

On the importance of adults in maintaining population habitat occupation of recruits as deduced from observed schooling behaviour of age-0 anchovy in the bay of Biscay

Pierre Petitgas, Pierre Beillois, Patrick Grellier, Jacques Massé

The paper presents data on the schooling behaviour of young of the year of anchovy in Biscay recorded during the acoustic survey JUVAGA performed by IFREMER in October 2003. At the end of the larval drift which lasts approximately 100 days, juveniles are found scattered in a vast area and particularly around the shelf breaks and in the outer ocean off the coasts of Spain and France. The survey took place at a time when part of the young of the year were recruited to the adult stock in the inner part of the French shelf and part was still independent of the adult stock occupying shelf break juvenile habitats off the Spanish coast. The recruited juveniles showed similar schooling behaviour than the adults they were mixed with. In contrast, the independent juveniles showed typical juvenile schooling behaviour forming subsurface schools by day and night which were easily disaggregated. Adults were present in the inner part of the French shelf but not off the Spanish coast. The probability for juveniles which would not find the adult part of stock at age-0 to recruit to the stock with good survival rate at later age-1 is questioned. A hypothesis is built and discussed on the importance for the recruits to find the adults thus allowing closure of the life cycle and maintenance of the population in its occupation of habitats.

P. Petitgas, P.Beillois, P.Grellier and J. Massé: IFREMER, BP 21105, F- 44311 cedex 03, Nantes, France [tel : +33 240 374163, fax: +33 240 374075, e-mail : Pierre.Petitgas@ifremer.fr, Pierre.Beillois@ifremer.fr, Patrick.Grellier@ifremer.fr, Jacques.Masse@ifremer.fr]

Introduction

It is commonly accepted that for marine invertebrate populations in which adults are fixed or with limited movements, larval stages represent the dispersal phase of the life cycle allowing for the juveniles to colonise new habitats alone. In contrast, for marine vertebrate populations in which adults have large capabilities for moving and socialising (e.g., schooling), the importance of adults in facilitating the life cycle closure may have been dramatically underestimated. The adult fish in a population could play an important role by maintaining habitat occupation, migration routes and transmitting knowledge across generations (Longhurst, 1998; Slotte, 2001; ICES, 2004). If such working hypothesis holds, important consequences can be deduced. For instance, environmental impact on a population would need to be revisited as an interaction between climate, ecosystem and population structure rather than a direct forcing on a particular biological process. And followingly, fishing would be understood to modify the interaction between a population and the environment because a change in population demography would result in modifying the occupation of habitats and the link between generations.

The paper reports acoustic observations on the schooling behaviour of juveniles of anchovy (*Engraulis encrasicolus*, L.) in the bay of Biscay. In October 2003 an acoustic survey on anchovy juveniles was performed by IFREMER (Juvaga-03) with the objective of validating a larval drift and survival model for recruitment prediction. We were looking for young juveniles at the end of their larval drift in the outer ocean habitats near the Spanish and French shelf breaks. Due to the late calendar timing of the survey (October) we found the juveniles at a time when part were independent of the adult stock and offshore and part were already mixed with the adult stock in the coastal habitats. Important differences in the schooling behaviour of the juveniles were observed when they were mixed with adults or alone and independent from them. This lead to confirm the importance of adults in the closure of the life cycle and the maintenance of the population in its occupation of habitats. Difficulty for juveniles to colonize habitats lost by adults is then discussed in the light of the decennial trend in abundance and spatial occupation of anchovy in Biscay.

Material and methods

Acoustic surveying. The survey was performed with R/V Thalassa, 8-15 October 2003. The acoustic equipment was a hull mounted SIMRAD EK500 echosounder 38 kHz with a nominal beam angle of 7.5°. The pulse duration was 1 ms and the ping repetition rate was 1 s⁻¹. The backscattered acoustic signal was digitised providing acoustic samples of 10 cm in height and 5 m in length which formed the echogram. Acoustic samples with a volume backscatter greater than -70 dB were saved. Echo processing was performed using the software MOVIES (Weill et al., 1993). Acoustic fish density

(echointegration) was expressed in sA ($m^{-2} \text{ n.m.}^{-2}$) units of an equivalent reflexion surface (nautical area scattering coefficient or NASC, MacLennan et al., 2002). The small duration of the survey imposed a survey strategy based on visiting particular areas of potential interest leaving vast unsampled areas. The acoustic methodology applied was that of the spring fisheries evaluation surveys (Massé, 1996; Petitgas, 2003) except that here, we targetted areas where anchovy was present. Acoustic prospection was performed during day-time. When possible, overnight transects were programmed to sail across already sampled areas where anchovy schools had been observed during previous day-time. Echotraces identification mid-water trawl hauls were undertaken conditionnally to the acoustic image. The trawl dimensions were 57x52 m, allowing an opening of approximately 20 m on the vertically and 30 m horizontally (60 m between the doors). The trawl was rigged differently for sampling the surface layer than for sampling deeper in the water column.

Categories of echotraces and their identification. Echogram images were empirically coded in 4 categories based on echotraces morphology and spatial occupation, following practice in spring surveys (Massé, 1996): D1, shoal aggregates near bottom (maximum altitude from bottom: 10 m); D2, well formed schools in mid-water; D3, shoal aggregates near surface (maximum depth from surface: 35 m); D4, well formed schools near surface (maximum depth from surface: 35 m). When sea bottom was greater than 50 m, differentiating echotypes was appropriate and each category could be identified separately: D1 or D2 were identified with a deep haul while D3 or D4 required a surface haul. In more coastal areas, differentiating echotypes was in general difficult except in particular situations (e.g., all echoes close to bottom). Appropriate vertical positioning of the trawl allowed to identify all vertical echotraces when sea bottom was smaller than 50 m. This was controlled on the echogram during fishing.

Trawl haul catch data. At each trawl haul, species were sorted, weighted and measured for length. A subsample of 50 randomly taken anchovies were further sampled (with length < 15 cm) for otolith age and growth determination in the laboratory, as well as allozyme diversity. On board, the age was determined by analysing the otolith of a small number of individuals (46 in all) to estimate the range of length values separating young of the year from age-1 fish and older.

Anchovy abundance around the trawl hauls. For each haul i , a horizontal portion H_i of the echogram was defined as that identified by the haul. These portions were 3-6 n.m. long. The French shelf in Biscay is a mixed species ecosystem where schools cannot be identified to species using their echotrace characteristics only. Schools can only be identified to species when the trawl catch is made of one species only. When the trawl catch is a mixture of species, fish abundance in the echotype identified by the trawl haul can only be disaggregated into species by using the species proportions and species length as provided by the trawl catch (Massé, 1996; Petitgas, 2003). The abundance of

species e (tonnes) over H_i is given by : $B_{e,i} = X_{e,i} \sum_{j \in H_i} D_{u,j}$ where D_u is the acoustic fish density for echotype D_u ($m^{-2} n.m.^{-2}$) and X_e is species e echointegration factor. The number of fish is then derived by dividing biomass by individual mean fish weight: $N_{e,i} = B_{e,i} / \bar{w}_{e,i}$. The species echointegration factor for haul i is given by: $X_{e,i} = K_{e,i} / \sum_e K_{e,i} \sigma_{e,i}$ with $\sigma_{e,i} = 4\pi \bar{l}_{e,i}^2 10^{-B_e/10} / \bar{w}_{e,i}$ where B_e is species e target strength parameter (see below) and K_e is species e proportion in weight in the trawl catch.

Schooling behaviour. Echotypes, species composition and anchovy length were spatially organised allowing for a stratification of the data. In each strata, trawl hauls and their associated echotypes were selected to document the strata characteristics in terms of anchovy schooling behaviour.

Schools characteristics. For some surface hauls, only juvenile anchovy was caught. The schools identified by such trawl hauls were analysed. They were captured by the image analysis procedure of the software MOVIES (Weill et al., 1993) and their parameters were estimated. Knowing the volume backscatter of the school (R_v in $dB m^{-3}$) and the target strength of the fish, it is possible to derive the number of fish per unit volume in the school and the total number of fish in the school. Target strength (dB) is related to fish length $TS_i = 20 \log(l) - B_e$. Mean fish length is estimated from the trawl catch. The coefficient B_e is species specific. For anchovy, we used the value given by Diner and Marchand (1995): $B_e = 71.2$. The school density in numbers per m^3 is given by: $N = 10^{(R_v - TS_i)/10}$. The volume backscatter of the school (R_v) was estimated as the average of all acoustic samples within the school.

Results

Geographical pattern at regional scale. Combining echotypes (Fig. 1) and results of trawl hauls (Fig. 2, Tables 1 and 2) allowed for distinguishing different zones of 4 types (Fig. 3). In zones 1, 2, 3, 5 (type 1 zone) only surface echotraces D3-D4 were seen which were identified 100 percent to anchovy young of the year. In zone 1 although echotraces were seen the trawl was ill-rigged and no catch was obtained. Zone 3 was identified by night-time acoustic recording but no trawl haul was performed. In all other zones, anchovy was mixed with other species and young of the year anchovies were mixed with adult anchovies. In coastal zones 4, 8, 10 (type 2 zones) echotypes D2-D3-D4 were present and identified all in one with one trawl haul. In coastal zone 9 anchovy was not seen (type 4 zone). In central zones 6 and 7 (type 3 zone) surface echotypes D3-D4 were well separated on the vertical from bottom echotypes (D1) and were identified with distinct pelagic trawl hauls. Adult anchovy was at the bottom when smaller sized anchovy was in the surface layer. More information than day-time acoustic

records was used to define zone limits. Night-time recordings were used to identify zone 3, define the northern limit of zone 2, the western limit of zone 4, and the southern limit of zone 8.

Length and age. The overall length distribution was obtained by a weighted average of the trawl haul length distributions. First in each zone, the zone average length distribution was estimated by weighting the haul length distributions by the number of anchovies (acoustically estimated) in the vicinity of the hauls. Then the overall distribution was estimated by weighting the zone distributions by the zone total fish numbers (acoustically estimated). The overall length distribution (Fig. 4) ranged from 6 cm to 20 cm with 50% of the individuals under 12 cm length. Otoliths age determination on a small number of individuals on board (Table 3) evidenced young of the year to be smaller than 14 cm.

Schooling behaviour of age-0 anchovies with and without adults. Age-0 anchovies were observed in various situations: in well formed characteristic shoals in the surface layer (0-35 m), extremely dispersed in the surface layer (0-35 m), or in similar schools than the adults in mid-water. When forming similar schools than the adults, age-0 anchovies were in the coastal areas (zones 4,8) with adults in the vicinity or mixed in the trawl catch. Trawl hauls 11 and 17 (Figs. 5, 6) are typical illustrative examples showing schools and length distributions. Schools were visually similar to the those observed in spring surveys, meaning that age-0 anchovy in the coastal zone would have acquired the adult schooling behaviour and would be fully recruited to the stock. Trawl haul 15 in zone 5 (Fig. 7) shows age-0 anchovy shoals in the surface layer independent from adult fish (pure anchovy catch, homogeneous length distribution, no adult fish in the vicinity). These shoals were visually similar to those of age-0 anchovy observed in 1999, meaning that they are specific to age-0 anchovy when still independent of the parental stock. At haul 10 in zone 4 (Fig. 8) age-0 anchovy was smaller than at haul 15, was mixed with other species, was close to adult fish and formed adult type schools, meaning that adult schooling behaviour would be acquired as a trait depending on the presence of adults in the vicinity rather than naturally in the ontogeny as fish length increased.

Day-night behaviour of age-0 anchovy surface schools when independent of adults. Age-0 anchovies independent of adults were found in the surface layers only and in the central part of the shelf or at shelf break (zones 1,2,3,5; Fig. 3). When in shoals (haul 15, Fig. 7) during day-time, they also stayed aggregated in similar shoals during night-time (Fig. 9), meaning that these fish had not acquired yet day-night schooling differences and stayed aggregated in a similar manner during day and night.

Aggregation/dispersion behaviour of age-0 anchovy surface schools when independent of adults. The Spanish shelf break (Fig. 1) was surveyed on October 8 and 9 after gale winds which had occurred from 3 to 6 October. We observed very few juvenile anchovy-like surface echotraces. The only echotraces observed in zone 1 (Fig. 3) corresponded to haul 4 (Fig. 10) but could not be ground

truthed due to an inappropriate rigging of the trawl. The area was surveyed before the gale winds by AZTI and echotraces such as those of trawl haul 4 (Fig. 10; top) were observed along the shelf break (G. Boyra, comm.pers.). Identification catches evidenced pure small sized anchovy with length smaller than 10 cm. We observed very dispersed anchovy in the surface layer on the French shelf break off Landes in zone 2 (Fig. 3) at trawl haul 7 (Fig. 10, down) with in the trawl catches small sized anchovy (length 7.9 cm; Table 2). Based on AZTI's observations, we considered that echotraces at haul 4 corresponded to anchovy with a similar length than at haul 7. We thought that we had observed two extreme aggregation states of age-0 anchovy in the surface layer: most dispersed at haul 7 and most aggregated at haul 4 (Fig. 10). Echogram portions during trawling at hauls 4 and 7 were selected and replayed for school extraction and school parameter estimation with the software MOVIES (Tables 4, 5). In the most dispersed state (haul 7 in zone 2; Fig. 3; Fig. 10 down; Table 5), schools were small grains of a few meters long with very little acoustic reverberation index and containing about ten individuals. These grains were nearly invisible sailing at 10 knots and potentially difficult to separate from plankton echoes. Reducing the surveying speed was essential to depict them. In the most aggregated state (haul 4 in zone 1, Fig. 3, Fig. 10 top, Table 5), schools were 20 m in length and several m in height, well visible on the echosounder sailing at 10 knots and contained several thousands of fish. It seemed that age-0 surface schools could disperse completely and that school cohesion was not very strong.

Conclusion and discussion

There was a continuous progression (Fig. 3) on the French shelf, from zone 5 (central shelf) where small sized anchovy was seen at surface with no adults in the surroundings, to zones 6,7 where small sized anchovy was at the surface when larger sized anchovy was underneath at the bottom, to zone 8 (coastal) where small and large size anchovies formed similar schools and were mixed in the catches. Such progression made one think that age-0 anchovies arrived progressively to the coast where they recruited to the adult stock and changed their schooling behaviour.

Before recruiting to the adult stock, age-0 anchovies showed particular schooling characteristics. They would stay in the surface layer (0-35 m) whatever the conditions (day-night cycle, wind), would aggregated in dense schools of tens of meters or be extremely dispersed in small grains hardly visible on the echogram. School aggregation/dispersion would be dependent on the meteorological condition with dispersion occurring under environmental forcing (e.g., wind). But when condition permitting, the fish would stay aggregated in schools by day and night. Therefore accessibility to the fish seemed heavily dependent on the meteorological conditions, making reliability of age-0 surveys for the direct estimation of recruitment questionable. Further, age-0 anchovy occupied the entire bay of Biscay,

from very off-shore areas where they are independent of adults to coastal areas where they are mixed with adults, imposing recruit surveys to cover the entire bay of Biscay.

Age-0 anchovies when independent from adults (not recruited to the adult stock) had a particular schooling behaviour, different than that when they were in contact with the adults. The acquisition of the adult schooling behaviour was observed to depend on the presence of adults in the vicinity of the age-0 fish rather than to develop naturally with ontogeny as fish length increased.

Age-0 anchovy independent of adults were observed off-shore only and in the surface layer (central French shelf and shelf breaks). Because contact with adults changed so dramatically the schooling behaviour of the juveniles, the question is raised whether contact with adults would enhance juvenile survival. It can be argued that juveniles could change their behaviour in the coastal areas even in the absence of adults. This situation was not observed. In French coastal areas, anchovy juveniles were always observed to be in contact with adults. In Spanish coastal areas, no adults nor juveniles were observed. Because of this contrast, the question is raised whether juveniles have the capability to colonise by their own, habitats unoccupied by adults. Could the adults have a facilitating effect in the maintenance of habitat occupation. These questions shed a novel light on the role of the different Spanish and French habitats for the viability of the Biscay anchovy stock. Junquera (1986) reports the progressive disappearance of old anchovy along the Spanish coast in the sixties and seventies from West to East. What is then the future of juveniles off the Spanish coast that do not encounter adults?

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Table 1 : correspondence between zone, trawl haul and echotrace category (see Figs 1, 2, 3)

zone number	zone type	Echotrace type	trawl haul number
1 : Shelf break off Spain	1	D3-D4	5
2 : Shelf break off Landes	1	D3-D4	5
3 : Surface layer on central southern shelf	1	D2-D3-D4	5
4 : Gironde	2	D3-D4	10,11,12
5 : Surface layer on central northern shelf	1	D3-D4	15, 22, 23
6 : Bottom layer on central northern shelf	3	D1	21
7 : mid water on central northern shelf	3	D2	17
8 : Loire	2	D2-D3-D4	18, 19
9 : Glénans-Groix	4	D2	24
10 : South Glénans	3	D2	25

Table 2 : Trawl haul characteristics. Nocha: code of haul, ke: proportion in weight of anchovy in the catch, Length: mean length of anchovy in the catch, Grade: number of individual anchovies per kg, Xe: echointegration coefficient for anchovy, D: acoustic backscatter around the haul ($m^2 \text{ n.m.}^{-2}$), Biom (t): anchovy biomass around the haul, N (10^3): nombre of anchovies (thousands of fish) around the haul

Nocha	ke	Length	Grade	Xe	D	Biom (t)	N (10^3)
7	1.000	7.92	316	0.0530	0.7	0.04	11.4
10	0.278	11.94	86	0.0317	308.7	9.78	843.9
11	0.368	14.69	44	0.0496	33.9	1.68	73.4
12	0.830	10.61	128	0.0623	1004.9	62.60	8005.6
15	0.999	12.45	86	0.0790	683.2	53.94	4623.2
17	0.924	15.82	36	0.1066	20.5	2.18	79.4
18	0.074	12.16	84	0.0106	150.0	1.60	134.7
19	0.207	12.51	70	0.0223	46.3	1.03	72.4
21	0.732	13.44	62	0.0494	41.4	2.05	126.6
22	0.050	15.86	33	0.0592	7.1	0.42	13.9
23	0.401	15.39	37	0.1044	28.0	2.92	106.9
25	0.001	12.79	72	0.0002	419.8	0.10	6.8

Table 3 : Pourcent age-0 individuals at length. N: number of individuals on which otolith reading was performed on board.

Longueur (cm)	11	12	13	14	15	16	17	18
Pourcent (%)	100	100	100	100	66	0	0	0
N	6	6	6	6	5	5	5	5

Table 4: Criteria used for the automated school object recognition procedure (software MOVIES). Are retained as school objects those echotraces for which parameter values are all (condition "and") greater or equal than the values in the table. σ_{ag} : multiple reflexion index (m^2) defined as the sum of the sample indices within the school, L: school length (m), H: school height (m), A: school area (m^2), R_v : school volume backscattering index ($dB m^{-3}$) defined as the average of the sample indices in the school, HW (horizontal whole): number of successive empty pings inside the school, VW (vertical whole): number of successive empty samples on a signly ping inside the school.

	Water layer	σ_{ag}	H	L	A	R_v	HW	VW
Dispersed Haul 7	12-32m	10^{-6}	0.5	0.5	0	-65	0	0
Aggregated Haul 4	12-32m	10^{-6}	1	3	3	-55	0	0

Table 5 : Characteristics of the age-0 anchovy schools when they are independent of adults in their most dispersed (Trawl haul 7, Fig. 10) and aggregated (Trawl haul 4, Fig. 10) states observed at 4 knots when trawling. R_v : volume backscattering index ($dB m^{-3}$), L: length (m), H: height (m), A: area (m^2), $V = A L$: volume (m^3), N_{pings} : number of pings that sampled the school, N_{sch} : number of schools along the trawled distance, N_d : school density in numbers of fish per m^3 , N_t : total number of fish in the school.

	R_v	L	H	A	V	Prof	N_{pings}	N_{sch}	N_d	N_t
Dispersed Haul 7	-57.25	3	0.8	1.85	5.55	31	2.7	128	2.2	12
Aggregated Haul 4	-46.66	18.31	3.53	25.06	459	19	20	42	4.5	2084

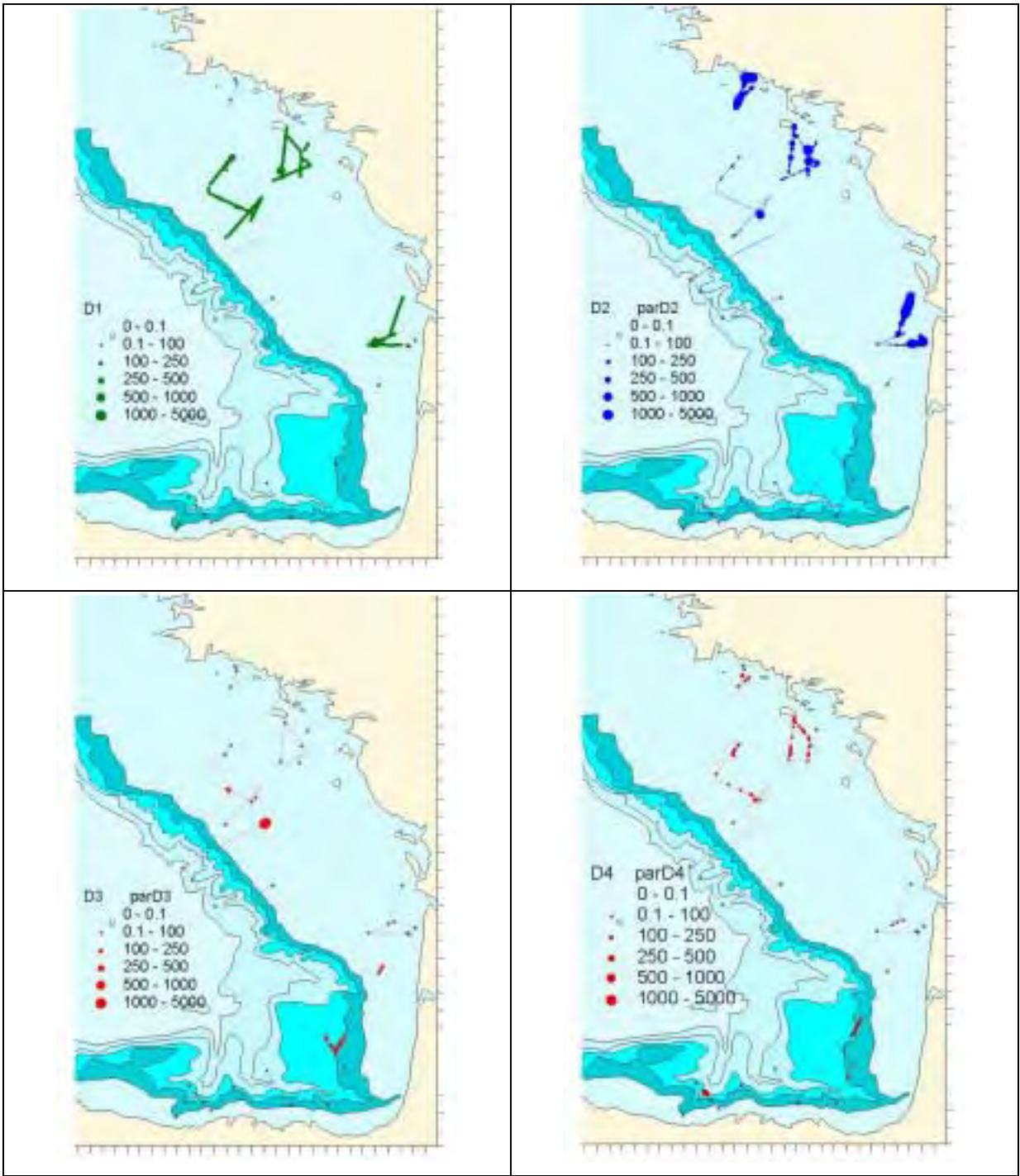


Figure 1 : Acoustic fish backscatter (s_A en $m^2 \cdot m.n.^{-2}$) in the different echotrace categories.

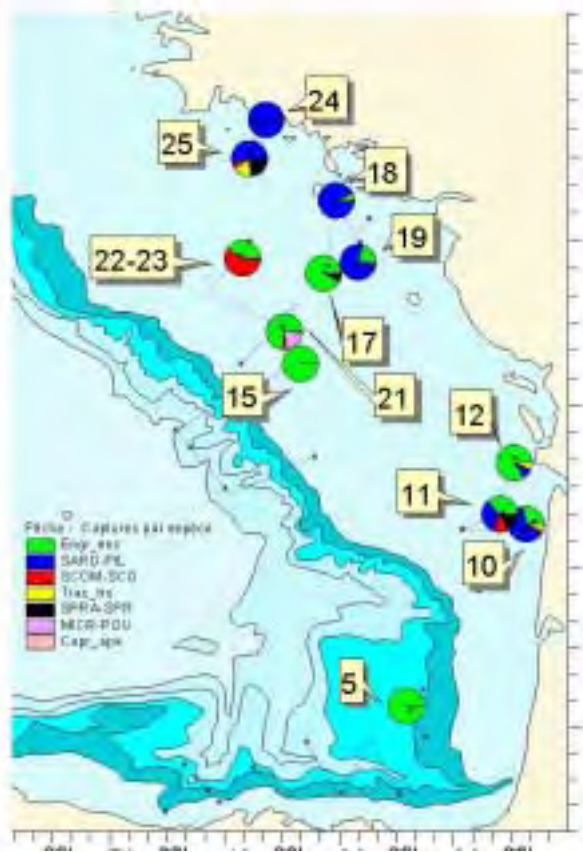


Figure 2 (left) : Weight proportion of species in the trawl catches. Numbers are trawl haul codes.

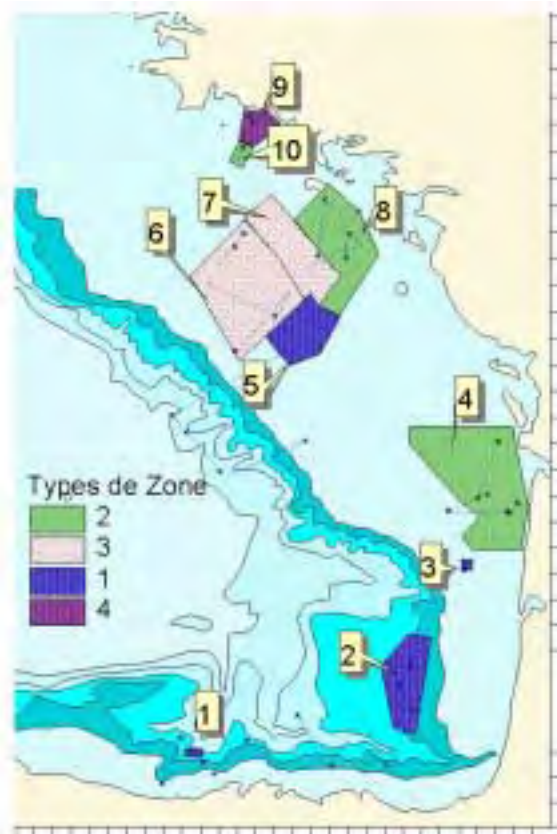
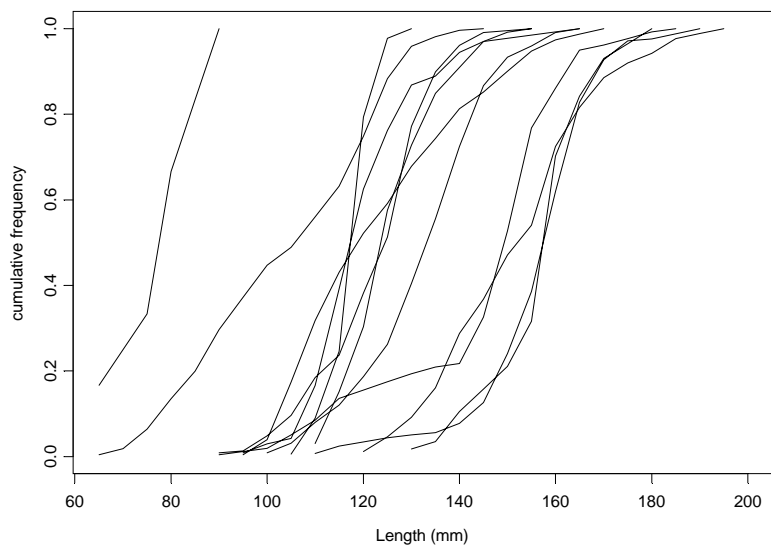
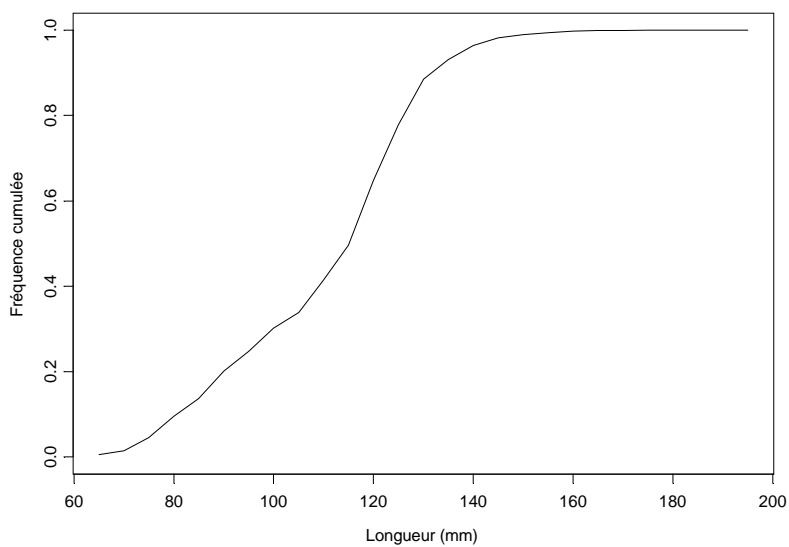


Figure 3 (right) : strata (zone) définition. zone categories are given in the legend. Zone 5 (type 1) is masked under zone 6 (type 3).



(a)



(b)

Figure 4: Cumulative frequency of anchovy length (mm). The curves give the proportion of individuals having a length smaller than the abscissa. Top (a): distributions the trawl haul catches superposed. Down (b): overall distribution estimated by weighting haul distributions with acoustically estimated fish numbers.

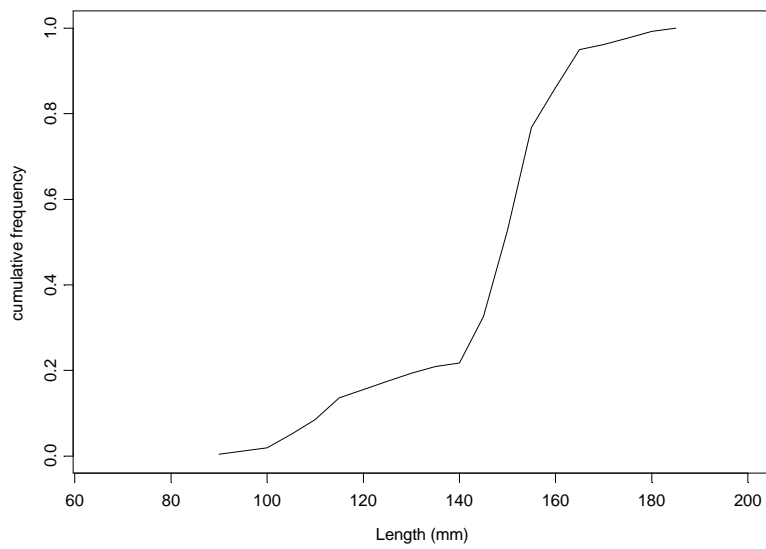
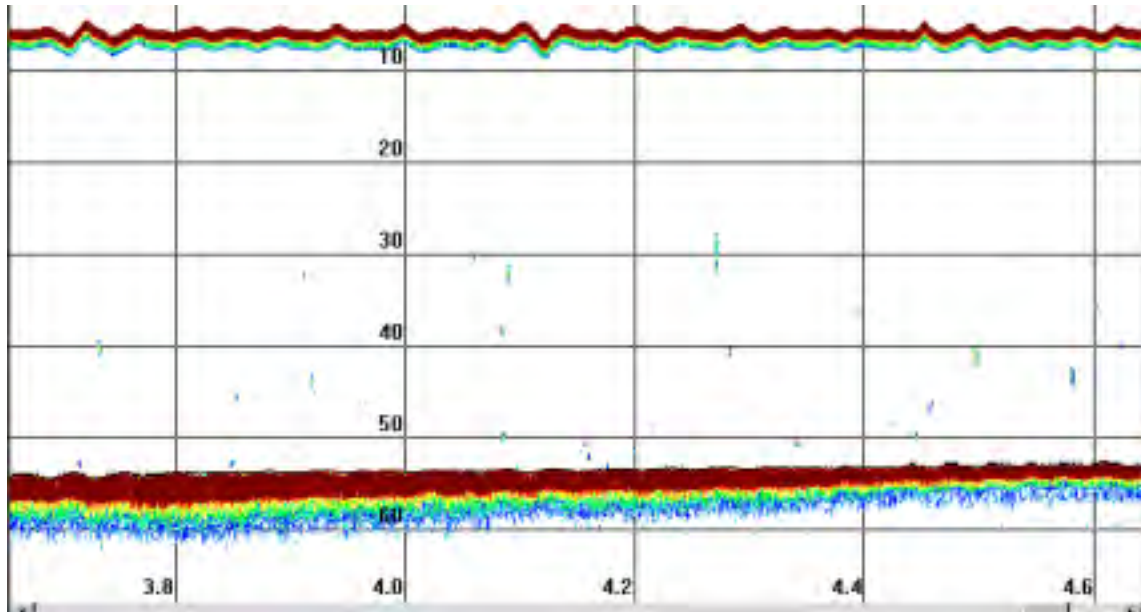


Figure 5: Trawl haul 11 in coastal zone 4. Top: acoustic image (Time 13:36:54 GMT; boat speed 10 knots; visualisation threshold -60 dB) identified as a mixture of species including anchovy (Fig. 2, Table 2). Down: cumulative distribution of anchovy length in the catch.

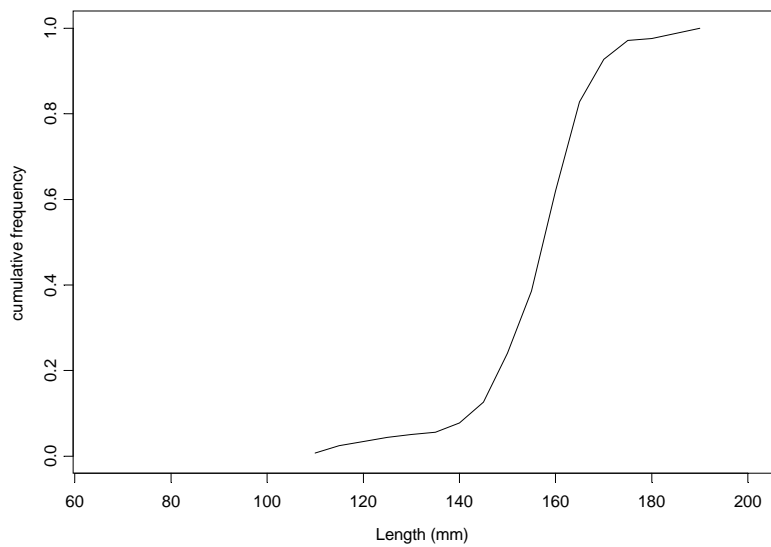
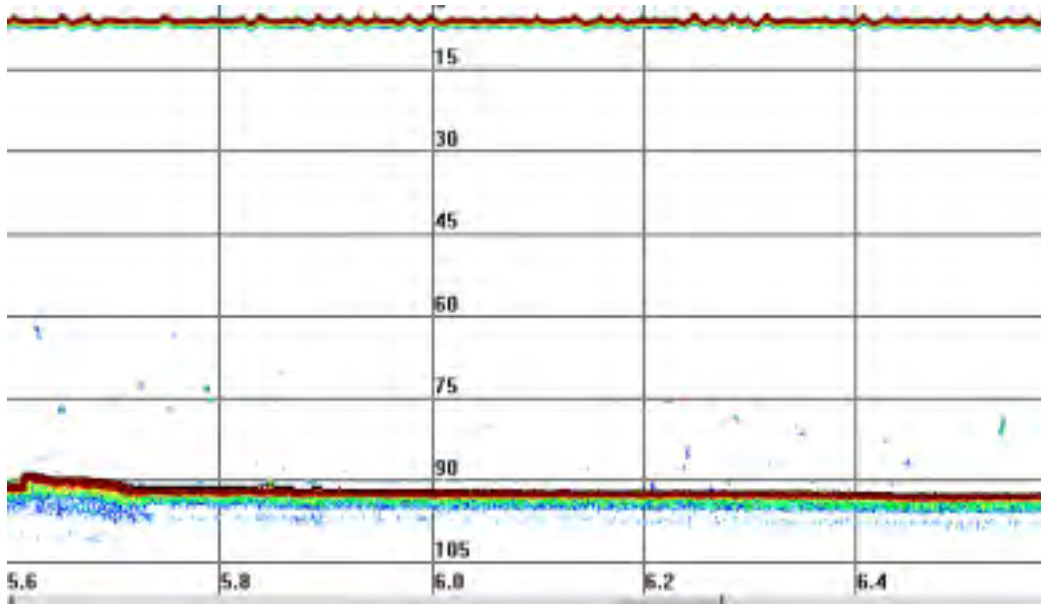


Figure 6: Trawl haul 17 in coastal zone 8. Top: acoustic image (Time10:00:00 GMT; boat speed 10 knots; visualisation threshold -60 dB) identified as a mixture of species including anchovy (Fig. 2, Table 2). Down: cumulative distribution of anchovy length in the catch.

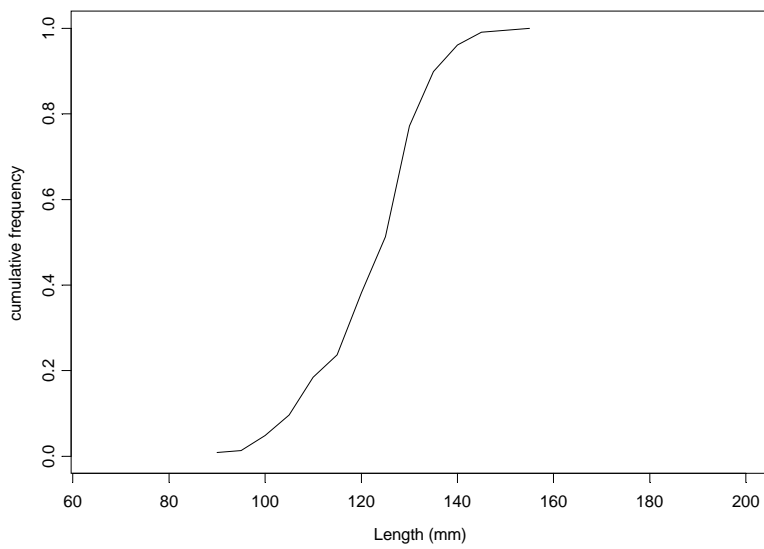
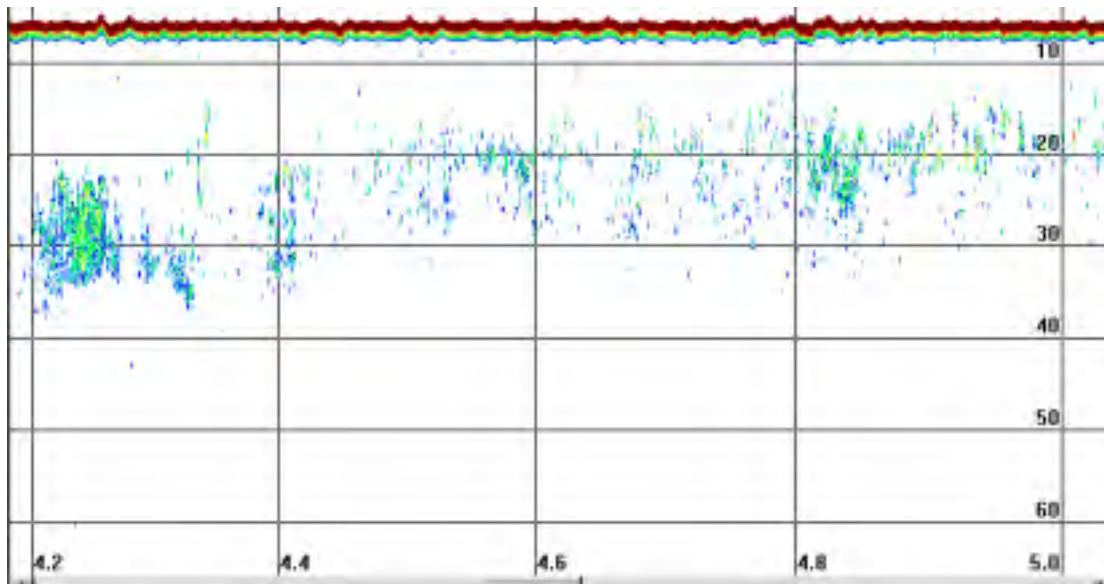


Figure 7: Trawl haul 15 in central zone 5. Top: Acoustic image (time 18:09:33 GMT; boat speed 9 knots; visualisation threshold -60 dB) identified as pure anchovy (Fig. 2, Table 2). Bottom: cumulative distribution of the anchovy length in the catch.

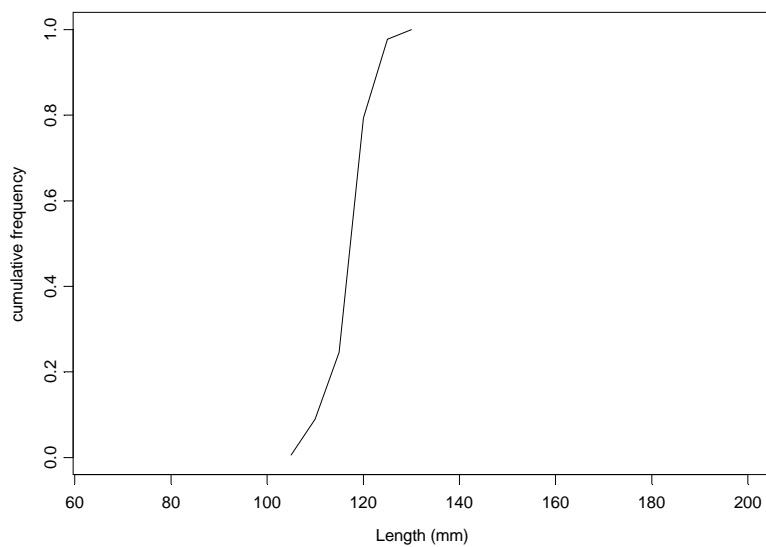
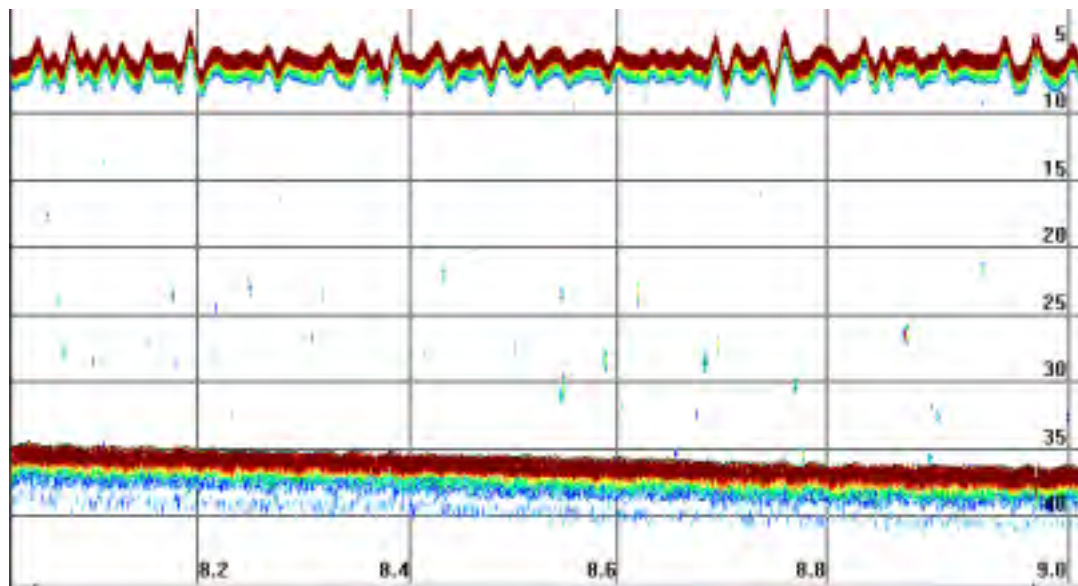


Figure 8: Trawl haul 10 in coastal zone 4. Top: acoustic image (Time 05:36:28 GMT; boat speed 10 knots; visualisation threshold -60 dB) identified as a mixture of species including anchovy (Fig. 2, Table 2). Down: cumulative distribution of anchovy length in the catch.

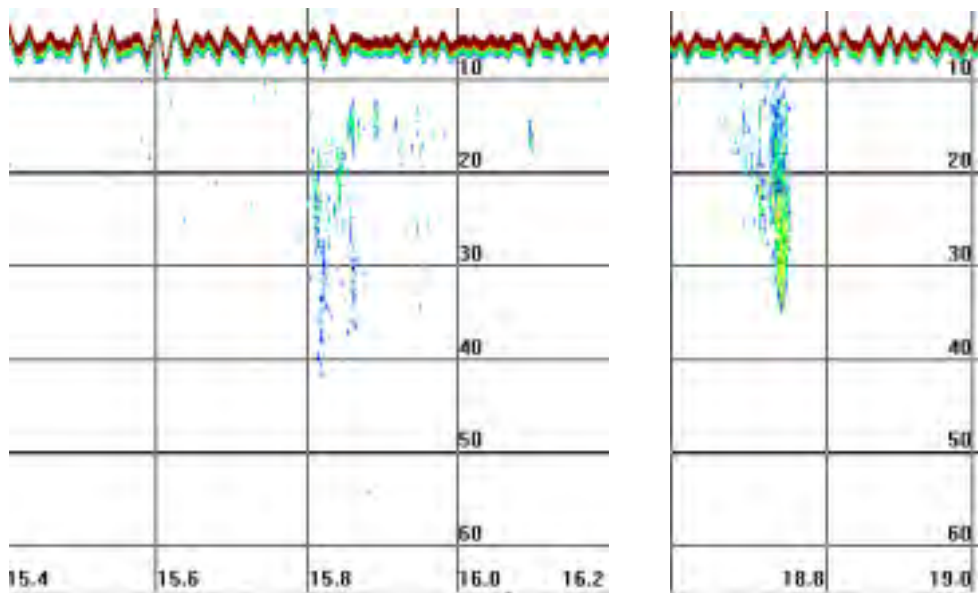
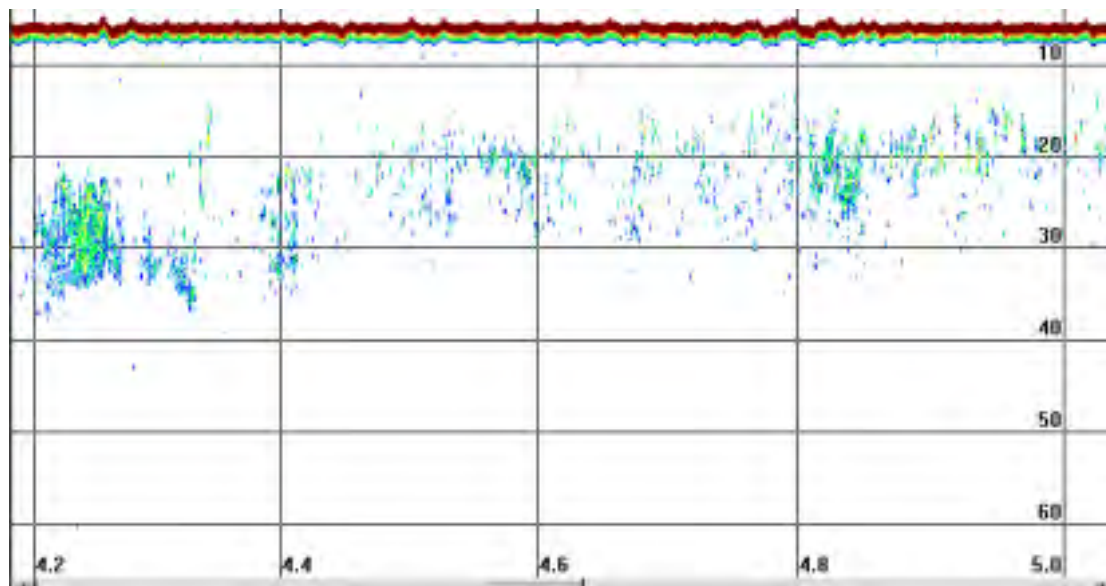


Figure 9: acoustic image at location of trawl haul 15 during day-time (top: time 18:09:33 GMT; boat speed 9 knots; visualisation threshold -60 dB) and night-time (down: time 02:12:00 GMT, boat speed 11 knots, visualisation threshold -60 dB).

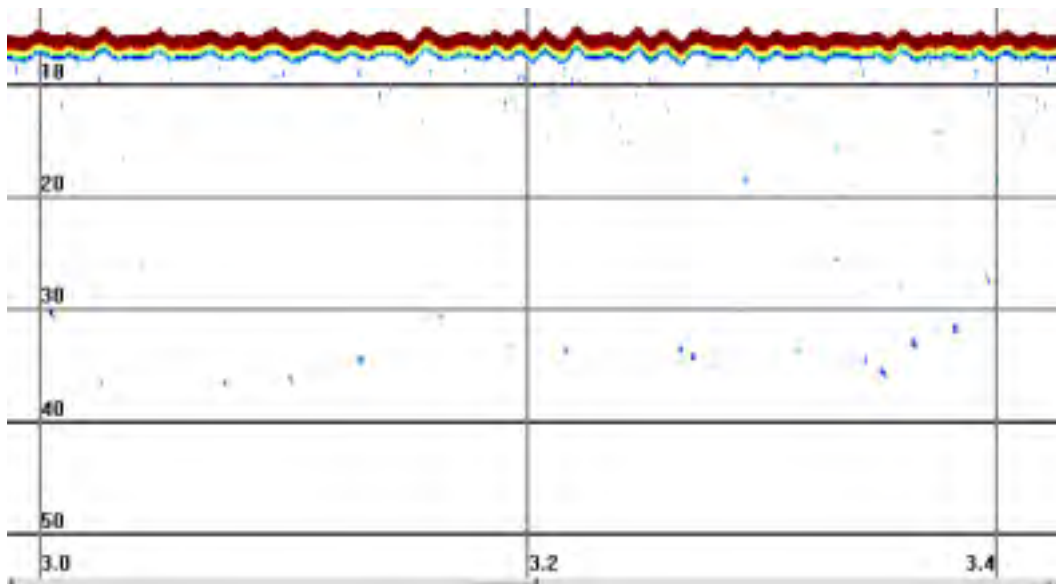
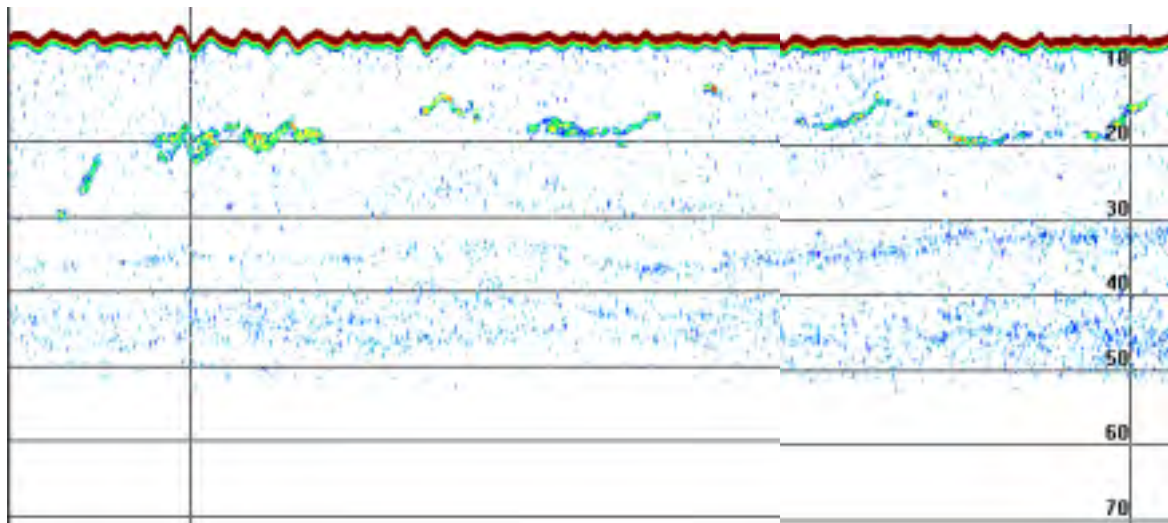


Figure 10: Acoustic image of age-0 anchovy schools when independent of adults, in the most concentrated and dispersed aggregation patterns observed during the survey. Top: at location of trawl haul 4 (Time 10:44:47 GMT; boat speed 3.5 knots; visualisation threshold -60 dB). Down: at location of trawl haul 7 (Time 19:00:00 GMT; boat speed 4 knots, visualisation threshold -60 dB).