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Variability and controls of otolith growth in the anchovy of the Bay of Biscay

Pierre Petitgas, Patrick Grellier, Erwan Duhamel, Martin Huret,
Jacques Massé, Mathieu Doray

Individual fish growth depends on internal population factors such as phenotypic variability as well as external factors such as past environmental conditions (temperature, food) and selective mortality (predation or fishing). In the anchovy, growth in the first year is key to population dynamics as it determines the potential energy allocated to reproduction as well as the capacity to occupy off-shore habitats. Further, in the recent past, the anchovy in the bay of Biscay has experienced collapse and recovery and the role played by growth in this history is unknown. Since 2001 with the spring acoustic survey series PelGas, we have monitored individual fish growth by measuring in the otolith the increments between annual rings, in addition to age determination. These data now allow to analyse the growth patterns in the population as well as the effects of environmental parameters and fishing on the apparent growth of individuals. We show that growth is related to a spatial pattern where smaller and lower growing individuals are more coastal than off-shore larger and faster growers. We evidence a temperature effect on the growth pattern where warm years are also those of faster growth. In contrast, fishing does not seem to affect the apparent growth. We also account for the variability of growth between individuals, which has stayed high throughout the series. The study implies a spatial substructure and segregation in this population where particular habitats could have played a fundamental role for the recovery of the population after its collapse.

Key words: Anchovy, Biscay, Otoliths, Growth, Metapopulation

Contact authors: Pierre Petitgas, IFREMER, Research Unit on Ecology and Models for Fisheries, rue de l'île d'Yeu, 44300, Nantes, France. tel: +33240374163, email: pierre.petitgas@ifremer.fr

Introduction

A fish population is classically conceptualised as a group of individual fishes that are all alike and that undergo the same life cycle pattern (Sinclair, 1988). Yet, some populations display within population life cycle diversity based on differential growth patterns of individual fishes, which trigger alternative life strategies and migration behaviours (e.g., Jonsson and Jonsson, 1993; Secor, 1999, Petitgas et al., 2010).

The anchovy population in the Bay of Biscay occupies two different types of spawning habitats, coastal habitats close to large estuaries and marine off-shore habitats (ICES, 2010a, chapter 8). Further, length at age is very variable among individuals of the same age class and year classes overlap greatly in length. In addition, larval dispersal kernels depend on spawning time and spawning sites (Huret et al., 2010). Thus differences in growth pattern among individuals may influence spawning habitat occupation, spawning windows and ultimately recruitment. The present study is one step in understanding theses mechanisms.

Material and Methods

The data come from the French survey series PELGAS, 2001-2011, undertaken in spring (May) during the spawning of anchovy and sardine. This is a pelagic fish oriented survey that also monitors the pelagic ecosystem (ICES, 2011b). Here, we used fish and hydrological data. Figure 1 gives as example the locations of trawl hauls and CTD casts in the PELGAS 2011 survey as well as the average map of the anchovy spatial distribution.

Sampling the fish for the otoliths. The fish data consist of otoliths (sagittae) extracted from individual fishes collected at trawl haul stations. Trawl hauls are performed opportunistically depending on echotraces encountered along the regularly spaced acoustic transects extending from coast to shelf break. At each trawl haul, the catch is sorted by species. The length distribution and the weight-length relationship of anchovy are estimated at each haul, using length classes of 0.5 cm. Based on such grouping, 40 fishes are further selected spanning the length range in the haul, for otolith age reading and micro-structure analysis. In May anchovy growth has resumed after winter and the border of the otolith is characteristic allowing to identify clearly the last winter ring (Uriarte et al., 2012). Both sagittae otoliths were extracted from each individual and kept in leukite.

Reading otolith annual growth increments. In addition to ageing, annual growth increments between winter rings were measured. This was done under light microscopy using a digital camera installed on the binocular and related to a PC. Measurements were performed using the image analysis software Visilog. Growth increments were measured along the major (longitudinal) axis of the otolith (Fig. 2). Because the position of the otolith centre (nucleus) is imprecisely defined, the diameter from winter ring to winter ring was measured then divided by 2. Increments during age 0 (i.e., between birth and the first winter) were measured on age 1 fish and noted R1. Increments during age 1 (between first and second winter) were measured on age 2 fish and noted R2-R1. Increments during age 2 (between first and second winter) were measured on age 3 fish and noted R3-R2 (Fig. 2). The data set covers the period 2001-2011 and comprises ~ 10 000 individual fishes where growth increments, age, location, bottom depth are documented.

Environmental indices. The hydrological data consist of indices derived from the CTD vertical profiles. The CTD stations are performed on a grid of stations covering the entire shelf and independently from the acoustic transect lines and trawl hauls. Indices derived from the CTD profiles (Huret et al., 2012) are the following: surface (5m) and bottom temperature and salinity, potential energy deficit (kg m^{-1} s^{-2}, index of vertical stratification), surface (5m) fluorescence (mg chla m^{-3}), vertically integrated fluorescence. Fluorescence data were centred to the mean in each year.

How to characterise the growth pattern. The otolith growth pattern was characterized by the bivariate distributions between growth annual increments at different ages. Bivariate distributions were summarized using gravity centre and inertia along its major and minor axis, as for spatial distributions (Woillez et al., 2009).

Environmental effects on growth. Growth increments were linearly regressed on hydrological indices to evidence environmental controls on growth across the years. Growth takes place predominantly in summer and autumn, after spring spawning. Here, hydrological indices were available for spring time only. We considered the conditions in the previous year (t-1) of the biological sampling (t). In doing so, we considered implicitly that the indices in spring were indicative of later conditions in the year. Hydrological indices were averaged over all stations providing one value per year for each index. Annual growth increments at age were averaged over all individuals per year and then regressed on each of the hydrological indices. For instance, increments during age 0 (i.e., between birth and the first winter) measured on age 1 fish in years t were regressed on the indices of the previous years t-1. Because increments during age 1 (between first and second winter) measured on age 2 fish were dependent on increments during age-0 (between birth and first winter), the residuals of that regression were first calculated and then linearly regressed on the hydrological indices. Residuals were calculated for years t and the indices for the previous years (t-1). The same procedure was applied for increments during age 2 (between second and third winter) measured on age 3 fish. The increments R3-R2 were regressed on increments R1 and the residuals of that regression were regressed on the environmental indices for years t-1. To identify which hydrological index correlated to growth increments, we selected the regressions that had a p-value <0.05 and explained more than 40% of the variability in the growth increments. The procedure is schematically summarized on Fig. 3.

Fishing effects on growth. Fishing may select fast growers. The fishery was entirely closed from mid 2005 to the end of 2009 due to low abundance and repeated low recruitments (ICES, 2011c). We tested whether fishing was directed towards a particular growth pattern by estimating growth during age 0 (increment R1) for the years when the fishery was opened and closed (2005-2009). Further we tested whether growth selective mortality occurred due to fishing by comparing increments R1 along the cohorts. Cohorts (starting at age 1) considered during the fishing period were 2000 to 2003 and 2010 and that during the fishing ban were 2006 to 2008.

Results

Growth pattern. Increments during age 1 (R2-R1: between first and second winter) were negatively correlated with increments during age 0 (R1: between birth and first winter) (Fig. 4), meaning that larger fishes at age 0 grew less during their subsequent year than did smaller fishes at age 0. Correlation between annual increments in subsequent ages were less correlated with age 0 increment. Thus, the bivariate distribution (R2-R1, R1) between growth during age-1 and growth during age-0 was the dominant characteristic of the growth pattern.

Spatial pattern. Gravity centre and inertia was computed on the bivariate distribution (R2-R1, R1) by depth strata (Fig. 5) on individuals of age-2. Individuals that showed larger growth during age-0 (larger R1) were found off-shore in deeper bottom depths, while those with smaller R1 were coastal. To understand whether such pattern was consistent over the ages, the mean R1 at age in the trawl hauls was also computed (Fig. 5). Whatever the age, individuals that grew larger before their first winter (greater R1) were encountered at deeper bottom depths. Indeed, the average distribution of anchovy (Fig. 1) shows a concentration on the outer shelf at 44-45°N and another one off the Gironde estuary at 45-46°N.

Survival pattern. Fishes belonging to the same cohorts from ages 1 to 3 were identified (9 cohorts from 2001 to 2011) and the evolution of the R1 plotted against age (Fig. 6). Individuals that grew larger before their first winter (larger R1) suffered a greater mortality as they were absent at ages 2 and 3. This is probably in relation with differential mortality on the habitats, smaller and coastal fishes having greater survival.

Environmental effects. The inter-annual variability in growth during age-0 (R1) and during age-1 (R2-R1) correlated positively with the index of water column stratification and bottom temperature respectively (Fig. 6). Water column stratification was estimated in spring at spawning time. Spring vertical stratification could influence hydrological conditions occurring later in the year (from summer to winter) for larvae and juvenile growth. Anchovy schools are predominantly (as observed in acoustic surveys) close to the bottom during day time, which may explain why bottom temperature was correlated with growth during age-1.

Effect of Fishing closure. Growth during age-0 (R1) as well as the bivariate distribution between growth during age-1 and age-0 (R2-R1, R1) did not differ between periods of fishing and no fishing (Fig. 8). Further the pattern of growth selective mortality did not differ between the two periods (Fig. 9). Though fishing can be expected to target larger individuals at age 1, the growth pattern did not seem to be affected by it. As larger individuals at age-1 suffer a greater mortality in offshore habitats than their smaller more coastal cohort congeners, natural (predation) mortality could display a selective pattern similar to that of fishing.

Conclusion, Discussion

Growth during age 0 (between birth and first winter) is determinant for population dynamics as it determines the spatial distribution (in particular the occupation of offshore habitats), growth in subsequent years (in particular reproductive potential) and survival.

The important variability in growth during age-0 among individuals of the same cohort could depend on the birth date and/or the encountered conditions. The spawning season lasts 3 to 4 months from April-May to July-August. Thus individuals born at the beginning of the spawning season will have a longer time for growth than those born at the end. Back-calculation of birth dates would help understand whether the variability in growth before the first winter reflects the birth dates of the recruits. This would require to access to daily otolith increments on age-1 fish otoliths, which could be possible with scanning electronic microscopy.

The anti-correlation between growth before the first winter and growth between the first and second winters could be related to a balance between growth and reproduction. The larger individuals at the end of the first winter could invest more in reproduction during their first year. This could be investigated using bioenergetic modelling.

Variation in growth during age 0 across years was correlated with water column vertical stratification. And that during age 1 was correlated with bottom temperature. We used spring hydrological conditions to characterize growth conditions over the year. We implicitly assumed correlation in hydrological conditions between spring and autumn. This is not unrealistic as spring conditions may influence the seasonal evolution of the environment, in particular spring river plumes and mixing (Huret et al., 2012). More work is needed on how spring conditions (e.g., vertical stratification) influence that in the following autumn and how spring conditions (e.g., bottom temperature) are influenced by that in the previous autumn. The correlation of the growth increment (R2-R1) residuals with bottom temperature from the same year were non significant, questioning how well spring bottom temperature is indicative of previous autumn (growth) conditions.

The relationships evidenced between the spatial distribution, the growth pattern and the environmental conditions could allow to predict anchovy distribution maps based on growth patterns forced by environmental conditions.

An important assumption implicit in the study was that the sampling was even across the distribution range, which is a reasonable assumption as the trawl hauls are located based on echo-traces.

When deriving the abundance index based on the acoustic survey a global age-length key is currently used. Because the spatial distribution and the growth patterns are well related, it could be appropriate to map the age-length key when assessing the anchovy population.

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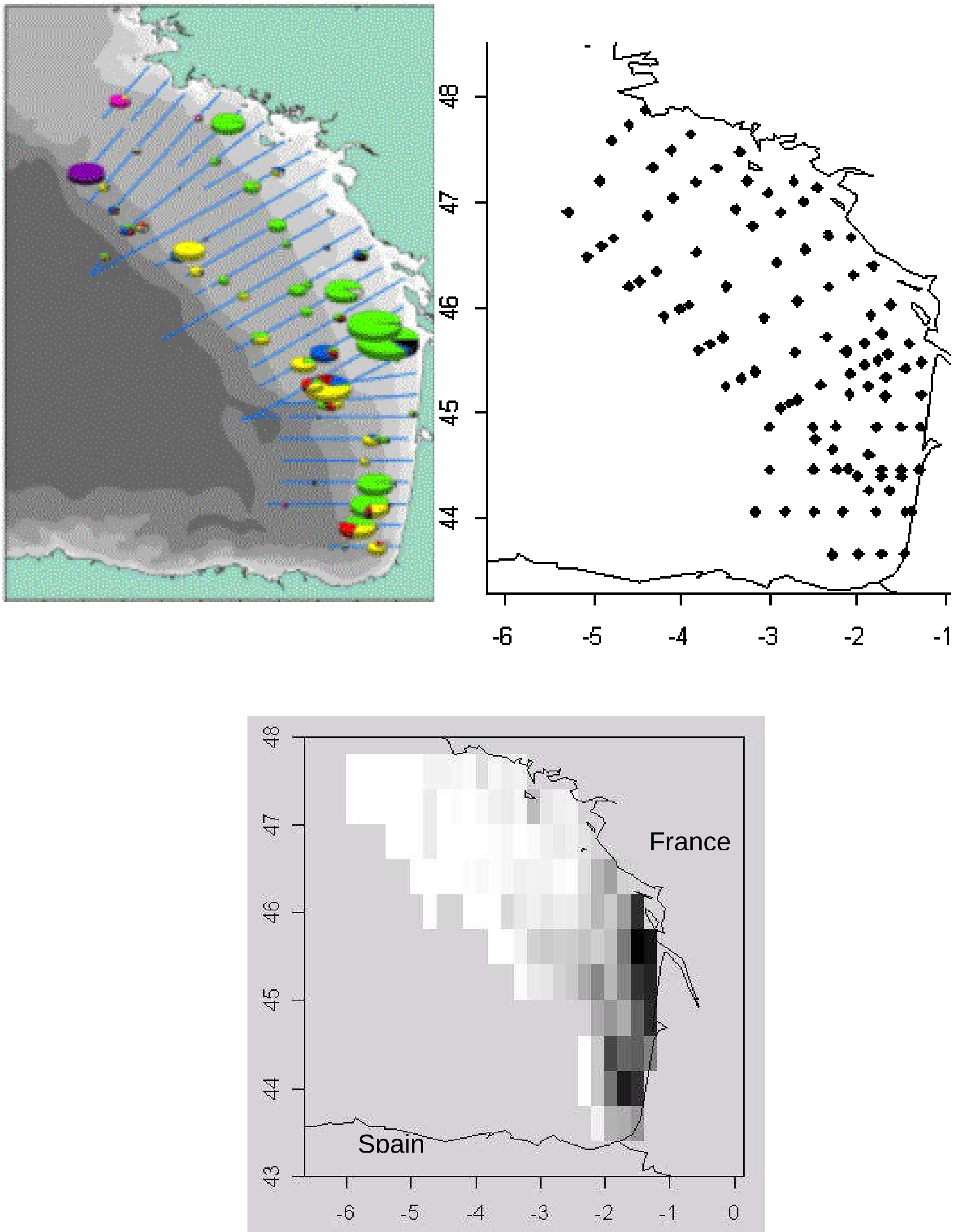


Fig. 1: Sampling. Top: Fish and environmental data collected during PELGAS 2011. Top left: trawl haul positions, where green corresponds to anchovy catch; the blue lines are the acoustics transects. Top right: CTD cast locations. Bottom: average map of anchovy abundance (tonnes per square nautical mile), 2001-2011.

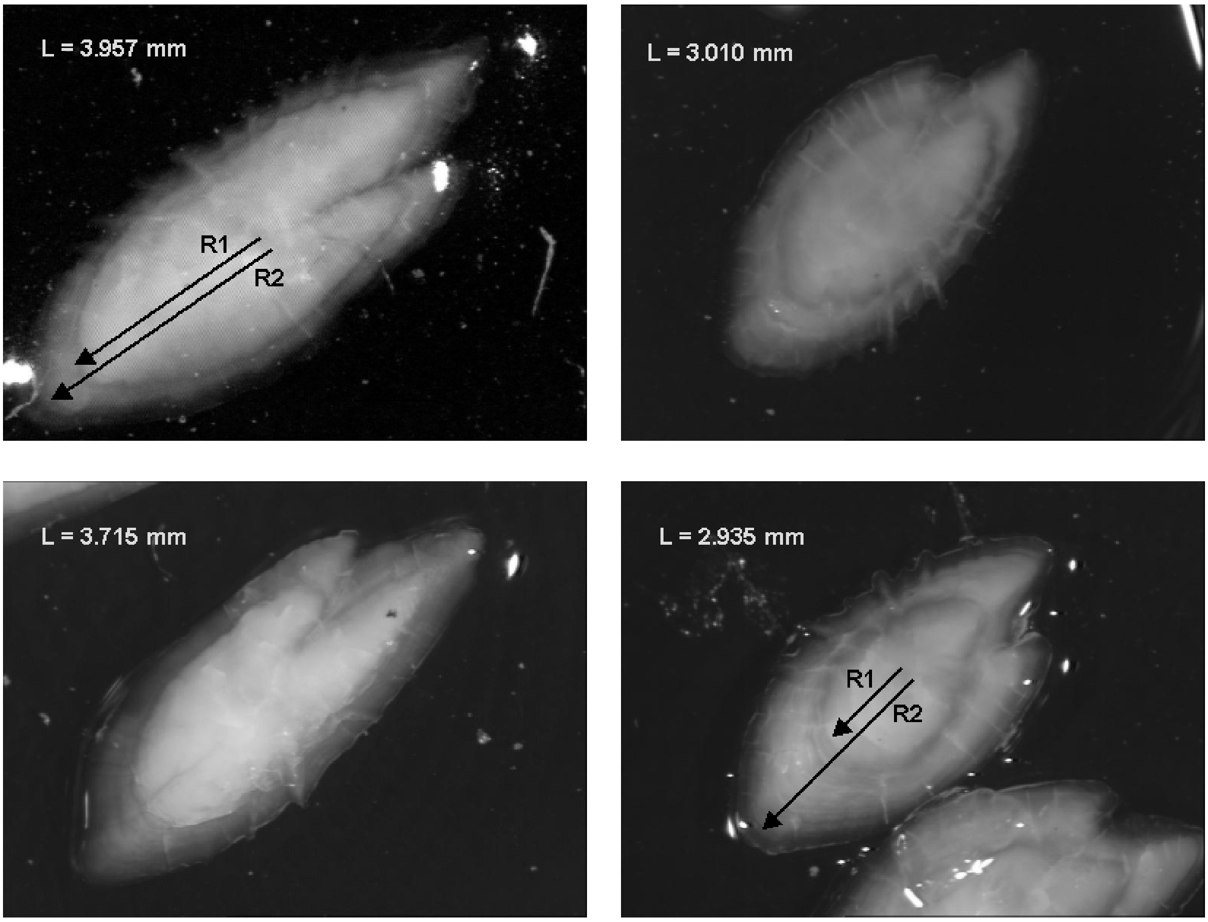


Fig. 2: Measurement of otolith annual growth on age 2 fish. All figures have the same scale. R1 represents the growth between birth and first winter and R2 that between birth and second winter. Left: Elongated otoliths showing larger growth during age 0 (R1) and smaller growth during age 1 (R2-R1). Right: Round otoliths showing smaller growth during age 0 and larger growth during age 1.

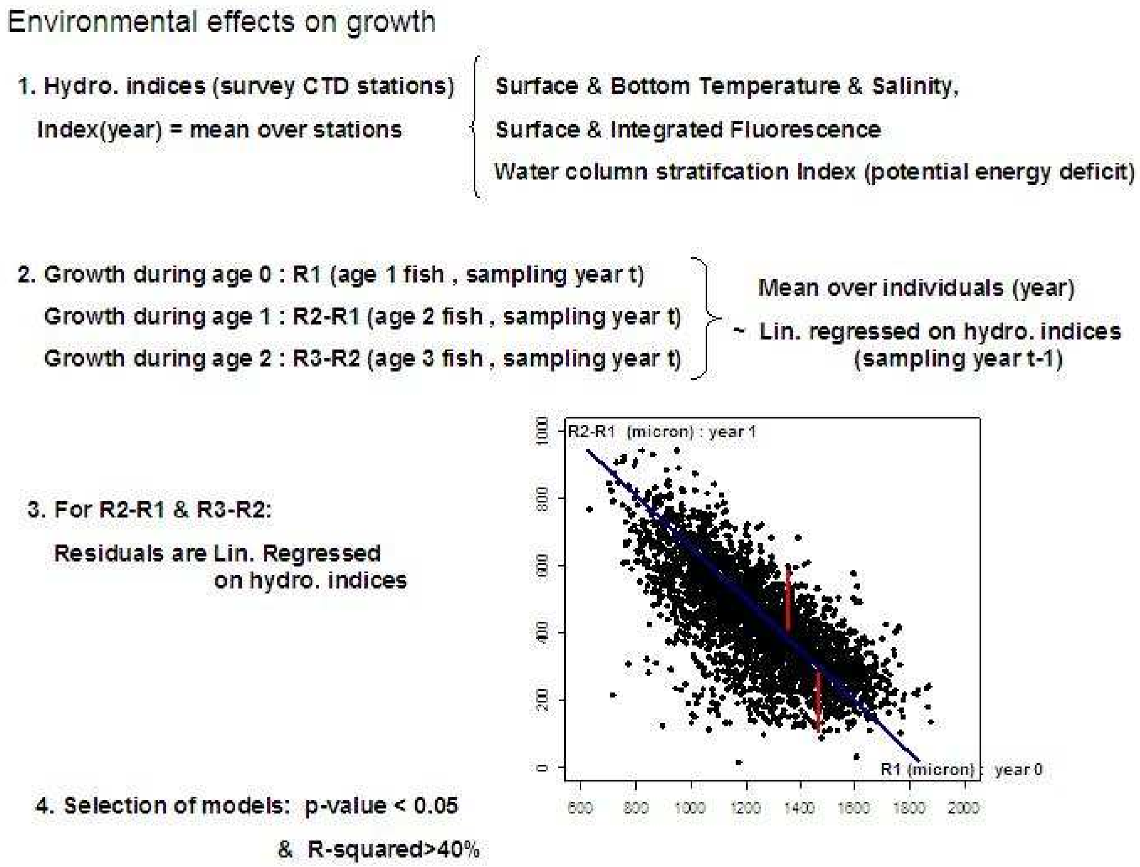


Fig. 3: schematics of the procedure used to regress otolith annual growth increments on hydrological indices.

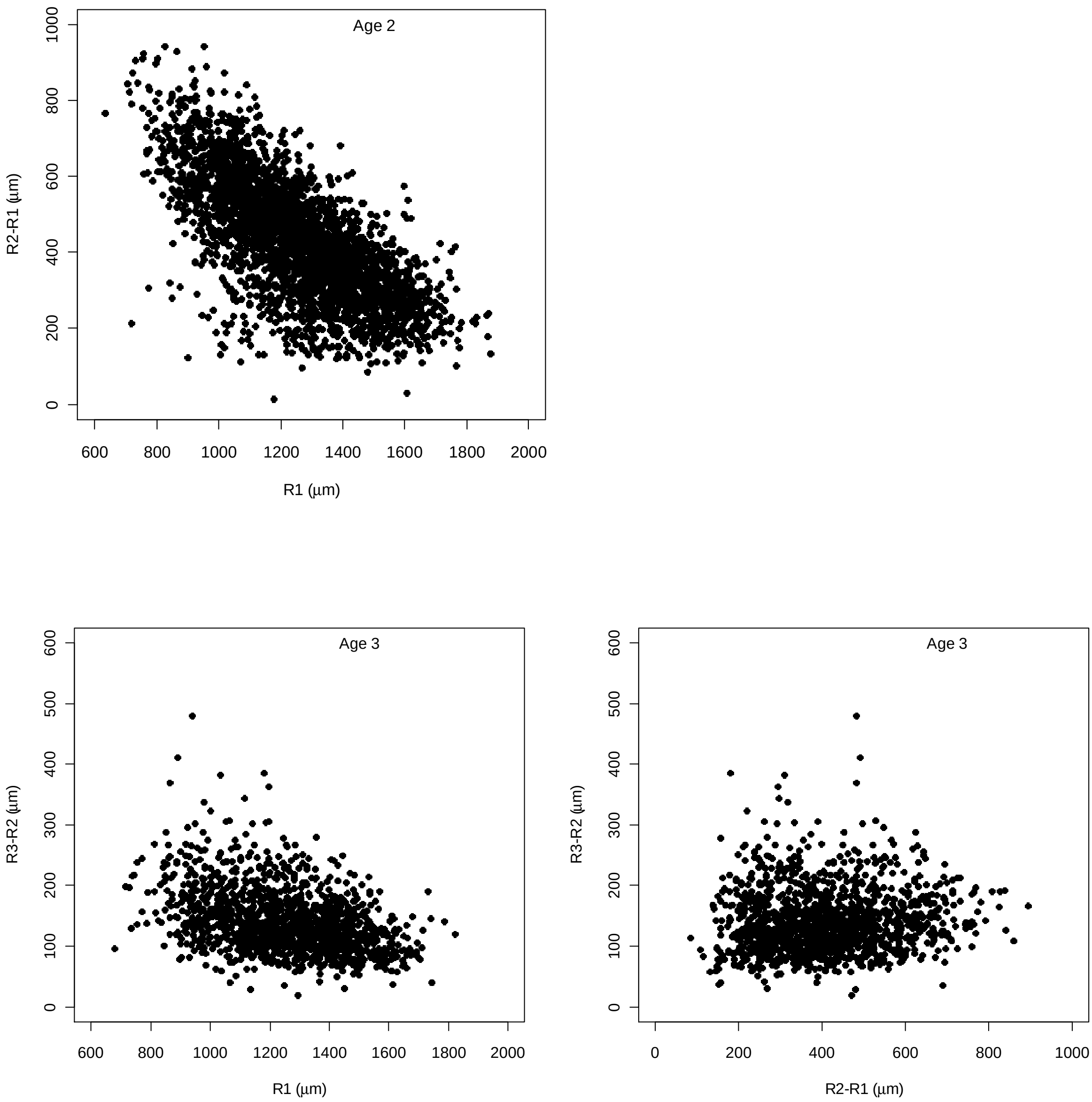
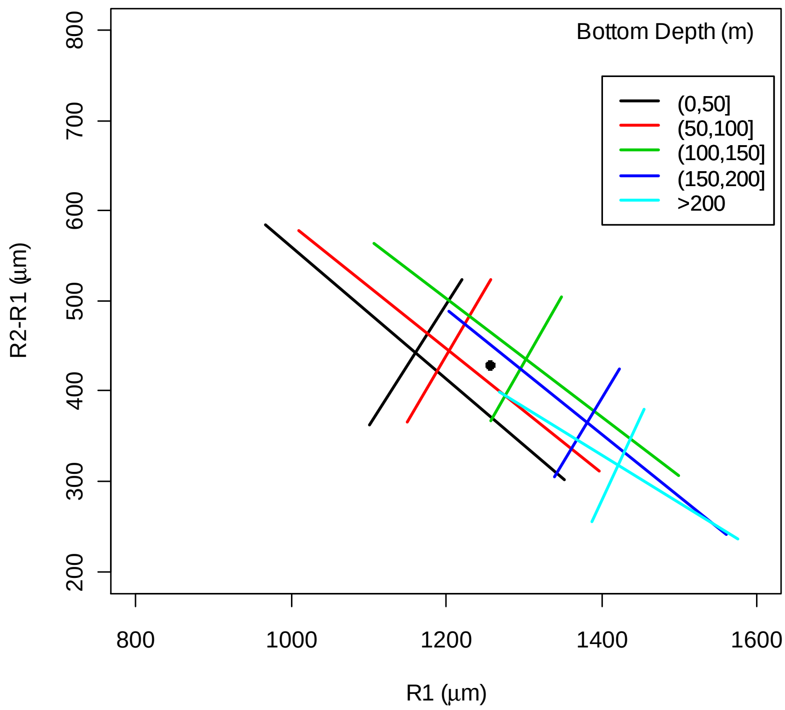


Fig. 4: Growth pattern. Correlation between growth increments during age-1 and age-0 (top left), during age-2 and age-0 (bottom left) and during age-2 and age-1 (bottom right).



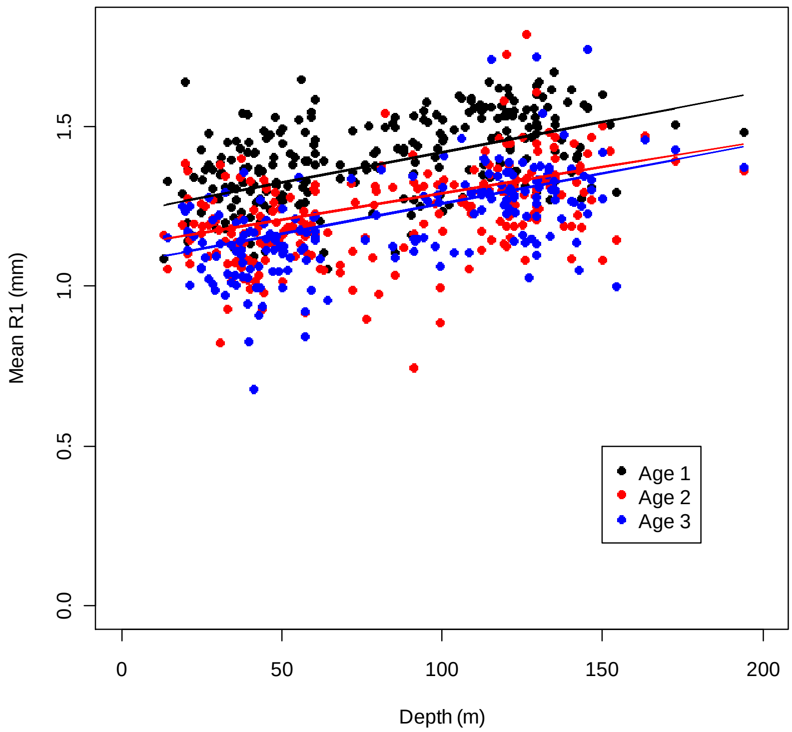


Fig. 5: Relationship between growth and spatial pattern. Top: gravity centre and inertia of bivariate distributions (R2-R1, R1) for different depth strata. Bottom: Mean R1 at age in the trawl hauls as a function of bottom depth.

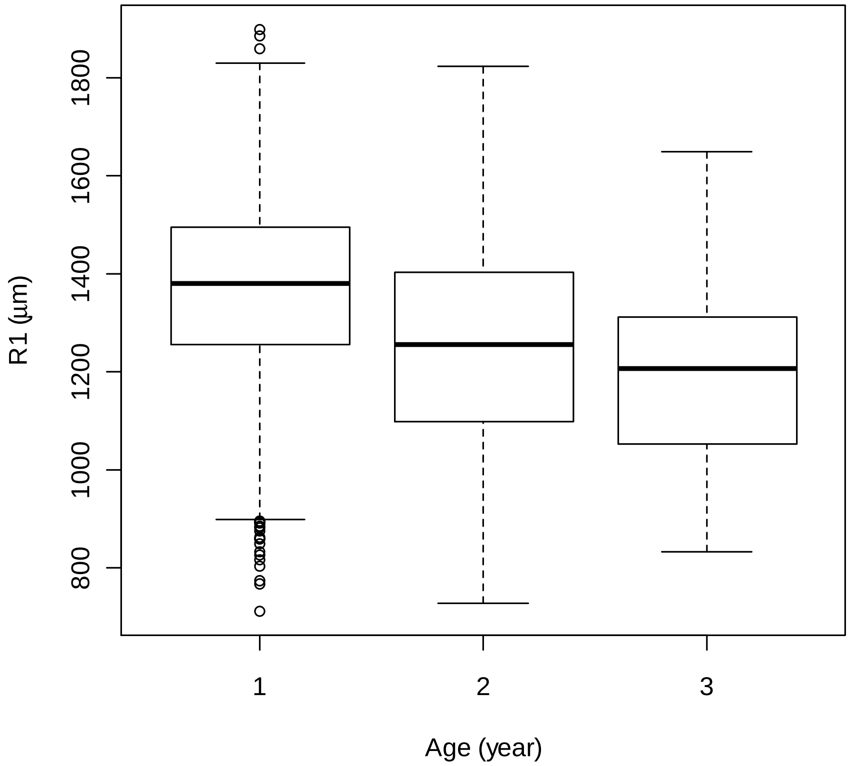
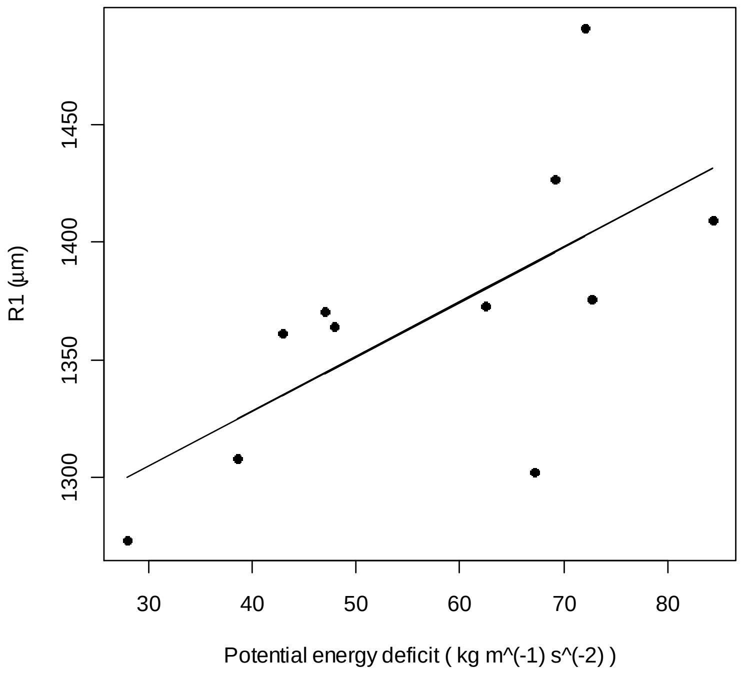


Fig. 6: Relationship between growth and survival. Boxplot of R1 as a function of age along cohorts (pooled) from 2001 to 2011.



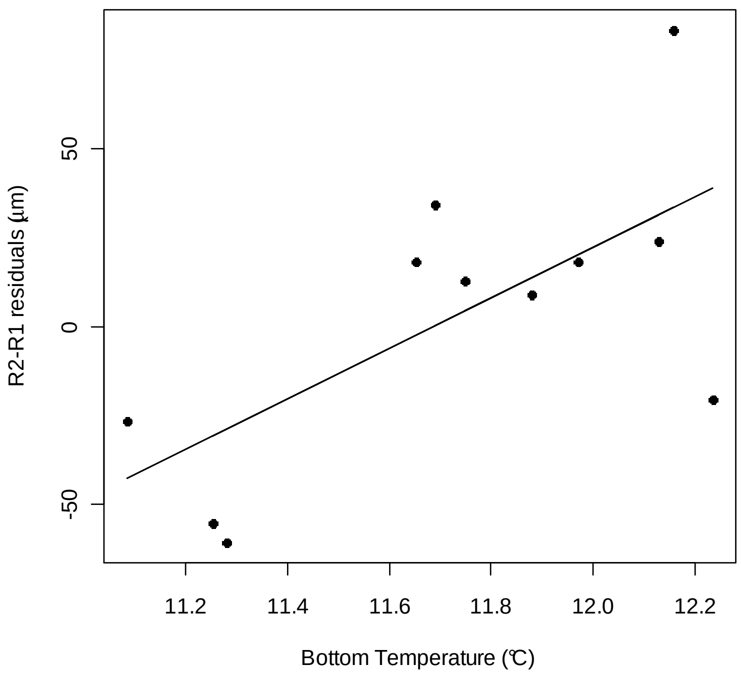
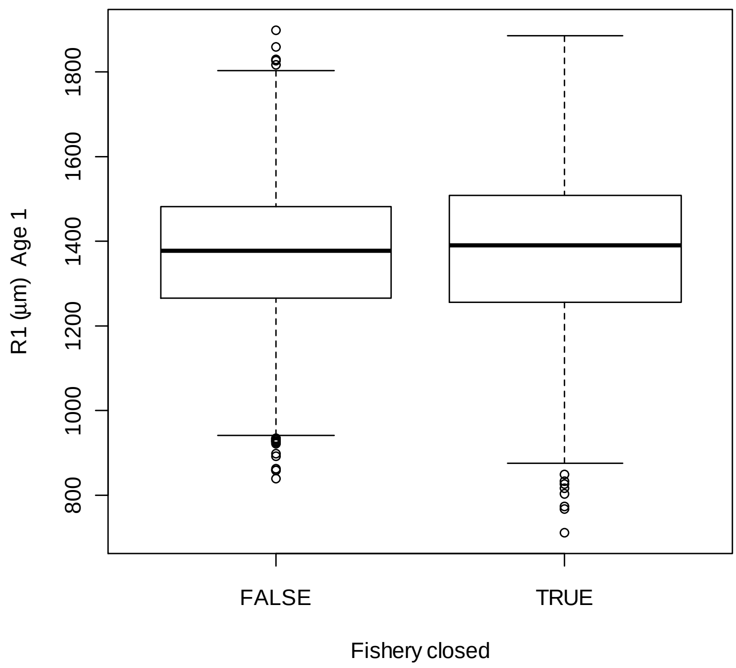


Fig. 7: Relationship between growth and environment. Selected significant regressions of growth increments on hydrological indices. Top: Mean R1 of age 1 fish as a function of the mean water column stratification index. Bottom: Mean residual R2-R1 of age 2 fish as a function of bottom temperature.



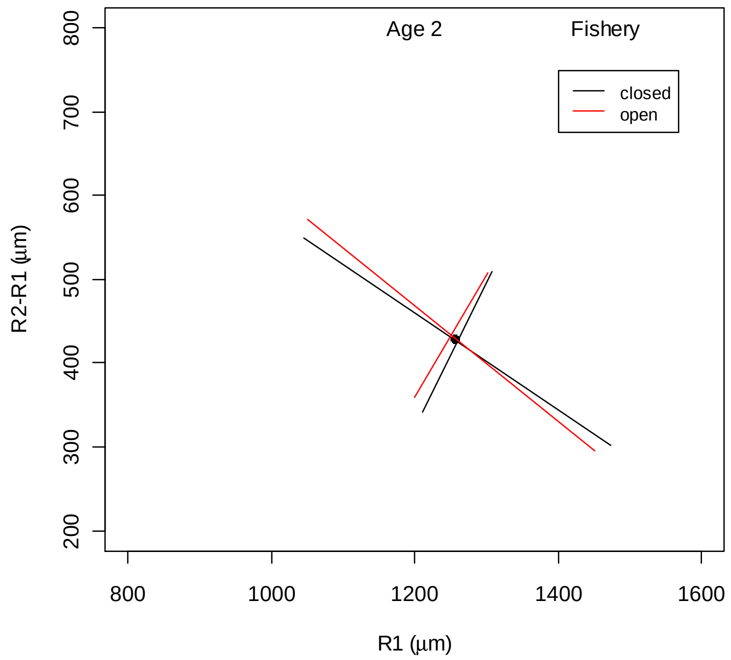


Fig. 8: Relationship between growth and fishing ban. Top: boxplot of growth at age-0 (R1) measured on age 1 fish for periods of fishing and no fishing. Left: gravity centre and inertia of the bivariate distribution (R2-R1, R1) for periods of fishing and no fishing.

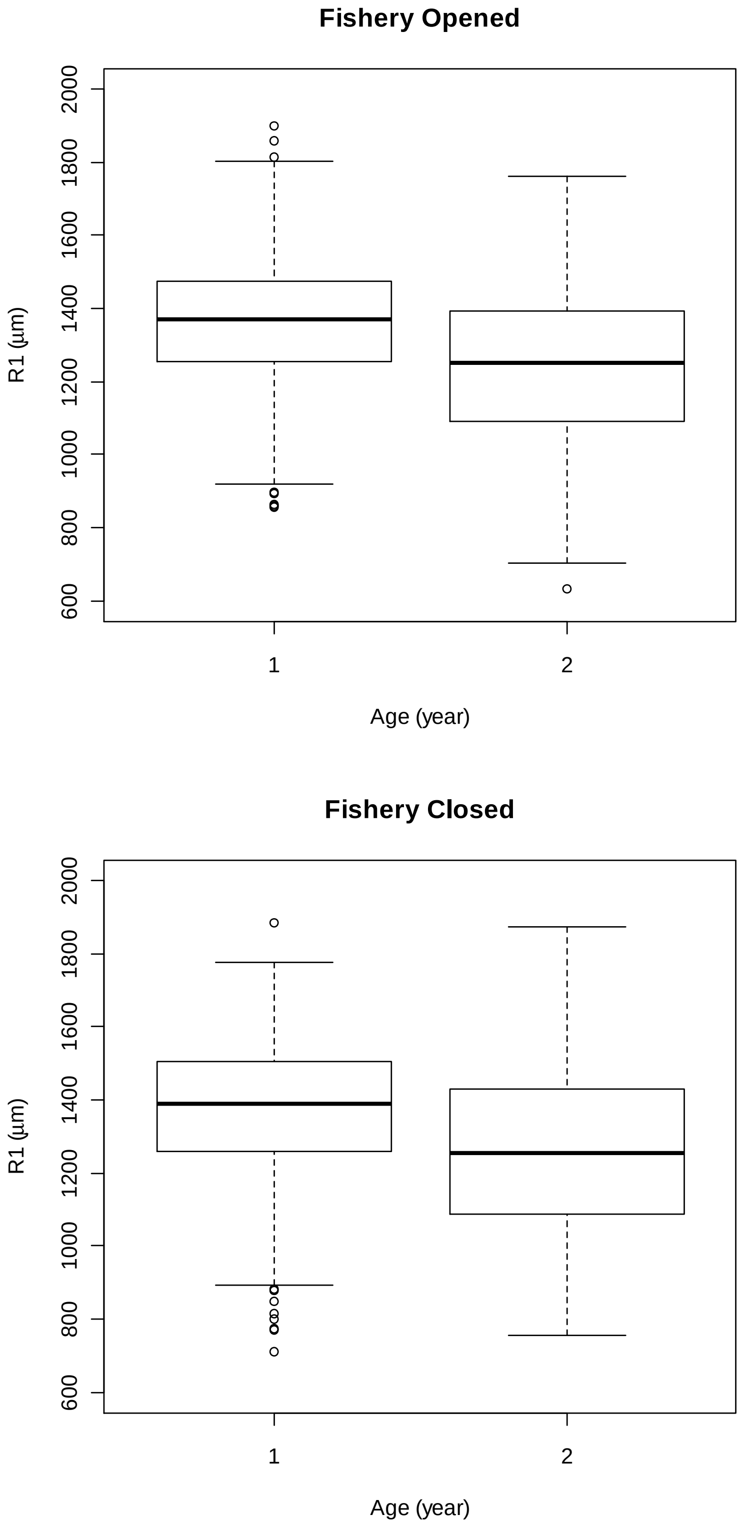


Fig. 9: Relationship between growth, survival and fishing ban. Boxplot of R1 (growth during age 0) as a function of age along cohorts (pooled) for two periods, when the fishery was opened (top) and when it was closed (bottom).