature at the Depth of the Principal DSL, and Predicted Biogeography for**
410 **the Period 2090-2100.**

411 (A) Present-day mesopelagic biogeography derived by K-means clustering of gridded PP ($\text{g C m}^{-2} \text{ day}^{-1}$; data from <http://www.science.oregonstate.edu/ocean.productivity/index.php>) and T_{PDSL} ($^{\circ}\text{C}$:
412 estimated from predicted values of Z_{PDSL} using data output from SODA [17]) values into ten classes
413 (see Table S1 for mean values).

414 (B) Future mesopelagic biogeography. Gridded cells attributed to their future appropriate class using
415 centroids from the present-day result.

416 Longhurst surface provinces [1] are overlaid and labelled. Each mesopelagic biogeography is formed
417 of ten classes (that form distinct mesopelagic provinces when resolved spatially), which are ranked
418 in order (from C1 to C10) of increasing backscatter values (proxies for mesopelagic biomass). See
419 also Figures S2 and S3 and Table S1.

421

422 **Figure 4: Global Change in PP_{bs} , an Inverse Proxy of Trophic Efficiency, and Principal DSL Depth for**
423 **Each Longhurst Surface Province for the Present-Day and Future, Assuming Future Conditions as**
424 **per Data Output from NEMO-MEDUSA-2.0 for the Period 2090-2100.**

425 (A) PP_{bs} (tonnes m^{-2} ; primary-producer biomass required to generate one unit of backscatter per m^2
426 from DSLs in the mesopelagic) calculated by surface province (see Supplemental Information). Error
427 bars are from regression model RMSE values.

428 (B) Predicted variability in the depth of the principle day-time DSL ($\widehat{Z_{\text{PDSL}}} = 483.8 + 1272 \times \tau - 143 \times \text{PP}$,
429 $\text{RMSE} = 28 \text{ m}$, where PP ($\text{g C m}^{-2} \text{ day}^{-1}$) is primary production (data from
430 <http://www.science.oregonstate.edu/ocean.productivity/index.php>) and τ (N m^{-2}), is wind stress,
431 taken from SODA [17]). See also Figure S1.

432 Surface provinces are grouped by Ocean and ranked by latitude from north to south: ARC is the
433 Arctic Ocean, IO is the Indian Ocean, SO is the Southern Ocean, and ANT represents the region of the
434 SO south of the Antarctic Polar Front. For the Pacific and Atlantic Oceans, provinces that are furthest
435 north (N), south (S) and those which reside closest to the equator (E) are indicated.