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Acoustic surveys for juvenile anchovy in the Bay of Biscay: abundance estimate as an indicator of the next year's recruitment and spatial distribution patterns

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A series of acoustic surveys (JUVENA) began in 2003 targeting juvenile anchovy (*Engraulis encrasicolus*) in the Bay of Biscay. A specific methodology was designed for mapping and estimating juvenile abundance annually, four months after the spawning season. After eight years of the survey, a consistent picture of the spatial pattern of the juvenile anchovy has emerged. Juveniles show a vertical and horizontal distribution pattern that depends on size. The younger individuals are found isolated from other species in waters closer to the surface, mainly off the shelf within the mid-southern region of the bay. The largest juveniles are usually found deeper and closer to the shore in the company of adult anchovy and other pelagic species. In these eight years, the survey has covered a wide range of juvenile abundances, and the estimates show a significant positive relationship between the juvenile biomasses and the one-year-old recruits of the following year. This demonstrates that the JUVENA index provides an early indication of the strength of next year's recruitment to the fishery and can therefore be used to improve the management advice for the fishery of this short-lived species.

Keywords: anchovy, juvenile, recruitment, spatial dynamics.

Introduction

The management of short-lived fish species such as small pelagics is conditioned by the annual recruitment to the population. For example, in the Bay of Biscay, age 1 anchovy (*Engraulis encrasicolus*) usually contribute about 75% of the total stock biomass (Uriarte *et al.*, 1996; ICES, 2010). In addition, recruitment in marine fish in general (Leggett and Deblois, 1994) and pelagic species in particular (Kawasaki, 1992) varies greatly and is influenced by environmental conditions (Borja *et al.*, 2008; Fernandes *et al.*, 2010), which limits the potential use of stock-recruitment relationships. It is therefore difficult to manage short-lived species based on annual advice due to the unknown increase in abundance that will represent the strength of next year's recruitment.

This problem has long been recognized (Hjort, 1914; Allain *et al.*, 2001), and approaches other than classical stock-recruitment relationships have been considered in order to improve information on the incoming recruitment. Some possible approaches are: (i) statistical relationships between environmental variables and recruitment; (ii) mechanistic models of early-stage survival; and (iii) direct surveys of early stages (Painting *et al.*, 1998). There is a vast amount of literature on environment–recruitment relationships. Several attempts have been made to predict recruitment based on environmental variables for the Bay of Biscay anchovy population (Allain *et al.*, 2001; Borja *et al.*, 2008); however, none of them obtained sufficient precision to improve management advice effectively (de Oliveira *et al.*, 2005; ICES, 2009). More robust data-mining approaches have recently been developed (Fernandes *et al.*, 2010), but they still need to be fully validated. Mechanistic models based on transport and survival (Allain *et al.*, 2007) are potentially useful, but there is still little information on the factors that determine mortality, and this limits how the model outputs can be applied.

The third possibility is to assess the abundance of an earlier stage as a proxy for the recruitment strength (Dragesund and Olsen, 1965; Larkin, 1976; Walters, 1989). As there is no significant correlation between egg and/or larval abundances and recruitment of small pelagic species (Peterman *et al.*, 1988) due to the high variability in mortality rates during early life stages, they cannot be used as a recruitment proxy. However, it is generally accepted that the recruitment strength is mainly determined by the mortality at the pre-juvenile stages (Leggett and Deblois, 1994), and can therefore be measured at later stages (Bradford, 1992). Attempts to determine the incoming recruitment strength based on later stages, such as post-larvae or juveniles, have proven successful (Hourston, 1958; Dragesund and Olsen, 1965; Koeller *et al.*, 1986; Axenrot and Hansson, 2003; Schweigert *et al.*, 2009) and have been incorporated into some fisheries management policies, such as those for South African anchovy (De Oliveira and Butterworth, 2004; Barange *et al.*, 2009).

In the Bay of Biscay, a succession of low recruitments since 2001 and the consequent closure of the fishery from 2005–2009 highlighted the need for an early indication of recruitment strength in order to improve management (Barange *et al.*, 2009). With this purpose in mind, an acoustic survey (JUVENA) for estimating the abundance of juvenile anchovy in early autumn was set up following methodologies derived from the European project JUVESU (Uriarte, 2002; Carrera *et al.*, 2006). The idea was to test the hypothesis that juvenile abundance estimates can provide a reliable indicator of the abundance of recruits that will enter the adult stock the following year. This requires that the most variable mortality rates occur at earlier life stages (i.e., egg, larvae and post-larvae) in spring and early summer; the variability in mortality rates would decrease afterwards, being the recruitment strength determined at the juvenile stage by the end of the summer.

There are some methodological challenges involved in sampling juvenile anchovy in the Bay of Biscay in early autumn. Anchovy have a vertical distribution that is very close to the surface (Uriarte *et al.*, 2001), and a considerable part of the population is found at 7.5–15 m depth, which is above the initial depth of the typical acoustic sampling range. In relation to the horizontal distribution, they can occupy a huge potential area that can extend from shallow coastal to off-shelf waters, and from the northern Spanish coast (43.5°N) to the western French coast up to 47°N (Martín, 1989; Uriarte *et al.*, 2001), which implies a great deal of sampling effort. The bulk of the juvenile population is found in the outer waters or off the shelf (in the typical fishing grounds for the tuna live-bait fishery in autumn, Martín, 1989; Lezama-Ochoa *et al.*, 2010), isolated from adults and other pelagic species. They are thus easily identifiable, but are occasionally found in the company of gelatinous plankton (Uriarte *et al.*, 2001). This distribution of juveniles has been suggested to correspond with the passive drift of eggs, larvae and early juveniles towards the southwest offshore waters as a result of the predominant northeasterly summer winds. At the end of summer the juveniles reach a size that makes them capable of migrating back towards nursery areas near the coast (Uriarte *et al.*, 2001; Irigoien *et al.*, 2008). However, some authors have questioned the capacity of this off-shelf part of the juvenile population to survive the winter and hence to contribute to the recruitment of one-year-old fish during the following year (Petitgas *et al.*, 2004). In general, it can be said that before the JUVENA survey series was launched, the juvenile stage of Bay of Biscay anchovy had been little studied and its ecology and spatial dynamics were poorly understood.

The objectives of this paper are to present the methodology developed in the JUVENA survey series to assess the juvenile anchovy in the Bay of Biscay, to show the abundances and spatial distribution patterns of this life stage obtained after eight years of surveys (from 2003–2010), and, finally, to determine the relationship between the juvenile and recruitment indices to evaluate the potential of JUVENA as a predictive tool for anchovy recruitment.

Material and methods

Sampling strategy

The JUVENA surveys were carried out annually from 2003–2010 between September and October in the Bay of Biscay (Table 1). In these months the juveniles have grown enough to be visible to the echosounders (allowing the tuna fishing fleet to target them as live bait) and normally occupy large outer and off-shelf areas in front of the northern Spanish and west French coasts (Cort *et al.*, 1976; Martin, 1989; Uriarte *et al.*, 2001). Acoustic sampling was performed during the day because at this time of year juveniles usually aggregate in schools in the upper layers of the water column during the day, and can be distinguished from plankton structures (Cort *et al.*, 1976; Uriarte *et al.*, 2001). The sampling was carried out following a regular grid formed by transects arranged perpendicular to the coast (Figure 1), spaced at 17.5 nmi (from 2003–2005) or 15 nmi (2006 onwards) to ensure their independence (Carrera *et al.*, 2006). Sampling started on the northern Spanish coast, going from west to east, and then moved to the north to cover the waters in front of the French coast of the Bay of Biscay. It is important to conduct the survey in the precise temporal window that extends from mid-August to mid-October, which is not too early, so juveniles can be detected and caught, and not too late, so they have not yet abandoned the offshore grounds.

The survey covered the entire expected spatial distribution of juvenile anchovy in these months of the year, from offshore areas well beyond the continental shelf to very coastal waters, because the spatial process of anchovy juvenile recruitment occurs from offshore areas towards the coast during autumn (Uriarte *et al.*, 2001). This exploration area can vary from year to year and is potentially large. Consequently, considerable effort was made to achieve the broadest possible coverage of the area by using an adaptive sampling strategy. In this strategy, the boundaries of the sampling area were defined according to the findings of each survey and the parallel information obtained from the commercial fishing fleet, which uses juvenile anchovy as live bait for tuna fishing. Along the Spanish and French coastlines, the minimum limits of the sampling area were set at 5°W and 46°N, respectively. According to previous information on juvenile distribution, this area was expected to contain the vast majority of the juvenile anchovy abundance (Cort *et al.*, 1976; Uriarte *et al.*, 2001; Carrera *et al.*, 2006). For practical reasons, a maximum surveying area was set within the limits 6°W and 48°N. Between these limits, the actual along-coastline boundaries were set each year at the points where there was a clear decrease in abundance or, if possible, a transect in which juvenile anchovy was not detected. The length of the transects extended from about the 20 m to at least the 1000 m isobaths, and, according to the adaptive scheme of the survey, if the detections continued they were enlarged offshore to 4 nmi beyond the last detection of an anchovy school. In addition, the information from the commercial live-bait tuna fishery collected before and during each survey was taken into account when decisions about the sampling strategy were made during the surveys. As a result of this sampling scheme, the years with a larger abundance of anchovy required a larger sampling coverage.

In the period from 2003–2004, the area was sampled with a single commercial purse-seiner subcontracted for the survey and equipped with scientific echosounders. In 2005 a second purse-seiner was added to the survey to provide extra fishing operations, and in 2006 a pelagic trawler with complete acoustic equipment, the RV "Emma Bardán", replaced the second purse-seiner (see

Table 1. Summary of sampling effort.

Year	Start of the survey	End of the survey	Number of vessels	Effective survey time (days)	Fishing operations	Anchovy-positive fishing operations	Inter-transect distance (nmi)	Sampled area (nmi^2)	Positive area (nmi^2)
2003	18/09	14/10	1	20	47	36	17.5	16 829	3 476
2004	19/09	19/10	1	18	21	9	17.5	12 736	1 907
2005	12/09	07/10	2	20	47	45	17.5	25 176	7 790
2006	13/09	14/10	2	42	80	52	15	27 125	7 063
2007	04/09	30/09	2	37	70	40	15	23 116	5 677
2008	26/08	25/09	2	33	85	46	15	23 325	6 895
2009	26/08	25/09	2	39	67	42	15	34 585	12 984
2010	1/09	30/09	2	40	79	60	15	40 500	21 110

Table 2 for vessel characteristics and equipment employed in each survey).

Data acquisition

The acoustic equipment included Simrad EK60 split-beam echosounders (Kongsberg Simrad AS, Kongsberg, Norway) of 38 and 120 kHz from 2003–2006, plus a 200-kHz transducer from 2007 (Table 2). The transducers were installed looking vertically downwards, at about 2.5 m depth, at the end of a tube attached to the side of the vessel in the case of the commercial fishing vessels, and on the vessel hull in the case of the research vessel. The transducers were calibrated using standard procedures (Foote *et al.*, 1987).

The water column was sampled acoustically to a depth of 200 m. Catches from the fishing hauls and echotrace characteristics were used to identify fish species and determine the population size structure. The fishing stations were decided based on the typology of the detected echoes, trying to identify each change in the detected typologies. Purse-seining was used to collect samples up to 2005 and then this was combined with pelagic trawls from 2006 onwards. To improve species identification in the first three surveys, when only purse-seiners were available, additional night fishing operations were performed by focusing bright light on the water to attract the fish from surrounding waters. In 2006 pelagic trawling was included in the surveys, which made it possible to fish at greater depths than the purse-seine range (50 m maximum). The purse-seiners generally covered the coastal areas and the waters off the shelf where juveniles occupy the surface waters and are accessible to the purse-seine fishing range. The pelagic trawler covered the intermediate shelf regions where it may be necessary to sample at all depth layers. In addition, when deep, anchovy-like aggregations were detected by the purse-seiners, the pelagic trawler temporally left its coverage area to carry out additional fishing operations in these areas.

For the years when pelagic trawling was carried out in the surveys (2006 onwards) we have assessed the fraction of juvenile biomass observed deeper than 45 m below the surface. This assessment was restricted to the areas over the shelf because pure aggregations of juveniles off the shelf were all above 45 m depth. This was done in order to determine by how much the limited vertical fishing range of purse-seines could have affected the detection and estimates of juvenile biomass in the years 2003–2005, when only this fishing gear was available, and to eventually correct the potential underestimation of the juvenile biomass detected over the shelf in those years.

Intercalibration of acoustic data between vessels

Since the 2006 survey, when the acoustic sampling was split between two vessels, intercalibration exercises between the two vessels were routinely carried out each year based on the intercalibration methodology described by Simmonds and MacLennan (2005). The intercalibration process consisted of comparing the echointegration of the bottom echo in areas with a smoothly variable bottom (visible as overlapping transects in Figure 1). A minimum distance of 30 nmi was covered simultaneously by the two vessels for these exercises (Figure 1). The NASC values (MacLennan *et al.*, 2002) obtained by the layer echointegration of both the water column and bottom echoes obtained by the two vessels were compared to detect recording biases or other potential problems.

Abundance estimates

Echograms were examined visually with the aid of the catch species composition to identify positive anchovy layers. Noise from bubbles, double echoes, and, when necessary, plankton were removed from the echograms. Acoustic data were processed in the positive strata by layer echo integration using an ESDU (Echo integration Sampling Distance Unit) of 0.1 nmi with the Movies+ software (Ifremer, France). Echoes were thresholded to − 60 dB and integrated into six depth channels: 7.5–15 m, 15–25 m, 25–35 m, 35–45 m, 45–70 m and 70–120 m (no anchovies were found below 120 m depth).

Generally, only the 38-kHz data were echointegrated, using the TS–length relationships agreed in ICES WGACEGG for the main species (ICES, 2006; Table 2). Each fishing haul was classified into species. A random sample of each species was measured to determine the length–frequency distribution of the different species in 0.5-cm classes for the smaller species (anchovy and sardine) and 1-cm classes for the rest. Complete biological sampling of anchovy was performed to analyse age, size and the size–weight ratio. The hauls were grouped by strata of homogeneous species and size composition. The species and size composition of each homogeneous stratum were obtained by averaging the composition (in numbers) of the individual hauls contained in the stratum weighted to the acoustic density in the vicinity (2 nmi diameter). The species and size composition of each stratum were used to obtain the mixed species echointegrator conversion factor (Simmonds and MacLennan, 2005) for converting the NASC values of each ESDU into numbers of each species. However, although the methodology involved estimating multiple species, the survey strategy was focused strongly on juvenile anchovy, and only the positive areas for anchovy were processed. Therefore, only estimates of this species were considered reliable and thus produced.

Anchovy juveniles (age $= 0$) and adults (age ≥ 1) were separated and treated as different species. To separate juveniles from adults, the length–frequency distribution of anchovy by haul was multiplied by a corresponding age–length key. The key was determined

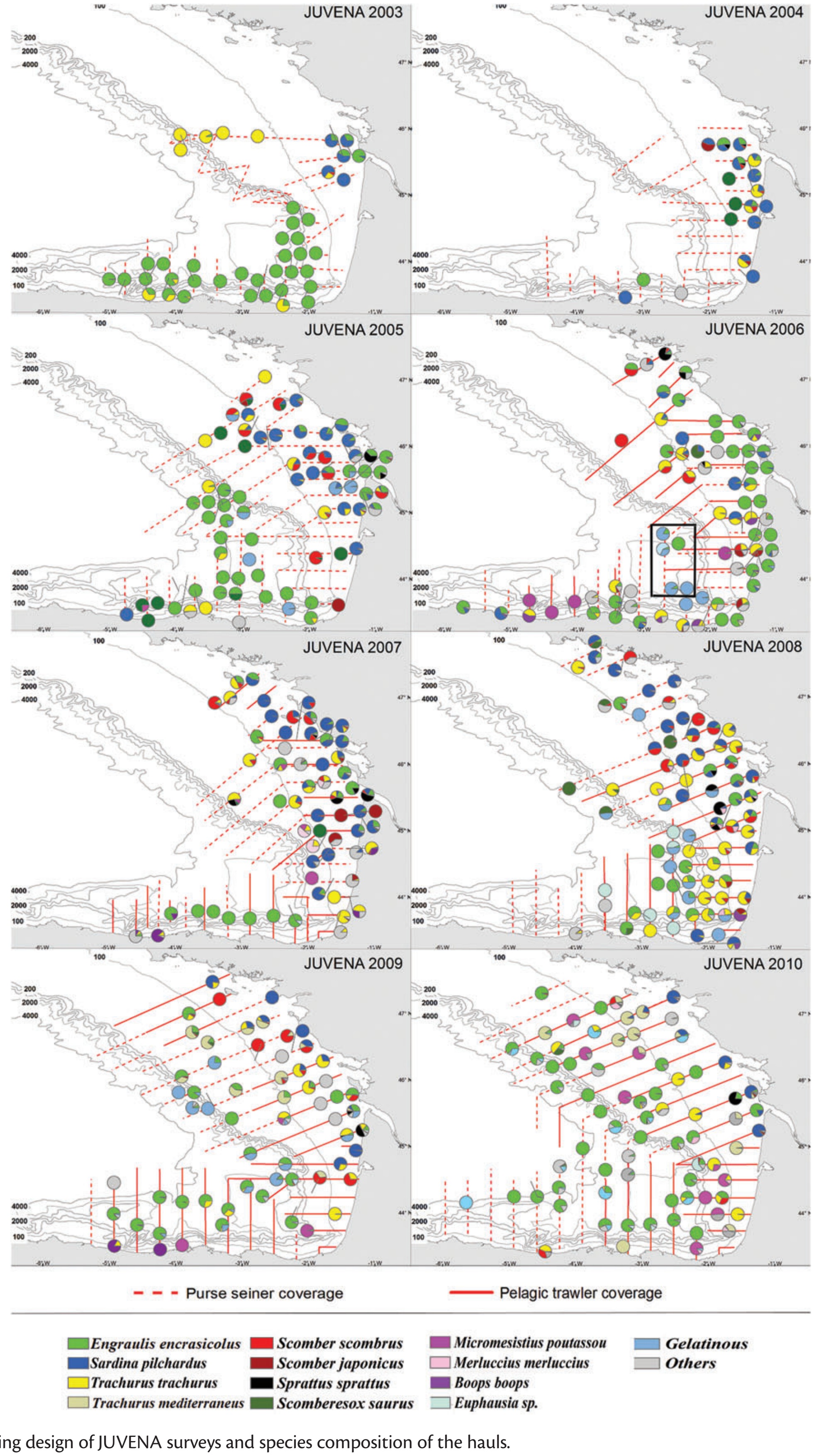

Figure 1. Sampling design of JUVENA surveys and species composition of the hauls.

Table 2. Vessels and equipment.

			Vessel 1	Vessel 2
Vessel	Name		Purse-seiners[a]	Emma Bardán
	Length (m)		30–35	27
	Side (m)		8	7
	Draft (m)		3.5–4	3.5
	Acoustic installation		side perch	hull
Acoustic Equipment	Transducer frequencies (kHz)		38, 120, (200)[b]	38, 120, 200
	Power (for 38, 120, 200 kHz) (W)		1200, 250, (210)[b]	1200, 250, 210
	Pulse duration (10^{-6}s)		1024	1024 (except in 2006: 256)
	Ping interval (s)		0.25–0.5	
Target Strength (b_{20})[c]	*Engraulis encrasicolus* *Sardina pilchardus* *Sprattus sprattus*	−72.6 dB	Degnbol *et al.* (1985)	
	Trachurus trachurus *Trachurus mediterraneus* *Scomber japonicas*	−68.7 dB	ICES (2006)	
	Scomber scombrus	−88 dB	Clay and Castonguay (1996)	
	Jellyfish (mean TS)	−81.7 dB	Average TS for jellyfish species in Simmonds and MacLennan (2005)	
Fishing gear	Pelagic trawl	No. of doors		2
		vert opening		15
		Mesh size (mm)		4
	Purse-seine	Depth	75	
		Perimeter	400	
		Mesh size (mm)	4	

[a]Vessel names: “Divino Jesus de Praga” (2003), “Nuevo Erreñezubi” (2004), “Mater Bi” (2005), “Gure Aita Joxe” (2005, 2008), “Itsas Lagunak” (2006, 2007, 2009).
[b]The 200 kHz transducer has been available on board purse-seiners since 2007. [c]TS of the mean pelagic species. The TS is obtained according to the relationship TS = b20 − 20log(L), where L is the standard length of the fish in centimetres.

every year for three broad areas: the purely juvenile area, the mixed-juvenile area (with a mix of juveniles and adults), and the Garonne river area (located at the coastal area around 45°40’N, also a mixed area but here adult anchovy were usually smaller than in the other areas). Finally, the abundance in numbers of juveniles and adults was multiplied by the mean weight to obtain the biomass per age and length class for each ESDU.

Near-field correction

Juvenile anchovy showed a near-surface distribution during the JUVENA survey period (Uriarte *et al.*, 2001). In order to achieve the best possible coverage of the vertical distribution of this species, in this work we started the echointegration at a range of 5 m from the transducer face (i.e. 7.5 m depth from the sea surface) rather than the 10.5 m (13 m depth) recommended to avoid integrating the near field of the 38-kHz transducer (Simmonds and MacLennan, 2005). Instead of ignoring these first layers, we estimated the bias produced by the near field in the 7.5–15 m echointegration channel and corrected for it in the biomass estimates. The details of this analysis can be found in the *Supplementary information* folder in the *ICES Journal of Marine Science* website.

Anchovy spatial distribution

Yearly maps of anchovy NASC values by ESDU along the survey transects were produced. In addition, a synoptic summary was made of the spatial distribution of anchovy juveniles throughout the study period in two different ways: yearly juvenile biomass values by ESDU were averaged between years over cells in a 30’ latitude and longitude grid. In addition, the overall probability of the presence of juvenile anchovy was also provided, calculated as the number of years the anchovy were present divided by the number of years the cell was sampled. The length and depth distributions of juveniles in each cell were also determined as averages over the series. Finally, we determined and plotted the interannual horizontal mean centre of gravity (Woillez *et al.*, 2009) of each 2-cm anchovy juvenile size class.

The biomass estimates and the processed data were plotted on maps using Surfer (Golden Software Inc., CO, USA), and ArcView GIS. Matlab (The Mathworks, Inc.) was used to summarize the data from the eight years.

Recruitment predictive capability

In order to estimate the recruitment predictive capability, the annual biomass estimates for anchovy juveniles were compared with the estimates of anchovy recruitment the following year. The recruitment is the biomass of age-1 anchovy in January of the following year, estimated according to the ICES assessment using a Bayesian model with inputs from catches and biomass estimates of two spring surveys: an acoustic one (PELGAS), conducted by Ifremer, and a survey based on DEPM (BIOMAN), conducted by AZTI (ICES, 2011). The biomass estimates were fitted by linear, log-linear and rank regressions between variables using the R software version 2.14.0 (R Development Core Team, 2011).

Results

Spatial coverage and fishing operations

The sampling coverage over the surveys (Figure 1) reflects the adaptive sampling scheme followed and shows the methodological changes made to improve the coverage, particularly since 2005. For example, the northern coverage along the French coast was considerably enlarged. The northern limit changed from 46°N in the first two years to beyond 47°N in the following years. The number of fishing operations has increased from 40 in 2003 to over 60 in the years since 2005 (Table 1); the small number of fishing operations carried out in 2004 was mainly because few anchovy were detected that year. The incorporation of the pelagic trawler in 2006 improved fishing flexibility, making it possible to fish near the bottom. This is shown in the fishing maps (Figure 1) by the increase in species variability (due to the addition of the close-to-the-bottom species). The potential coverage limitations are discussed in the *Supplementary data* for this article at *ICES Journal of Marine Science* online.

Spatial occupation patterns of anchovy juveniles

For each year the juvenile anchovy population could be divided into two clearly distinguishable groups. One part of the population consisted of practically purely juvenile anchovy (not mixed with adults), and the other part was mixed with, or in the proximity of, adults. The purely juvenile group was located in the southwestern part of the Bay of Biscay, normally off the shelf or in the outer part of it (white strata in Figure 2), and the mixed group was located to the northeast in shelf waters of < 130 m depth. The only exception was in 2006, when the typical off-shelf location of pure juveniles was seen only during the first three days of the survey, then, after two days of rough weather conditions (wind speeds over 11 ms^{-1}), the distribution of this purely juvenile group shifted towards shallow coastal waters all along the Spanish and French coasts (up to 45°N) (Figure 2).

In each group, juveniles were found in a different species composition context and bathymetrical distribution pattern. In the purely juvenile region, anchovy were generally the only or the largely predominant species (the percentage of anchovy individuals in these strata was always > 90%), mixed sometimes with smaller proportions of salp, jellyfish, and juvenile horse mackerel (Figure 1). In the mixed group, juvenile anchovy was found mixed in variable proportions with adult anchovy (the adult proportion increasing towards the northeast, Figure 3) and other pelagic species, mainly sardine, horse mackerel, mackerel and sprat (Figure 1).

The trends in density and area of occupation of juvenile anchovy were different for each group (Figure 4). In general, the densities were larger for the purely juvenile aggregations than for the mixed adult–juvenile aggregations; however, no clear prevalence was observed in the spatial occupation patterns. For regions with purely juvenile aggregations, the density varied greatly from very low values (< 5 t per square nautical mile) to values up to ten times higher. For regions with mixed juvenile–adult aggregations, the densities did not vary much, showing low-density values that were about the same as those of the off-shelf aggregations; however, the highest density values were lower. The areas occupied by juveniles in the first two years of the time-series (Table 1) were < 5000 square nautical miles. This then increased and remained rather constant above this value from 2005–2008, mainly due to an increase in the area occupied by the mixed-juvenile group over the shelf (Figures 2 and 4). In the last two years the occupied areas continually expanded (with no visible gaps) towards the offshore and northern regions, but not towards the west. In 2010, there was a drastic increase in the area of occupation, mainly off or at the outer part of the shelf, i.e. in the areas occupied by the purely juvenile anchovy group.

For the years that had the highest juvenile biomass estimates, the largest biomass contributions were invariably observed in the purely juvenile areas (Figure 4). This region contained on average 58% of the total biomass. This average increased to 75% when the least abundant years (2004, 2007 and 2008) were excluded, and reached up to 95% of the total biomass in 2010, when the strongest recruitment in the JUVENA series was recorded. The contribution of the mixed-juvenile region to the biomass was quite constant across the series, and in the years with the highest total juvenile abundance the contribution was relatively weak.

A sub-area of the off-shelf region, south of 45°N and around 2–3°W, accounted on average for the highest abundance of juvenile anchovy in the Bay of Biscay (Figure 5, top panel). In the southern part of this area there was a high probability that juvenile anchovy would be present (Figure 5, bottom panel). Another area with a high probability of the presence of juvenile anchovy was the Garonne plume (French coast between 45° and 46°N); however, in this area, the mean abundances were much lower.

The minimum sampling area established for interannual comparison, i.e. the area sampled in the years 2003 and 2004 (which was restricted to the south of 46°N, Figure 2), accounted on average for 86% of the juvenile biomass found in the JUVENA series (Figure 6, top panel). When 2003 and 2004 were excluded from this average (so that only the years with good northern coverage were included) (see Figure 1 and Table 1), the percentage of juvenile biomass to the north of 46°N was 16%, with a maximum percentage (in year 2006) of 40% of the total juvenile biomass. In practical terms, this implies that in the years when the northern regions were not sufficiently covered at the beginning of the series (2003 and 2004), on average about 14% of the juvenile biomass was probably missed.

In terms of the size–age composition of the anchovy (Figure 3; Figure 5, top panel), the offshore or pure-juvenile group was generally composed mainly of the smallest juveniles with a mean size of ~ 9 cm. In the inshore areas, the mean size of the juveniles was ~ 12 cm, whereas the mean size of the adults observed throughout these surveys was 13.5 cm. The size distribution was in agreement with the age distribution pattern (Figure 3). The horizontal distribution of the centre of masses in each size class (Figure 5, top panel) displayed a clear gradient towards the north in combination with another offshore–inshore gradient. This shows that juveniles probably moved from the southwestern off-shelf areas to the northeastern inshore areas.

Vertical distribution of anchovy juveniles

Anchovy juveniles showed different vertical distribution patterns according to the horizontal distribution and bathymetry. The purely juvenile anchovy aggregations, which mainly occupied off-shelf waters, were located in the first 45 m of the water column (Figure 5, bottom panel). As the juveniles came closer to the shore they started to sink deeper until eventually they resembled the typical adult anchovy aggregations about 10–20 m above the seafloor (Massé, 1996). In the shallow coastal areas they were observed in various typologies, occupying all the layers in the water column (Figure 5, bottom panel). On average, throughout the series, about 92% of juvenile anchovy biomass was located above 45 m depth (Figure 6), i.e. within the purse-seine range. When only the surveys carried out since 2006 (from this date a pelagic trawler allowed the entire water column to be sampled) were considered, the percentage only decreased to 88%.

Another interesting pattern that was observed concerned the mean depth of the different length classes of juvenile anchovy (Figure 7). The mean depth of juveniles gradually and consistently

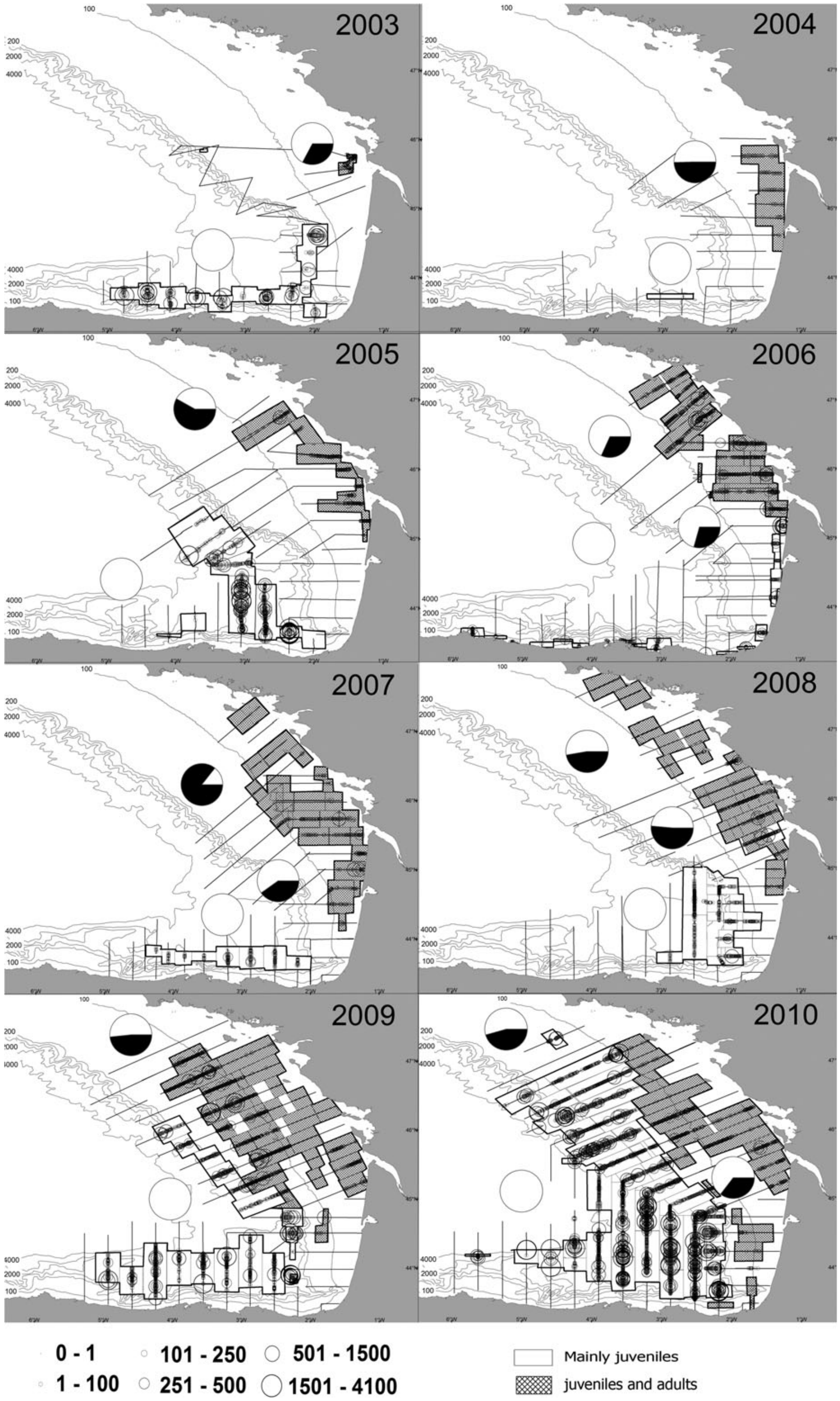

Figure 2. Anchovy biomass (bubbles) in kilogram by elementary distance sampling units of 0.1 nmi (185.2 m) and positive anchovy areas along the surveyed transects. The pie charts represent the mean percentage of juveniles (white) and adults (black) of the fishing hauls in each area.

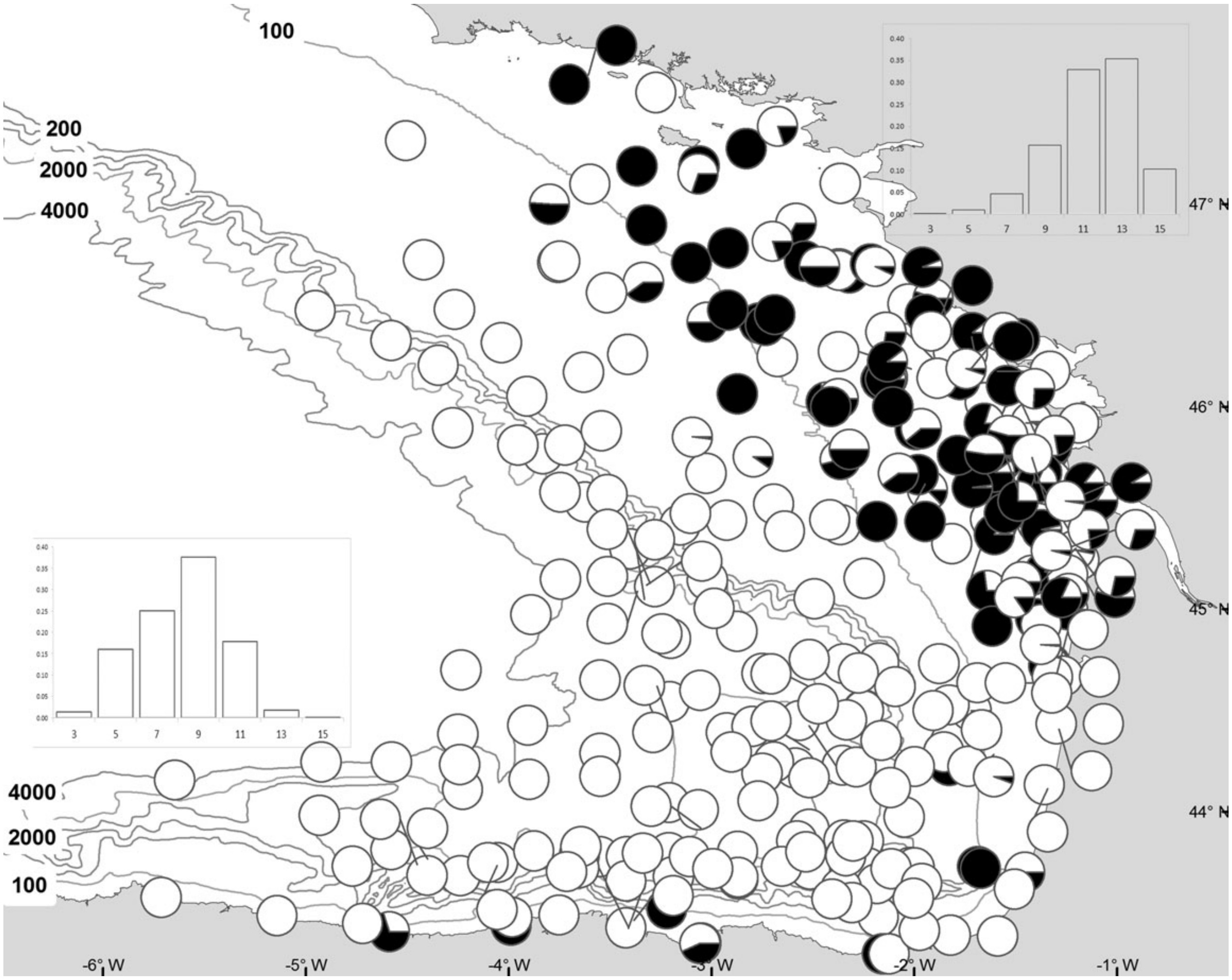

Figure 3. Age composition of anchovy for the seven years of the survey. The pie charts represent the mean percentage of juveniles (white) and adults (black) of the fishing hauls at each fishing site. The bars show the length distribution in centimetres of juvenile anchovy from the pure (left) and mixed (top-right corner) areas.

increased according to their body length at a rate of almost 2.5 m per growing centimetre. The mean length of juveniles in the echointegrated depth layers also showed a consistent and continuous pattern, with the mean lengths increasing from < 9 cm at the first depth layer to ~ 11.5 cm at the deepest layer.

Anchovy biomass estimates and recruitment prediction

A wide range of acoustic estimates of juvenile anchovy biomass was assessed over the JUVENA series (Figure 4). The estimates showed differences of more than two orders of magnitude between the lowest value in 2004 and the highest value obtained in 2010.

The series of juvenile anchovy biomass estimates showed a good parallelism to the independent estimates of anchovy biomass at age-1 recruitment at the beginning of the following year (Figure 8). Both quantitative linear (Pearson) and non-parametric rank (Spearman) correlations showed highly significant values (the coefficients of determination were 0. 93 and 0.86, respectively, with probabilities of being random below 0.0001 and 0.001, respectively). These significant relationships were not dependent on the extreme values of the series: both correlation results (at an alpha of 1%) continued to be significant even when the highest or lowest juvenile index from the JUVENA series was excluded from the analysis. Several quantitative linear or log-linear models can be fitted to series of recruitment based on the juvenile abundance indexes from JUVENA. The best fitting was achieved by the log-linear model, i.e. a potential model in linear scale, with coefficient of determination of 0.95 and p-value $= 5e - e5$ (Figure 8).

Concerning the main observed groups, the biomass of the purely juvenile group was significantly correlated with recruitment, explaining 87% of the recruitment variability, while the biomass of the mixed-juvenile and adult group showed no significant relationship and explained less than 20% of the recruitment variability.

The main error sources involving the estimation of juvenile anchovy biomass along the temporal series of JUVENA surveys were analysed to check their impact on the recruitment prediction capacity. Applying the corrections derived from the potential sources of bias, either one by one or all at the same time, did not affect the significance of the relationships between the JUVENA index and the next year's recruitment, which remained highly significant in all cases. Refer to the *Supplementary data* for this article at *ICES Journal of Marine Science* online for further details.

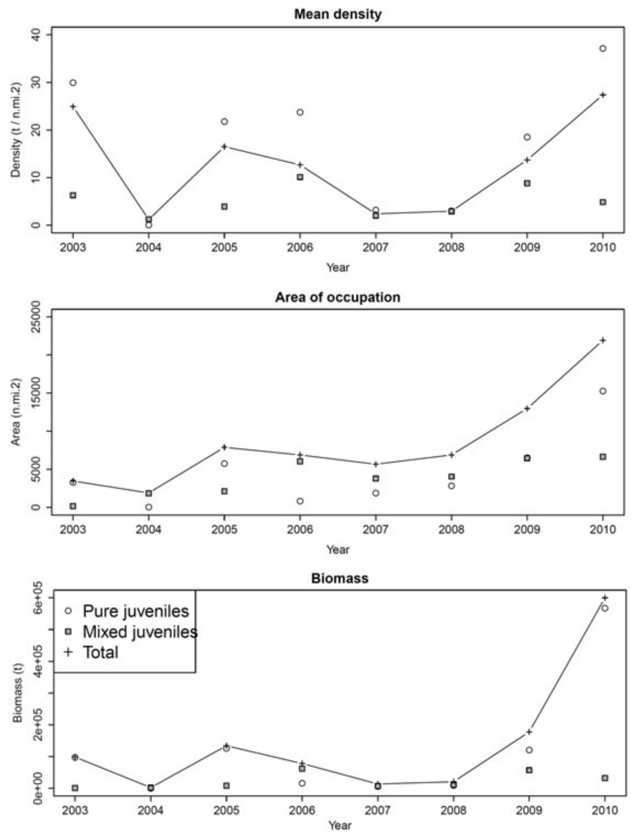

Figure 4. Mean density, area of occupation and biomass of juvenile anchovy during the eight annual surveys, differentiating the contribution of the two main groups of juveniles observed: the pure juvenile group located off the shelf or at its outer part and the group of juveniles mixed with adults located at the inner part of the shelf.

Discussion

Spatial occupation patterns

The spatial distribution of juvenile anchovy in the Bay of Biscay shows clear differences between the two main groups in this particular season (Figure 2). The purely juvenile group, isolated from adult anchovy (Figure 3) and from most of the other small pelagic species (Figure 1), occupies the first 45 m of the water column in the daytime (Figure 7) and is distributed off or in the outer part of the shelf. The mixed-juvenile group is found on the inner shelf, mixed in variable proportions with adults and other species; it is more deeply distributed and starting to show the typically adult nycthemeral behaviour (Figure 7). The purely juvenile group also contains most of the juvenile biomass in abundant years (Figure 4). In addition, Bachiller *et al.* (2013) recently found that the purely juvenile group has better feeding conditions than the mixed group in spite of occupying an area with lower prey abundance. These authors suggest that this *a priori* worse situation may be compensated for by the lower predation risk and the higher visibility caused by the lower water turbidity. This is the case in the slope waters of the Bay of Biscay (Irigoien *et al.*, 2007), which provide better feeding conditions for a selective hunter species like juvenile anchovy (Van der Lingen *et al.*, 2006).

The purely juvenile group seems to have spatial dynamics in which both the mean density and the area change with population abundance; therefore, the combination of a high mean density and a high occupation area can produce huge abundances, as occurred in 2010. In contrast, in the mixed region, the density of juvenile anchovy was rather constant, and the biomass changes were mainly related to the range of the occupied area (Figure 2). According to these trends, the two groups correspond to different spatial dynamics models (Petitgas, 1998): a constant density model for the mixed-juvenile group, and a varying density and area model for the purely juvenile group. In both cases the biomass depends on the range of the occupied area, which highlights the importance of correctly defining its boundaries to obtain a correct estimate of the biomass level. This type of spatial dynamics (expansion of the occupied area according to the abundance) has already been shown for adult anchovy stock by Uriarte *et al.* (1996) and Somarakis *et al.* (2004). Other pelagics show similar spatial dynamics, e.g. Japanese sardine (Zenitani and Yamada, 2000).

The occupation of the off-shelf waters by purely juvenile anchovy is consistent throughout the series and agrees with previous works on juvenile anchovy in the Bay of Biscay (Uriarte *et al.*, 1996, 2001; Carrera *et al.*, 2006; Lezama-Ochoa *et al.*, 2010). Uriarte *et al.* (2001) described a large juvenile abundance in the French outer-shelf waters (as in 2009 and 2010) in the 1999 JUVESU survey, which was followed by strong recruitment in 2000 (ICES, 2010).

The off-shelf distribution of the bulk of the juveniles is the result of a southwest drift of eggs and larvae from the usual spawning grounds over the shelf as a consequence of the wind regimes and currents in late spring and summer in the Bay of Biscay (Borja *et al.*, 2008; Allain *et al.*, 2001; Uriarte *et al.*, 2001; Irigoien *et al.*, 2008). An autumn migration pattern of juveniles towards the shelf as they grow and develop sufficient swimming abilities is necessary in order for them to return to the spawning grounds and thus complete their life cycle (Cort *et al.*, 1976; Uriarte *et al.*, 2001; Irigoien *et al.*, 2008). This autumn migration of juveniles also matches the spatial distribution patterns of juvenile anchovy according to size observed in the JUVENA survey. Small juveniles (from 3–11 cm in length) show a gradual shift from the areas off the shelf in the central Bay of Biscay (Figure 4) in a north-northeast direction towards the French shelf; while the largest juveniles and the bulk of the adults are already found on the French shelf. These migration patterns are in agreement with the patterns observed by Aldanondo *et al.* (2010), who used otolith chemistry to show that anchovies born in low salinity waters drift to higher salinity waters and return back after the development of their swimming skills. Curiously, these size distribution patterns are almost opposite to the patterns of adult anchovy during the spawning season (Motos *et al.*, 1996; Petitgas *et al.*, 2011), in which the small adults (mainly the age 1 recruits) are located on the inner continental shelf, whereas the largest ones (mainly age 2 and older) occupy the outer shelf and slope waters.

Concerning the vertical distribution, the presence of a local abundance maximum in deep waters only for the mixed group (Figure 5, bottom panel; Figure 7) suggests that some of the juveniles of this group already perform the daily vertical migrations characteristic of the adults. This is in agreement with previous reports on Bay of Biscay juvenile anchovy (Uriarte *et al.*, 2001; Petitgas *et al.*, 2004; Carrera *et al.*, 2006). It is still unclear whether the observed change in this behaviour is mediated by adults (Petitgas *et al.*, 2004). Although some of our observations (particularly the capture of near-bottom purely juvenile schools in the northern shelf areas) do not support this idea on a small scale, the persistent

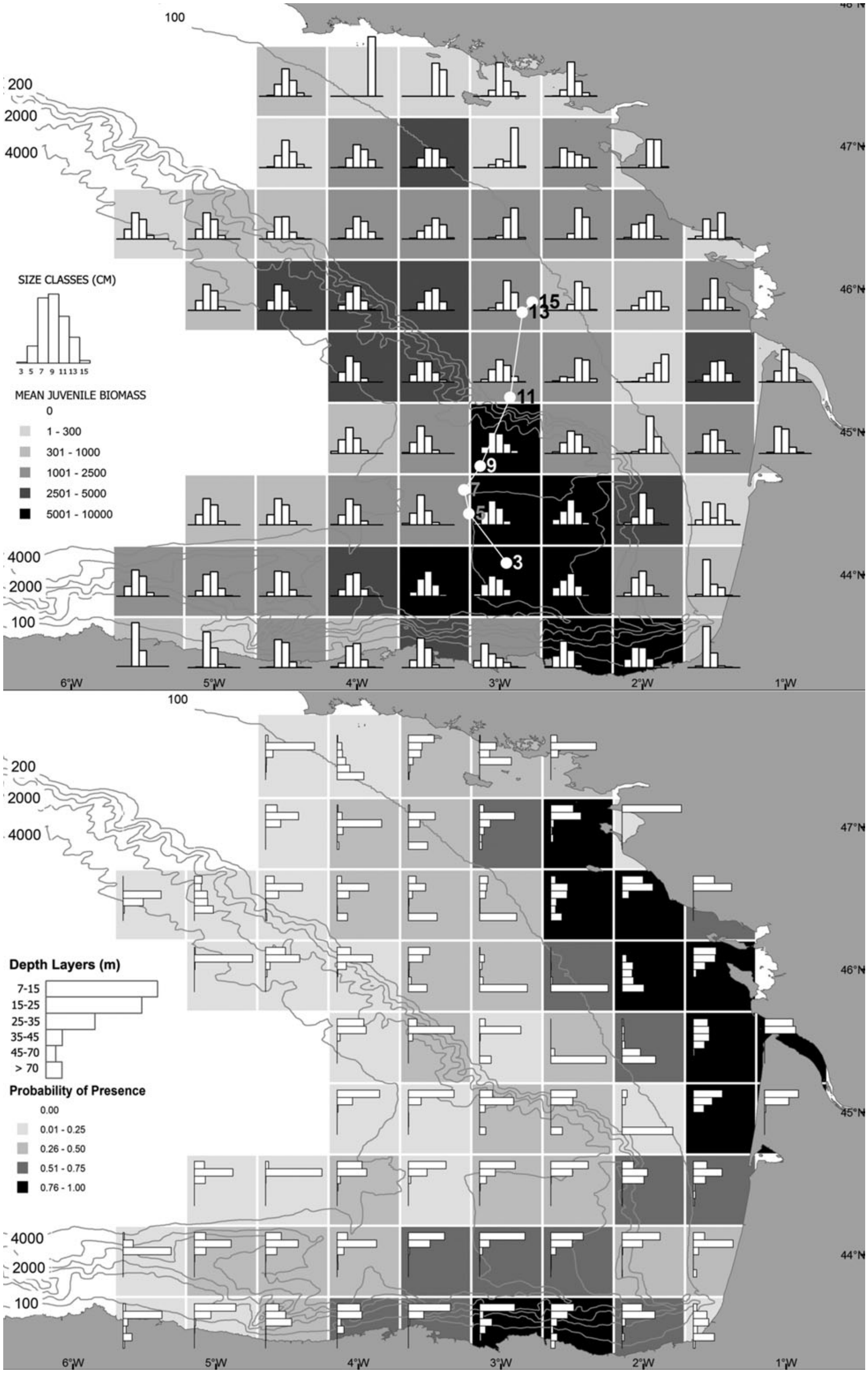

Figure 5. Top panel: the grey level represents the mean aggregated biomass (in tones) of juvenile anchovy in geographic 30 nmi side squares; the vertical bars show the size distribution inside each square; and the connected white dots, the location of the centre of mass of each size class. Bottom panel: overall horizontal probability of the presence of juvenile anchovy in 30 nmi side geographic squares; the horizontal bars represent the vertical distribution of juvenile anchovy in each square. The figure is intended to provide a kind of overall "3D map" of the juvenile anchovy distribution.

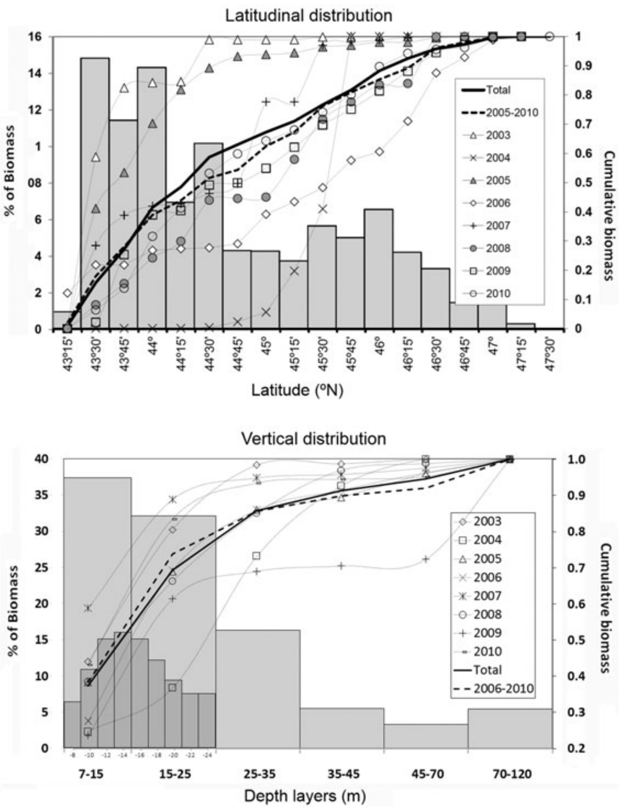

Figure 6. Top panel: percentage (grey bars) and cumulative (lines) biomass of juvenile anchovy against latitude. The dashed line shows the results for 2005 – 2009, when there was a larger coverage of the northern shelf region than in 2003 and 2004. Bottom panel: percentage (light grey bars) and cumulative (lines) vertical distribution of juvenile anchovy biomass according to the integration layers used in the project. The dashed line shows the contribution of 2006 – 2009, in which the pelagic trawler was available. The dark grey bars represent a higher-resolution vertical distribution of the first two depth layers, showing that the biomass does not increase continuously to the surface, but has a maximum at 14 m depth.

lack of near-bottom juveniles in areas empty of adults (such as the whole north coast of Spain) tends to support it on larger regional scales.

Recruitment forecasting capability

The main aim of this work was to test whether the abundance of juveniles in autumn constitutes a reliable indicator of the strength of recruitment to the adult stock each year in the Bay of Biscay. The hypothesis has been confirmed by the significant positive correlations between the biomass estimates of juveniles and the next year's age-1 recruits (Figure 8). This relationship is not too dependent on any particular point of the series, neither the maximum nor the minimum.

Of course, the positive correlation between juvenile abundance and subsequent recruitment at age-1 ought to be presumed because they are successive estimates of the abundance of the same cohort. It should be noted, however, that obtaining a good relationship between the juvenile and age-1 anchovy abundance estimates first requires that the surveying and acoustic estimation methodology are correctly implemented in order to determine the juvenile biomass, and second that the interannual variability in the survival rates between these two stages of the same cohort are low during late autumn and winter. High variability in survival rates could have corrupted the expected correlation between juveniles and subsequent recruits. Therefore, the confirmation of this good relationship indicates that the JUVENA series has produced a reliable index of juvenile abundance (provided that the ICES assessment is correct, at least in relative terms), and also that the year-class strength of anchovy in the Bay of Biscay is already determined by the end of the summer, when the mean age of the juveniles is usually between 2 and 4 months (Aldanondo *et al.*, 2010). This means that, for Bay of Biscay anchovy, as for other species (Leggett and Deblois, 1994), the high variability in the year-class strength is generated from the varying survival rates during the earliest life stages of its life cycle (eggs and larvae). Our results are in agreement with previous reports of a correlation between juvenile abundance and year-class strength found for other species and populations (Hourston, 1958; Koeller *et al.*, 1986; Axenrot and Hansson, 2003; Gudmundsdottir *et al.*, 2007; Schweigert *et al.*, 2009). Furthermore, in some cases the year-class strength has also been reported to relate to earlier pre-recruit abundances, such as postlarval abundance (Fossum, 1996; de Barros and Toresen, 1998; Fox, 2001; Oeberst *et al.*, 2009).

The mean rate of juvenile to recruitment estimates across the time-series is 2.7. Although it is tempting to try to use this rate to infer juvenile mortality during winter, there are important methodological differences concerning the ways of obtaining the estimates of juvenile biomass and recruitment that prevent us from considering them at the same scale. The juvenile index is based solely on acoustics, while the recruitment index is based on a Bayesian assessment combining three different inputs: acoustics, DEPM and fleet catches, which have some internal unsolved discrepancies (Ibaibarriaga *et al.*, 2008; ICES, 2012). Moreover, the different vertical distributions, aggregation patterns and gonadal contents between spring (spawning) and autumn (mostly immature juvenile) anchovy are likely to produce different TS-length relationships, which are currently not properly taken into account in the acoustic estimates. Consequently, at the moment the most robust and consistent use of the JUVENA index is to consider it as a relative index, as the mortalities inferred from the rates of the two indices are not reliable. Therefore, the fact that the estimate of juvenile biomass in 2004 was less than the subsequent estimate of recruits in spring 2005 is not considered relevant. First, the extremely low abundance of that year class made the estimate of its abundance in autumn and spring more imprecise than that in other years, potentially increasing the expected discrepancy between the indices; and second, that the 2004 juvenile biomass, the lowest of the series, coincides with the lowest of the recruitment series is evidence that the estimate for that year provided highly informative content.

Our results for juvenile anchovy do not fit the entrainment hypothesis (Petitgas *et al.*, 2006, 2010) according to which the adults of certain pelagic species transfer the knowledge of the homing migrations necessary for completing the life cycle. In the case of the Bay of Biscay anchovy, it is obvious that the juveniles migrate towards the continental shelf without the aid of the adults, as there are no adults off the shelf (Figure 3). In addition, if this hypothesis holds true, then a reduced survival rate of the purely juvenile group will be expected, whereas according to our data it is the purely juvenile group, and not the mixed one, that is significantly correlated with the recruitment. Perhaps the entrainment for the Bay of Biscay anchovy involves transferring behavioural knowledge (the nycthemeral behaviour, as postulated by Petitgas *et al.*, 2004)

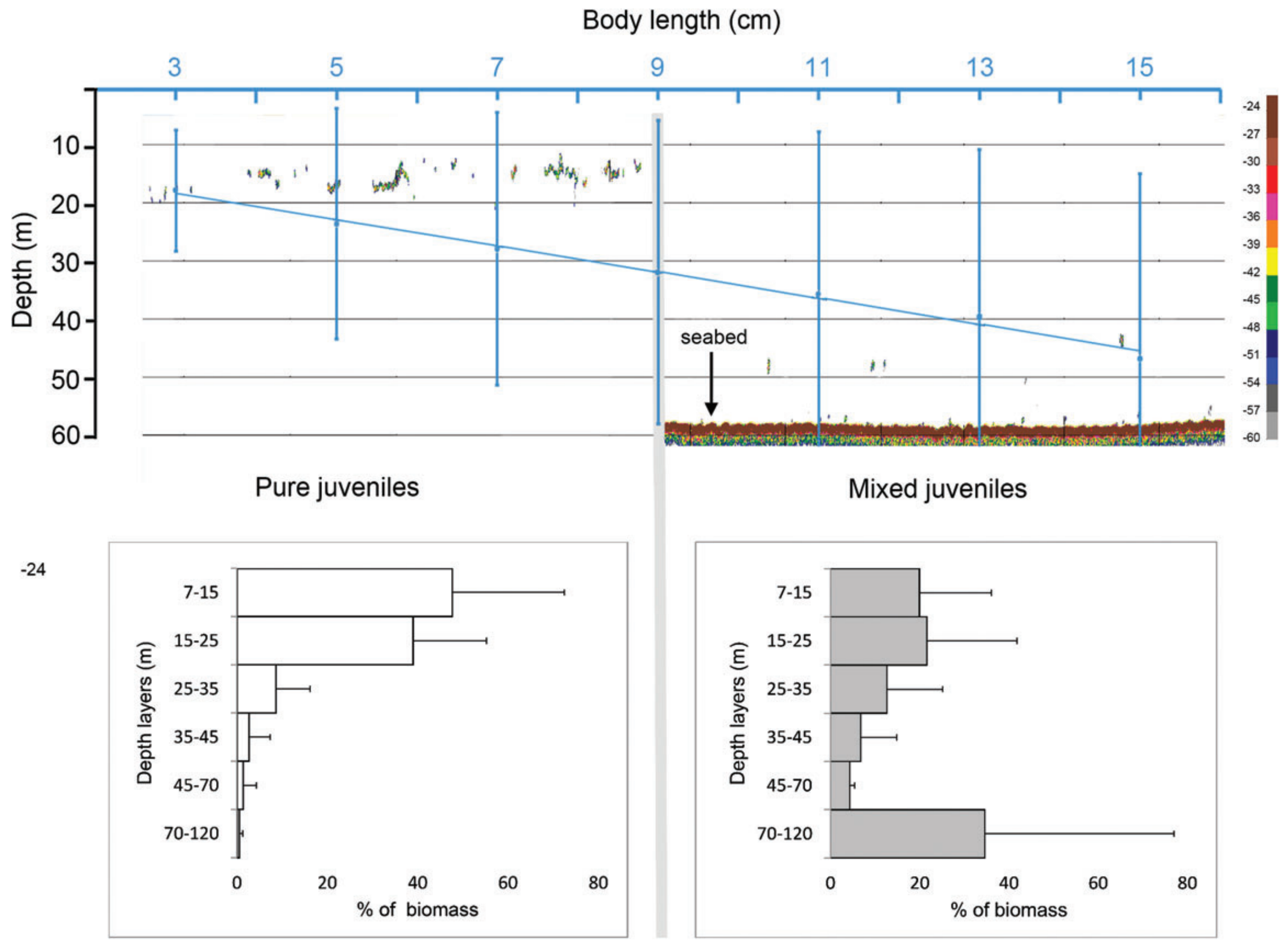

Figure 7. Top panel: sample echograms of anchovy juveniles at −60 dB threshold. On the left, close-to-surface pure juvenile aggregations, and on the right juveniles mixed with adults in the typical adult-like near-bottom schools. The horizontal extent of each echogram is about 1 nmi. Overlapped with the echograms blue dots with vertical error bars represent the mean depth of anchovy juvenile length classes and associated confidence intervals at 99% confidence levels. The mean depth increased linearly with body length, being the fitted linear regression: depth (m) = − 11.14 – 2.27*length (cm); $R^2 = 0.99$. Bottom: Mean vertical distribution of acoustic density of juvenile anchovy obtained for years 2006 – 2010 for the two different groups observed. A colour version of this figure can be accessed online.

rather than the migration routes. Or, alternatively, the entrainment may involve the transference of migration routes taking place a few months later, in late spring and summer, after the spawning season, when both the recruits and the older adults are known to jointly carry out the trophic migrations towards the north (Uriarte *et al.*, 1996). In any case, the closure of the life cycle of Bay of Biscay anchovy and the differences in life-cycle strategy between anchovy and other pelagic species remain unexplained and should be further studied.

In the study period there has been a broad range of recruitment levels, from an extremely low level in 2004, which caused the collapse of the fishery, to one of the highest recruitment levels of the entire recruitment time-series in 2011. The good correlations shown in our results suggest that the JUVENA index can be used to provide an indication of the next year's recruitment at age-1, not only in qualitative terms but also in quantitative ones. However, although linear and log-linear models were shown to be good candidates, the objective of defining the best quantitative modelling was not considered in this paper and has been left to stock assessment modellers to be investigated in the near future when a few more medium and strong year classes become available.

Currently, information provided by the JUVENA index is not systematically used by ICES for providing management advice. However, at the end of 2009, managers used this information to reopen the anchovy fishery with a low TAC (ICES, 2010). Different methods for using this information could be adopted, such as using the values of the juvenile index to construct recruitment scenarios for short-term projections of the latest stock assessment results (as proposed by Ibaibarriaga *et al.*, 2010). In any case, we leave it to ICES to decide how the index should be used, while this work is focused on building and testing the index.

In general terms, having an early indication of the recruitment strength would allow the fishing effort to be managed better by minimizing the risk of depleting the population by overfishing (Walters, 1989; De Oliveira and Butterworth, 2004). Schweigert *et al.* (2009) highlighted the importance of this information, even in the case of a non-significant relationship. The JUVENA index not only provides a significant relationship with recruitment; it also fits conveniently into the existing timetable: in this region, the management of the anchovy fishery is based on direct assessment surveys carried out in spring that provide their advice at the end of the spawning season. By that time a significant part of the annual anchovy fishery has

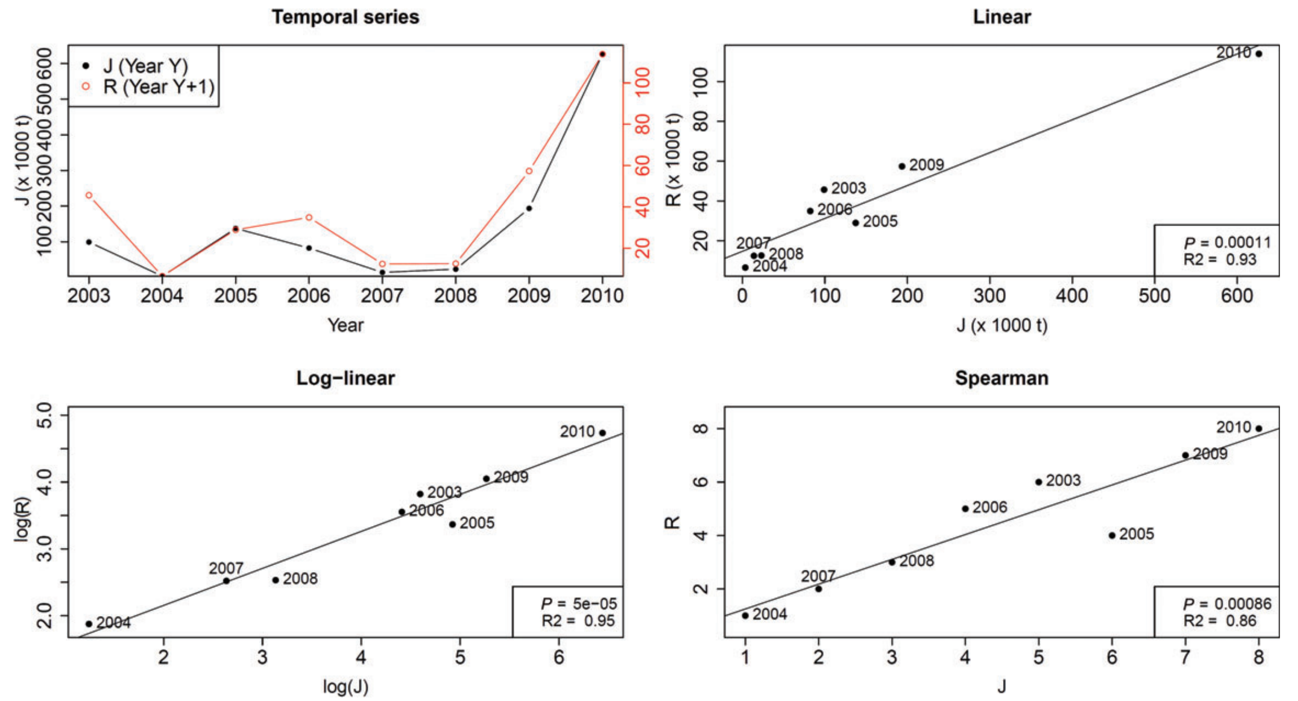

Figure 8. Temporal series of juvenile (J) against recruitment (R) indices and fitting of different regression models between them: linear, log-linear and Spearman. A colour version of this figure can be accessed online.

already ended, which logically limits the effectiveness of the management measures. In this case, an early indication of the recruitment level, such as that provided by the JUVENA index, would allow precautionary measures to be applied several months before the next spawning period and the start of the fishery activity. This information could substantially improve the management of the Bay of Biscay anchovy fishery, helping to prevent collapses such as have occurred in recent years.

Supplementary data

The following supplementary material is available at *ICES Journal of Marine Science* online. A working document entitled "Uncertainties and alternative estimates of the JUVENA index according to its special methodology and assumptions" describes the procedure of assessing the main uncertainties faced in the juvenile anchovy biomass estimation process. In addition, a set of echogram images is provided as examples of juvenile anchovy detections during the JUVENA surveys.

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