

Could Biscay Bay Anchovy recruit through a spatial loophole?

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Abstract

In the Bay of Biscay, anchovy juveniles are regularly observed off the shelf whereas spawning occurs over the shelf, mainly in the river plumes. This distribution of the juveniles can be interpreted as advective losses of the population recruiting over the shelf. However, recent research suggests an alternative interpretation based on the possibility of the population exploiting the off the shelf waters for recruitment through a loophole of lower predation. In this article, we test this second hypothesis through a review of the information available about different processes in the Bay of Biscay (anchovy distribution, size at age spatial differences, recruitment timing and spatial distribution and potential predators distribution). We also develop a model to explore recruitment success when predation risk is positively correlated with feeding opportunities. We conclude that the hypothesis of anchovy using off-shore (oceanic) waters as a spatial loophole for recruitment cannot be excluded.

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1. Introduction

A recent paper by Bakun and Broad (2003) has the great merit of having brought back some basic concepts of ecology to fisheries science: (1) populations of opportunistic species explode when re-colonising a perturbed ecosystem. (2) Mortality of early stages is a fundamental parameter in population dynamics, in particular for species with high reproductive potential, including most fish. Fisheries science sometimes tend to rely too much on bottom-up mechanisms, growth is believed to be the sole cause of recruitment variability, and small environmental signals are believed to yield large variability in recruitment. We sometimes forget the evasive effects of small changes in mortality rates, and that high growth often tend to be accompanied by reduced survival (Munch and Conover, 2004).

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The term loophole refers to interactions between strategies and environmental conditions producing gaps in the biological control that result in a significant mortality reduction of such early stages. Although related, a difference should be made between the factors a larvae can control through behaviour (both phenotypic plasticity and genetically fixed behaviours), which is the classical behavioural ecology perspective, and those that arise due to large-scale environmental variability that are not influenced by the larval behaviour. In this paper we use “loophole” *sensu* Bakun and Broad (2003) as an interaction between reproductive strategy and large-scale environment variability (spatial or temporal) resulting in a significant reduction of the mortality. Bakun and Broad (2003) describe two such potential gaps: (1) anchovies exploding in the Humboldt upwelling system that is frequently perturbed by El Niño. (2) Tuna populations spawning in oligotrophic oceanic waters with low food concentrations but also low predatory pressure. Another example of this second strategy is probably the Chilean Jack Mackerel dispersing to spawn in the oligotrophic oceanic waters of the Southern Pacific gyre (Cubillos et al., 2005; Barbieri et al., 2005) instead of using the much richer waters of the adjacent Humboldt system.

Favourable mechanisms for the recruitment of European anchovy (*Engraulis encrasicolus*) are generally interpreted in terms of another concept developed by Bakun (1996), the triad of retention, enrichment and concentration. However, that concept was developed in the context of upwelling systems where advective transport is very strong and waters outside the upwelling very poor. European anchovy generally lives in large bay-like systems (Bay of Biscay, Bay of Cadiz, Gulf of Lion, Adriatic Sea, etc.) where enrichment is often due to large rivers (Adour, Gironde, Gualdaquivir, Ebro, Rhone, Po).

In the Bay of Biscay (Fig. 1) in particular a number of observations seem to be in contradiction with the retention hypothesis. Age 0 juveniles are often found off the shelf (Uriarte et al., 2001) whereas age 1 adults

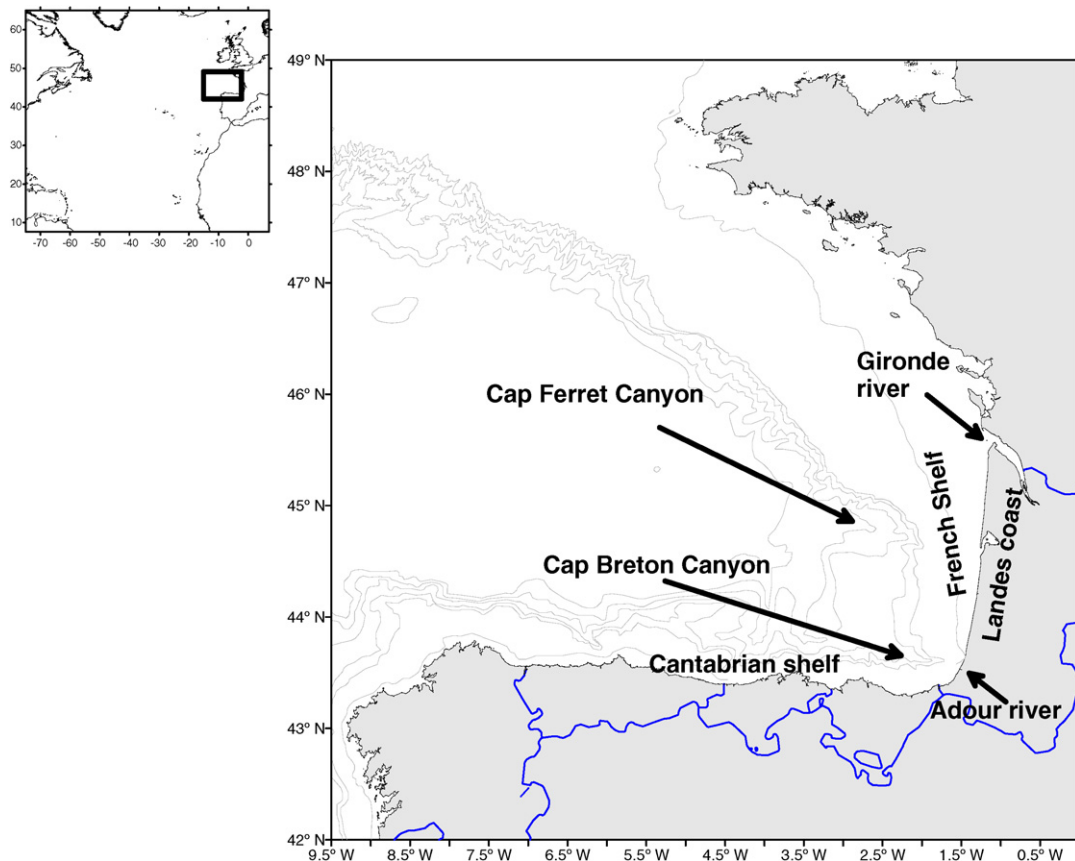


Fig. 1. Map of the study area showing the main geographical features indicated in the text.

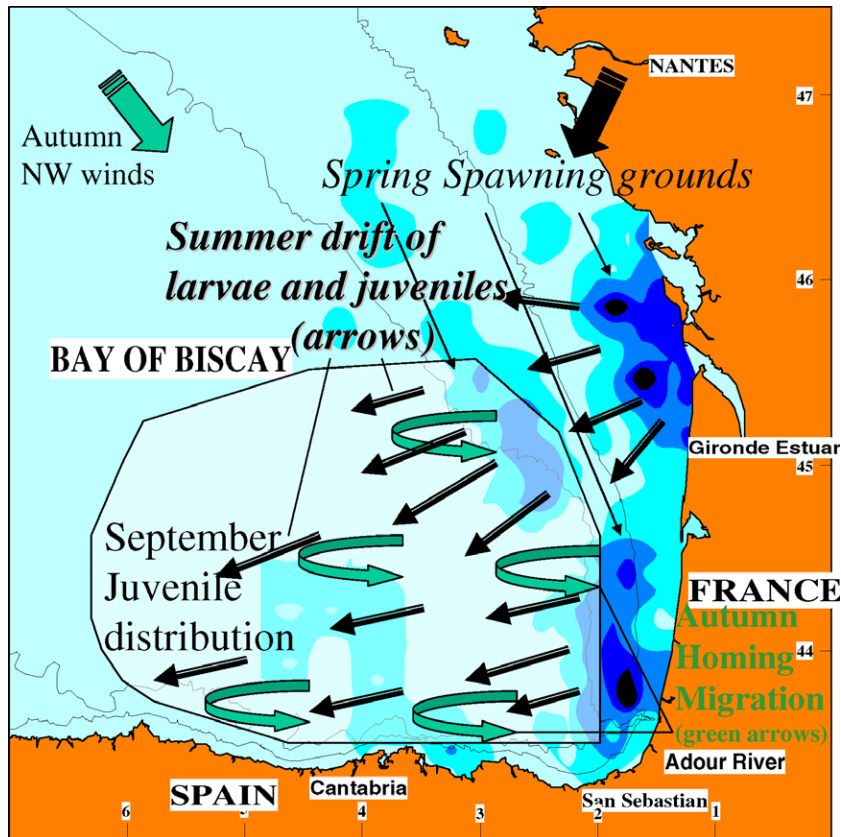


Fig. 2. Scheme of the proposed spatial pattern of recruitment of the Bay of Biscay anchovy. Adapted from Uriarte et al. (2001).

appear on the shelf and most of the spawning occurs in the river plumes and partially on the shelf-break but virtually no spawning occurs off the shelf (Motos et al., 1996). Furthermore, high recruitments are associated with winds favouring upwelling (Borja et al., 1996, 1998; Allain et al., 2001), which in the Bay of Biscay does not necessarily mean higher productivity (most nutrients supplied by rivers), but more likely with increased transport off the shelf.

From the observed pattern Uriarte et al. (2001) proposed that a significant part of the larvae were advected off the shelf and returned to the shelf as juveniles (Fig. 2). In the frame of a “Bakun triad” interpretation of the recruitment, the juveniles off the shelf would most likely be lost from the population. However, the spatial “loophole” concept suggests an alternative hypothesis: the spatio-temporal loophole (the off-shore loop) may transport old larvae and early juveniles into regions with low predatory pressure (off the shelf) before returning to the shelf as older juveniles, less susceptible to predation by planktivorous fishes.

In the context of the GLOBEC initiative for integration and synthesis (www.globec.org) the objective of this paper is to explore the likelihood of such an alternative hypothesis using different sources of information available about processes in the Bay of Biscay.

2. Timing of the anchovy life cycle in the Bay of Biscay

Fig. 3 synthesises the timing of spawning and recruitment of anchovy in the Bay of Biscay. Spawning begins in mid March at temperatures around 13 °C, to peak in May–June with temperatures around 18 °C, and decline in July. Larvae appear in April and are generally present until August. Larvae metamorphose into juveniles around the age of 30–40 days and the first juveniles generally appear at the beginning of August and are present well into November. In years with average recruitment, age 1 anchovies are around

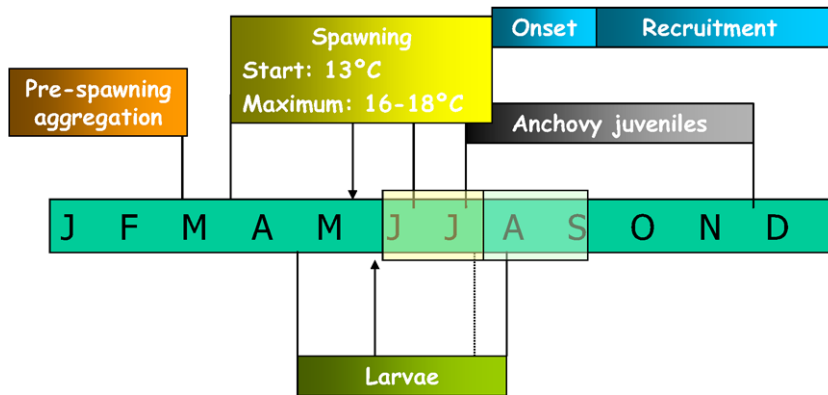


Fig. 3. Synthetic schema of the anchovy spawning and recruitment timing in the Bay of Biscay.

70–80% of the spawning population the following year and therefore the strength of the recruitment into mature individual is due to the survival of larvae and juveniles during the previous summer.

3. Spawning, larvae and juveniles distribution

The spawning area of anchovy in the Bay of Biscay is well known because annual evaluation of the biomass has been carried out since 1988 using the daily egg production method which requires a high resolution data on the distribution of the eggs (Motos et al., 2005). The main spawning area for anchovy in the Bay of Biscay

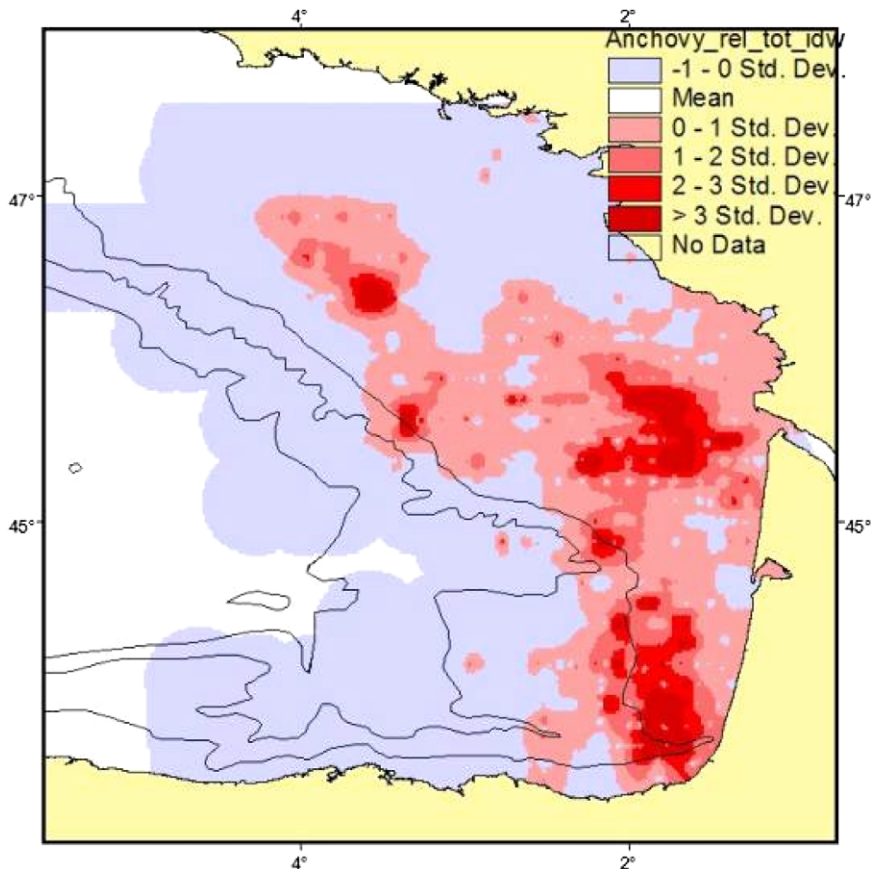


Fig. 4. Average spawning area of anchovy in the Bay of Biscay for the period 1988-2004.

are the Gironde river plume, the Adour river plume and some areas of the shelf-break (Motos et al., 1996; see also Fig. 4). Data for larval distributions are scarce. However specific surveys targeting larvae distribution during June–July were carried out in 2004 and 2005. The highest concentrations of early larvae correspond with the spawning area, mainly around the river plumes. However, the age of the larvae, the average size and maximum sizes found increase from the river plume to the off the shelf direction (Etxebeste et al., 2007; see also Fig. 5). That is, larvae are small and abundant in the river plumes and larger and less abundant

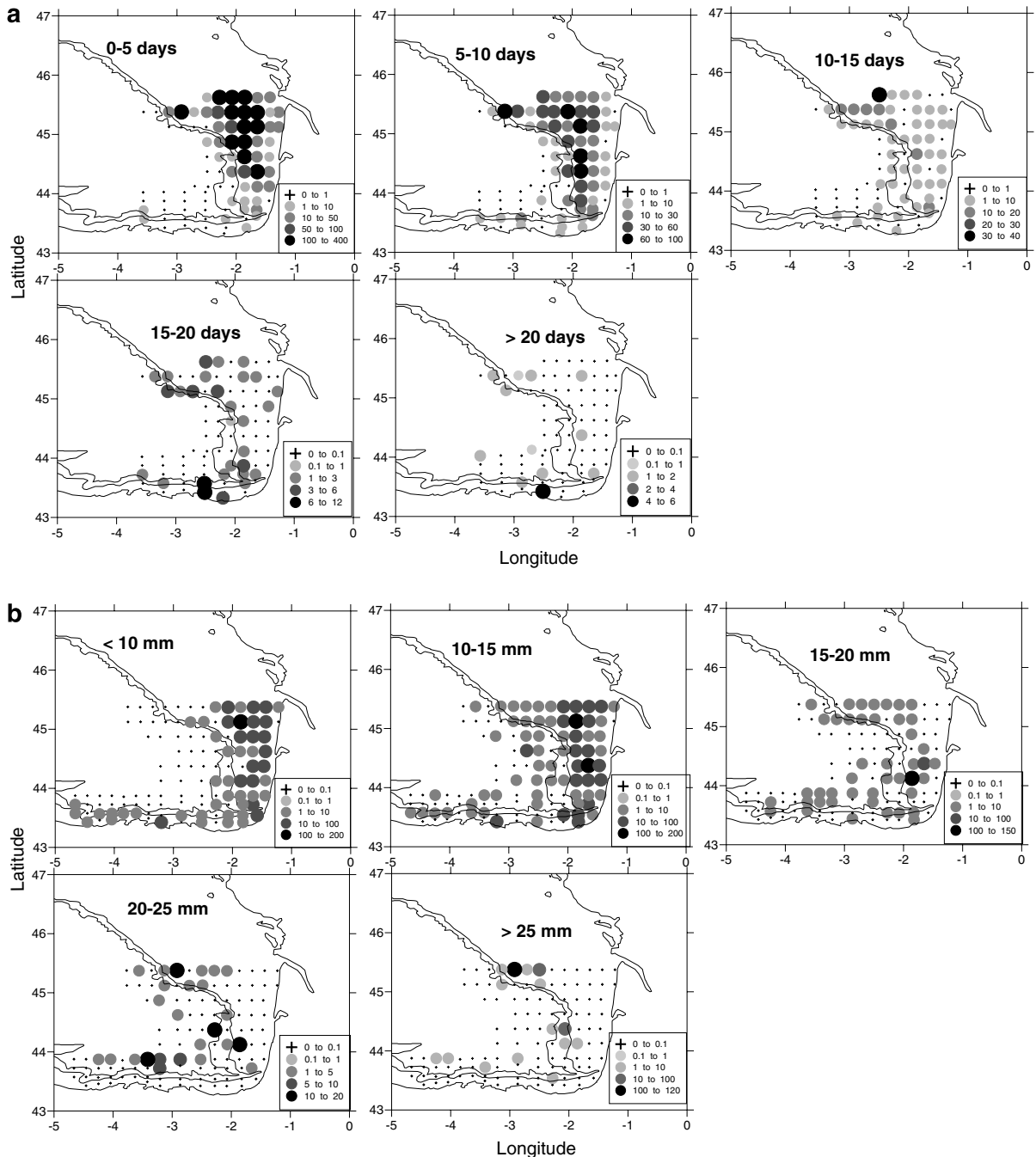


Fig. 5. (a) Distribution of anchovy larvae abundances (ind m^{-2}) by age classes in June 2004. Modified from Etxebeste et al., 2007. (b) Distribution of anchovy larvae abundances (ind m^{-2}) by size classes in July 2005 (Etxebeste et al., 2007).

when distancing from the plumes which suggests a drift. Surveys targeting juveniles are also limited but have been carried out during 1998, 1999, 2003, 2004, and 2005 in the period September–October. Additional information on distribution has been obtained from fishermen that use anchovy juveniles as live bait to fish tuna during the summer–autumn period. Contrary to eggs and early larvae, larger larvae and juveniles are often found off the shelf. There is also a size segregation with smaller juveniles being found off the shelf and larger ones inside (Fig. 6). The complete egg/small larvae/large larvae/small juvenile/large juvenile distribution picture suggests a transport cycle as suggested by Uriarte et al. (2001) (Fig. 2) where anchovy is advected off the shelf as old larvae and returns as juvenile.

Instead of having old larvae and young juveniles off the shelf, an alternative possibility could be that individuals remaining on the shelf grow faster and consequently are larger than those found off the shelf. However otholith aging of the individuals has shown no significant difference in the size at age between individuals captured on or off the shelf (Fig. 7). As shown by the gap in sizes in Fig. 6, larvae near metamorphosis are difficult to capture because fast enough to escape plankton samplers but not yet enough aggregated so as to be easily captured by fishing gears. However, the smaller juveniles found off the shelf appear to be younger individuals confirming the transport cycle hypothesis. Furthermore, an analysis showed that recent larval growth in the

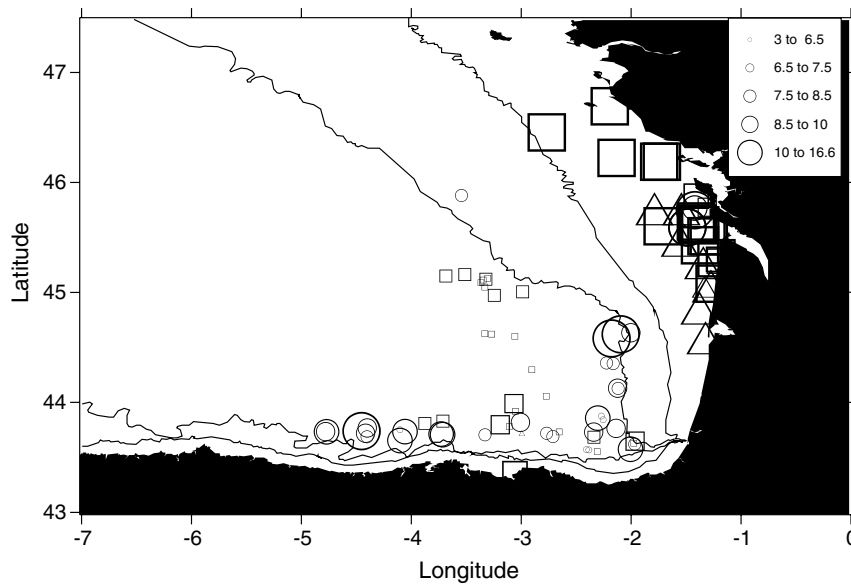


Fig. 6. Anchovy juveniles distribution and size (length, cm) modes for 2003 (circles), 2004 (triangles) and 2005 (squares) September–October surveys.

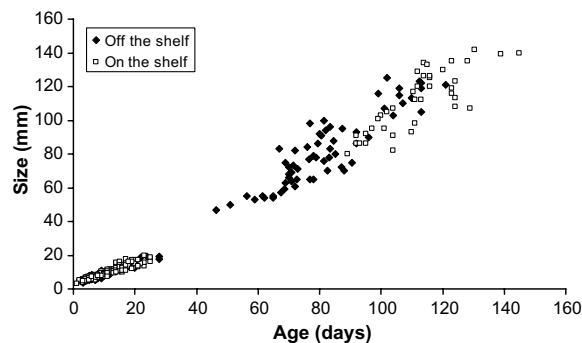


Fig. 7. Age–size relation for larvae and juveniles collected on the shelf (empty squares) and off the shelf (filled diamond) during the 2003–2004 surveys.

area of the Gironde river plume was slightly higher than in other areas. Otherwise no significant differences in larvae growth rate between in and off the shelf were detected (Etxebeste et al., 2007).

4. Consistent pattern or casual observation?

One question that immediately arises in relation with the conceptual recruitment pattern proposed by Uriarte et al. (2001) is whether the juveniles observed off the shelf are representative of their distribution or it is just something occasional occurring only in some years or concerning a very small part of the juvenile population. Two sources of information indicate that the summer off-shore distribution of juveniles corresponds to a consistent spatial pattern throughout the years: catches of juvenile anchovy as live bait for the tuna fishing boats are usually made in August and September in off the shelf areas beyond the Cantabrian and French shelf, whilst they are scarce on the shelf, except for the live bait catches of 1 year old anchovies which are usually taken close to the Gironde Estuary (Cort et al., 1976; Martin, 1989; Uriarte et al., 2001). In addition, we do have something almost similar to a fleet of autonomous underwater vehicles covering off the shelf waters in summer: the tuna populations migrating into the Bay of Biscay in summer (albacore and bluefin tuna). Because it is a traditional and profitable fishery there is a good database on the temporal and spatial location of catches. Interestingly the seasonal migration of juvenile albacore and bluefin tuna into the Bay of Biscay (Fig. 8) coincides with the recruitment period of anchovy in summer (Fig. 9). Albacore in particular performs a long trophic migration from wintering areas in the center Atlantic towards the South of Ireland following a temperature window of around 17–18 °C. Reaching the Bay of Biscay the largest part of the population enters the Bay of Biscay where temperatures 2–3 °C higher are found, whereas another part of the population follows the 17 °C isotherm to the South of Ireland (Ortiz de Zárate and Cort, 1998; Sagarminaga and Arrizabalaga, 2006). For both species, catches in the Bay of Biscay concentrate in a narrow time window, with most of the catches occurring between July and September (Fig. 9). Also, albacore and bluefin are mainly captured off the shelf. Fishermen using live bait to capture albacore with pole and line techniques prefer anchovy to any other bait such as small sardine or horse mackerel (pers. comm.) and gut contents analysis of tuna in the Bay of

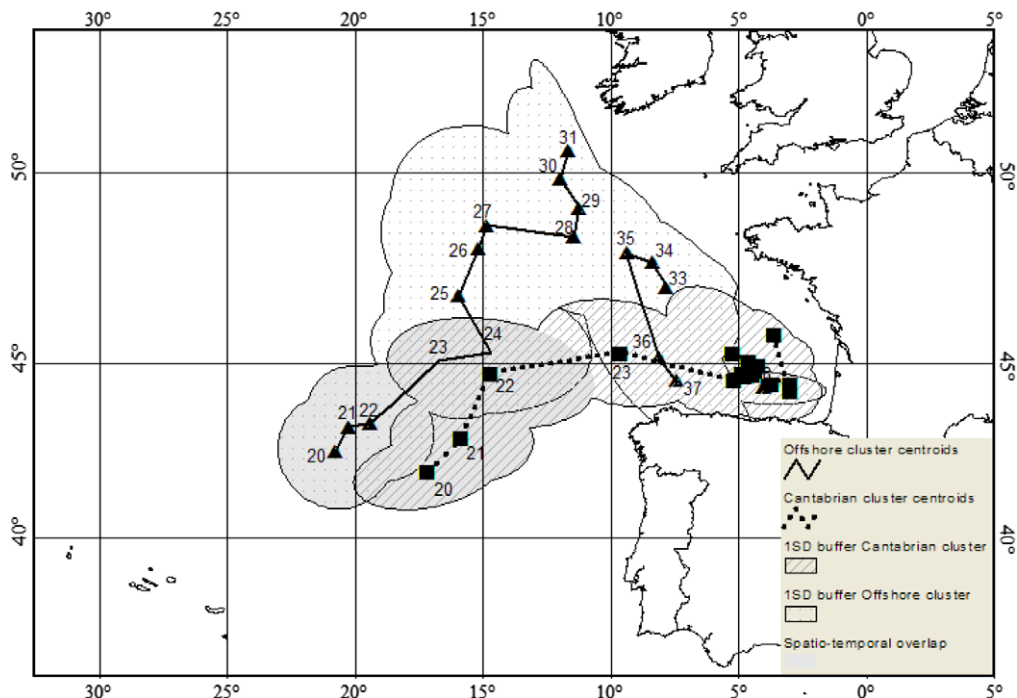


Fig. 8. Weekly evolution of albacore trolling fishing grounds, following albacore migration patterns. Modified from Sagarminaga and Arrizabalaga (2006).

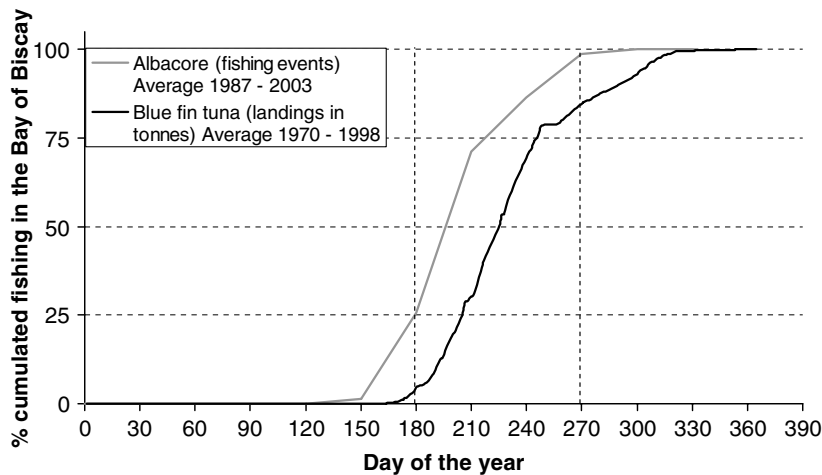


Fig. 9. Average phenology of the baitboat bluefin and trolling albacore catches in the Bay of Biscay. Gray line for the albacore catch events (average 1987–2003). Black line for bluefin landings in tonnes (average 1970–1998). The vertical bars indicate the main recruitment period as indicated in Fig. 3.

Biscay indicate that anchovy, together with euphasids and myctophids, is an usual prey item of albacore and bluefin tuna in the Bay of Biscay (Goñi, 2004; Ortiz de Zárate, 1987; Ortiz de Zárate and Cort, 1986). The population of tuna seasonally migrating into the Bay of Biscay has been captured at least for as long as there are records. These data indicate that during that period of the year tuna populations do find abundant food off the shelf water in the Bay of Biscay, supporting the idea that the presence of juvenile anchovy off the shelf waters is neither occasional nor in small numbers. In fact, two of the new series of surveys on juveniles performed from 2003 to 2005, revealed most of juvenile anchovy located off shelf waters (Boyra et al., 2005a,b ms.) as was the case in the 1998 and 1999 surveys (Uriarte et al., 2001), despite some detections over the shelf (Petitgas et al., 2004).

5. General circulation patterns in the Bay of Biscay

An important test for the spatial loophole hypothesis is whether the average circulation patterns fit with the proposed trajectory. The proposed hypothesis would not make evolutionary sense if the general circulation patterns were to produce such a trajectory only occasionally. That is, if in most years there was no transport off the shelf, or if on the contrary, the transport was generally so strong that there was no possibility to return to the shelf during the same year.

The Bay of Biscay tends to be a relatively stagnant part of the North Atlantic Ocean, situated in between the subtropical gyre with the Azores current and the subpolar gyre with the North Atlantic current. The slope water circulation is highly variable with the season as shown by current and temperature measurements along the north Spanish continental slope (Pingree and Le Cann, 1990). In the winter, the southward component of wind stress relaxes, allowing an eastward warm poleward surface flow to develop off the Iberian Peninsula. Part of the flow continues northwestward as a slope current (Fig. 10: slope current) and another part of the flow pursues its poleward advance across the Landes Plateau and the continental slope of Cape Ferret canyon (Fig. 9: shelf residual circulation). Furthermore, a relevant characteristic of the poleward flow is its inability to follow the abrupt changes of topography, such as Cap Breton or Cap Ferret Canyons (Pingree and Le Cann, 1990). At these locations, the slope water can be collected into anticyclonic eddies, called Slope Water Oceanic eDDIES (SWODDIES) by Pingree and Le Cann (1992), and then be injected into oceanic regions, usually through a westward motion (Fig. 10: eddies). These Swoddies are seasonally recurrent features that might trap and transport biological material from the shelf and slope as well as enhance primary production (Fig. 11, Smith et al., 1996; Fernandez et al., 2004).

In early spring, the thaw brings large quantities of fresh water to the French shelf. The resulting low salinity waters over the French shelf are less dense than those on the shelf-break and the flow is in an east-

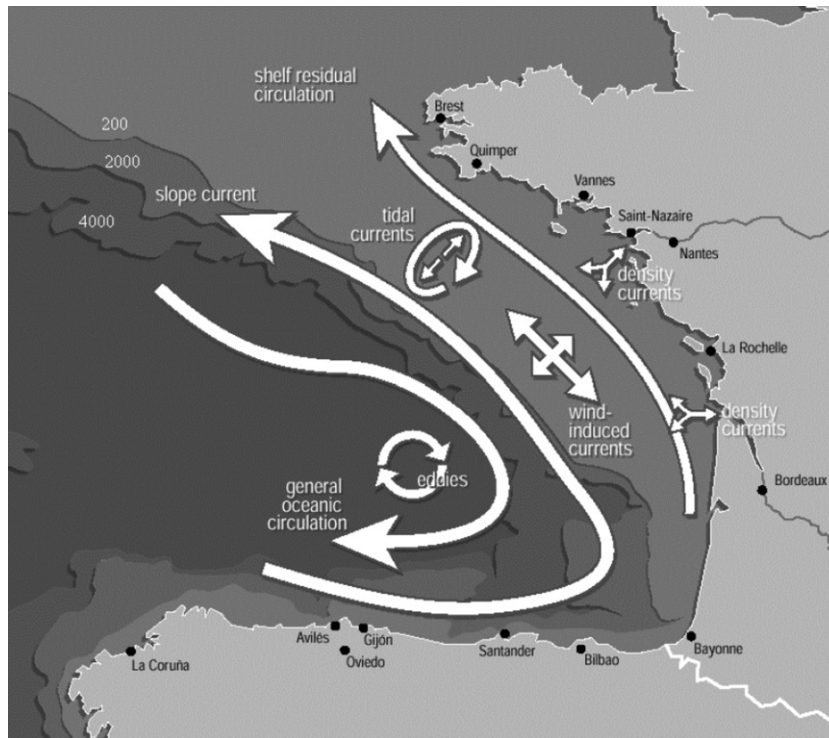


Fig. 10. Schematic illustration of Bay of Biscay circulation summarized by Kouttsikopoulos and Le Cann (1996) following OSPAR 2000.

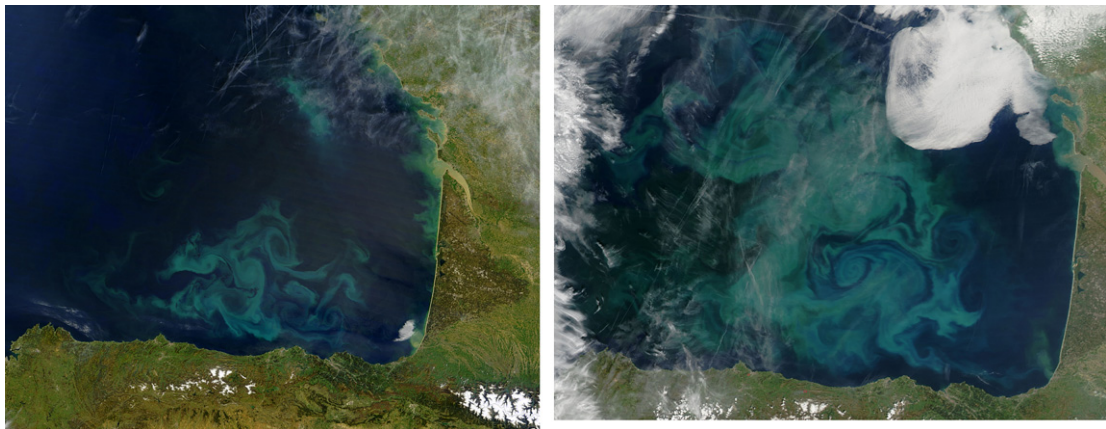


Fig. 11. Satellite images of the Bay of Biscay showing phytoplankton blooms associated to eddies in April 2004 (left) and April 2005 (right).

ward direction. In late spring and summer, prevailing winds change, being more often of an easterly component, and cause upwelling of cool water and westward flow near the sea surface south of the Bay of Biscay.

Let us underscore that drastic changes of the parameters that govern the shelf dynamics occur precisely during the anchovy spawning period (decrease of the freshwater runoff; change in dominant winds; increase of solar heating) (Kouttsikopoulos and Le Cann, 1996). Another interesting feature is that, during summer, water off the shelf in the southern part of the Bay is warmer than those in the river plumes. Therefore, in terms of temperature, growth could be better off the shelf than on the shelf. To conclude, it can be argued that larvae

advected off the French shelf should not be transported too far and can be carried back to the Northern Spanish coast or the French shelf by the current system.

6. Food concentration

Fish larvae and juvenile do need food. Plankton distribution data off the shelf in the Biscay Bay are scarce. However, from the mesozooplankton data collected during DEPM survey from 1999 to 2005 and nano-micro-

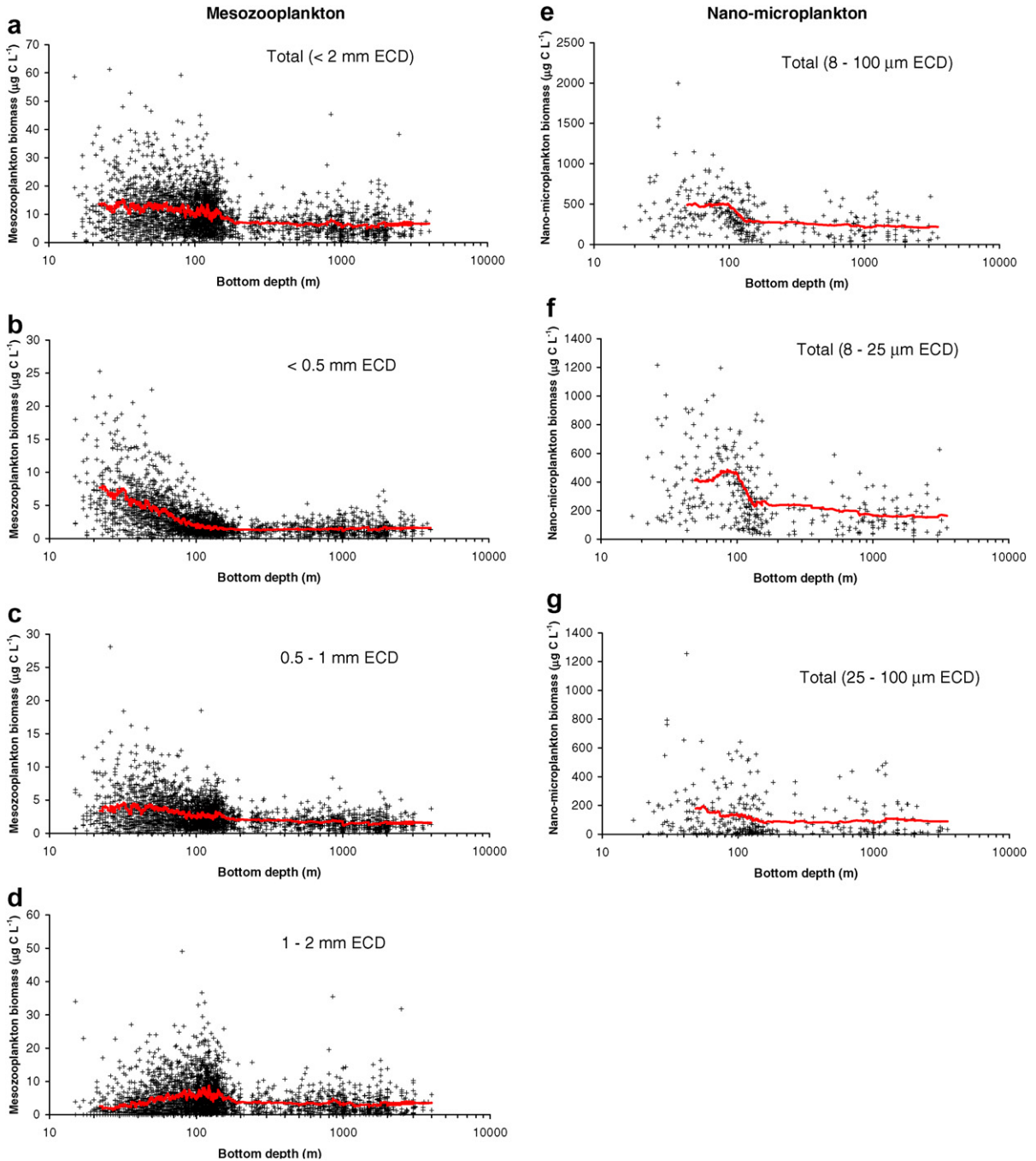


Fig. 12. Nano-microplankton and mesozooplankton concentration ($\mu\text{g C l}^{-1}$) in the Bay of Biscay as a function of bottom depth.

plankton data collected during three consecutive surveys in 2004 it can be observed that, as in other areas, in the Bay of Biscay the plankton concentration on the shelf is higher than off the shelf. In terms of mesozooplankton total biomass on the shelf is about twice that found off the shelf (average on the shelf of around 12 mg C m^{-3} against 6 mg C m^{-3} off the shelf, considering the shelf-break at 200 m depth) (Fig. 12a). However the distribution varies with size. For small mesozooplankton the concentration in coastal waters is about six times higher than off the shelf, (Fig. 12b), whereas for larger mesozooplankton the differences are much smaller, and actually for mesozooplankton between 1 and 2 mm equivalent circular diameter (ECD) the higher concentrations are found at the shelf-break, concentration in coastal waters being similar or lower to those off the shelf. In terms of nano- and microplankton the situation is similar, total concentration and that of the smaller particles is higher on the shelf than off the shelf (Fig. 12e and f). But for the largest microplankton there is a significant reduction of the difference between concentrations on the shelf and off the shelf (Fig. 12g). To our knowledge there is no published information about the diet of anchovy larvae and juveniles in the Bay of Biscay. The only study on the diet of anchovy in the Bay of Biscay was carried out on adults (Plounevez and Champalbert, 1999). Interestingly these authors find a situation where, despite total zooplankton concentration in the plume of the Gironde being twice that found off the shelf, the gut fullness index off the shelf was twice that measured in the river plume (Plounevez and Champalbert, 1999). This clearly indicates that diet is not a simple function of total food concentration, but also of food composition and probably of time allocated to feeding as a result of trade off between ingestion and risk of being predated. In addition, as they grow, anchovy larvae target larger particles (Conway et al., 1998; Schmitt, 1986). Therefore, the differences in available and suitable prey field for the larvae on the shelf and off the shelf waters decreases with age. Furthermore, off the shelf waters in the Bay of Biscay are often enriched by eddies pumping deep waters to the surface. This stimulates primary production inside the eddies (Fig. 11), and increases zooplankton densities (Fernandez et al., 2004). Actually, because eddies are often generated at the shelf-break the zooplankton community inside the eddies differs by containing a high percentage of species typical for the shelf (Fernandez et al., 2004). That is, although waters off the shelf certainly present lower food concentrations, old larvae and juveniles would not find themselves in an extreme oligotrophic environment.

7. Distribution of potential predators

There is an apparent contradiction between tuna migration into the Bay of Biscay off the shelf waters during the recruitment to juvenile period and the proposed loophole concept of lower predation rates. However the risk of predation by tuna has to be evaluated in relation to three factors: (1) tuna off the shelf are likely to prefer juveniles to larvae (3–13 cm range with preference for 4–5 cm, Ortiz de Zárate and Cort, 1986). So it is after a certain growth that anchovy become a target for tuna, when approaching sizes and swimming capacities that allow a gradual return to the shelf as suggested by Uriarte et al. (2001).

(2) On the other hand the shelf is occupied by a large concentrations of planktivorous fish such as mackerel, horse mackerel, sprat, sardine and anchovy itself, all potential predators on anchovy eggs and larvae (Cabral and Murta, 2002; Olaso et al., 1999; Assis et al., 1992; Szeinfeld, 1991; Valdés et al., 1987; Alheit, 1987; Macpherson, 1979). As an example, Szeinfeld (1991) estimated that up to 56% of the total anchovy egg mortality in South African waters was the result of sardine predation. In addition some of the pelagic (e.g. horse mackerel) and demersal fish such as hake predate on anchovy juveniles (Olaso et al., 1999; Guichet, 1995). More importantly, the spawning period for some of these species inhabiting the shelf is earlier than that of anchovy (Ibarrriaga et al., 2007), and the larvae and juveniles of these species can be active predators of the newly born anchovies. For example, the larvae of mackerel begin feeding on fish larvae as soon as they reach 5–6 mm (Fortier and Villeneuve, 1996; Conway et al., 1999). So, the potential predators are not only the adult fish, but also the early stages of those born before. To that, one needs to add cannibalism by anchovy itself on eggs and larvae (Valdés et al., 1987; Takasuka et al., 2004). Szeinfeld (1991) estimates the 6% of anchovy egg mortality in South African waters was due to cannibalism. Interestingly, Takasuka et al. (2004) find that size-selective mortality of anchovy larvae was directed negatively for cannibalism by anchovy juveniles and positively for predation by skipjack tunas. That is, the cannibalised larvae had lower growth rates than the larvae from the original population in the same larval size range but on the other hand, a similar comparison showed no differences in larval growth rates for predation by skipjack tunas. If the same applied to tuna and anchovy in

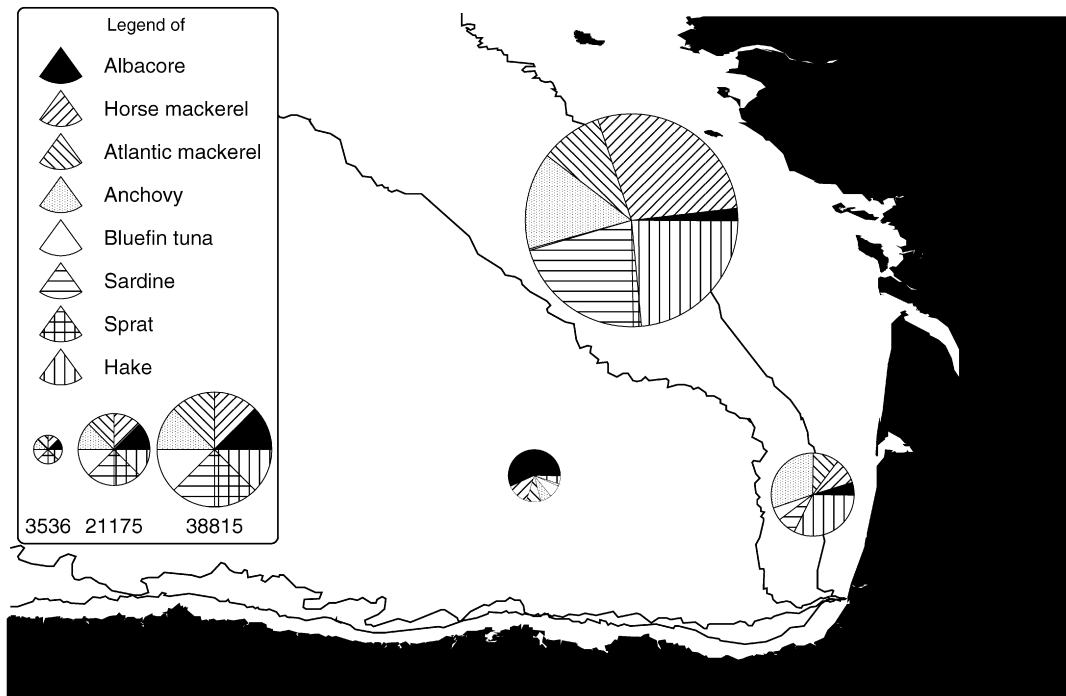


Fig. 13. Average (1973–2004) landings in tonnes per ICES area (VIIIa, VIIIb and VIII d). Source: ICES catches data base.

the Bay of Biscay fast growing larvae would have lower mortality on the shelf where intraguild predation and cannibalism dominates. But, off the shelf, where tuna dominate, mortality would be less related to the growth rate, and therefore food availability would have a lower impact on the survival.

(3) The biomass of the potential predators on the shelf is significantly larger than that of the tuna population migrating into the Bay of Biscay during summer. Considering only the landings of commercial species recorded (which excludes juveniles of the different species and does not include the bias of targeted fisheries), catches over the shelf areas (ICES areas VIII a and b) are 10 to 3 times higher than those off the shelf (ICES area VIII d) (Fig. 13). For potential predators on anchovy egg and larvae (as sardine, mackerel or horse mackerel) where independent estimates of biomass over the Cantabrian and French shelf regions exist (acoustic surveys) the populations are often about 10 times larger than the anchovy population (ICES, 2005, 2006).

8. Modelling the loophole

Growth (or feeding) and predation risk is usually viewed as conflicting processes, increased growth often comes at the cost of increased risk of predation. This trade-off can be either behavioural, where foraging activities involve some increase in risk of encountering predators (McNamara and Houston, 1987; Lima and Dill, 1990) or physiological, if high growth rates reduce prey escape abilities in some way (Billerbeck et al., 2001; Lankford et al., 2001). Alternatively – and consistent with the ‘loophole’ concept, it may be viewed as a trade-off faced by spawners between placing eggs and larvae in regions with high growth and predation rates versus regions with low growth and predation rates. If larval behaviour determines drift routes, then the dilemma applies to larvae and the relevant behavioural traits (swimming, vertical positioning) are subject to natural selection.

To illustrate this point we have developed a simple model of a larva in different environmental types. We applied the growth model for larval fish developed by Fiksen and Folkvord (1999), where growth is a satiating function of daily food ration:

$$g(i, T) = K(T)(1 - e^{-\beta i}) - r_0(T), \quad (1)$$

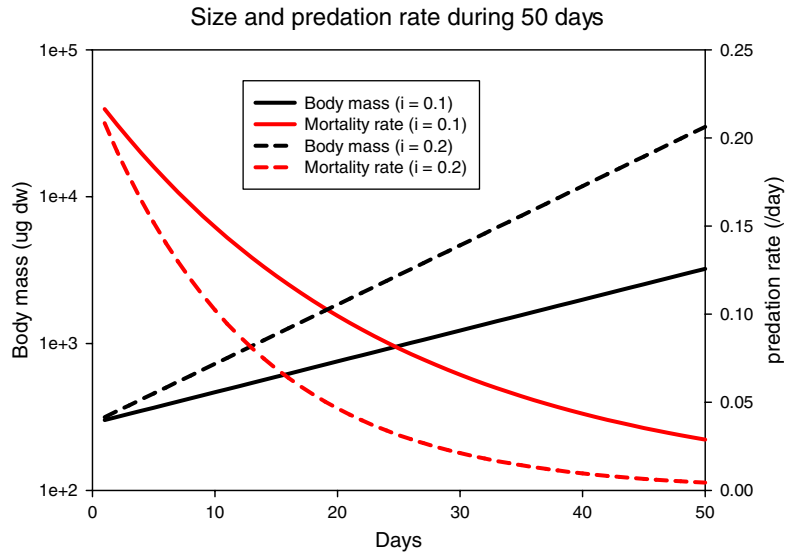


Fig. 14. An illustration of size-development and instantaneous mortality rate over 50 days using Eqs. (1) and (2). The difference recruitment success measured as the probability of survival to a given size would be significant between these two scenarios ($i = 0.1$ and $i = 0.2$).

where T is temperature, $K(T)$ limited growth, $r_0(T)$ metabolic rate, and β is a shape constant. Because data on anchovy physiology are scarce, we have used the same values as in [Fiksen and Folkvord \(1999\)](#), therefore, our modelled anchovy is physiologically a herring. The daily ration (i) in fractions of body mass determines growth rates at any given temperature. In addition, the rate of mortality (day^{-1}) in larval fish is typically dropping rapidly with size (W_g ; g dry body mass, [McGurk, 1986](#)):

$$\mu(W) = 2.2 \times 10^{-4} W_g^{-0.85}. \tag{2}$$

A simple realisation of body mass and instantaneous mortality rate over 50 days with ration = 0.1 and 0.2 are presented in [Fig. 14](#). This illustrates the benefit of rapid growth, or high food intake if there is no connection between ingestion rate and mortality, and is the traditional argument of why recruitment success is sensitive to growth rates.

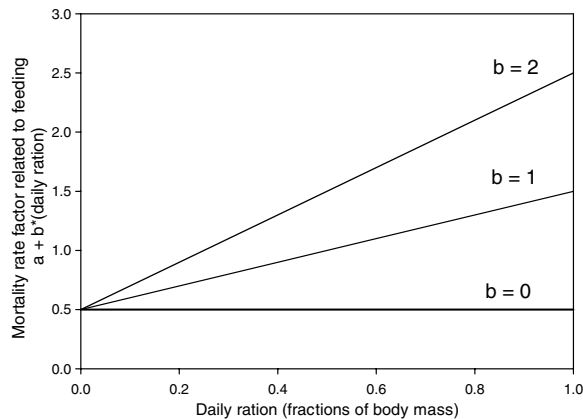


Fig. 15. Various scenarios of the relationship between feeding and mortality rate. Here, the factor $a + bi$ is multiplied with the size-dependent mortality rate ([McGurk, 1986](#)) to mimic cases where increased daily ingestion rates are associated with risk.

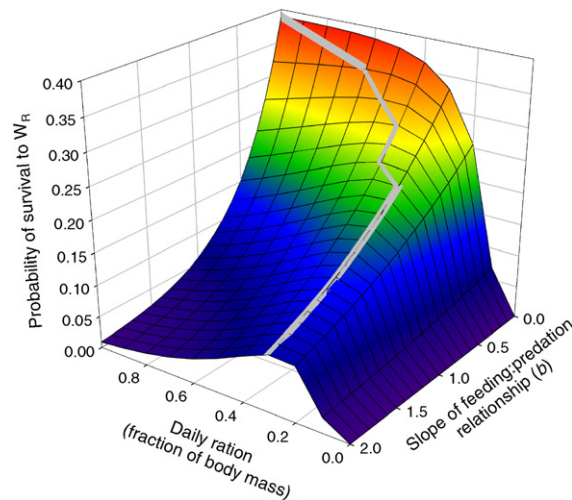


Fig. 16. The probability of survival (from 0.28 mg dw) to a given size ($W_R = 0.1$ g dw) for larval fish under combinations of daily food rations and relations between feeding and mortality rates. When feeding and mortality are correlated, survival to a given size is maximised at relatively low food intakes (grey line).

If, however, feeding is positively related to predation risk, due to behavioural, physiological or through spatial correlations between food and predator abundance, then Eq. (2) must be modified:

$$\mu(i, W) = (a + b \cdot i) \cdot 2.2 \times 10^{-4} W_g^{-0.85}. \quad (3)$$

In this case, the factor b determines the strength of the linkage between feeding opportunities and predation rate, while a simply scales the overall level of mortality (Fig. 15).

The degree of correlation between feeding and mortality determines at which level of food intake survival to a given size is maximised (Fig. 16). At strong correlations (high values of b) survival peaks at lower foraging efforts or in regions with low food and predator abundance. The ‘loophole-strategy’ would then be to have low rations (but not too low), slower growth, but at lower mortality rates.

9. Discussion

At least three distinct zooplankton communities (river plume, mid-shelf and shelf-break) can be found across the shelf (Albaina and Irigoien, 2004) in front of the Gironde. This horizontal segregation of the zooplankton communities shows that physical processes, probably related to the vertical structure such as internal waves (Pingree et al., 1986) can be retention mechanisms on the shelf. As observed for other anchovy species (Hewitt, 1981a,b; Hunter and Coyne, 1982; Vasconcellos et al., 1998), *E. encrasicolus* in the Bay of Biscay initiate schooling behaviour between 10 and 15 mm in length (Etxebeste et al., 2007). This indicates that at a relatively early stage the swimming capacity of anchovy is significant and sufficient to actively use physical retention mechanisms as do zooplankton. The fact that old anchovy larvae are found off the shelf whereas the zooplankton characteristic from its spawning habitat remains in the plume area suggests that anchovy do not suffer the same evolutionary pressure on behavioural mechanisms favouring retention. That difference in evolutionary pressure could be explained by higher success off the shelf, through what we have called a spatial loophole.

The observations reported here do not allow rejection of the hypothesis that anchovy in the Bay of Biscay might be recruiting through such a spatial loophole. The size and abundance distribution of larvae and juveniles (smaller larvae on the shelf and larger ones off the shelf and viceversa for juveniles) strongly suggests off-shore transport of the larvae and return by the juveniles. As the size–age relation shows, this is not due to differential growth on and off the shelf and this pattern has now been observed for several years (Juesu and Juvena campaigns, 1998, 1999, 2003, 2004, 2005; Uriarte et al., 2001 and Boyra et al., 2005; unpublished).

Furthermore, the annual migration of albacore and bluefin tuna in off-shelf waters of the Bay of Biscay coincide with the anchovy recruitment period and the areas where the bulk of juveniles are caught as live bait. This is a recurrent pattern and indicates that the percentage of anchovy leaving the shelf must be significant. In any case the biological production of the waters off the shelf during that period has to be relatively high if able to influence the migration of large predators such as tuna (Sagarminaga and Arrizabalaga, 2006). The general circulation in the Bay of Biscay is slow (Pingree and Le Cann, 1990) and includes mechanisms such as the off the shelf counter-current that limit advection and could even favour return to the southern French and Cantabrian shelf. Without taking into account modulating factors such as prey selection effects (Plounevez and Champalbert, 1999), enrichment due to eddies (Fernandez et al., 2004) and the switch to larger prey as the larvae grow, the food concentration available for the larvae off the shelf would be roughly half that on the shelf. This is a significant difference in potential food concentration but it does not attain order of magnitude differences expected in truly oligotrophic waters. Furthermore, the model illustrates a point often ignored in fisheries science: if feeding is positively connected to predation risk, due to behavioural or physiological mechanisms or through spatial correlations between food and predator abundance, survival to a given size is maximised at lower rations. In fact, the best indication of the profitability of the off-shelf strategy is the fact that juveniles found off the shelf are alive and have size at age not different from those found on the shelf.

Do these observations imply that all the anchovy recruitment in the Bay of Biscay occurs through the spatial loophole described previously? Certainly not. Our age–size observations show no difference on and off the shelf, and contradicts predictions from an individual based modelling exercise suggesting significant growth differences (Allain et al., 2003). It remains certain that more food is available on the shelf. The lack of difference in size at age between individuals captured on and off the shelf could be due to several reasons: (1) a majority of the population moving in and out which would result in a homogeneous pattern for the population, (2) temperature dependent growth would reduce differences since water in the river plumes are colder than in oceanic areas during summer, (3) a behavioural interaction between feeding and predation risk as suggested by our model, (4) a combination of these factors with individuals moving through areas with different temperature, food and predation risk. The results from Etxebeste et al. (2007), showing small to non-significant differences in the recent growth for larvae collected in the different areas, suggest that there are not remarkable differences in the growing conditions between areas. (5) positive size-dependence in predation risk on-shore could lead to under-estimation of growth in this region. Increasing predation rates with size is likely for prey of planktivorous fish (abundant in on-shelf areas), since larger larvae tend to be detected at greater distance (Folkvord and Hunter, 1986).

Furthermore, the anchovy population in the Bay of Biscay is relatively isolated from other populations (the closest large population is in the Bay of Cadiz) and it can be considered as self-sustained. In variable environments such as Bay of Biscay, genetic lineages that put “all their eggs in one basket” too often run high risk of extinction. In these variable environments, ensuring that some offspring always survive (even in bad years) is a winning strategy. It is likely that there are a variety of zones and conditions to recruit on and off the shelf, and probably the areas and conditions vary depending on the environmental conditions (transport, temperature and abundance of predators). If off-shelf regions are more risky than on-shelf regions in terms of losing all the eggs, then a spawning strategy where eggs are spread to different regions may be selected for. Actually, what the model developed here indicates, is not that the recruitment occurs at certain point of the ingestion–predation space, but that there are various combinations of food and predatory risk that allow relatively good recruitment – depending on the nature of the feeding-to-risk relationship. Although commonly associated in behavioural ecology, fishery science has often carried out sensitivity analyses on growth and mortality rates, but rarely connected them. However, what the review presented here clearly indicates is that studies investigating recruitment should not consider food independently of the associated risk of predation.

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