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**Contribution to project objectives** – with this deliverable, the project has contributed to the achievement of the following objectives (from Annex I / DOW, Section B1.1.):

N.º	Objective	Yes	No
1	Reduce uncertainties in our knowledge of the functioning of Tropical Atlantic (TA) climate, particularly climate-related ocean processes (including stratification) and dynamics, coupled ocean, atmosphere, and land interactions; and internal and externally forced climate variability.		x
2	Better understand the impact of model systematic error and its reduction on seasonal-to-decadal climate predictions and on climate change projections.		x
3	Improve the simulation and prediction TA climate on seasonal and longer time scales, and contribute to better quantification of climate change impacts in the region.		x
4	Improve understanding of the cumulative effects of the multiple stressors of climate variability, greenhouse-gas induced climate change (including warming and deoxygenation), and fisheries on marine ecosystems, functional diversity, and ecosystem services (e.g., fisheries) in the TA.	x	
5	Assess the socio-economic vulnerabilities and evaluate the resilience of the welfare of West African fishing communities to climate-driven ecosystem shifts and global markets.	x	

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**Deviation from planned efforts for this deliverable:**

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**Executive Summary:**

Objectives for D12.1 were to analyse large-scale changes in range and assemblage properties in the pelagic food web and analyse cumulative impacts on the fish compartment and associated ecosystem services.

This report summarizes work carried out within PREFACE WP 12.1 based on data from mesopelagic sampling during the PREFACE surveys in 2014 and 2015 and the compilation of historical data. In particular this report provides evidence that (1) the concept to compare historical and present samples could be realized methodologically, and that (2) a biological model can be developed in line with the PREFACE rationale to analyse changes in the environment and biota, link these to modelling and use the knowledge of changes to enhance capacities of understanding future developments, which is needed for D12.2.

Aspects of change in more coastal environments due to changes in ocean oxygen conditions are not included in this report (stations closer to the Senegalese coast) and will be considered in D12.2 due to the fact that reconstruction data on past oxygen conditions are yet not perfectly available.

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## Preface

Objectives for D12.1 (Retrospective bioclimatic analysis) were to analyse large-scale changes in range and assemblage properties in the pelagic food web and analyze cumulative impacts on the fish compartment and associated ecosystem services.

This report summarizes work carried out within PREFACE WP 12.1 based on data from mesopelagic sampling during the PREFACE surveys in 2014 and 2015 and the compilation of historical data. In particular this report provides evidence whether (1) the concept to compare historical and present samples could be realized methodologically, and whether (2) a biological model can be developed in line with the PREFACE rationale to analyse changes in the environment and biota, link these to modelling and use the knowledge of changes to enhance capacities of understanding future developments, which is needed for D12.2.

Aspects of change in more coastal environments due to changes in ocean oxygen conditions are not included in this report (stations closer to the Senegalese coast) will be a matter of D12.2 due to the fact that reconstruction data on past oxygen conditions are yet not perfectly available.

## Introduction

Mesopelagic assemblages can be differentiated with regards to biogeographic affiliation and water depth. Ross et al. (2010) showed that community structure changes with depth and differentiate between shallow (<400 m) and deeper stations (about 600 m). Fock (2009), Fock et al. (2004) and Olivar et al. (2017) indicated that water mass structure in the Atlantic is an essential parameter for mesopelagic assemblage structure.

Recent findings on warming trends (Cheng et al., 2017; Hausfather et al., 2017) indicate a significant thermal change of the upper ocean during the last 50 years. Accordingly, different modelling approaches indicate significant climate impacts on mesopelagic assemblages (Klevjer et al., 2016; Proud et al., 2017), however mainly with a focus on proxy parameters such as changes in scattering layer depth rather than dedicated analyses of species composition present and past.

## Methods

### Historical sampling

Sampling was carried out from 1966 to 1983, of which samples from 1966 to 1968 were used because of sampling season and area. Samples were taken at night to have consistent sampling with regards to the diurnal vertical migration of mesopelagic fishes. A 1600 meshes pelagic trawl (MT 1600) was deployed, spanning 20m vertically and 30m horizontally, equipped with two 8m<sup>2</sup> Süberkrub doors. Normally, an inlet was fixed to the codend with 10mm stretched mesh size, further complemented by a small cloth inlay to preserve the catch (Post, 1987). This configuration is likely to underestimate the abundance of specimens < 30mm standard length (SL) (Gartner et al., 1989), but the application of large commercial nets has the advantage of likely better catchability for larger and

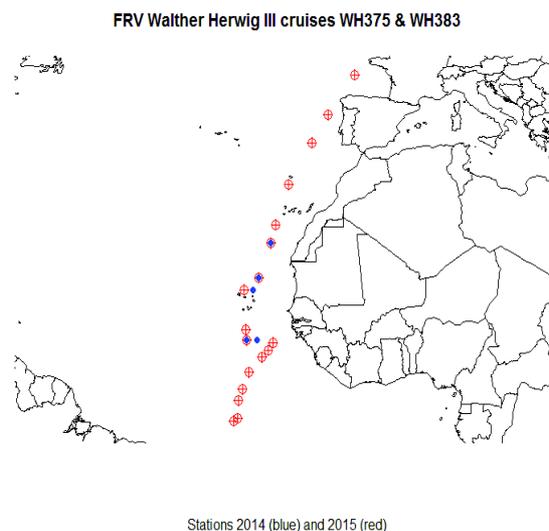
rarer species due to the higher sampled volume of water (Krefft, 1976, 1974; Merrett et al., 1986). During retrieval, the net was hauled speedily in order to avoid contamination of deep hauls with specimens from shallower depths (Krefft, 1976). Trawl samples were thus carried out as double oblique hauls. For a nominal trawling speed of 3.5 kn, ship speed was usually reduced to 2.5 kn during lowering, and to 1.5 kn during retrieval of the net (Krefft, 1967). After retrieval, the forenet area was carefully sampled by hand before winding it to the drum.

Sampling depths were selected based on echo soundings.

### Sampling in 2014/2015

A pelagic research trawl, i.e. "Aalnetz", was deployed during nighttime, with a mouth opening equivalent to the MT1600 trawl, app. 20 by 30 m depending on trawling speed and water depth. Minimum mesh size was 20 mm with an inlet with 1.7 mm mesh size fixed to the last section of the codend to gently preserve the delicate fish.

The codend was further equipped with an opening-closing device with three net bags, so that depth stratified sampling was possible. Sampling depths were selected based on echo soundings and thus could be slightly different to historical sampling (Fig. 1, see Annex 1 for sampling information).



**Figure 1 : Station plot for PREFACE sampling in 2014 and 2015, this study, consistent with historical trawling stations 1966-68.**

### Evaluating the comparability of survey results past and present

Samples taken with different trawls can be affected by net effects in several ways (Heino et al., 2012):

- Area of net opening
- Ease of avoidance of net
- Retention through mesh selection

- Herding effect

Given that the PREFACE gear ("Aalnetz") was rigged comparably to historically used gear ("MT1600"), and was of equivalent dimensions, net avoidance and selection issues need to be considered in particular.

We follow the approach of Harrison (1967) to review the following size-dependent criteria:

- Similarity in size range and cohort structure
- Similarity in size range
- Similarity in cohort structure

Differences in size spectra would for instance indicate net avoidance (larger specimens) or reduced selectivity (smaller specimens), whereas changes in cohort structure would point at selectivity issues. A comparison with results from Olivar et al. (Olivar et al., 2017) from 2015, applying a smaller net (5 \* 7 m, so-called "Mesopelagos" net), shows the suitability of size-dependent criteria. Their maximum sizes are on average smaller than the maximum sizes found in this study from the same place, the same year and at the same time-of-year (Table 1).

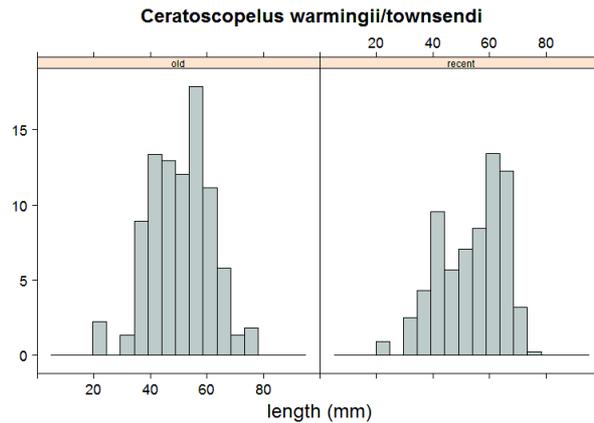
**Table 1: Comparison of maximum body sizes for selected mesopelagic species collected by "Mesopelagos" net or by "Aalnetz", both cruises in the 2015 in the tropical-subtropical North Atlantic.**

Sizes in mm standard length (SL).

Species	Mesopelagos (Olivar et al. 2017)	This study
<i>Diplophos taenia</i> (Stomiiformes)	58	150
<i>Chauliodus sloani</i> (Stomiiformes)	194	248
<i>Argyropelecus sladeni</i> (Stomiiformes)	40	83
<i>Argyropelecus hemigymnus</i> (Stomiiformes)	28	39
<i>Diaphus rafinesquii</i> (Myctophiformes)	72	84

For one species, *Ceratoscopelus warmingii* (Myctophiformes), "Mesopelagos" maximum size was larger (82 mm SL) than in this study (76 mm SL). For this species however, cohort structure varied considerably between both surveys, i.e. modal values were indicated at 19 and 40 mm SL in Olivar et al. (2017), whereas in this study, we identified a young cohort at 20 mm SL, but two major size groups at about 40 mm SL and 60 mm SL (Figure 1), of which the latter was missing in the "Mesopelagos" catches. Many larger species with good swimming capabilities were underrepresented in "Mesopelagos" catches, although abundant in this study, e.g. *Electrona risso* (Myctoph.).

For smaller species, maximum sizes did not differ between the "Mesopelagos" and the "Aalnetz" catches, e.g. *Diogenichthys atlanticus* (Myctoph., 24 to 24.3 mm SL), *Benthosema suborbitale* (Myctoph., 34 to 33.4 mm SL).



**Figure 2: Cohort structure of *Ceratoscopelus warmingii* (Myctophiformes) in this study (recent, "Aalnetz") and in historical samples (old, MT1600). *C. warmingii* was formerly named as *C. townsendi*.**

Size dependent criteria were applied to six selected species, representative of different taxa (Stomiiformes, Myctophiformes, Beryciformes), based on size frequency distributions as shown in Figure 2 (Table 2). In most cases, significant differences arise from shifts of abundance within a given size range and cohort structure, so that we conclude that the survey results from historical and present sampling are comparable in terms of methodology, and that differences would reflect changes in environmental factors such as climate induced effects. Several publications suggest changes in size as an effect of increasing oxygen demand (e.g. Cheung et al., 2012), an assumption that can be tested with this approach.

**Table 2 : Application of size-dependent similarity criteria to evaluate differences between historical (MT1600) and present sampling ("Aalnetz"). Figures except for *C. warmingii* given in Annex 2.**

Species	Similarity in terms pf...	Significance and difference
<i>Argyropelecus affinis</i> (Stom.)	Size range and cohort structure	No significant difference
<i>Electrona risso</i> (Myctoph.)	Size range and cohort structure	No significant difference
<i>Hygophum macrochir</i> (Myctoph.)	Size range and cohort structure	Significant difference, stronger cohort at 52 mm as compared to historical sampling
<i>Ceratoscopelus warmingii</i> (Myctoph.)	Size range and cohort structure	Significant difference, stronger cohort at 60+ mm as compared to historical sampling, see Fig. 1
<i>Diretmus argenteus</i> (Berycif.)	Size range and cohort structure	Significant difference, smaller cohort less abundant
<i>Diretmoides pauciradiatus</i>	Cohort structure	Significant difference, cohort at 60-70 mm SL complemented by new cohort at 100+ mm SL.

## Analytical procedures

Univariate diagnostics were applied to investigate whether simple patterns were present in the data. Multivariate diagnostics were applied on assemblage level, and species-wise bioclimatic modelling was undertaken for selected species which were not included in the multivariate analysis, i.e. the latter approach is better suitable for less abundant species.

## Univariate bioclimatic diagnostics

4 different parameters were generated to allow for quick inspection of the data set:

- Abundance weighted mean depth
- Abundance weighted mean latitude
- Maximum latitude
- Minimum latitude

General calculation details for abundance weighted indices is given in Olivar et al. (2017).

Eel-like species were excluded from this analysis because these were likely included in the historical samples from handpicking the forenet, whereas so-called "deck catch" including handpicked specimens was not included in the analysis for 2015, since it could not properly be assigned to a certain catching depth. This exclusion refers to chauliodids, stomiids, and serrivomerids.

## Multivariate bioclimatic diagnostics

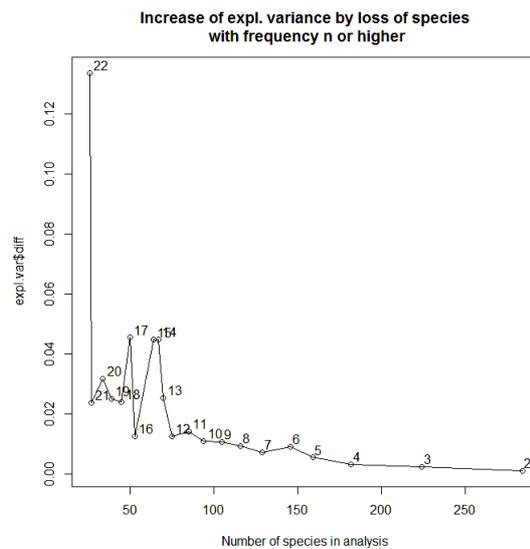
Principal components analysis (PCA) appeared as suitable method to objectively structure data (Kenny et al., 2009), given that unidirectional approaches such as species stacking (Distler et al., 2015) appear to be difficult in the first place, i.e. species removals will likely be compensated for by substitutions from other species.

PCA was carried out in two different modes, i.e. based on presence-absence species data in line with most bioclimatic modelling approaches (see next section), and  $\log(x+1)$ -transformed species abundance data scaled to 30 minutes trawling.

The survey design 2015 was aligned to historical sampling in 1966 and 1968, and spring samples from these cruises were applied for comparison with 2015 samples, being also a spring survey.

PCA suffers from the double-zero problem, i.e. stations become apparently similar due to species with zero abundances in both samples, though these species could be ecologically quite different (Zuur et al., 2007). This appears as arch-effect mainly on the second principal component (PC2).

PCA performance can be characterized by the degree of explained variance of the original data set. With  $n$  variables,  $n$  PCs explain 100 % variability. Reducing the number of variables in the analysis accordingly leads to simpler PC structure, thus subsequently more variance contained in each PC. In previous studies we excluded singletons and doubletons by rule-of-thumb (Fock, 2009), but in this study we developed a selection algorithm to analyse this change in explained variance for the first 4 PCs in relation to the number of excluded species. Exclusion criterion was frequency, i.e. the number of occurrences in samples in a given data set.

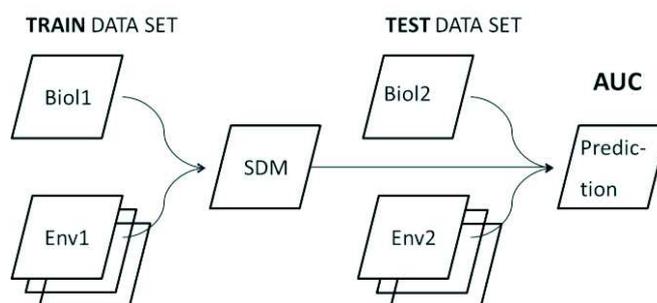


**Figure 3 : Results of the species selection algorithm for PCA based on first 4 PCs, conducted in p/a modus. Similar results for  $\log(x+1)$  data.**

Starting with 407 species including samples from historical and present sampling (frequency 1 or higher), 284 species remained for frequency 2 or higher, about 150 species with frequencies of 5 or higher etc. (Fig. 3). It is evident, that at each reduction step the increase in explained variance by lost species increases, but from  $n=12$  to  $n=13$  the PC structure becomes increasingly simple thus indicating that at this step we start losing essential information in the data set. All further PCAs were carried out with  $n>11$ .

## Bioclimatic modelling

The bioclimatic envelope modelling applied in PREFACE WP12.1 is based on p/a-distribution patterns reflecting physiology-based utilization of habitat and the projection of these patterns as an effect of changes in environmental conditions. We follow the common approach to evaluate several models in parallel (Jones et al., 2012) in order to derive an unbiased understanding of distributional change. MAXENT, BIOCLIM and DOMAIN models were applied (Carpenter et al., 1993; Elith et al., 2011), with sea basslet *Bathysphyraenops simplex* as model organism.



**Figure 4 : Workflow for bioclimatic modelling.** Biol1,2 – biological data sets, Env1,2 – environmental predictors, SDM – species distribution model, AUC – Area-under-curve test criterion

The workflow comprises to develop the model with a training data set, test the model with a test data set and check the goodness-of-fit of the predictions by means of the AUC criterion (Figure 4). In a third step (not shown in the figure), the data set Env2 can be replaced with data from climate change scenarios to project a future distribution state of the species. Environmental data were acquired from World Ocean Atlas (WOA) as decadal climatologies for salinity, temperature and oxygen for water depths 0-100, 100-300 and 300-500 m. For historical oxygen contents, a linear approximation was undertaken based on data in Stramma et al. (2012).

## Statistical treatment

For the analysis of differences of species size ranges and cohort structure, and of differences in univariate bioclimatic diagnostics, a resampling procedure was developed to avoid biases due to inevitably different sampling designs between historical sampling and sampling carried out in 2015.

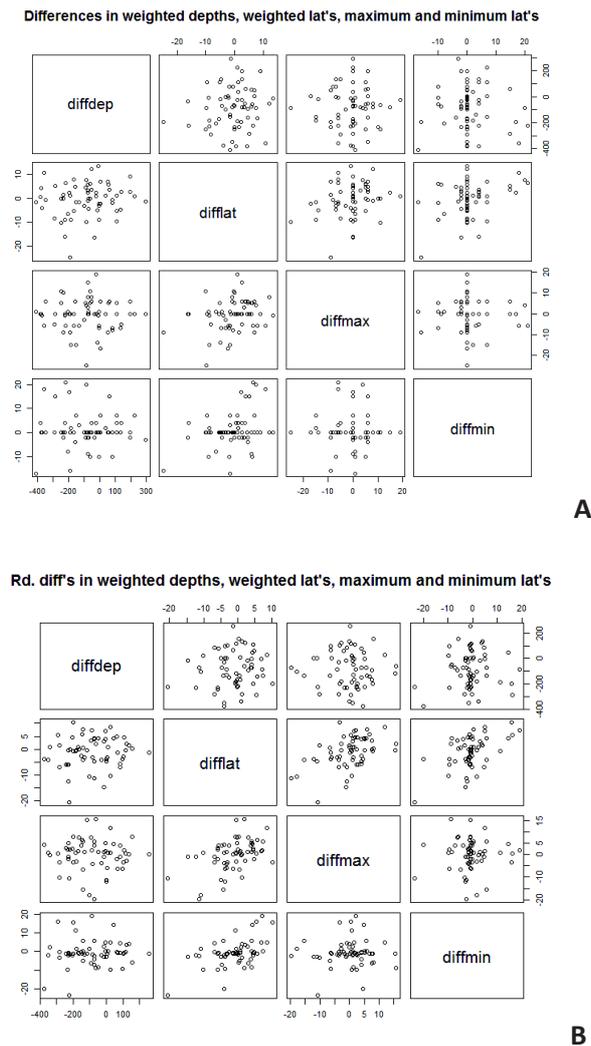
Samples were indexed as 'historical' or 'recent' period, and statistical random sampling with replacement was conducted to get subsamples, from which the respective parameters were derived.

## Results

### Univariate diagnostics

Positive and negative differences between periods in terms of weighted mean depth, weighted mean latitude, minimum and maximum latitude were found (Fig. 5). Positive differences indicate that species appeared further north in 2015 (weighted mean latitude, maximum latitude, minimum latitude) or appeared shallower in 2015 (weighted mean depth, Fig. 5). The difference in minimum latitude (diffmin) is not informative given that the analysis was limited by its southern boundary, the Equator, and accordingly many species show zero change in their southern limit.

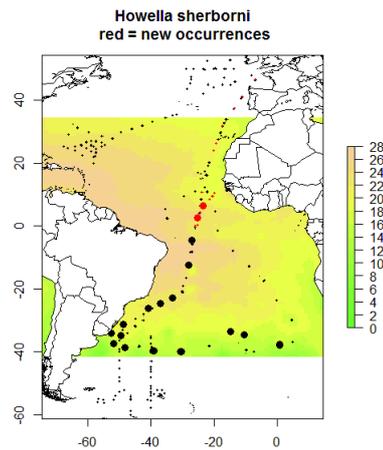
For non-randomized data, positive correlations appear for diffdep-diffplat ( $r=0.12$ ) and diffmax-diffplat ( $r=0.27$ ), of which only the correlation diffmax-diffplat re-appears in the randomized data set ( $r=0.46$ ,  $p<0.001$ ), whereas diffdep-diffplat drops to  $r=0.10$  (Fig. 5B). This suggests a relationship between changes in abundance weighted mean latitude and changes in maximum latitude in a way that positive responses were accompanied by increases in abundance in survey space, whereas negative responses were accompanied by decreases of abundance in survey space in relation to latitude. This will be discussed in the next section ('Multivariate diagnostics') with regards to the flattening of the main species gradient. However, the possible explanation that negatively responding species would increasingly move downward in the water column is not supported by the weak diffdep-diffplat correlation. Survey space here not only refers to latitudinal coverage, but also water depth to which sampling was undertaken.



**Figure 5 : Paired scatterplots for univariate diagnostics (A), and paired scatterplot for univariate diagnostics after randomization (Rd.) (B).** diffdep – difference in weighted mean depth 2015 to 1966/68, difflat – difference in weighted mean latitude 2015 to 1966/68, diffmax – difference in weighted maximum latitude, diffmin – difference in weighted minimum latitude. Randomizations include 100 repetitions with 500 data points in each period.

## Multivariate diagnostics

The frequency filter in PCA with  $n > 11$  prevents the inclusion of some rare but very informative species in the analysis. The boreal myctophid *Notoscopelus kroeyeri* appeared in the Bay of Biscay in 1966/68, but was not present in 2015. Sherborne's basslet *Howella sherborni* appeared south of the equator in historical samples, but now extended its habitat to about  $10^{\circ}\text{N}$  (Fig. 6). Likewise, the sea basslet *Bathysphraenops simplex* extended its range from tropical to subtropical, now reaching the Canaries. The analysis for *B. simplex* will be documented in the next section ('Bioclimatic modelling').

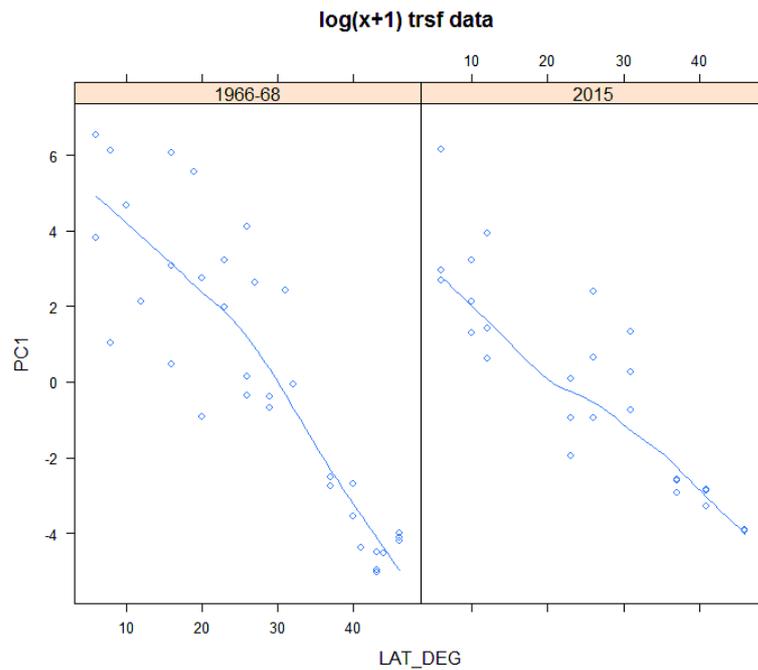


**Figure 6 : Range extension of Sherborne's basslet in the 2015 PREFACE cruise, as compared to historical fundings (black dot).** Crosses indicate sampling locations where this species was not encountered. WOA surface layer temperature in background.

For pa-data, the first 4 axes explained 47.9 % of total variance (%: 18.7, 14.4, 8.0, 6.7), which is the same level of explained variance as for  $\log(x+1)$  transformed data (%: 47.9; per PC 15.7, 14.27, 11.3, 6.6). However, the first 2 PCs explained more variance in pa-analysis than in abundance weighted  $\log(x+1)$  mode, which is due to the more simple data structure in presence-absence data.

PCA indicates that in particular PC1 and PC4 are interesting in terms of climate change (Fig. 7). PC1 indicates a significant flattening of the latitudinal gradient. The section 20°N to 40°N indicates that this flattening took place at a rate of app. 1° lat per decade. The flattening is consistent with the positive correlation between  $\text{difflat}$  and  $\text{diffmax}$ , with many species having negative  $\text{difflat}$ . Negative  $\text{difflat}$  would move the center of distribution closer to the Equator, thus eliminating the bump observed in PC1 for the period 1966-68. Numerically the presence of negative  $\text{difflat}$  species in 2015 is shown by the fact that absolute loadings for station at low latitude is about the same as for 1966-68. In turn, species extending their range northwards (positive  $\text{difflat}$  and positive  $\text{diffmax}$ ) would diminish the influence of true northern species in the analysis.

Species loadings are presented in Annex 4.



**Figure 7 : PC1 by latitude North and period for log-transformed data.** LOESS smoother applied.

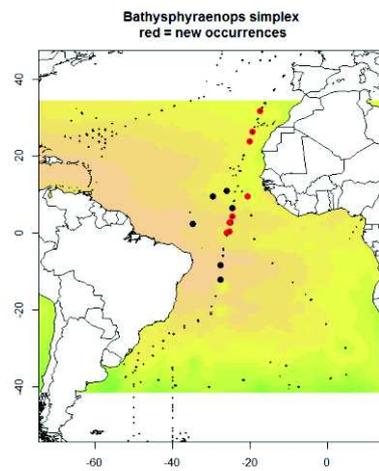
PC4 (Annex 3) shows a negative pattern for 2015 and a strictly positive pattern 1966-68. This reflects in particular species with increased abundances in 2015 (negative) or increased abundances in 1966-68 (positive). PC2 shows the arch effect mentioned for data along a strong gradient, and PC3 appears only little informative.

At species level, positive-positive loadings for PC1 and PC4 resp. would indicate non expanding species with decreasing abundances (examples given with loadings  $> 0.1$ ; here : *Photostomias guernei* (PSTOGUE)), whereas negative-negative loadings would indicate expanding species with increasing abundance level (example: *Ceratoscopelus maderensis* (CERMAD)) .

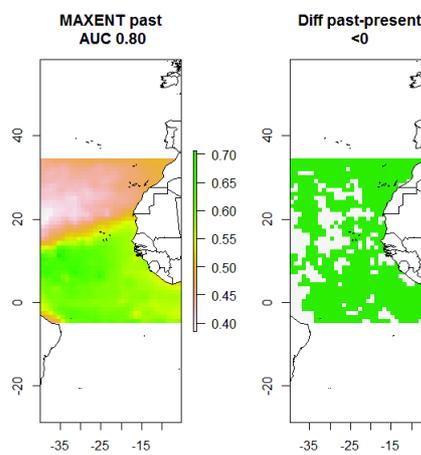
### Bioclimatic modelling

*Bathysphyaenops simplex* expanded northwards (Fig. 8 A). The best model to mirror this expansion is MAXENT, which reaches an AUC of 0.8 as compared to DOMAIN (0.69) and BIOCLIM (0.60).

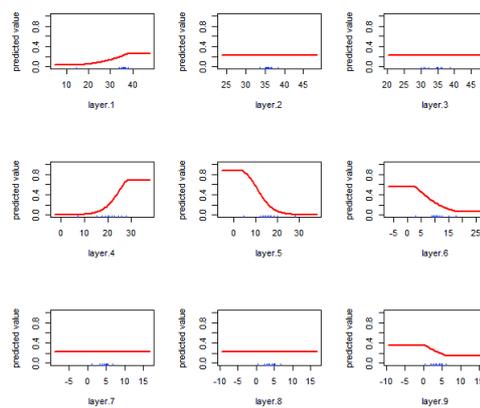
The influence of environmental predictors is different, and in some cases they are not informative, e.g. salinity 100-300 and 300-500, and oxygen 0-100 and 100-300. This analysis underlines the importance of including oxygen data in modelling the distribution of pelagic species in the Atlantic.



A



B



C

**Figure 8 : Range extension of sea basslet *B. simplex* in the 2015 PREFACE cruise, as compared to historical fundings (black dot) (A), MAXENT modelling of present distribution (B, left panel, scale probability) and predicted change of suitability in relation to past conditions (right panel, green area), and influence of environmental predictors (C, left to right: 0-100, 100-300, 300-500, top to bottom: salinity, temperature, oxygen). Crosses in (A) indicate historical sampling locations where this species was not encountered. WOA surface layer temperature in background in (A).**

## Outlook: Towards D12.2

Two aspects of D12.1 are essential for the development of D12.2 (Bioclimatic modeling: Bioclimatic modeling tuna and prey field dynamics according to scenarios).

The flattening of PC1 as shown in multivariate diagnostics suggests a linear relationship

$$PC1 = f(T)a_0 + f(T)lat ,$$

which can be re-written as generalized additive model of the form

$$PC1 = a_0 + f(T) + f(lat) + f(T, lat)$$

With regards to PC4, species bioclimatic modelling with regards to important tuna forage fishes will indicate changes in food supply. Important forage species for tuna are myctophids, gonostomatids, and in particular photichthyds, e.g. *Vinciguerria nimbaria* (Menard et al., 2000; Ménard and Marchal, 2003). At higher latitude, PC1 was negative, thus PC4 suggests that several species of myctophids with additional negative loadings on PC1 will increase in abundance, e.g. *Ceratoscopelus maderensis*, *Diaphus rafinesquii*, *Lampanyctus crocodilus*, together with Grey's deepsea smelt *Bathylagichthys greyae*. However, *V. nimbaria* was not correlated to PC4 (loading 0.02) indicating no change in overall abundance.

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**Annex 1**

Sampling information WH383

CRUISE	ST_NO	Net	Daytime	Year	Month	Day	LAT_DECD	LON_DECD	BOTTOM	FI_DUR1	Start	Stop	Speed	FI_DEPTH
WH383	306	N1	Night	2015	3	23	10.59	-19.92	4716	30	22:40	23:10	3.3	51
WH383	306	N2	Night	2015	3	23	10.59	-19.92	4716	30	23:30	00:00	3.1	166
WH383	306	N3	Night	2015	3	24	10.59	-19.92	4716	30	00:20	00:50	3.1	397
WH383	309	N1	Day	2015	3	24	9.56	-20.60	3836	30	12:41	13:11	3.1	337
WH383	309	N2	Day	2015	3	24	9.56	-20.60	3836	30	13:36	14:06	3	390
WH383	309	N3	Day	2015	3	24	9.56	-20.60	3836	30	14:31	15:01	3.2	509
WH383	311	N1	Night	2015	3	24	9.54	-20.59	3842	30	22:30	23:00	3	47
WH383	311	N2	Night	2015	3	24	9.54	-20.59	3842	30	23:20	23:50	3.1	246
WH383	311	N3	Night	2015	3	25	9.54	-20.59	3842	30	00:10	00:40	2.9	397
WH383	315	N1	Night	2015	3	25	8.48	-21.57	4296	30	22:28	22:58	3	52
WH383	315	N2	Night	2015	3	25	8.48	-21.57	4296	30	23:18	23:48	3.1	228
WH383	315	N3	Night	2015	3	26	8.48	-21.57	4296	30	00:08	00:38	3.1	368
WH383	318	N1	Night	2015	3	26	6.48	-23.55	4058	30	22:50	23:20	3	57
WH383	318	N2	Night	2015	3	26	6.48	-23.55	4058	30	23:40	00:10	2.9	208
WH383	318	N3	Night	2015	3	27	6.48	-23.55	4058	30	00:30	01:00	3.1	388
WH383	321	N1	Night	2015	3	27	4.17	-24.63	4570	30	23:30	00:00	3.1	51
WH383	321	N2	Night	2015	3	28	4.17	-24.63	4570	30	00:20	00:50	3	134
WH383	321	N3	Night	2015	3	28	4.17	-24.63	4570	30	01:10	01:40	2.9	409
WH383	324	N1	Night	2015	3	28	2.67	-25.22	3783	30	23:30	00:00	3.3	46
WH383	324	N2	Night	2015	3	28	2.67	-25.22	3783	30	00:20	00:50	3.2	139
WH383	324	N3	Night	2015	3	29	2.67	-25.22	3783	30	01:10	01:40	3.1	449
WH383	327	N1	Night	2015	3	29	0.30	-25.29	3047	30	23:30	00:00	3.2	59
WH383	327	N2	Night	2015	3	30	0.30	-25.29	3047	30	00:20	00:50	3.1	380
WH383	327	N3	Night	2015	3	30	0.30	-25.29	3047	30	01:10	01:40	3	473
WH383	330	N1	Day	2015	3	30	0.03	-25.97	3701	30	13:35	14:05	2.8	323
WH383	330	N2	Day	2015	3	30	0.03	-25.97	3701	30	14:25	14:55	2.8	468
WH383	330	N3	Day	2015	3	30	0.03	-25.97	3701	30	15:15	15:45	3.2	617
WH383	333	N1	Night	2015	3	31	0.03	-25.95	3703	30	00:47	01:17	3.8	55
WH383	333	N2	Night	2015	3	31	0.03	-25.95	3703	30	01:37	02:07	2.9	373
WH383	333	N3	Night	2015	3	31	0.03	-25.95	3703	30	02:27	02:57	3	476
WH383	337	N1	Night	2015	4	2	10.80	-23.90	5361	30	23:30	00:00	3	50
WH383	337	N2	Night	2015	4	3	10.80	-23.90	5361	30	00:20	00:50	2.8	375
WH383	337	N3	Night	2015	4	3	10.80	-23.90	5361	30	01:10	01:40	2.9	587
WH383	340	N1	Night	2015	4	3	12.30	-23.08	4998	30	23:30	00:00	3.1	44
WH383	340	N2	Night	2015	4	4	12.30	-23.08	4998	30	00:20	00:50	2.9	378
WH383	340	N3	Night	2015	4	4	12.30	-23.08	4998	30	01:10	01:40	3	555
WH383	341	N1	Night	2015	4	7	17.61	-24.30	3622	30	00:35	01:05	3	48
WH383	341	N2	Night	2015	4	7	17.61	-24.30	3622	30	01:25	01:55	3	365
WH383	341	N3	Night	2015	4	7	17.61	-24.30	3622	30	02:15	02:45	3	581
WH383	344	N1	Day	2015	4	8	17.64	-24.29	3596	30	13:40	14:10	3	331
WH383	344	N2	Day	2015	4	8	17.64	-24.29	3596	30	14:30	15:00	3	397
WH383	344	N3	Day	2015	4	8	17.64	-24.29	3596	30	15:20	15:50	3.1	519

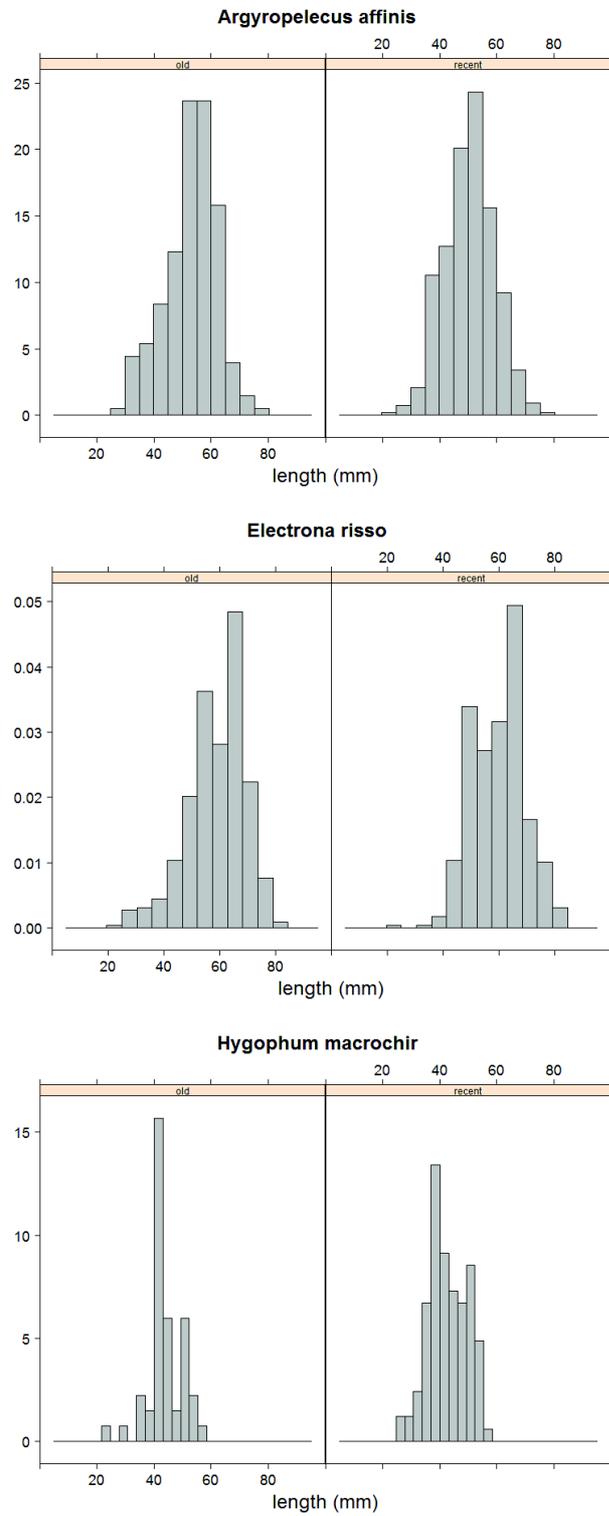
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### Retrospective bioclimatic analysis

WH383	349	N1	Night	2015	4	9	19.21	-21.96	3517	30	23:30	00:00	3.2	58
WH383	349	N2	Night	2015	4	10	19.21	-21.96	3517	30	00:20	00:50	2.8	376
WH383	349	N3	Night	2015	4	10	19.21	-21.96	3517	30	01:10	01:40	2.9	504
WH383	352	N1	Night	2015	4	11	23.87	-20.05	3776	30	22:30	23:00	2.9	51
WH383	352	N2	Night	2015	4	11	23.87	-20.05	3776	30	23:20	23:50	2.6	398
WH383	352	N3	Night	2015	4	12	23.87	-20.05	3776	30	00:10	00:40	2.9	535
WH383	355	N1	Night	2015	4	12	26.36	-19.35	3812	30	22:30	23:00	3.2	50
WH383	355	N2	Night	2015	4	12	26.36	-19.35	3812	30	23:20	23:50	3	456
WH383	355	N3	Night	2015	4	13	26.36	-19.35	3812	30	00:10	00:40	3	544
WH383	358	N1	Night	2015	4	14	31.70	-17.33	4478	30	22:30	23:00	3	53
WH383	358	N2	Night	2015	4	14	31.70	-17.33	4478	30	23:25	23:55	3.2	430.5
WH383	358	N3	Night	2015	4	15	31.70	-17.33	4478	30	00:10	00:40	3.5	546
WH383	361	N1	Night	2015	4	16	37.38	-13.71	4247	30	21:30	22:00	3	0
WH383	361	N2	Night	2015	4	16	37.38	-13.71	4247	30	22:25	22:55	2.9	180
WH383	361	N3	Night	2015	4	16	37.38	-13.71	4247	30	23:10	23:40	3	454
WH383	363	N1	Night	2015	4	17	41.04	-11.19	4224	30	22:30	23:00	2.8	67
WH383	363	N2	Night	2015	4	17	41.04	-11.19	4224	30	23:25	23:55	2.8	446
WH383	363	N3	Night	2015	4	18	41.04	-11.19	4224	30	00:15	00:45	3	536
WH383	367	N1	Night	2015	4	19	46.49	-6.89	4704	30	22:30	23:00	3.3	61
WH383	367	N2	Night	2015	4	19	46.49	-6.89	4704	30	23:25	23:55	3	446
WH383	367	N3	Night	2015	4	20	46.49	-6.89	4704	30	00:15	00:45	2.8	542

## Annex 2

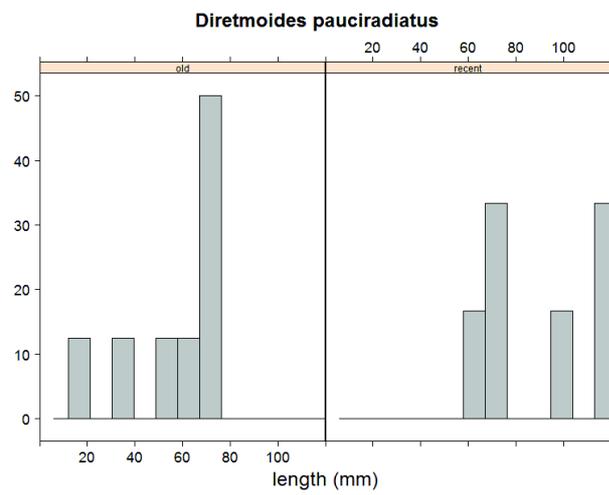
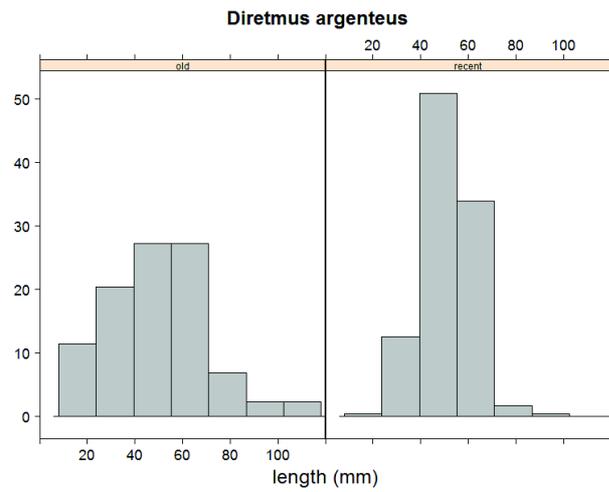
Additional figures for the comparison of size ranges and cohort structure, see text for explanations



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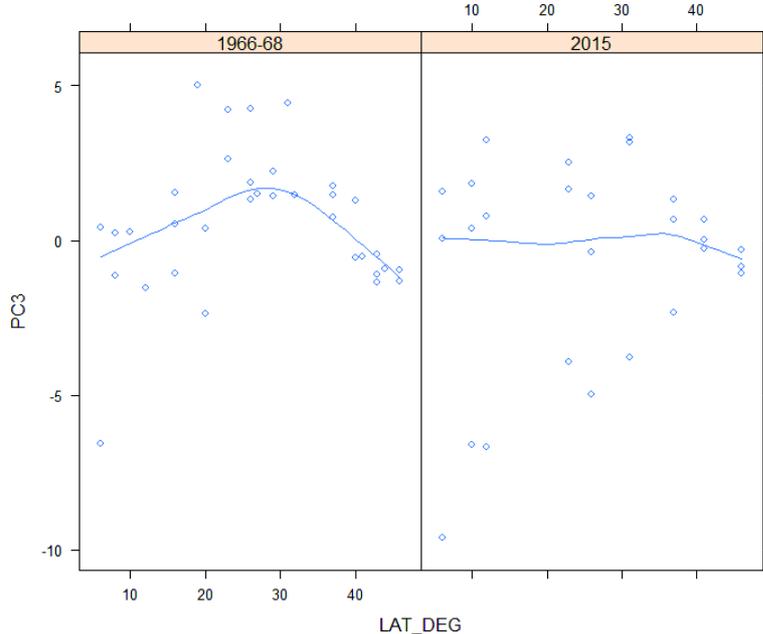
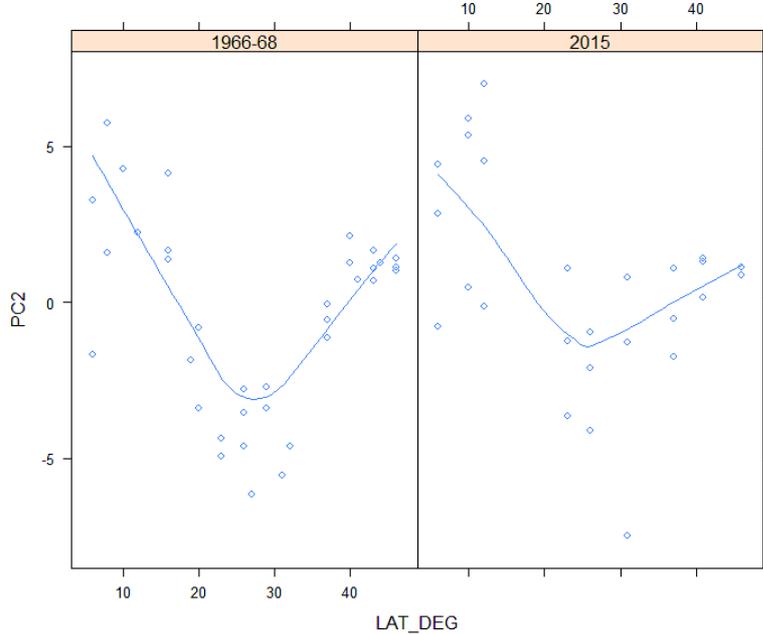
### Retrospective bioclimatic analysis

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### Annex 3

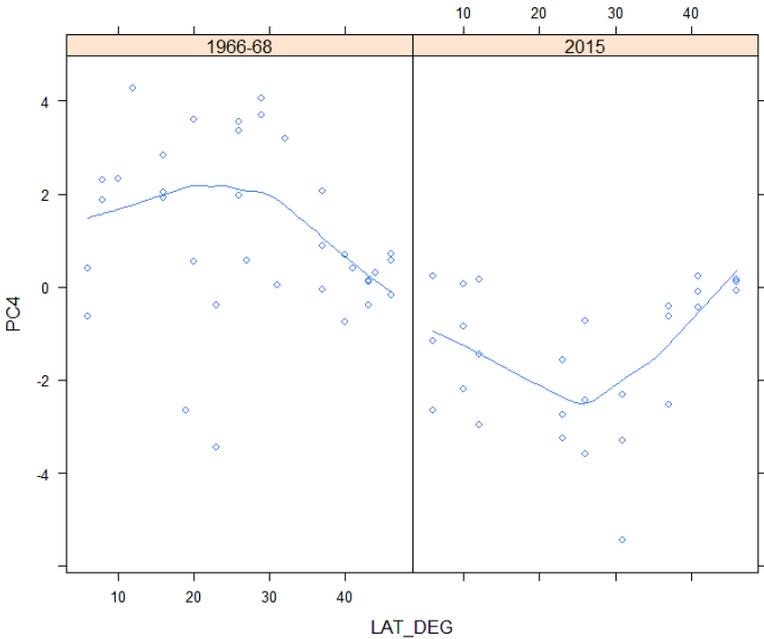
PC2-4 plots by latitude N and period, log(x+1) transformed data



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Retrospective bioclimatic analysis

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## Annex 4

Species loadings, PCA on log(x+1) data for species with frequencies  $n > 11$ .

SPECIES	PC1	PC2	PC3	PC4
ANOCOR	<b>0.15</b>	0.00	0.14	0.02
ARGACU	0.06	<b>-0.13</b>	0.19	<b>-0.12</b>
ARGGIG	0.11	0.18	0.09	<b>-0.09</b>
ARGHEM	<b>-0.06</b>	<b>-0.02</b>	0.09	<b>-0.09</b>
ARGSLA	0.17	0.18	0.05	0.04
ASTIND	0.15	<b>-0.00</b>	<b>-0.01</b>	<b>-0.08</b>
ASTRICH	0.20	0.13	<b>-0.10</b>	0.04
BATYARG	0.14	0.13	0.07	0.02
BATYLON	0.04	<b>-0.17</b>	0.10	0.09
BENGLA	<b>-0.19</b>	0.06	<b>-0.05</b>	0.01
BLAGGR	<b>-0.01</b>	<b>-0.14</b>	<b>-0.09</b>	<b>-0.21</b>
BOLIND	0.06	<b>-0.12</b>	<b>-0.13</b>	<b>-0.24</b>
BONPED	0.14	0.14	0.12	<b>-0.09</b>
CERMAD	<b>-0.16</b>	<b>-0.03</b>	<b>-0.07</b>	<b>-0.10</b>
CERWAR	<b>0.22</b>	<b>-0.17</b>	<b>-0.06</b>	<b>-0.02</b>
CHAUDA	0.02	<b>-0.21</b>	0.16	0.11
CHAUSCH	<b>0.18</b>	0.17	0.05	<b>-0.00</b>
CHAUSL	<b>-0.05</b>	<b>-0.04</b>	0.07	<b>-0.01</b>
CYC_SP	<b>-0.01</b>	0.12	0.08	<b>-0.08</b>
DIADUM	0.17	<b>-0.01</b>	<b>-0.09</b>	0.02
DIAHOL	<b>-0.01</b>	0.08	<b>-0.02</b>	<b>-0.04</b>
DIAMOL	<b>0.16</b>	<b>-0.17</b>	<b>-0.11</b>	0.07
DIAPER	0.10	<b>-0.09</b>	<b>-0.11</b>	<b>-0.03</b>
DIARAF	0.04	<b>-0.17</b>	0.09	<b>-0.26</b>
DIAVAN	<b>0.13</b>	0.08	<b>-0.20</b>	0.08
DIPTAE	<b>0.19</b>	<b>-0.05</b>	<b>-0.16</b>	<b>-0.06</b>
DIRARG	<b>0.12</b>	0.18	0.11	<b>-0.14</b>
ELECRI	0.05	0.19	0.05	0.01
EUSTOOB	0.08	<b>-0.13</b>	0.07	<b>0.28</b>
GONDAT	0.10	0.04	0.18	<b>-0.17</b>
GONELO	0.09	<b>-0.15</b>	0.18	0.15
HOWATL	0.09	0.01	0.15	<b>-0.16</b>
HYGBEN	0.01	<b>-0.09</b>	0.06	<b>-0.01</b>
HYGHYG	0.06	<b>-0.22</b>	0.02	<b>-0.18</b>
HYGMAC	<b>0.16</b>	0.11	<b>-0.20</b>	0.04
HYGREI	<b>0.16</b>	<b>-0.12</b>	<b>-0.18</b>	<b>-0.03</b>
HYGTAA	<b>0.15</b>	<b>-0.06</b>	<b>-0.17</b>	0.01
IDIFAS	0.03	<b>-0.18</b>	0.13	<b>0.24</b>
LAMALA	<b>0.19</b>	0.00	<b>-0.10</b>	0.08
LAMATE	0.03	<b>-0.12</b>	0.19	<b>-0.11</b>
LAMCRO	<b>-0.16</b>	0.01	<b>-0.04</b>	<b>-0.05</b>
LAMCUP	<b>0.13</b>	0.00	0.03	0.15
LAMFES	<b>0.13</b>	<b>-0.13</b>	0.15	0.12

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LAMLIN	<b>0.10</b>	0.06	0.08	<b>-0.11</b>
LAMPHO	<b>0.13</b>	<b>-0.18</b>	0.05	<b>-0.05</b>
LAMPUS	<b>-0.04</b>	<b>-0.09</b>	<b>-0.05</b>	<b>-0.04</b>
LEPGAU	0.05	<b>-0.22</b>	<b>-0.00</b>	<b>-0.13</b>
LEPGUE	<b>0.20</b>	0.11	<b>-0.19</b>	0.06
LEPPYR	0.07	<b>-0.06</b>	0.07	<b>0.31</b>
LOBDOF	0.13	<b>-0.12</b>	<b>-0.09</b>	0.10
LOGGEM	0.07	<b>-0.19</b>	0.18	<b>-0.09</b>
MAROBT	0.09	<b>-0.11</b>	0.16	<b>-0.04</b>
MELBER	0.04	<b>-0.01</b>	0.11	<b>-0.02</b>
MELTYP	0.11	0.11	0.14	<b>-0.16</b>
MELZUG	<b>0.16</b>	0.18	0.10	<b>-0.03</b>
MYC	0.09	<b>-0.09</b>	<b>-0.25</b>	<b>-0.14</b>
NEMSCO	0.15	<b>-0.04</b>	0.03	0.11
NOTOCAU	0.09	<b>-0.12</b>	0.02	<b>-0.21</b>
NOTORE	<b>0.19</b>	<b>-0.06</b>	<b>-0.13</b>	<b>-0.10</b>
PSTOGUE	<b>0.11</b>	<b>-0.09</b>	0.14	<b>0.26</b>
SCOMIZ	<b>0.19</b>	0.19	0.09	<b>-0.02</b>
SEAKOE	0.02	0.09	0.09	<b>-0.07</b>
SERBEA	0.08	0.12	0.09	0.09
SERBRE	0.09	0.07	0.11	<b>-0.09</b>
STEDIA	0.13	0.13	0.13	<b>-0.09</b>
STOBOA	<b>-0.04</b>	0.08	<b>-0.02</b>	0.17
SYMVER	<b>-0.03</b>	<b>-0.03</b>	<b>-0.17</b>	<b>-0.08</b>
VINNIM	0.18	<b>-0.01</b>	<b>-0.23</b>	0.02