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Spatial distribution and inter-annual variations in the size frequency distribution and abundances of *Pleuragramma antarcticum* larvae in the Dumont d'Urville Sea from 2004 to 2010

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Abstract:

This paper investigates the abundance and distribution of Pleuragramma antarcticum larvae by size class in the Dumont d'Urville Sea from 2004 to 2010. Samples were collected between Dumont d'Urville station and the Mertz Glacier Tongue onboard the RV l'Astrolabe for studying the inter-annual and spatial distribution of fish larvae and the TRV Umitaka Maru for looking at life stages vertical distributions. The seabed depression adjacent to the Mertz Glacier Tongue and in Commonwealth Bay hosted high abundances of small P. antarcticum larvae, while larger larvae were found in lower abundance and further offshore. We found that canyons, sea ice, stability of the water column and temperatures are important features for determining suitable areas for young larvae.

Keywords : Pleuragramma antarcticum; East Antarctic shelf; Fish larvae; Life cycle; Inter-annual variations

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Running-title: spatio-temporal distribution of *Pleuragramma antarcticum* larvae

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Abstract

This paper investigates the abundance and distribution of *Pleuragramma antarcticum* larvae by size class in the Dumont d'Urville Sea from 2004 to 2010. Samples were collected from Dumont d'Urville station to the Mertz Glacier Tongue on board the RV "l'Astrolabe" for studying the interannual and spatial distribution of fish larvae and the RV "Umitaka Maru" for looking at life stages vertical distributions. The seabed depression adjacent to the Astrolabe Glacier supported high abundances of small *P. antarcticum* larvae while larger larvae were found in lower abundance and further offshore. We assumed that canyons, seaice, stability of the water column and temperatures are important features for determining suitable areas for young larvae.

Key words:

Pleuragramma antarcticum, East Antarctic shelf, fish larvae, life cycle; interannual variations

1 Introduction

Long term synoptic monitoring of polar oceans has always been a challenge and annual mesoscale surveys are rare. In the pelagic zone, while the areas dominated by Antarctic krill (*Euphausia superba*) are quite well studied, monitoring is needed to study the trophic web in the neritic zone. The Dumont d'Urville Sea ranging from Terre Adélie to the Mertz Glacier Tongue (MGT) in George V Land, East Antarctica, was studied during the Collaborative East Antarctic Marine Census (CEAMARC) which is a contribution to the Census of Antarctic Marine Life. Three ships investigated the area but two studied the pelagic zone: the Japanese RV "Umitaka Maru" and the French RV "Astrolabe". The objectives were to study the marine biota over the East Antarctic continental shelf in relation to environmental parameters, to draw ecoregions (Koubbi et al., 2010) and to establish baseline information that could be used to track changes over time. This study area will be a legacy site for future comparability studies. The present study concerns mainly the long term monitoring of *Pleuragramma antarcticum* larvae conducted as part of the multi-annual ICO^{2}TA programme (Integrated Coastal Ocean Observations in Terre Adélie) supported by the French Polar Institute, IPEV (Institut Paul Emile Victor). The vertical distribution pattern of juvenile and adult will also be discussed. This programme is part of CEAMARC and started in 2004 for the study of fish larvae.

One aim of the sampling network during the CEAMARC and ICO^{2}TA surveys was to conduct a regionalisation of this area. Ecoregionalisation is a combination of regional geographic, oceanographic and biogeographic features (Koubbi et al., 2010). An ecoregion is "a recognizable space which can be distinguished by its abiotic characteristics and associated biological assemblage, operating at particular spatial and temporal scales" (ICES, 2005). Ecoregionalisation can help prioritize conservation efforts by determining, for example, Habitat Areas of Particular Concern (HAPC) which are defined by their ecological function or their rarity. Determining Essential Fish Habitat (EFH) is part of this process. EFH are "those waters and substrate necessary to fish for spawning, breeding, feeding, or growth to maturity". Some Antarctic fish species show a spatial and temporal repartition of life stages (Koubbi et al. 2009). Spawning grounds, nurseries of juveniles and trophic areas of adults are spatially separated as shown by Harden-Jones (1968). The main question is to understand what determines the position of spawning grounds especially for a pelagic species such as *P. antarcticum*. Is it determined geographically or environmentally? How do the larvae disperse from these spawning grounds and what environmental factors influence larval distribution? To answer these questions, we need information about the regional characteristics of the study area.

The ICO^{2}TA programme surveys the zone between the coast and the continental shelf, from the vicinity of Dumont d'Urville station (139ºE) to the Mertz Glacier Tongue (MGT; 146ºE) (Figure 1). In the Dumont d'Urville Sea, Koubbi et al. (2010) completed two regionalisations based on fish assemblages: one using pelagic fish and another with demersal fish. Other studies on hydrology, plankton and benthos allow further differentiation of regions.

The regionalisation based on demersal fish showed a clear difference between continental margins, inner-shelf depressions, banks and coastal zones with the highest diversity in the two deep basins (Koubbi et al., 2010). We assume that George V Basin is richer in species because there is a permanent polyna, complex water masses due to the formation of Antarctic bottom waters and because it is limited to the north by a sill. For the Adélie Basin, this depression is not limited by a sill at the level of the continental margin. The benthic communities were studied using underwater video by Gutt et al. (2007) for the coastal zone near Dumont D'Urville station and by Post et al. (2010) for the shelf area. Smaller deep canyons are also observed along the coast. As in the Georges V or Adélie basins, their depth can reach 500 m or more than 1000 m, for example near the Astrolabe glacier next to Dumont d'Urville Station. Iceberg scouring creates patterns of deposit attracting filter-feeding benthic communities in various stages of maturity and recolonisation. These communities are also influenced by hydrology, topography and past environment.

Water mass characteristics depend on bathymetry, advection linked to wind, including strong katabatic winds in this area (Wendler et al., 1997) and ice cover. The Dumont D'Urville Sea is an area of particular interest because it is so dynamic and is currently undergoing some significant changes. Two major areas were observed over the shelf during the CEAMARC surveys (Koubbi et al., 2010). The first is to the west of Commonwealth Bay, which has less vertical stratification compared to the second zone to the east of this bay. Modified Circumpolar Deep Water (MCDW) enters the Adelie Depression through the sill and follows the eastern side of the basin towards the MGT. The high salinity Shelf Water (HSSW), produced by cooling and seaice formation in winter, was also found on the eastern side of the basin (deeper than the incoming MCDW) during CEAMARC. Water over the shallow banks was mostly Antarctic surface water (relatively fresh, compared to MCDW and HSSW).

The Mertz Glacier Polynya (MGP), centered on ~ 67° S, 145° E, and bays (e.g. Commonwealth Bay) are major sites of the formation of cold, high-density water that contributes to Antarctic Bottom Water (AABW) production, which is globally significant (Massom *et al.,* 2001). The MGP is a seasonally recurrent ice factory, the shape and size of which has been controlled by the Mertz Glacier Tongue (MGT), katabatic winds, weather conditions and the location of very large grounded icebergs and other ice features such as pack ice and sea ice. An important cyclonic gyre transports water within the depression (Williams and Bindoff, 2003). Changes in the size and shape of the MGP could have a significant effect on the ocean freshwater budget, global thermohaline circulation (closely linked to global climate), and on regional sea ice production (Massom and Stammerjohn, 2010). Antarctic sea ice provides a habitat for a range of organisms (phytoplankton, mesozooplankton, Euphausiids, cryopelagic fish and top predators) which have adapted to the conditions (Loots et al., 2009; Lubin and Massom, 2006) and provide food for pelagic species throughout the winter.

The regionalisation based on pelagic fish was more relevant for the oceanic zone than for the shelf area, showing the importance of frontal zones associated with the southern boundary and the shelf break. Pelagic Fish assemblages were clearly identified between (1) the oceanic zone with mesopelagic fish offshore and icefish juveniles near the shelf break and (2) the neritic zone highly dominated by *Pleuragramma antarcticum* and early life stages of Notothenioids. Over the shelf, there is only a slight difference between the upper 50 m layer and the rest of the water mass. There are few studies to characterize ecoregions based on plankton. Some of them are mainly over the oceanic zone, e.g. East BROKE (Nicol et al., 2000 and Hosie et al., 2000) and Japanese surveys

(Chiba et al., 2000). The neritic zone was mainly explored during ICO²TA. Beans et al. (2008), Swadling et al. (submitted and this issue), Vallet et al. (2009 and this issue) identified neritic spatial assemblages of phytoplankton, mesozooplankton and Euphausiids respectively. Spatial differences do not seem stable every summer (Swadling et al., this issue). However, Beans et al. (2008) have identified 3 different zones according to phytoplankton assemblages, water stratification and nutrients and Vallet et al. (2009 and this issue) see spatial segregation of Euphausiid life stages. If there are differences between assemblages in the George V basin, the Adélie bank and the Adélie Basin, they may be weakened depending on the weather, the sea ice and the stratification of the water mass.

The pelagic part of ICO²TA focuses on the control of the pelagic ecosystem by few species of micronekton or plankton. *Pleuragramma antarcticum* (Antarctic silverfish) is often considered a keystone species of the high Antarctic zone, much like *Euphausia superba* (Antarctic krill) is for waters beyond the continental shelf (Guglielmo *et al.*, 1998; Fuiman *et al.*, 2002) or *Euphausia crystallorophias* (ice krill) for the neritic zone (Vallet et al., 2009 and this issue). These species can highly dominate the micronekton.

Is there a wasp waist control in the pelagic East Antarctic neritic zone? Wasp waist control was described by Cury et al. (2000) for productive oceanic zones such as upwelling regions . It occurs when there is a large number of species at the lower trophic level (plankton) and large populations of top predators. In between, there is an intermediate trophic level occupied by only few species of small plankton-feeding pelagic species. In the case of the East Antarctic shelf, this intermediate level is occupied by the Antarctic Silverfish and Euphausiids. This level is crucial because population crashes and sudden recoveries have been observed worldwide for most of the micronekton species due to overexploitation but also to environmental changes. Most of these species belonged to the family Clupeidae, a family absent in the Southern Ocean, showing particular life history traits adapted to the pelagic environment which allow large biomass.

P. antarcticum occupies the pelagic niche, as do Clupeids in other oceans. It is a member of the predominantly neritic benthic order Notothenioidei but, unlike most of the other species, it is pelagic where it dominates; it inhabits both open waters and areas of pack ice and can be found from the surface layers to depths of up to 900 metres (De Witt, 1970 and Fuiman et al., 2002). This species is the only Notothenioid fish in which all stages of development take place throughout the water column; other species may be cryopelagic, such as *Pagothenia borchgrevinki,* or spend part of their life in the water column (mainly during the larval or juvenile stage), such as species of the genus Trematomus or icefish (Koubbi et al., 2009).

Spawning is thought to occur in late winter-early spring, with eggs hatching in November-December; however, this pattern is likely to vary between regions according to local conditions (Vacchi *et al.*, 2004). Newly hatched larvae range in size from approximately 6-10 mm (Regan, 1916; Vacchi *et al.*, 2004). It is thought that *P. antarcticum* spawns in areas close to ice-shelves and glaciers, or over deep coastal canyons (Hubold and Ekau, 1987; Eastman, 1993). On hatching, larvae are carried by the prevailing currents to nursery areas near the shelf break. Like many Antarctic fish species, larval development proceeds relatively slowly, *P. antarcticum* comprises the majority of ichthyoplankton of the neritic zone, sometimes accounting for more than 98% (Guglielmo et al., 1998, Vacchi et al., 1999, Hoddell et al., 2001, Granata et al., 2002, Koubbi et al., 1997 and 2009). Few studies on the distribution of *P. antarcticum* larvae exist in the Dumont d'Urville Sea, one on the coastal zone of the Dumont d'Urville station (140°E) by Koubbi et al. (1997), one including the oceanic zone by Hoddell et al. (2001) and the most recent from Koubbi et al. (2009) describing the spatial distribution of larvae collected in 2004 in the Dumont d'Urville Sea. From studies in the Ross Sea or around the Antarctic Peninsula, we know that *P. antarcticum* larvae forage on copepods, microzooplankton, planktonic eggs, euphausiids and amphipods (Takahashi and Nemoto, 1984, Kellermann et al., 1987, Granata et al., 2009). However, in the Dumont D'Urville Sea, Koubbi et al. (2007) and Vallet et al. (this issue) demonstrate that the larvae are omnivorous.

The vertical distribution of *P. antarcticum* larvae and juveniles in the western Ross Sea, where larvae are more abundant in the upper water layer (150m) while juveniles and adults are often distributed at greater depths (Granata et al., 2009) supports this hypothesis. Juveniles and adults are carnivorous, feeding mainly on copepods and Euphausiids (Hubold, 1985; Kellermann, 1987; Hubold & Ekau, 1990; Granata et al. 2009). The change of diet between the larval and juvenile stage from omnivory to larger crustacean prey is confirmed by lipid trophic markers (Mayzaud et al., this issue). Eastman (1985) and Cherel et al. (this issue) show that this species can occasionally feed near the bottom. It was captured by beam trawl during the CEAMARC surveys (Causse et al., this issue). Finally, this species is also an important prey for top predators (Ridoux and Offredo, 1989; Ainley et al., 1991; La Mesa et al., 2004; Smith et al., 2007; Cherel et al., this issue).

The horizontal and vertical segregation of life stages such as the differences in foraging prevent the exposure of larvae from predation and competition by juveniles and adults.

In this paper, we seek to identify the underlying features of the distribution of *P. antarcticum* larvae in the Dumont d'Urville Sea (East Antarctic shelf). Spatial segregation of larval, juvenile and adult life stages is also considered.

2 Materials and Methods

2.1 Sample Collection

Since 2003, the vessel Astrolabe has been adapted for coastal oceanographic surveys with the assistance of IPEV. Data and samples for fish larvae were collected every January from 2004 to 2010 from this vessel (figure 1). Sampling usually started near January 9th except in 2004 and 2007, when surveys were later in January. Time of sampling was linked to the logistics of Dumont d'Urville and Dome C scientific stations. The maximum survey duration was 11 days. 132 stations were investigated for the study of fish larvae (Table 1) from 139°E to 145°E and from 65°30'S to 67°S.

The sampling network varied from year to year depending on the weather, sea-ice and sea conditions. From 2004 to 2006, location of the westernmost sampling stations was constrained by a study on the foraging of Adélie Penguins tracked by Argos.

Other samples from the RV "Umitaka Maru" were considered in this study to determine the vertical distribution of life stages and growth rate. 24 stations were sampled from January 29th to February 12th 2008 from 62°S to 67°S and from 140°E to

145°E.

At each station, a CTD was deployed from the surface to a minimum depth of 200 m (the maximum depth reached by bongo nets for sampling larvae), or close to the seafloor for sites shallower than 200 m, to obtain vertical profiles of temperature and salinity. Temperature and salinity were used to calculate density. Mean values of temperature, salinity and density were calculated for 0-100m and 100-200 m layers.

An investigation of the interannual variability of sea ice concentration (SIC) in the Dumont D'Urville sea area near Terre Adélie for the period 2003 to 2009 was performed using satellite remotely sensed data. Values for this parameter were determined on a regular spatial grid in the study area for each year of the study from 2003 to 2009. The Aqua Advanced Scanning Radiometer- EOS (AMSR-E) dataset used for this study is derived by Hamburg University (http://ftp-projects.zmaw.de/seaice/AMSR-E_ASI_IceConc/hdf/s6250/). It is the highest resolution (6.25 km) satellite sea ice concentration product available and can be obtained in near real time on a daily basis. For each year, 52 weekly-representative satellite datasets were used. Each of the 52 datasets was processed (using the ArcGIS S*ingle Output Map Algebra* tool) to produce 52 binary maps for each of three SIC categories; Open Water (0 to 10% SIC), Transition (10 to 80% SIC) and Pack Ice (80 to 100 % SIC). The 52 binary maps for each SIC category were then added together (using the ArcGIS S*ingle Output Map Algebra* tool) to determine the number of weeks at each SIC category for each raster cell. ArcGIS *Zonal Statistics* tool was used to average the raster values for each SIC category within each of the spatial grid squares in the study area. For the present paper, only the category corresponding to Pack Ice was retained.

On the Astrolabe, ichthyoplankton was collected using a double frame 500 µm bongo net (Smith and Richardson, 1977) towed in oblique hauls between 0 and 200 m, at a speed of between 2 and 3 knots. For each haul, the volume of filtered water was calculated using a flow meter attached to the net. On Umitaka Maru, the different life stages considered in this study were collected by an IYGPT (International Young Gadoid Pelagic Trawl) at depths of 50, 200, 500 and 1000 m (Koubbi et al., 2010). Since the mesh size of this net was 100 mm in the front, then tapering through 80 mm–40 mm–20 mm to 10 mm mesh size in the cod end, data from young larvae (<30mm) were not taken into account for this part of the analysis. *P. antarcticum* larvae used in this study were collected using one of the two bongo nets on the Astrolabe. Samples were preserved in 5 % seawater buffered formalin. *P. antarcticum* larvae were identified based on their morphology and pigmentation as described by Kellermann (1990) and the total number of larvae identified at each station was recorded to calculate the total abundance of *P. antarcticum* larvae per 100 m^3. Standard length (SL) measurements were taken for 40 – 50 larvae from each station, or as many as it was possible to measure for smaller samples. Larvae were allocated to millimetre size classes by rounding SL measurements down to the nearest millimetre. Mean abundance per SL classes was also calculated for each station.

Standard lengths of juveniles and adults were also measured to the millimetre on a subsample of maximum 50 individuals per catch from IYGPT which was used on the Umitaka Maru.

2.2 Data Analysis

A Geographic Information System (GIS) (ArcGIS; ESRI) was used to study the spatial pattern of abundances of *P. antarcticum* larvae and environmental conditions. The study area was defined in ArcGis in a shapefile feature class from Antarctic Digital Database from the Scientific Committee on Antarctic Research (SCAR).

Interpolations using Inverse Distance Weight (with a weight=2) with the software SURFER were done for studying the yearly variations of temperature, salinity and concentration of pack ice for the study period.

Length Frequency Distributions (LFD) of the different life stages with their associated growth were studied. The software Statgraphics was used to determine the best linear regression to estimate the daily growth of *P. antarcticum* larvae in January and February. As the maximum duration of surveys was 10 days, measurements from all surveys held on Astrolabe from 2004 to 2010 and Umitaka Maru 2008 were pooled together for fish larvae analysis. Only taxa from the Umitaka Maru cruise were used for calculating the growth rate between larvae, juveniles and adults.

For each bongo sample from the Astrolabe, abundance of larvae per millimetre size class was computed considering LFD and total abundance of larvae. Abundance data was divided amongst 22 size classes. A log (x + 1) transformation was applied to the abundance data prior to the analysis. Multivariate analysis of the abundance data was conducted using Correspondence Analysis. Correspondence analysis is a descriptive/exploratory technique designed to analyse multivariate data and decompose it into a small number of summary variables to represent low dimensional plots (Quinn and Keough 2002). Environmental and temporal variables (including sea temperature, salinity, latitude, longitude, day and year) were included as additional variables into the analysis. As both variables (size classes) and observations (stations) had the same weight, they can be represented in the same geometric space due to barycentric projection (Benzécri, 1973). This analysis should allow for detecting any spatial or interannual differences in the distribution of the larvae according to their size.

3 Results

3.1 Environmental parameters

Ranges of temperature and salinity were the lowest for the deep layer with a decreasing trend in temperature until 2009 and a slightly increasing trend in salinity (figure 2). The surface layer also showed major differences between years when considering ranges of temperature and salinity. Ranges of both parameters increased in 2008 and were the highest in 2009. Maximum values of each parameter show that during summer 2005 and 2006, the temperatures were at their lowest maximal values (-0.7°C). This was also the case for the mean temperatures (-1.06°C). In 2008, 2009 and 2010, we observed the lowest values of minimum temperature in the surface layer (<-1.28°C). The salinities in the surface layer tended to increase when considering only the maximal and mean values. However the lowest value was observed in 2009.

Mean values of temperature and salinity for the 0-100 m layer were also plotted according to the longitude (figure 3). For temperature, a pattern was observed among years. At longitudes 139°E and 140°E, spatial differences might be due to the latitudinal gradient linked to the sampling design occurring since 2005 from the coast to the shelf break. This problem was limited for the area within 141°E and 146°E as the same latitudinal range was sampled every year. The highest values of temperature were observed at the western part of the sampling network and the lowest near the MGT. For all longitudes (except from 143°E-144°E), the trend was towards cooling. Minimum values were observed in 2005, 2006 and 2009. The highest values of temperature and lowest values of salinity were globally observed in 2003 and 2004. Salinities were higher after 2005 for the whole area.

The duration of pack ice cover for years 2003 to 2009 was expressed as the number of weeks per year with 80-100% of sea ice concentration which corresponds to pack ice (figure 4). The pack ice location and coverage varied among years. A global trend towards longer periods of high concentration and shorter periods of low concentration was observed. In 2004, 2006 and 2009, there was less pack ice than in other years. 2008 (the year of the CEAMARC surveys) appeared to be the year with the longest period of pack ice over the study period. The duration of pack ice cover was lower for MGP (from 144°E to 145°E) than for the rest of the study area. The MGP can be seen as a relatively consistent feature from year to year in terms of its location and extent. This area is covered in Pack Ice for fewer weeks than the rest of the study area. However the greatest duration of pack ice for this area is observed in 2008.

West of 142°E and except along 140°E, pack ice duration is highest with at least 30 weeks per year, the maximum observed for this area was in 2005 and 2008.

3.2 Life stages distribution

3.2.1 Larval distribution

Abundances varied from 0 to 3356 larvae per 100 m^{-3} with an average of 63 +/- 310 larvae per 100 m^{-3}. The map of abundance data from all years of the survey (2004-2010) suggested that the highest larval abundances were found near Commonwealth Bay, alongside the MGT in Buchanan Bay and in the vicinity of the Adélie depression (figure

5). Relatively high abundances were also found close to the coast west of Dumont d'Urville station. Abundances were lower over the shallower waters of the western Adélie Bank.

3.2.2 Length analysis of larvae

A subsample of 2561 larvae was measured to study the size distribution over the years (Table 2). Standard lengths varied from 5 to 27 mm. Plotting size class maximal abundance for all stations sampled between 2004 and 2010 (figure 6) revealed that there were some interannual variations of abundance. Highest larval abundances were observed in 2005, 2009 and 2010. While 2005 was the year with the smaller size classes, the years 2004 and 2007 were those with the larger size classes and the lowest larval abundances.

A correspondence analysis was performed to explore size class abundances (20 classes of 1mm from SL 6mm to 25 mm) for the 125 sampling stations with positive larval catch. The correspondence analysis showed that the first axis accounted for 27.2 % of the total variance, with the first two axes accounting together for 41.2 %. The correspondence analysis biplot revealed a Gutmann effect, meaning that both axes one and two had a strong influence on the data (Figures 7 and 8).

Plotting the scores of the stations along axis one according to their longitude revealed three main zones with high scores on this axis (high scores indicate smaller larvae) – one directly offshore from Dumont d'Urville station (140°E), one in Commonwealth Bay (143°E), and another alongside the MGT (145°E) (figure 9). Lower scores (i.e. larger larvae) occurred over the Adélie Bank and between Commonwealth Bay and the Adélie Depression.

Major differences in the abundance size pattern occured in 2005 and 2006 with the highest scores on axis 1 linked to the smallest larvae (figure 10).

Environmental, geographical and temporal variables were projected as supplementary variables onto the first two axes of the analysis (figure 11) to understand the size distribution of larvae. Larvae sampled later in the month tended to be larger. Interannual variations were observed as shown in figure 10. Years 2005 and 2006 were on the positive part of axis 1, where higher proportions of small larvae were observed. Years 2004 and 2007 were on the negative part of axis 1, where larvae were larger and this was related to the timing of the sampling. Year 2010 was in the negative part of axis 2 where larvae were of medium size and very abundant.

Geographical location was also a strong indicator of larval size. Smaller larvae tended to be found at higher latitudes and longitudes (i.e. close to the coast and to the east of the study zone) and were more associated with greater depths linked to innershelf depressions (positive part of axis 1). Hydrological conditions were represented as the mean values and standard deviations (SD) of temperature, salinity and density at the 0-100 m surface layer and the 100-200 m layer. Mean surface temperature was in the negative part of axis 1 where larger larvae were found. Standard deviation of bottom (linked to axis 1) and surface density (linked to axis 2) was also quite important in this analysis.

3.3 Life stages size spectra and growth

Length frequency distribution of the Antarctic silverfish (n=1002) from the Japanese cruise 2007-2008 are presented in figure 12. Fish less than 30 mm SL were larvae. Specimens between 30-70 mm SL were juveniles of age 1year and those from 70-

110 mm SL were juveniles of age 2 years. Those greater than 110 mm SL corresponded to adults.

Size distribution was used to study the daily growth of fish larvae. However, because of limited data per year, specimens from the different surveys were pooled together. The growth rate of fish larvae was estimated to be 0.17 mm SL*d^{-1} (figure 13). Assuming that newly hatched larvae were ~6mm SL with a growth rate of 0.17 mm SL*d^{-1}, larvae caught were between 4-9 weeks old for the Astrolabe cruise and between 8-12 weeks old for the Umitaka Maru cruise. Hatching probably occurred between late-November to mid-December.

The growth rate between larvae caught in 2007 by the Astrolabe and juveniles of 1 year caught in 2008 by the Umitaka Maru was calculated to determine the growth during the first year (figure 14). Growth rate is estimated to 0.08mm SL*d^{-1}. The linear regression model according to the day of sampling shows a significant relation with R^2=91.45%. 224 larvae (15.70 sd 2.5 mm SL) and 366 juveniles of age 1 (49.21 sd 6.04 mm SL) were used.

Specimens of each age class from the same survey (Umitaka Maru 2008) were used to compute the growth of *P. antarcticum* in this area (figure 15). The equation from the exponential regression model is: SL (mm) = exp (2.25 + 0.74*year). Linear regression was also calculated for the same data to allow comparison between growth models of this study with previous works. Growth rate for one year was estimated at 39.54 mm SL, (0.10 mm SL per day).

The Antarctic silverfish shows a well defined vertical distribution pattern. While small juveniles were present throughout the water column, large individuals were present only in bottom samples (figure 16).

4 Discussion

The age groups identified in this study are comparable to those reported in previous works. Hubold (1984) attributed to age 0 (larvae) specimens from 8 to 25 mm SL; those of 30-50 mm SL were attributed to age 1 and 50-80mm SL to age 2+. Longer specimens were defined as adults. Other studies in the Antarctic Peninsula (Liu and Chen, 1995) determined from size frequency distributions that specimens between 26 to 54 mm SL belong to age group 1 and estimated that those fishes were 12-13 months old. From the same study individuals between 65-82 mm SL were attributed to age group 2 (probably ~2 years old). Our results agree with previous studies as fish larvae have lengths < 30 mm SL. Juveniles are separated in two groups and the limit between age 1 and age 2 in all studies is between 50-70 mm SL depending on the study area and period of sampling. Adults are probably separated into two age groups as suggested by Hubold (1984) but the small number of large specimens in this study did not allow us to separate them. The LFD of *P. antarcticum* from Umitaka Maru (2008) in relation to sampling depth is in good agreement with Hubold (1984) and Granata et al. (2002). Hubold (1985) stated that this strategy of segregation of life stages reduces intraspecific competition; the larvae are mainly in the upper 200 m layer.

Combining data from the 2004 to 2010 seasons in the Dumont d'Urville Sea allows us to understand the early life history of *P. antarcticum* during the summer period to explore interannual variations. *P. antarcticum* has a relatively high fecundity for an

Antarctic species, with individual absolute fecundity ranging between 4315 and 17774 eggs (Gerasimchook, 1987), and the larvae showing high rates of mortality. This is reflected by the decreasing abundance of the larger size classes in all years of the programme. The high fecundity explains why the larvae are more than 99% dominant in the samples (Koubbi et al., 1997 & 2009) as we observed abundances ranging from 0 to a maximum of 3356 larvae per 100 m^{-3} with an average value of 63 +/- 310 larvae per 100 m^{-3}. The high variability observed among samples show that these larvae live in dense swarms. The other Notothenioid fish in this area have a different strategy (except for some icefish larvae and *Trematomus newnesi*) with fewer offspring per year and in some cases, parental care (Koubbi et al., 2009).

The geographic and multivariate analysis results support the hypothesis that *P. antarcticum* larvae hatch close to shore, gradually being carried towards the innershelf depression and banks as they increase in size (Hubold, 1984; Koubbi *et al.*, 2009). Larvae caught during these surveys were between 4 and 9 weeks old for those caught in early-mid January and 8-12 weeks old for those caught at the end of January and early February. It is possible to calculate the hatching date for the area which is between late-November and mid-December. This is similar to those that were found in the Ross Sea (early-mid December) by Guglielmo et al. (1998).

The size distribution of larvae showed that Buchanan Bay near the Mertz Glacier Tongue and Commonwealth Bay are sites of high larval abundance, and the Adélie basin seems to be a second site of important larval abundance. This general pattern was observed over the years of the study showing that coastal areas with deep canyons are favourable to the small larvae. This time repeatable pattern of larval distribution suggests that homing could be a key mechanism for spawning of *P. antarcticum*. Homing reflects the capacity of fish to return to the same spawning areas from year to year. In geographical homing, i.e. natal homing (Papi, 1992), these areas are determined geographically and fish return to spawn at the same place where they were born. Larval distribution of *P. antarcticum* seems to be geographically determined as small larvae are preferably found near to the coast whereas larger larvae are located more offshore. Recently, environmental homing (Cury, 1994; Baras, 1996) has been proposed for anchovy as a generalisation of natal homing where spawning areas are environmentally determined and fish return to spawn in environmental conditions they experienced at the larval stage (Brochier et al., in press). Is it the case in sea ice ecosystems dominated by important geographical and oceanographic features like canyons, polynyas and katabatic winds? This strong attachment of adults to their spawning sites may not lead to larvae being released in optimal areas each year due to inter-annual variations in environmental conditions. However, this might ensure a good larval survival rate over the long term, as it prevents a systematic change in spawning distribution from occurring in response to years of exceptional environmental conditions (Corten, 2002). This conservatism of fish spawning grounds has been demonstrated for North Sea herring where the knowledge of spawning location is provided by old adults and transmitted across generations by entrainment mechanisms (Petitgas *et al.*, 2006). While this may lead to innovative spawning behaviour in distribution pattern in case of strong year class, this may also create a time lag in the detectable impact of long term environmental change on spawning distribution (Corten, 2002). However, this attachment to spawning grounds for *P. antarcticum* still has to be confirmed by genetic studies.

Coastal canyons are known to be favourable for spawning grounds and young larval development. This is the case for the subantarctic zone, for example the Kerguelen Islands where fjords and bays are known to be very productive because of the presence of coastal gyres in stratified and sheltered areas (Koubbi et al., 2001). Some species like the icefish *Champsocephalus gunnari*, the dominant pelagic fish of this area, have some of their spawning grounds in such canyon. The topography of a canyon provides many sheltered areas if the larvae are close to the bottom. Near Dumont d'Urville station (Koubbi, unpublished results), we observed large and dense swarms of larvae near the bottom and particularly in or nearby areas of canyons.

Beside geography, are there some common environmental similarities among the potential spawning grounds and will their environmental differences help us to determine the most suitable ones for *P. antarcticum* fish larvae? Several records in the 90s of early stages of *P. antarcticum* in the Ross and Weddell seas in waters adjacent to the continental ice shelves suggest that *P. antarcticum* larvae are associated with sea-ice early in their life history (Kellermann, 1986). More recently *P. antarcticum* eggs have been found within the sea-ice in the Ross Sea (Vacchi *et al.*, 2004; Bottaro et al., 2009), and young larvae are often found close to areas of sea-ice. Our results show that young larvae are located near polynyas with the major one being the MGP as shown by the analysis of sea ice. This is a large and permanent polynya observed every year with slight interannual differences. The second polynya influencing young larvae is located on the shelf at 140°E but the intensity of this one varies between years. The MGP accounts for only 0.001% of the total sea ice area in Antarctica but is responsible for 1% of total annual sea ice production (Tamura *et al*., 2008). Antarctic sea ice provides a habitat for a range of organisms such as grazers (copepods,…), and is a site of enhanced primary production during winter that is favorable to the development of young larvae. Koubbi et al. (2007), Vallet et al. (this issue) and Mayzaud et al. (this issue) have shown that larvae are omnivorous; they are mainly foraging on phytoplankton and copepods.

The multivariate analysis showed that standard deviation of density seemed to be an important factor for explaining young larval abundances. The standard deviation is a way of determining if the water column was stratified or not. In this study, areas of greater differences in density are found in the Eastern part of the surveyed area from Commonwealth Bay to the MGT. The MGP and Commonwealth Bay have been separately identified by Massom *et al.* (2001) as major sites of the formation of cold, high-density water that contribute significantly, on a global scale to Antarctic Bottom Water (AABW) production. This probably induces high stratification in these areas, helping to create more stable environments for the young larvae. Beans et al. (2008) have shown that the MGP is very different from the remaining zones. Diatom, ciliate and dinoflagellate abundances were at a maximum in January 2004. Among the diatom community, a very low diversity of principally small diatoms was observed (*Fragilariopsis spp*. dominated the community). The 139-140°E zone was dominated by predominantly larger species such as *C. pennatum* and *Rhizosolenia spp*. These are typically associated with open ocean conditions and would thrive better in these mixed waters than the smaller pennate diatoms. The third zone was located over the shallower and warmer shelf waters. During the January 2004 study, this area was characterized by minimal chlorophyll a concentrations and average diatom abundances with a high diversity. This zone seems to be characterized by the presence and high abundance of

Chaetoceros spp., in particular *C. criophilus*. Vallet et al. (this issue) show the importance of these species in the foraging of fish larvae. The geographic pattern of Beans et al. (2008) has to be confirmed for the other years as the 2004 survey took place later in January. However, we can estimate that the differences between the eastern and the western part of the study area in terms of stratification is constant but can be changed occasionally according to storms and katabatic winds which are frequent and strong in this area. If water stability is important for young larvae, these differences of water stratification between the three areas where the young larvae were found can explain why higher abundances were found in the MGP than in 140°E.

The transport of larvae from the ice edge to the shelf break is probably influenced by the strong katabatic winds in the area, as suggested for *P. antarcticum* larvae in the Weddell Sea (Hubold, 1984). An important gyre transport of waters within the George V Basin allows some retention of larvae in this area. However, this is not sufficient as larvae are also found on the Adélie bank and in the Adélie Basin. Even older larvae are less abundant north of the Adélie basin. This show the importance of having some retention process either linked to the topography (canyons) or to the circulation. Environmental conditions studied in the multivariate analysis show the importance of the surface temperature and its relationship to areas with the most suitable trophic conditions for larger larvae. The shelf break is generally associated with a high concentration of biological activity, and presumably provides a rich food source for developing *P. antarcticum*. The larval growth rate found in this study (0.17 mm SL*d^{-1}) is comparable to the Western Ross sea where values of 0.10-0.20 mm SL*d^{-1} were found by Granata et al. (2009). However, these values are slightly lower than the growth rates of 0.24 mm

SL*d^{-1} found in the Weddell Sea (Keller, 1983; Hubold, 1985) or 0.32 mm SL*d^{-1}of the Antarctic Peninsula (Kellermann, 1986). These results suggest differences in larval growth between regions of the Southern Ocean as already postulated by Radtke et al. (1993) or Granata et al. (2009).

Average growth rates between developmental stages show that during the first year of life this rate is about 0.08 mm SL*d^{-1}. The same growth value was determined in the Ross Sea (Guglielmo et al., 1998). Differences between stages is around 30-40 mm SL for the first two years of life, so the average growth rate per day would be between 0.08-0.10 mm SL*d^{-1}. Differences between the growth rate estimated for fish larvae during summer (0.17 mm SL*d^{-1}) and those calculated per year (equivalent of 0.8-0.10 mm SL*d^{-1}), reflect seasonal and age variations in growth rate. It has been suggested that the growth increment of Antarctic fishes is linked to the period of the year when their energy intake from food is in excess of their daily energetic requirements, probably there is a cyclic growth patterns with increased growth rates during the peak of phytoplankton production (White, 1977) leading to a less important growth rate in winter compared with summer.

Antarctic marine ecosystems are strongly linked to the dynamic, seasonal variability of sea ice advance and retreat (Massom and Stammerjohn, 2010). The trend in sea ice concentration (SIC) over the study period 2003 to 2009 was towards longer periods of high sea ice concentration and shorter periods of low sea ice concentration. Not all polynyas in this areas respond the same way to interannual variations, the MGP is more stable than the one on 140°E. As the surveys (except in 2004 and 2007) occurred more or less at the same time of year, we can compare abundance patterns linked to larval size. For 2004 and 2007, as the surveys were ten days later than the other ones from the Astrolabe, the size were the greatest and the abundances the lowest. We cannot use these surveys such as the one from Umitaka Maru (late January – beginning of February) for looking at interannual variations but we have used them for estimating larval growth. The remaining surveys showed some important differences between 2005, 2006 and the other years. The size distribution of larvae for these surveys, particularly for 2005, was shifted to the smaller size with 4-5 mm less in SL average than the other surveys. The temperatures observed during these two years were colder which can explain a delay in the larval development. Another explanation is that the pack ice duration was maximum in 2005. Clarke (1980, 1988) has suggested that food availability rather than temperature may usually limit the growth of polar marine ectotherms. Longer pack ice duration could reduce the intensity of light. In these conditions food quality is believe to be poorer (Clarke, 1988, Hagen, 1988). A combination of these factors probably reduces the food energy intake of fish larvae leading to a slower growth rate.

In light of events in February 2010 which saw the MGT calve, releasing a massive ~80 X ~40 km iceberg, it is very likely that significant changes will occur in the area west of where the former MGT was located, and this includes the changes to the MGP sea ice factory (Legresy *et al.,* 2010). The implications for marine ecosystems in this region as a result of such regional changes will be significant in terms of sea ice formation, formation of Antarctic bottom water and also concerning the stability of the water mass and the circulation pattern. All these parameters were determined as important for the early life stages of *P. antarcticum* as they provided stability, production of suitable preys and a circulation pattern favorable to the retention of larger larvae over the shelf. As we estimate that *P. antarcticum* plays a key role in the wasp-waist control of the pelagic ecosystem of the Dumont d'Urville Sea, this species can be considered as an indicator of the future changes that may occur in this area.

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Figure 1

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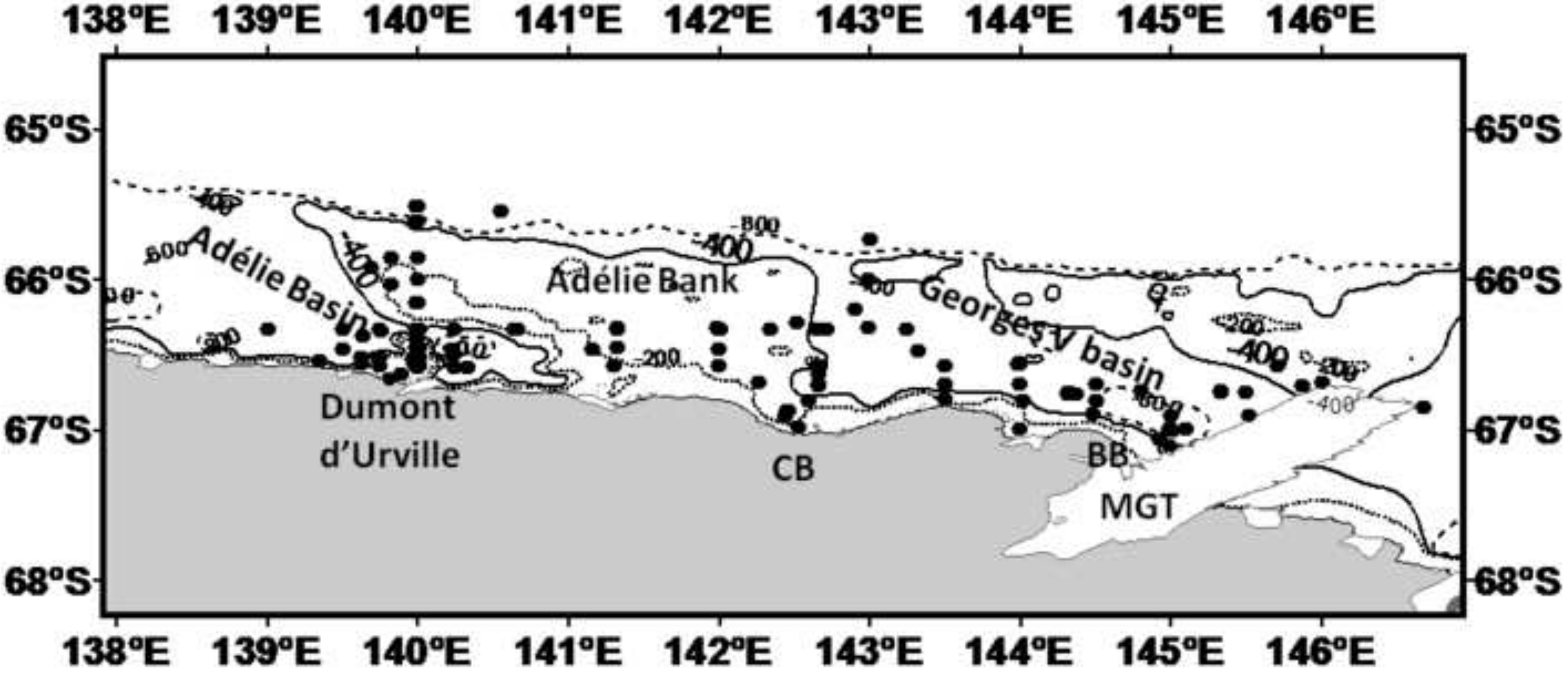

Figure 2

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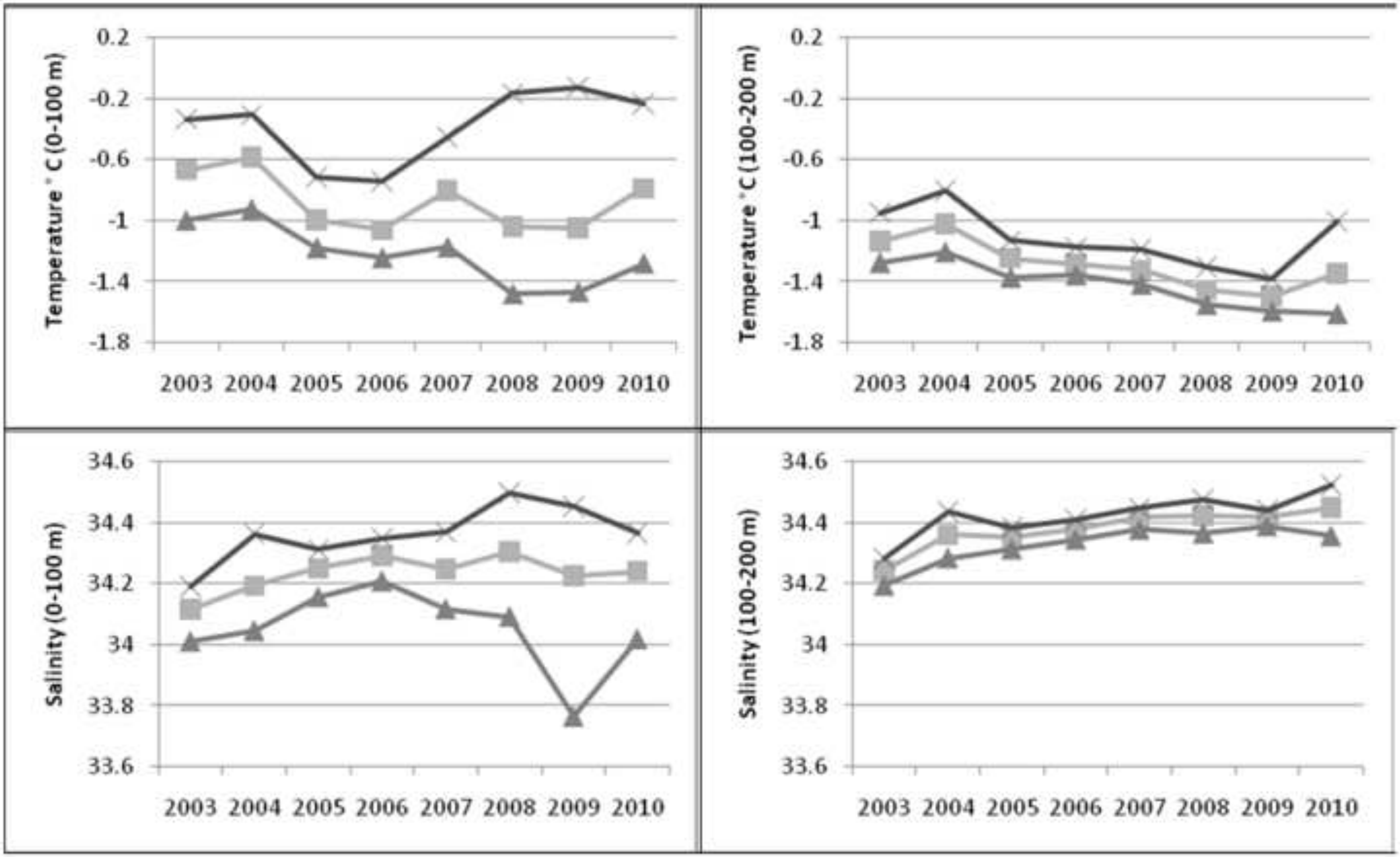

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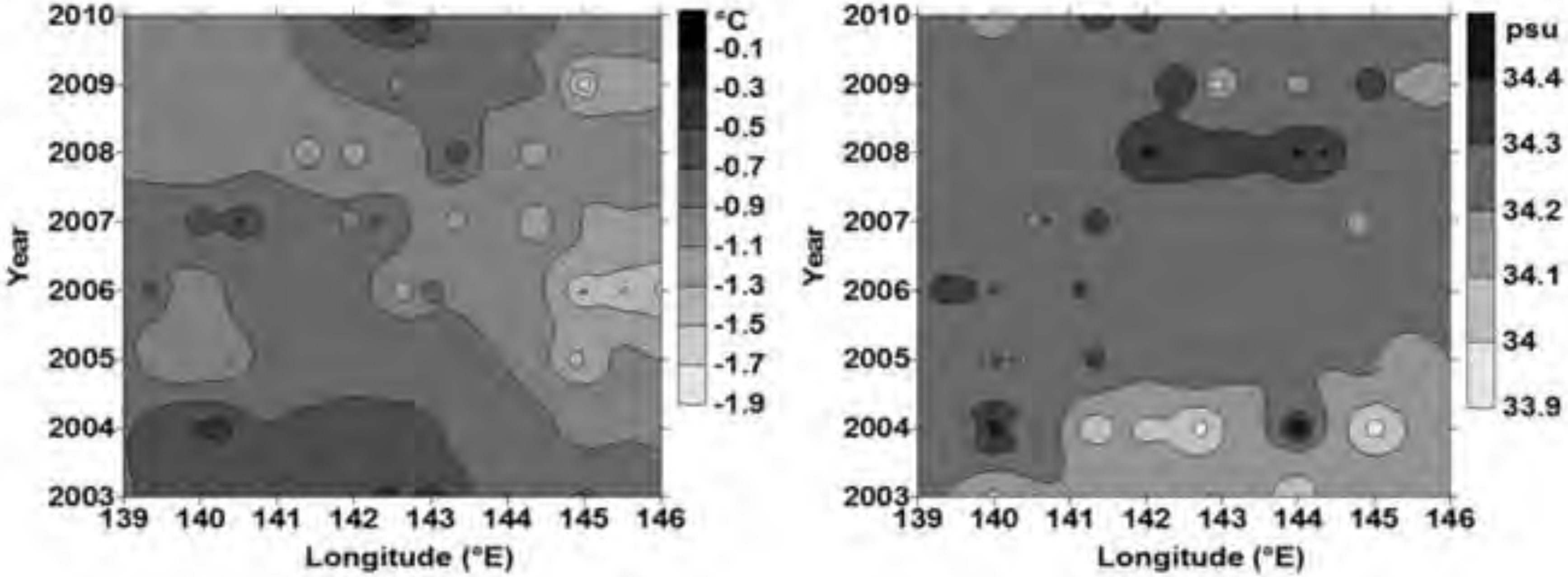
Year
2010
2009
2008
2007
2006
2005
2004
2003
139 140 141 142 143 144 145 146
Longitude (°E)
°C
-0.1
-0.3
-0.5
-0.7
-0.9
-1.1
-1.3
-1.5
-1.7
-1.9
Year
2010
2009
2008
2007
2006
2005
2004
2003
139 140 141 142 143 144 145 146
Longitude (°E)
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34.1
34
33.9

Figure 4

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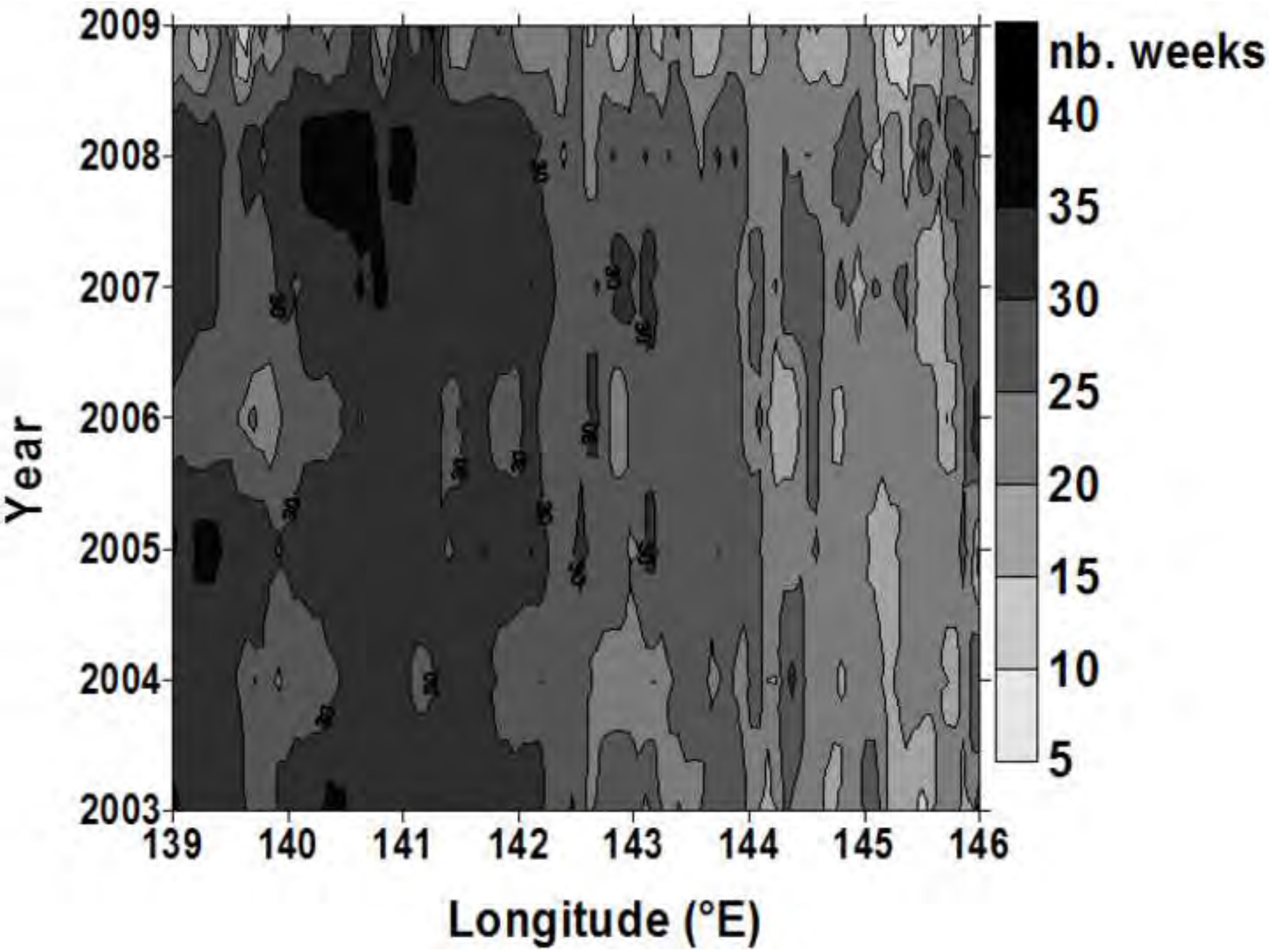

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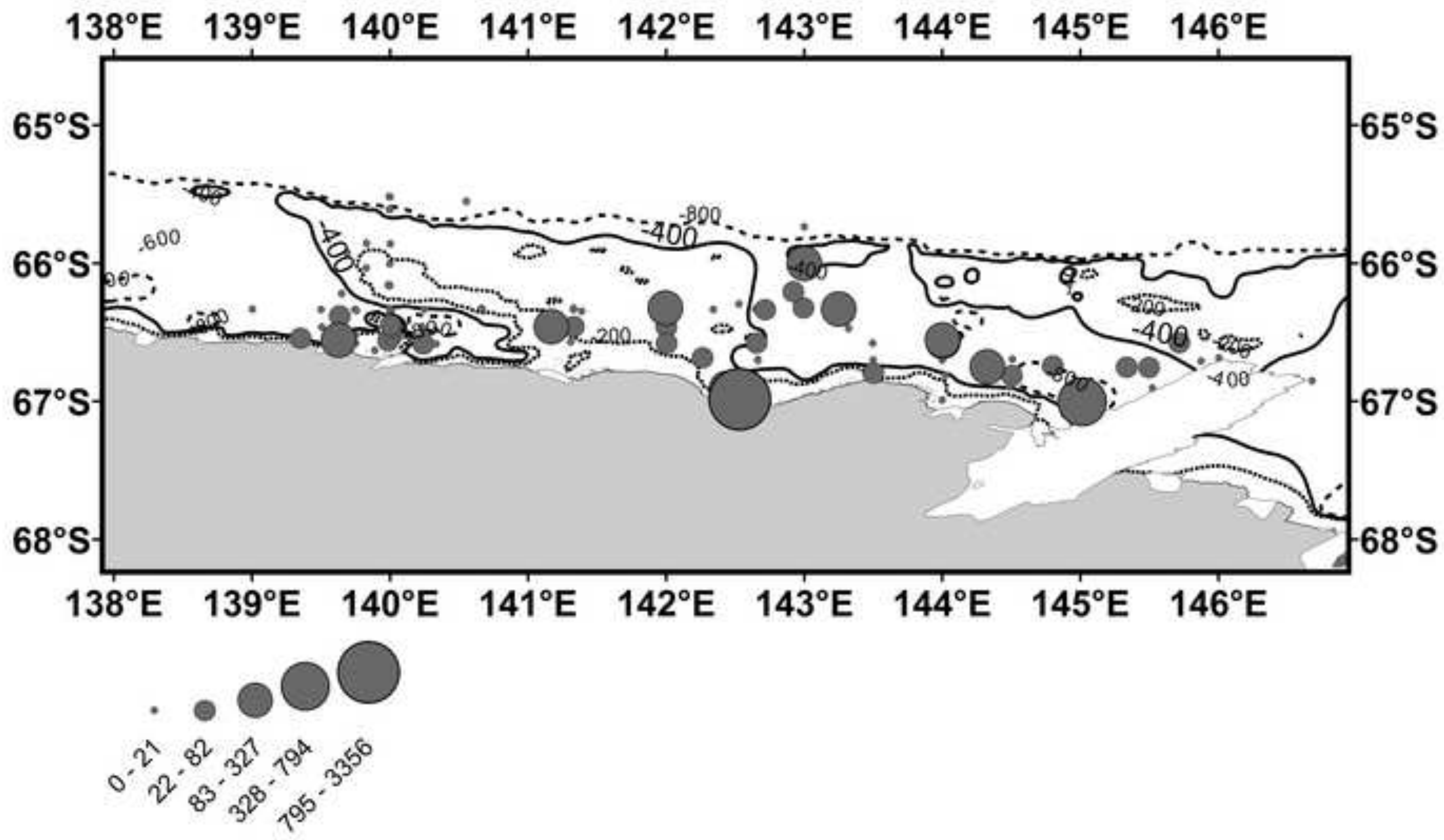
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-400
-600
-200
0 - 21
22 - 82
83 - 327
328 - 794
795 - 3356

Figure 6

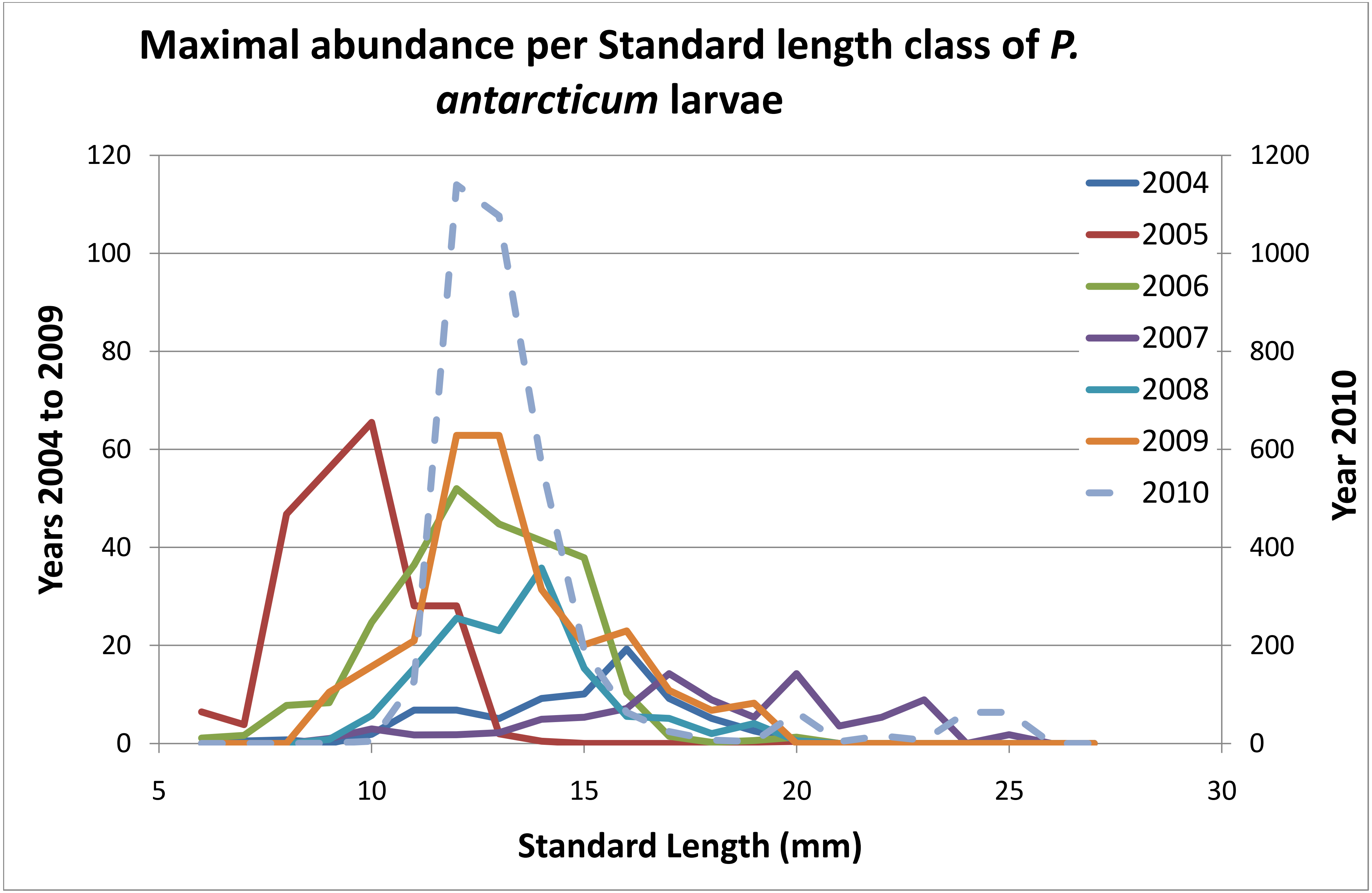
Maximal abundance per Standard length class of *P. antarcticum* larvae
Years 2004 to 2009
Year 2010
Standard Length (mm)
120
100
80
60
40
20
0
1200
1000
800
600
400
200
0
5
10
15
20
25
30
2004
2005
2006
2007
2008
2009
2010

Figure 7

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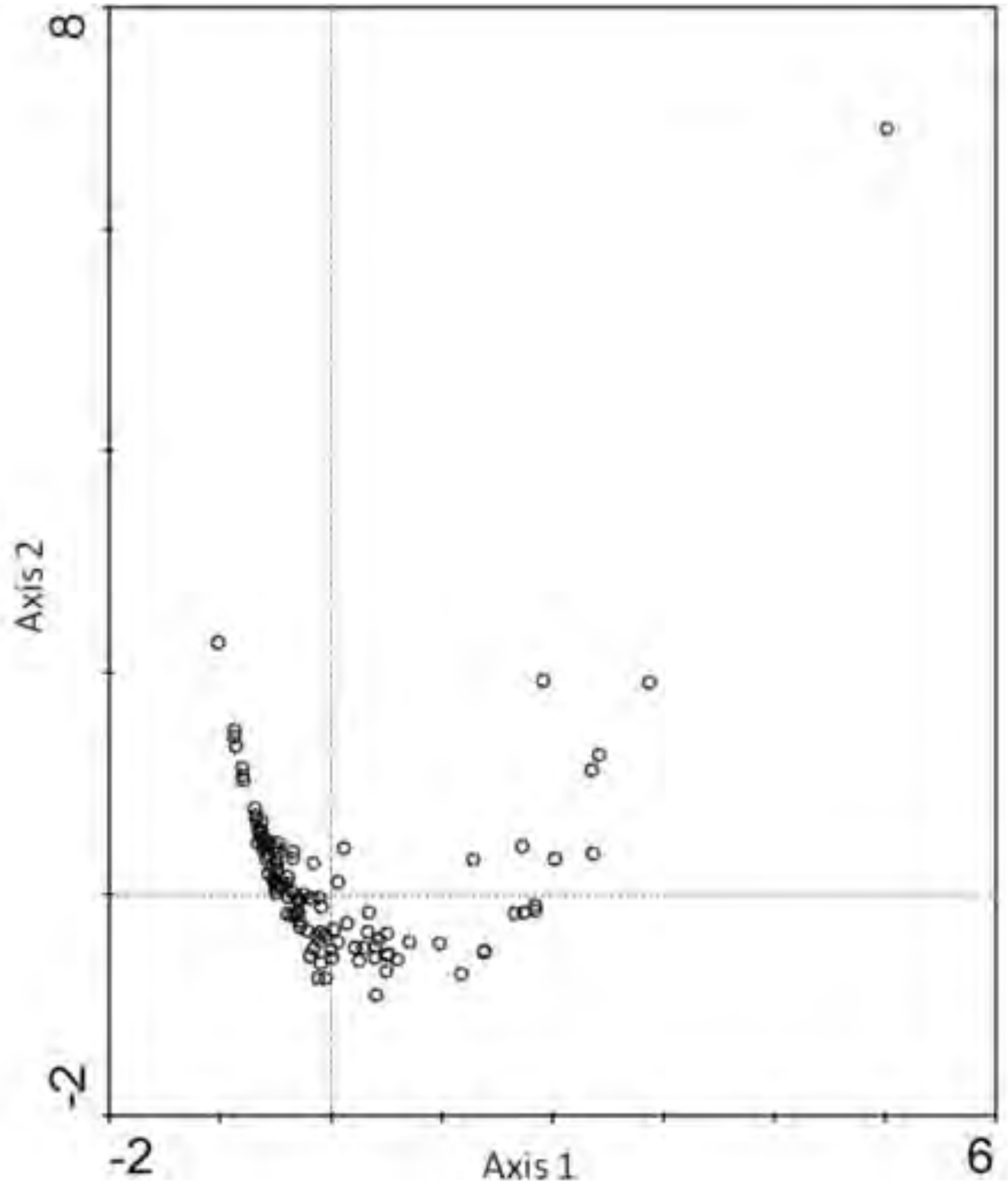

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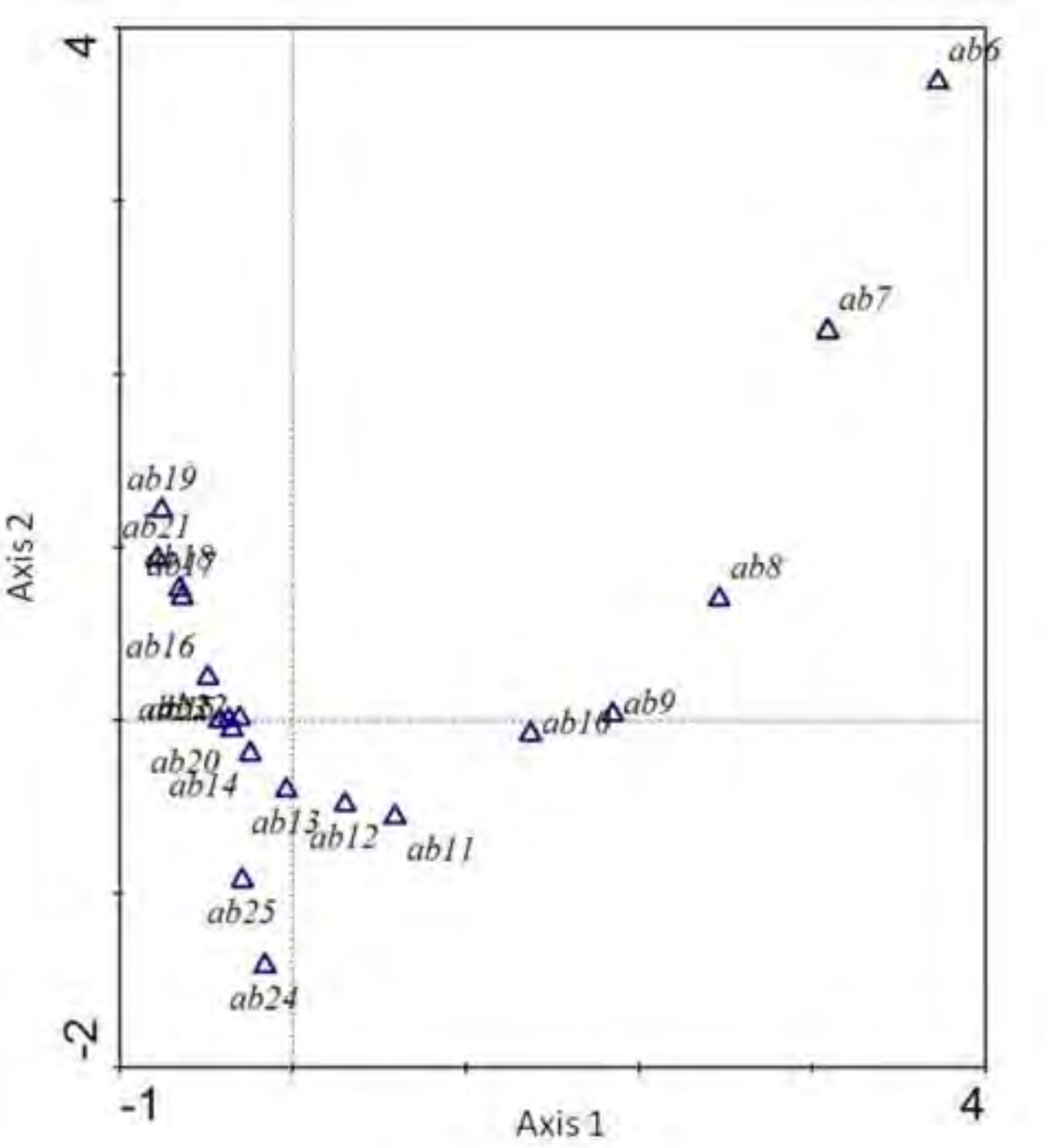
4
-2
Axis 2
-1
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Axis 1
ab6
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ab21
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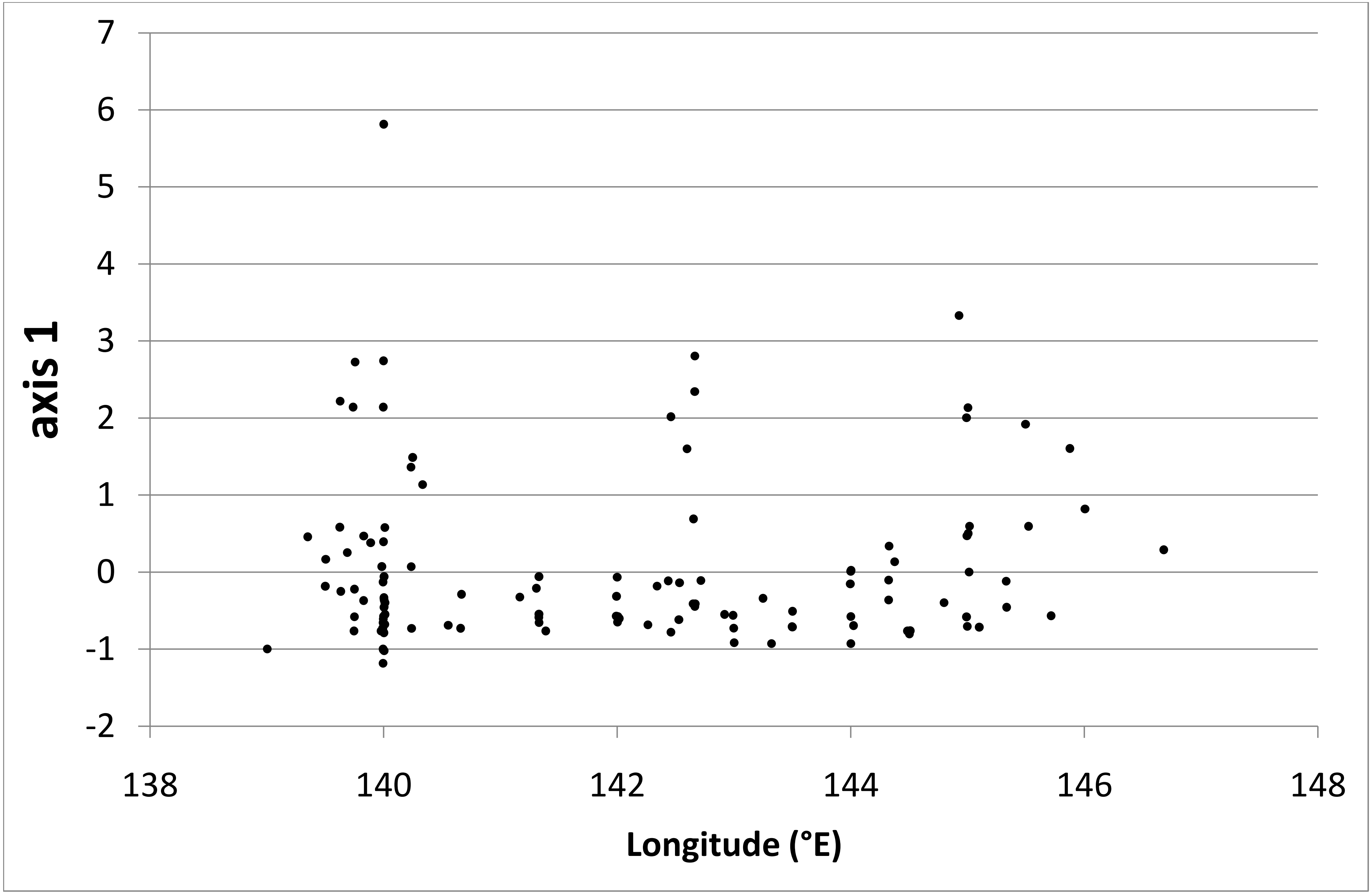
ab24

Figure 9



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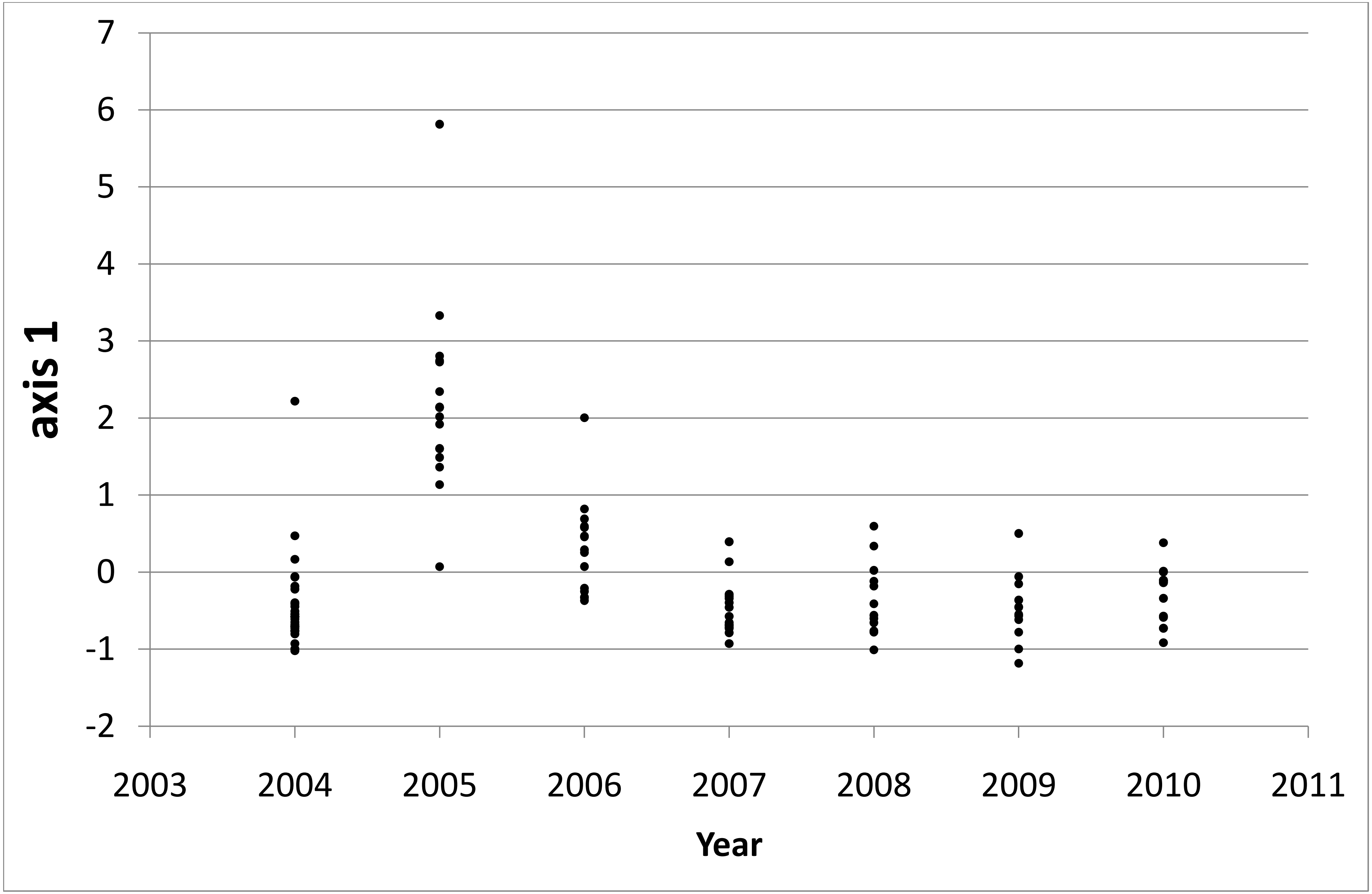
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2003
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2006
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2010
2011
Year

Figure 11

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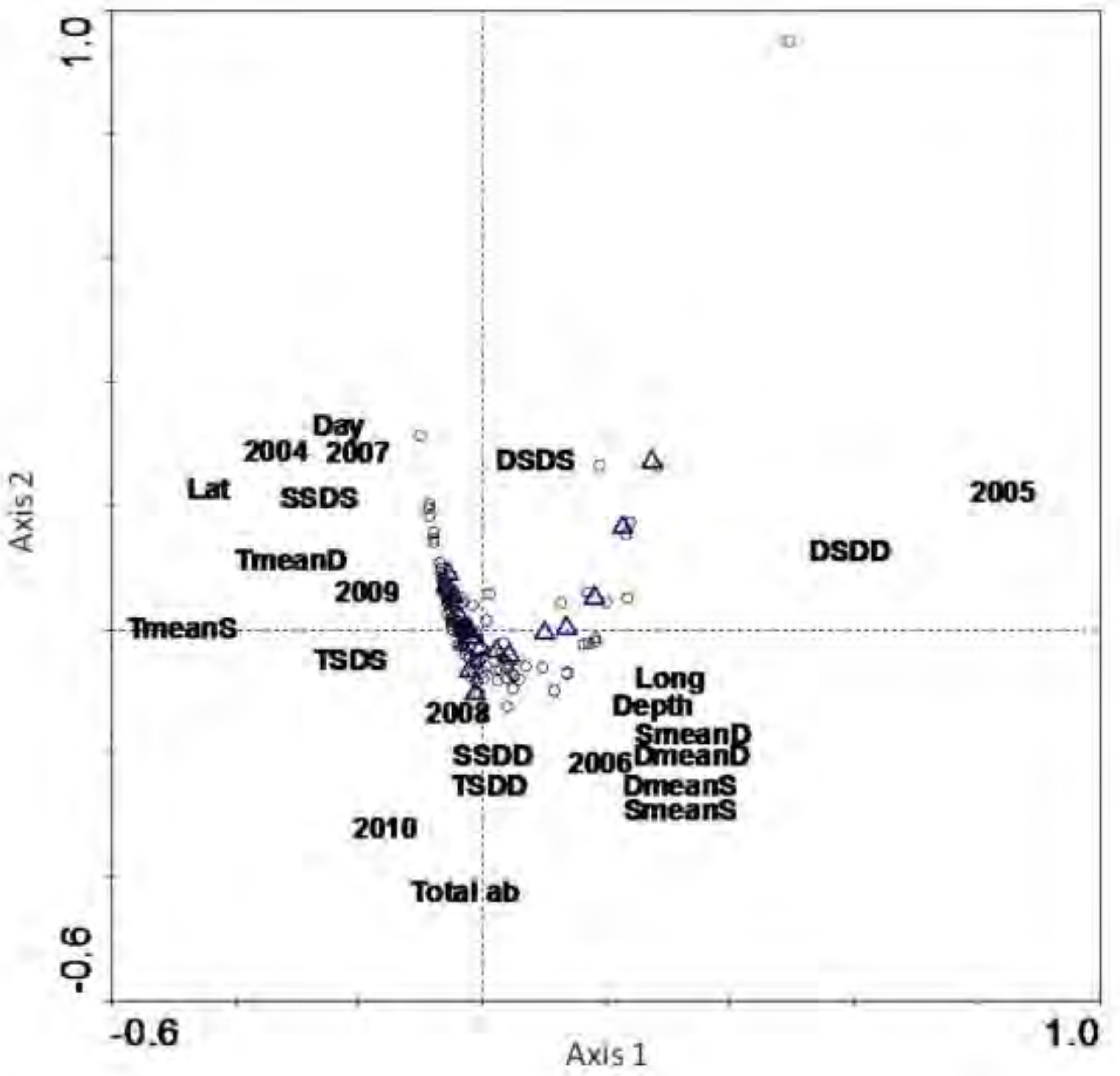

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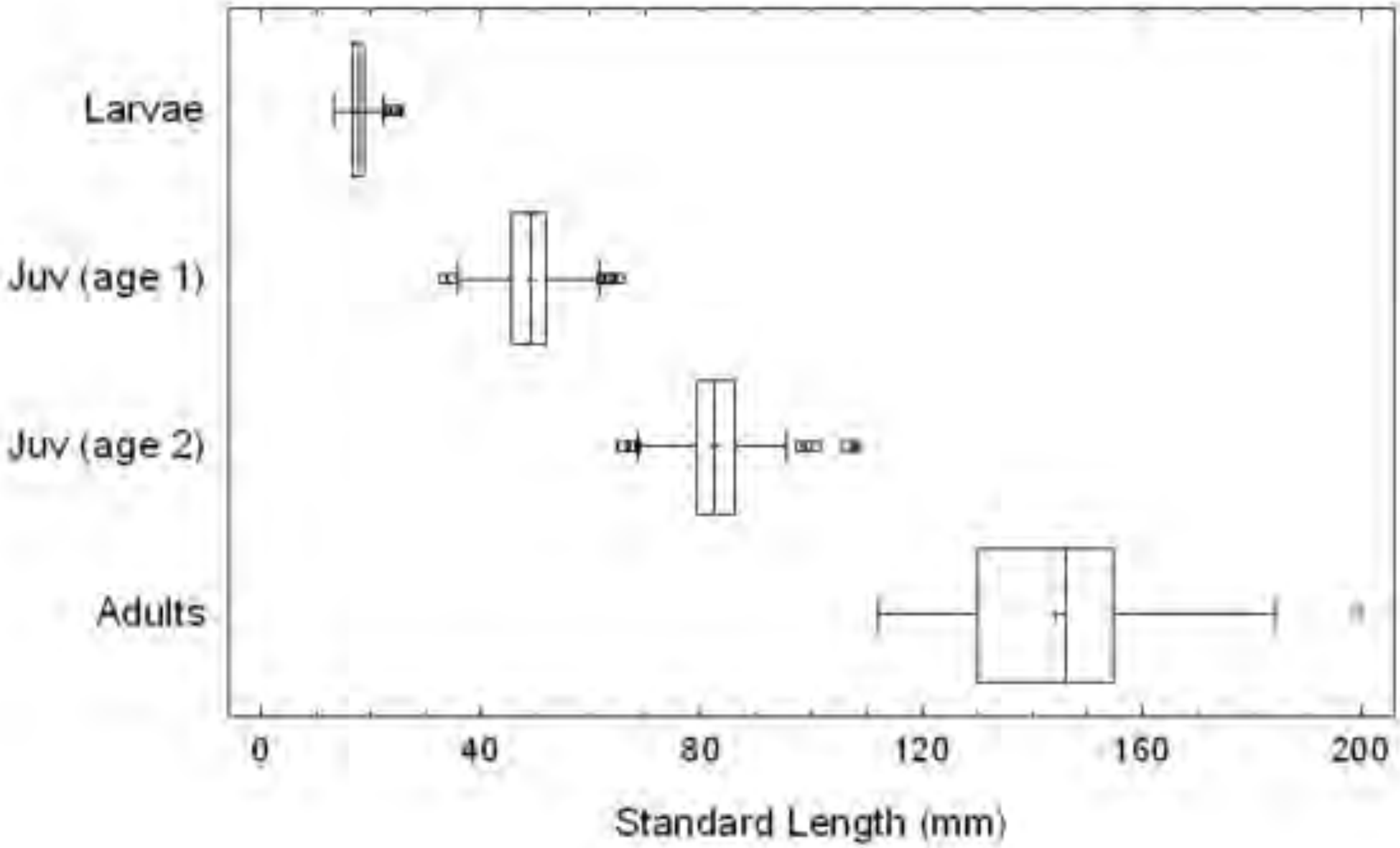

Figure 13

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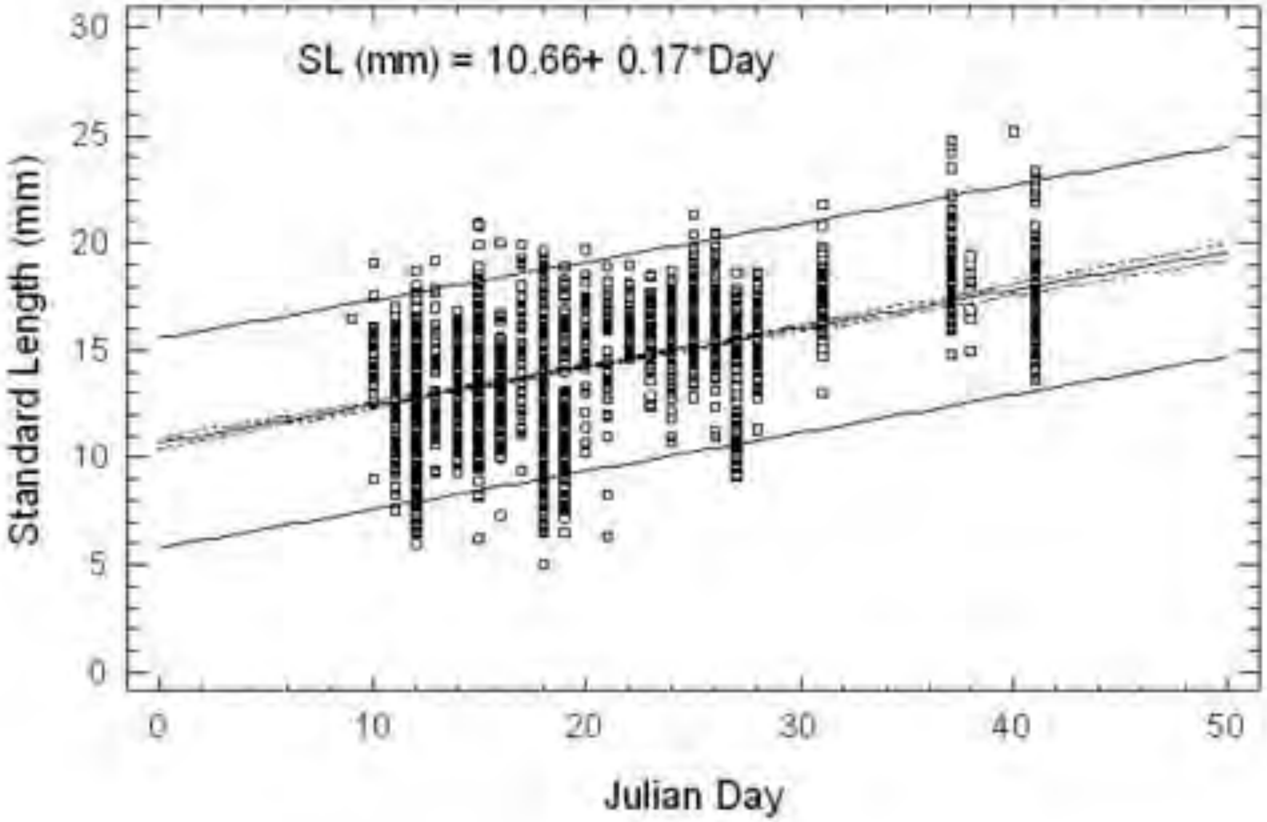

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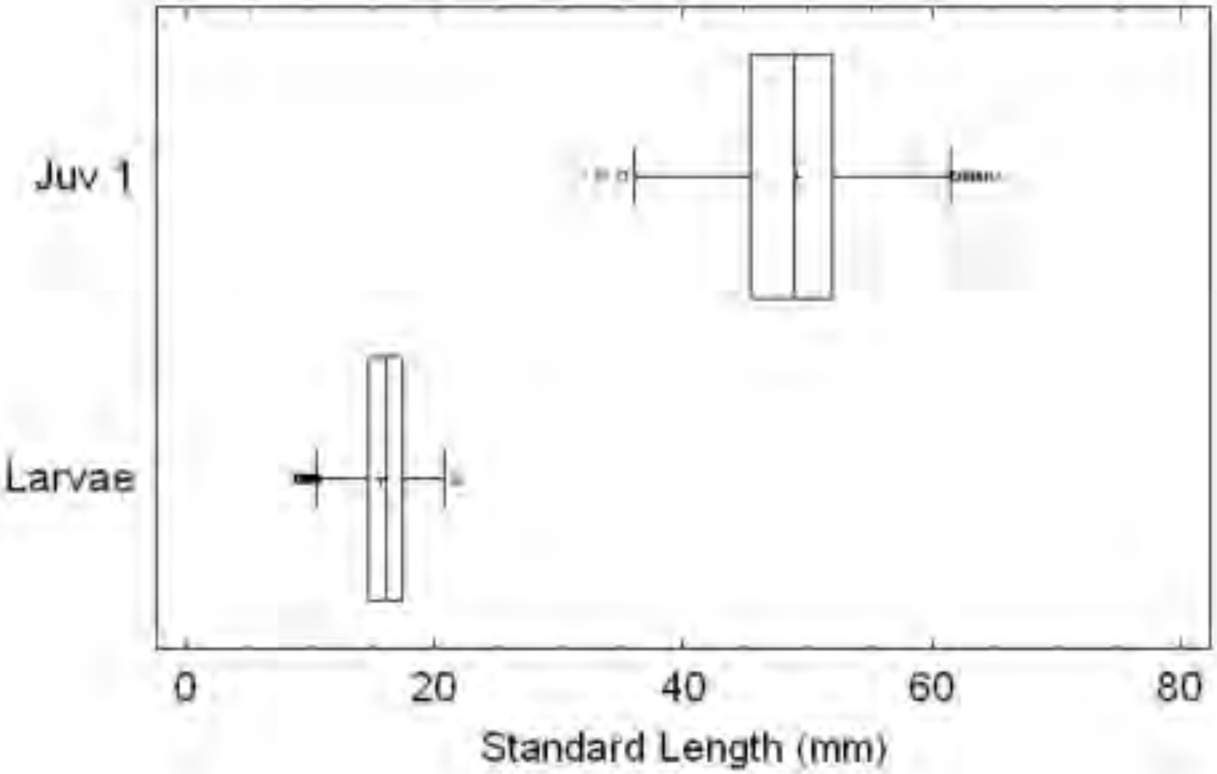

Figure 15
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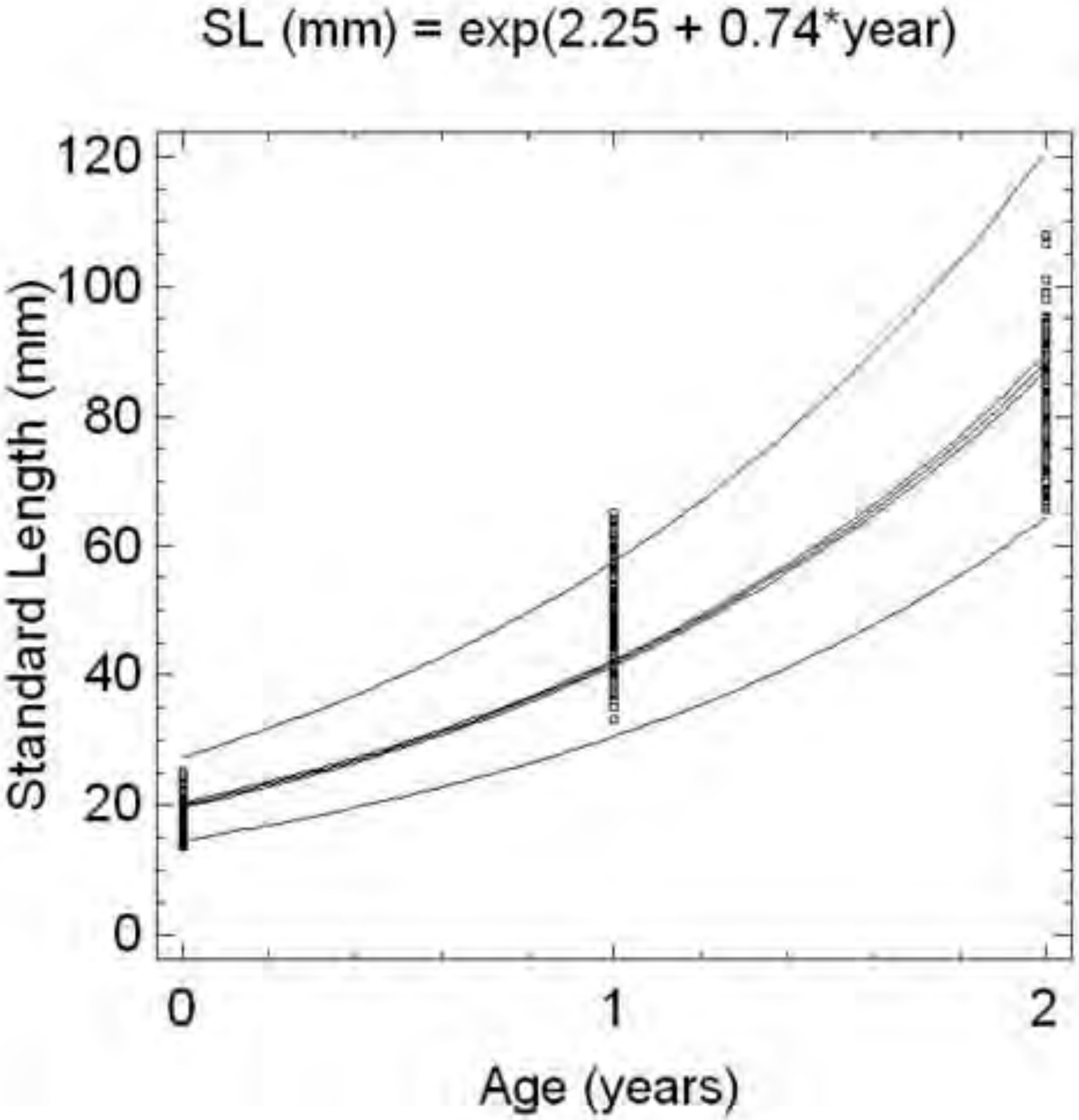

Figure 16
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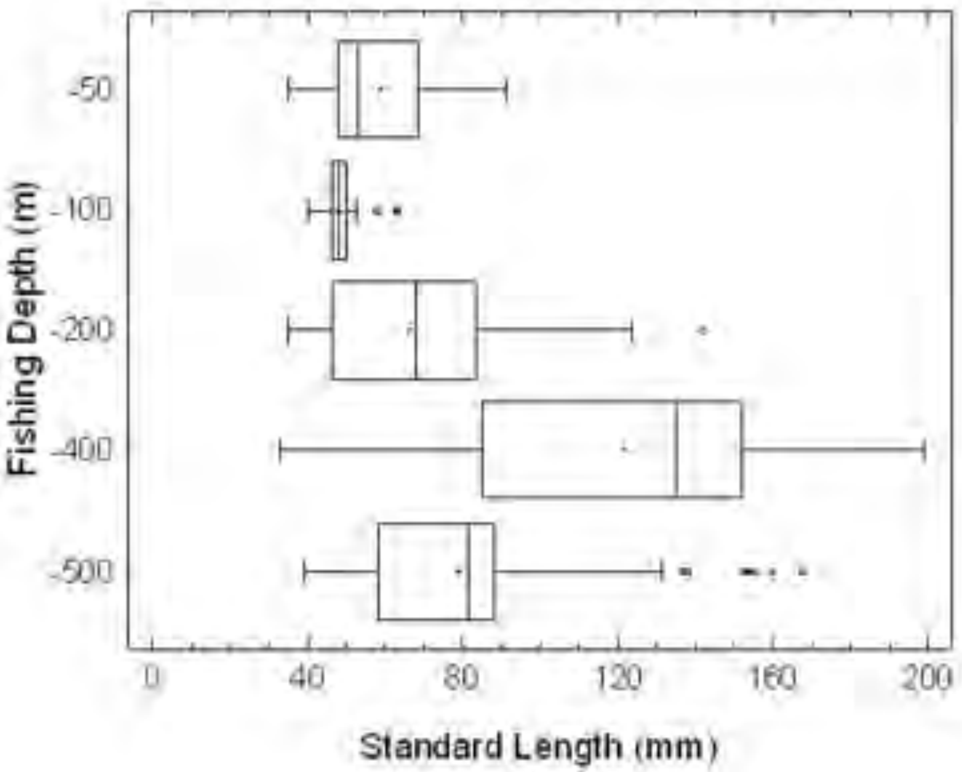

Table 1

Year	Start	End	Number of stations
2004	19/01	28/01	38
2005	10/01	19/01	23
2006	09/01	18/01	24
2007	24/01	01/02	15
2008	10/01	18/01	17
2009	10/01	17/01	15
2010	10/01	21/01	17

Table 2

Year	nb of larvae	Mean	standard dev.
2 004	455	15.9	1.7
2 005	209	10.3	2.0
2 006	590	11.9	2.2
2 007	223	15.7	2.5
2 008	391	14.0	1.9
2 009	127	15.5	1.8
2 010	566	14.1	1.7
Total	2 561	13.8	2.6