

THE BIOLOGY AND FISHERIES OF EUROPEAN HAKE, *MERLUCCIOUS MERLUCCIOUS*, IN THE NORTH-EAST ATLANTIC

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Abstract

The aim of this chapter is to review the biology and fishery, including the management, of European hake in the north-east Atlantic. The European hake is widely distributed throughout the north-east Atlantic, from Norway in the north to the Guinea Gulf in the south, and throughout the Mediterranean and Black Sea, being more abundant from the British Isles to the south of Spain. In this area, ICES (International Council for the Exploration of the Sea) recognises the existence of two stocks: the northern stock and the southern stock. Both stocks have been extensively and intensively harvested and since the beginning

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of the 90s have been considered to be outside safe biological limits. The northern stock, however, is currently considered to lie within safe biological limits. In any case, recovery plans were implemented for the northern stock in 2004 and for the southern stock in 2006. Despite its commercial importance, knowledge of the biology and ecology of the European hake in the North Atlantic is still quite scarce. For example, recent investigations suggest that European hake grows much faster, by a factor of two, than was considered previously. This faster growth also affects the maturity-at-age pattern of hake and the agreed maturity-at-age ogive used in the assessments. European hake is a top predator in the demersal community in the north-east Atlantic area; mainly preying on blue whiting, horse mackerel and other cupleids. In relation to the reproductive biology, European hake is considered to be a batch spawner species with indeterminate fecundity and spawning activity all year round. All these characteristics could, in turn, be interpreted as European hake adopting a more opportunistic life strategy, which is unusual for a gadoid and demersal species, and raises several questions about hake biology and ecology that require further investigation.

1. INTRODUCTION

1.1. Classification and the origin of ‘hake’

According to the *American Heritage Dictionary of the English Language*, the word ‘hake’ originated from the Old or Middle English word ‘haca’; this means ‘hook’, and defines the form of the shape of its lower jaw. The term ‘hake’ mainly refers to fish of the genera *Merluccius*, although other cod-like fish are also known as hake, for example, fishes of the genera *Urophycis* (Flick *et al.*, 1990; Pitcher and Alheit, 1995).

The first reference to fish of the actual genera *Merluccius* is found in the book *De aquatibus* by Belon (1553), where a fish of the name ‘Marlutiu vulgari’ was described. The origin of the name *Merluccius* came from the Latin name ‘Marlutiu’ and was described by Belon, who denominated the fish, actually known as *Merluccius merluccius*, as ‘Marlutiu’—Maris lucium—(Mar: sea; lutiu: pike), due to its similar appearance to pike (Fig. 2.1).

In the ‘Sistema Naturae’, the binomial system of nomenclature developed in the mid 1700s by Carlo Linnaeus, ‘Marlutio vulgari’ was described and classified as *Gadus merluccius*; this was included within the Family Gadidae and the genus *Gadus*, which is closely related to other cod species. This species was raised to the rank of genus by Rafinesque (1810), who first described the genus *Merluccius* based upon the type species *M. smiridus* (the actual *M. merluccius*) inhabiting the north-east Atlantic. The type species used to describe the genus *Merluccius* for the first time was the same fish first described by Belon (1553), that is, Marlutio vulgari.

DE AQUATILIBVS LIB. I.

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Hepar in duos lobos distinctum. Stomachus oblongus, innumeris appendicibus ad pilorum circumseptus, à quo ieiunum oritur, laxum ac pallidum, de quo item Ileon duobus semicirculis ad rectum descendens, gracile id quidem ac rubicundum. Folliculum itē habet candidissimum, spiræ annexum, quo in natatione plurimū adiuuatur. Calculos in capite duos cādidos habet: iis propemodum similes qui in Sparo reperiuntur. Cæterū Atherinis ac delectamentis marinis, vt & Gobionibus vefcitur.

Οὐραος, Græcis: Latinis, Afellus: Vulgo, Marlucius: Genuensibus,
Nafello: Romanis, Merluçço.

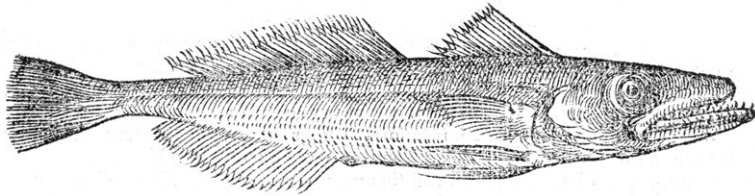


Figure 2.1 Figure of *Marlutio vulgari* first described in the book *De Aquatibus* by [Belon \(1553\)](#). Reproduced with the permission of Goettingen State and University Library as the holder of the original *De Aquatibus*—[Belon \(1553\)](#).

However, at that time, all the known species of the genus *Merluccius* were included within the Family Gadidae; they were raised to the rank of Family and included in the family Merlucciidae by [Adams \(1864\)](#). The characteristics of the Family Merlucciidae were described by [Gill \(1884\)](#) as ‘Gadidae with a moderate caudal region coniform behind and with the caudal rays procurrent forward, the anus sub-median, moderate sub-orbital bones, terminal mouth, sub-jugular ventrals; dorsal double, a short anterior and long posterior one, a long anal corresponding to the second dorsal; ribs wide, approximated and channeled below or with inflected sides and paired excavated frontal bones with divergent crests continuous from the forked occipital crest’.

In recent times, [Cohen et al. \(1990\)](#) included four genera in the Family Merlucciidae: the abovementioned *Merluccius* ([Rafinesque, 1810](#)), *Macruronus* ([Günther, 1873](#)), *Lyconus* ([Günther, 1887](#)) and *Steindachneria* ([Goode and Bean, 1896](#)). The first three belong to the sub-Family Merlucciinae, with the last under the sub-Family Steindachneriinae. In contrast, [Lloris et al. \(2003\)](#) presented a different classification, where the Family Merlucciidae was divided into five genera (*Merluccius*, *Macruronus*, *Lyconus*, *Lyconodes* and *Steindachneria*) included in three sub-Families (Merlucciinae, Macruroninae and Steindachneriinae). The differences in the latter approach are that a new sub-Family is described (Macruroninae) which included three genera (*Lyconus*, *Lyconodes* and *Macruronus*); furthermore, only the genus *Merluccius* belonged to the sub-Family Merlucciinae. Nevertheless, the evolutionary status of the Family Merlucciidae is still a subject of debate among fish taxonomists in relation to the extent of the Family or the phylogenetic

relationships between different genera of the Family, or the inclusion, or not, within the Family Gadidae.

Regardless of such past and ongoing extensive debates, that is, to provide Merlucciidae with a Family status or locate it under the Family Gadidae, most authors give a Family rank to Merlucciidae, including the genus *Merluccius* within this Family. In fact, there are 13 recognised species of the genus *Merluccius*, which makes it the most diverse genus within the Merlucciidae Family (Table 2.1). Apart from the 13 recognised species, Mathews (1985) postulated a new species, *M. hernandezi*, separated from *M. angustimanus*. However, most recent authors considered this species as a sub-population of *M. angustimanus* (Lloris *et al.*, 2003).

The distribution of the extant species of the genus *Merluccius* is very broad, spanning the continental shelves and slopes of most of the world's temperate and subtropical regions (Cohen *et al.*, 1990). They are distributed throughout both sides of the Atlantic, along the north-eastern and south-eastern, and north-western and south-western Atlantic, the Mediterranean Sea and the Red Sea; along the eastern Pacific Ocean and off southern New Zealand. There have also been isolated observations in the Indian Ocean off the south and south-east of Madagascar (Lloris *et al.*, 2003; Fig. 2.2). The distribution of extant hake occurs in both the northern and southern hemisphere, showing an antitropical distribution (Grant and Leslie, 2001).

1.2. Phylogeny and biogeography of hake

Although there is not yet a general consensus, various hypotheses have been proposed in relation to the phylogeny and biogeography of hake. The hypotheses presented up until now were based upon studies using different approaches, such as ichthyological information (Inada, 1981), parasitological information (Fernández, 1985; Kabata and Ho, 1981; Szidat, 1955), cladistic analysis (Ho, 1990) and the most recent ones based upon genetic studies (Grant and Leslie, 2001; Quinteiro *et al.*, 2000; Roldán *et al.*, 1999; Stepien and Rosenblatt, 1996).

Most of the authors proposed a north-eastern Atlantic ancestor for the genus *Merluccius*; this diverged into two major *Merluccius* lineages which evolved independently: one along the west coast of Europe and the other along the east coast of America to the Pacific, through the Panama seaway. However, there were some major discrepancies between the different views in relation to the evolution of these two major lineages. The exceptions to this general theory were proposed by Szidat (1955, 1961) and Ho (1974, 1990). For example, based upon the distribution of hake parasites, Szidat (1955, 1961) suggested a north Pacific origin, whereas Ho (1974) proposed a western Atlantic origin for *Merluccius* species.

In contrast to latter proposals, Inada (1981) and Kabata and Ho (1981) proposed two different hypotheses for the origin and biogeography of hake;

Table 2.1 Actually recognised species of the genus *Merluccius*, their distribution as well as the common name

Scientific name	Described by	Common name	Distribution	Latitude
<i>Merluccius albidus</i>	Mitchill (1818)	Offshore hake	North-west, Central-west Atlantic	20–35° N
<i>Merluccius angustimanus</i>	Garman (1899)	Panama hake	North-Central east Pacific	5–23° N
<i>Merluccius australis</i>	Hutton (1872)	Southern hake	South-east and South-west Pacific	South of 51° S
		Austral hake		40–57° S
		Antarctic queen hake		South of 40° S
		New Zealand hake		
<i>Merluccius bilinearis</i>	Mitchill (1814)	Silver hake	North-west Atlantic	36–47° N
<i>Merluccius capensis</i>	Castelnau (1861)	Cape hake	South-east Atlantic	0–34° S
		Shallow-water hake		
<i>Merluccius gayi</i>	Guichenot (1848)	Chilean hake	South-east Pacific	23–47° S
		Peruvian hake		3–10° S
<i>Merluccius hubbsi</i>	Marini (1933)	Argentine hake	South-west Atlantic	25–54° S
<i>Merluccius merluccius</i>	Linnaeus (1758)	European hake	North-east Atlantic	21–62° N
<i>Merluccius paradoxus</i>	Franca (1960)	Deepwater Cape hake	South-east Atlantic	South of 22° S
		Deepwater hake		
<i>Merluccius patagonicus</i>	Lloris and Matallanas (2003)	Patagonian hake	South-west Atlantic	45–49° S
<i>Merluccius polli</i>	Cadenat (1950)	Benguela hake	South-east Atlantic	20° N–19° S
<i>Merluccius productus</i>	Ayres (1855)	Merluza norteña	North-east Pacific	25–51° N
		North Pacific hake		
		Pacific hake		
		Pacific whiting		
<i>Merluccius senegalensis</i>	Cadenat (1950)	Senegalese hake	South-east Atlantic	10–33° N

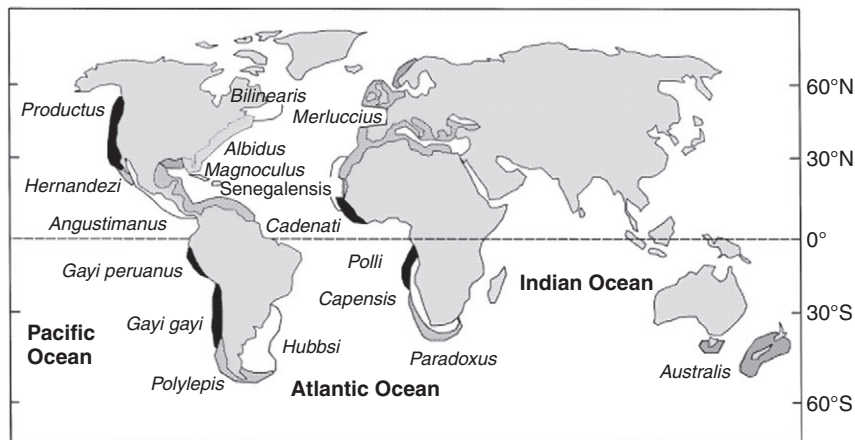


Figure 2.2 Geographical distribution of hakes (genus *Merluccius*); reproduced from Grant and Leslie (2001).

these were similar in the major points of discussion. For example, both views postulated an eastern North Atlantic origin of hake, with *M. merluccius* considered as the most ancestral; this was followed by a southward dispersal in two directions (see above). Hake entered the Pacific through the Panama seaway, before the formation of the Panama Isthmus. However, these authors did not agree in relation to the origin of the Argentine hake *M. hubbsi*. Inada (1981) suggested a south-western Pacific origin for Argentine hake around Cape Horn, whereas Kabata and Ho (1981) proposed that Argentine hake were derived from the western North Atlantic; this was based upon the dissimilarities between Argentine hake and Pacific hake parasites. Other studies utilising the distribution of parasites approach were in agreement with the conclusion of Kabata and Ho (Fernández, 1985).

More recently, Ho (1990) undertook a revision of Inada's study using cladistic analysis; this model suggested a western North Atlantic origin of hake, with *M. albidus* being the most ancestral hake species. This ancestral species vicariated in two lineages; one following a northwards dispersal, forming the north-western Atlantic and Pacific species, and the another migrating along South America and then dispersing eastwards across the tropical Atlantic to Africa, whose descendants gave rise to all extant hake in the western South Atlantic and the eastern Atlantic. In contrast to the findings of Inada (1981) and Kabata and Ho (1981), the phylogenetic results of Ho (1990) considered *M. merluccius* as the most recent species and therefore, it could not be considered as the ancestral species. Moreover, Ho (1990) agreed with the postulated western North Atlantic origin of Argentine hake by Kabata and Ho (1981), but differed with the postulated derivation from the eastern South Pacific (Inada, 1981).

Furthermore, [Roldán *et al.* \(1999\)](#), in a similar way to [Ho \(1990\)](#), based on genetic studies of nine out of the 13 recognised species, concluded that *M. merluccius* is the most recent derivation of the Euro-African species. As such, these authors supported an eastern Atlantic warm-water origin, beyond the eastern North Atlantic origin postulated by [Inada \(1981\)](#) and [Kabata and Ho \(1981\)](#). However, the findings of [Roldán *et al.* \(1999\)](#) disagreed with Ho's proposed origin (1990) of the genus within western Atlantic warm waters; this was because they postulated that *M. polli* and *M. paradoxus* in the eastern Atlantic as the descendants of an early Old-World *Merluccius*. On the contrary, [Ho \(1990\)](#) considered *M. albidus* as the direct descendant of hake ancestors.

Recently, [Grant and Leslie \(2001\)](#) presented a comprehensive genetic study with regard to the origin and biogeography of hake. New genetic data were presented, as well as the revision of data published by [Roldán *et al.* \(1999\)](#), [Stepien and Rosenblatt \(1996\)](#) and [Quinteiro *et al.* \(2000\)](#).

Figure 2.3 of [Grant and Leslie \(2001\)](#) shows hake phylogenetic tree summarising their phylogenetic and biogeography hypothesis. In agreement with previous authors, [Grant and Leslie \(2001\)](#) proposed a fundamental subdivision between Euro-African and American (including South Pacific) hake species, identifying them as Old-World and New-World taxa, respectively. This proposed division would have occurred in the Miocene

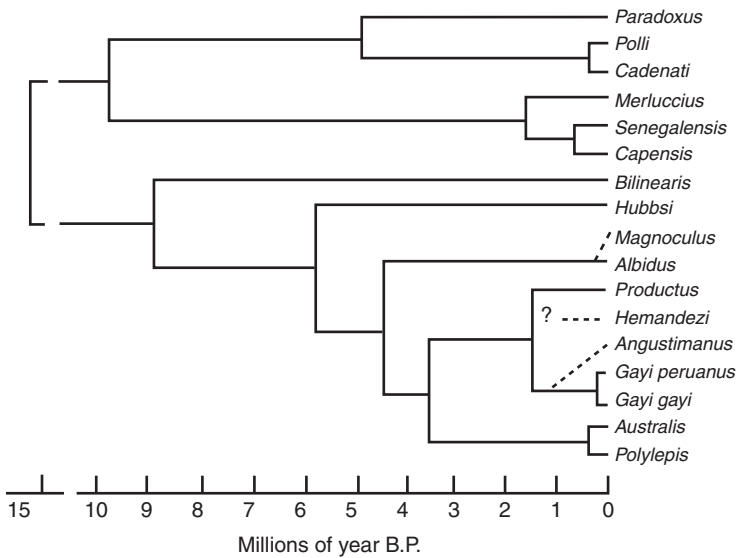


Figure 2.3 Phylogenetic hypothesis of hakes (genus *Merluccius*) based on all available data ([Grant and Leslie, 2001](#); [Roldán *et al.*, 1999](#); [Stepien and Rosenblatt, 1996](#); reproduced from [Grant and Leslie, 2001](#)).

10–15 Ma (million years ago). Furthermore, these authors divided the Old-World species into two sub-groups: *M. Paradoxus*, *M. polli* and *M. cadenati* formed one group, whereas *M. merluccius*, *M. senegalensis* and *M. capensis* belonged to the second group. This division supported the findings of [Roldán et al. \(1999\)](#). With regard to the relationships between the New-World species, these investigations reported that *M. bilinearis* is the most distant species, or the first descendant of the ancestor of the New-World species, followed by *M. hubbsi* and *M. albidus*. The rest of the four main species (*M. gayi*, *M. productus*, *M. polylepis* and *M. australis*) formed a group of derived species, with the first two and last two being sister species, respectively. A similar phylogenetic tree, with respect to the New-World species, was also found by [Roldán et al. \(1999\)](#).

The phylogenetic tree, in which all the taxa are identified and positioned in a hierarchical system of sister species, is a necessary step towards creating robust biogeographical models. [Grant and Leslie \(2001\)](#) postulated the most recent, and probably the most plausible, biogeographical hypothesis for the origin of hake by using such a phylogenetic tree. In agreement with most of the authors, they proposed a north-eastern Atlantic origin of hake, where the shallow epicontinental seas between Europe and Asia were occupied by ancestral *Merluccius*. Evidence of a north-eastern Atlantic-Arctic origin of the genus *Merluccius* was provided when fossils of *Merluccius* appeared in Middle and Upper Oligocene sediments in Europe ([Fedotov, 1976](#); [Inada, 1981](#); [Kabata and Ho, 1981](#); [Svetovidov, 1948](#)). In other words, these authors hypothesised a North Atlantic origin of hake ancestors which gave rise to the lineages of the Old- and New-World hake.

The results of [Grant and Leslie \(2001\)](#) are in agreement with most of the biogeographical models, such as those of [Kabata and Ho \(1981\)](#), [Inada \(1981\)](#) and [Fernández \(1985\)](#); whereas they are in disagreement with those of [Szidat \(1961\)](#), [Ho \(1990\)](#) and [Roldán et al. \(1999\)](#). Nevertheless, the genetic evidence, in addition to the European fossil record for hake, places the balance of evidence in favour of a North Atlantic origin of hakes.

[Grant and Leslie \(2001\)](#) postulated different tectonic and oceanic events to explain the divergence of hake ancestors into two different lineages, that is, the eastern Atlantic or Old-World hake and the western Atlantic-Pacific or New-World hake. On the one hand, there was the separation of the tectonic plates of Europe and North America and the subsequent expansion of the North Atlantic basin ([Van Andel, 1976](#)), and on the other, there was the cooling of North Atlantic waters which started in the Oligocene and finished in the mid-Miocene, around 15 Ma ([Savin et al., 1975](#)). The cooling of continental waters acted as a precursor for the southwards migration of the ancestral hake distribution, along the western and eastern Atlantic; this was facilitated by the expansion of the North Atlantic basin ([Grant and Leslie, 2001](#); [Fig. 2.4](#)).

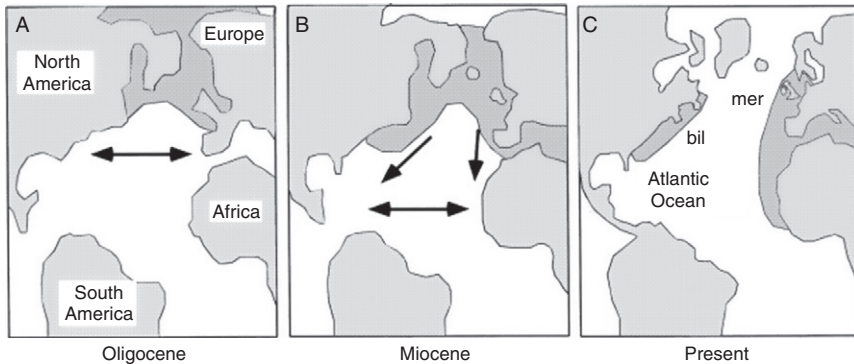


Figure 2.4 Theory for the initial separation of the hake ancestor in two different lineages, that is, Old- and New-world hakes (reproduced from [Grant and Leslie, 2001](#)).

Contrary to the publications of [Kabata and Ho \(1981\)](#) and [Inada \(1981\)](#), who suggested that African hake species originated from the north-eastern Atlantic ancestors as the hake moved southwards, [Grant and Leslie \(2001\)](#) proposed two different lineages within European and African hake; this was based upon their phylogenetic tree of sister taxa and two different radiations of ancestral *M. merluccius*. In the first radiation, during the mid-Miocene and around 10–15 Ma, an early *M. paradoxus* was established; it dispersed northwards to form the population of *M. cadenati* in the late Miocene or early Pliocene. From this population, a recent southerly displacement led to the origination of the last species of the ‘paradoxus’ lineage (*M. polli*) ([Fig. 2.5](#)). In the second radiation, the ancestral *M. merluccius* spread southwards to form the cape hake, *M. capensis*, which later back distributed northwards to give rise to *M. senegalensis* around 2 Ma (the ‘capensis’ lineage).

The origin and dispersal of the American hake species, as presented by [Grant and Leslie \(2001\)](#), are similar to the zoogeographical models presented by previous authors ([Ho, 1990](#); [Inada, 1981](#); [Kabata and Ho, 1981](#); [Roldán et al., 1999](#)). With the exception of [Kabata and Ho \(1981\)](#), who considered *M. albidus* the ancestor of all extant hake, all of these investigations considered *M. bilinearis* as inhabiting the north-western Atlantic and being the most ancient precursor of the New-World hake species. Regardless of which species was the ancestor, all of the authors proposed that the ancestor of American hake moved through the submerged Panamanian Isthmus in the mid-to-late Miocene to establish the eastern Pacific species (*M. gayi*, *M. productus*, *M. albidus* and *M. angustimanus*); this was before the closure of the Panamanian Isthmus around 3.5 Ma ([Keigwin, 1978, 1982](#)). However, [Grant and Leslie \(2001\)](#) proposed a slightly different scenario, whereby the ancestor *M. bilinearis* gave rise to *M. productus*, *M. gayi* and *M. albidus*, and then *M. gayi* subsequently became the ancestor of *M. angustimanus*, moving back towards the north ([Fig. 2.6](#)).

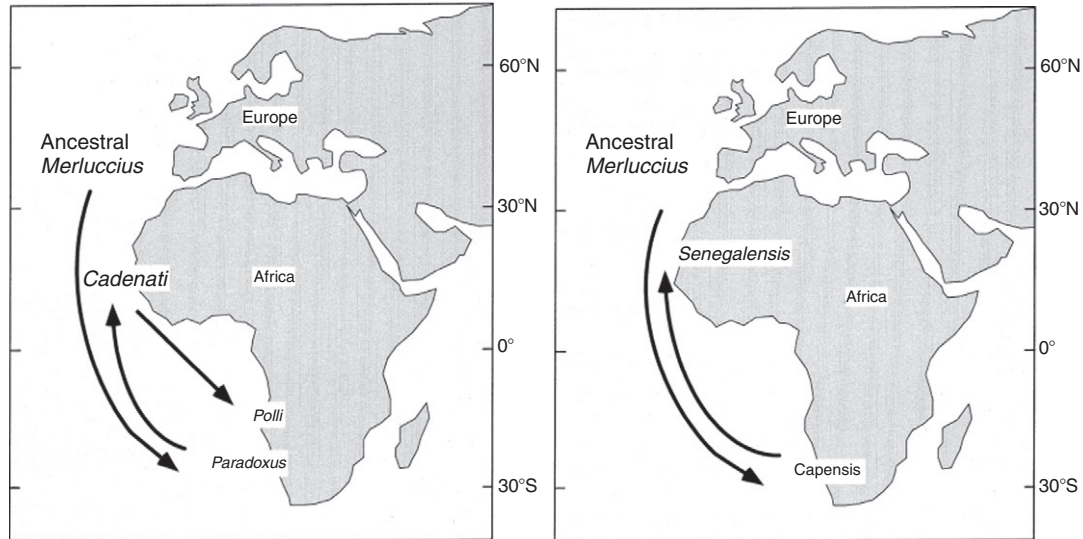


Figure 2.5 Geographical reproduction of the dispersal of hake ancestor in the North-east Atlantic postulated by [Grant and Leslie \(2001\)](#): the 'paradoxus' lineage (left) and the 'capensis' lineage (right) (reproduced from [Grant and Leslie, 2001](#)).

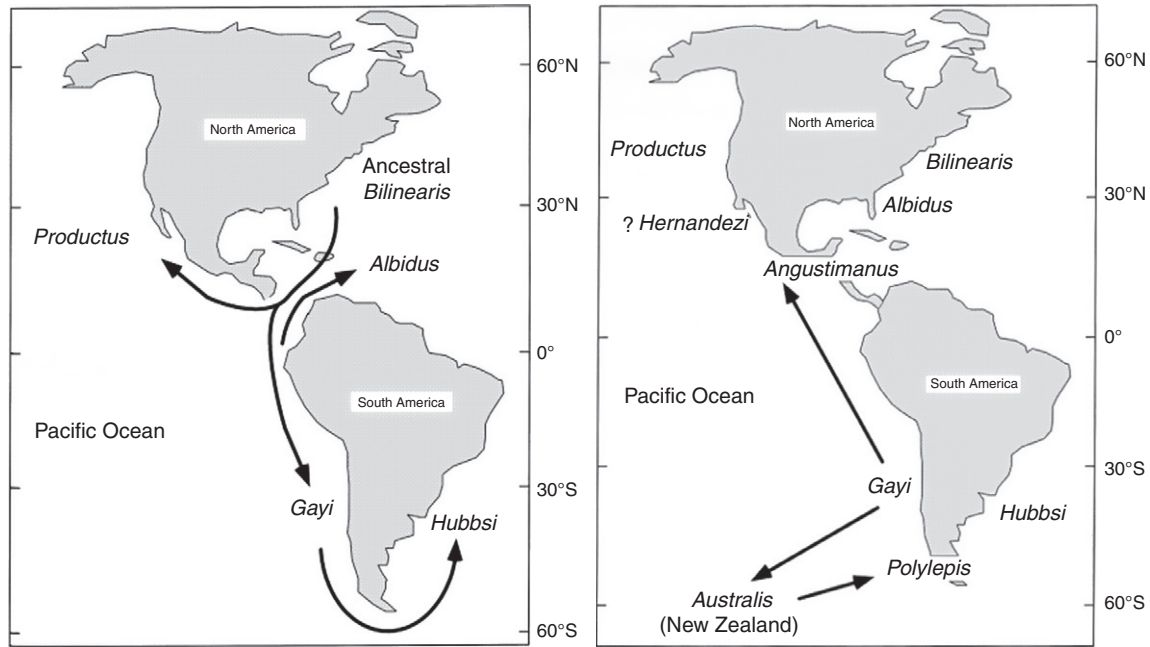


Figure 2.6 Geographical reproduction of the most recent description of ancestral Atlantic hake dispersal into the eastern Pacific Ocean (reproduced from [Grant and Leslie, 2001](#)).

The main discrepancies between the different authors are centred around the interpretation of the origin of (i) the Argentine hake and (ii) the Australian and South Pacific hake. For example, [Kabata and Ho \(1981\) and Ho \(1990\)](#) postulated a North Atlantic origin for the Argentine hake, whereas [Inada \(1981\)](#), [Stepien and Rosenblatt \(1996\)](#), [Roldán *et al.* \(1999\)](#), [Quinteiro *et al.* \(2000\)](#) and [Grant and Leslie \(2001\)](#) suggested a South Pacific origin, around Cape Horn. Genetic evidence recently presented by authors has shown that *M. hubbsi* and *M. bilinearis* are the most distant species within phylogenetic trees; as such, the scenario of a North Atlantic origin is improbable. [Inada \(1981\)](#) proposed a South African origin for the Australian lineage. In contrast, [Kabata and Ho \(1981\) and Ho \(1990\)](#) suggested an Argentine origin for Australian hake due to the southwards dispersal of *M. hubbsi*, whereas [Roldán *et al.* \(1999\)](#) and [Grant and Leslie \(2001\)](#) postulated that *M. gayi* was the ancestor of the Australian lineage. Moreover, these latter authors suggested that *M. polylepis* in South America was established after the return dispersal of *M. australis* ([Fig. 2.6](#)).

In summary, most of the authors agreed on a north-eastern origin of hake, with *M. merluccius* being the most ancestral of the extant hake species, which gave rise to two major lineages: one which formed all of the north-eastern Atlantic species and the other which migrated westwards through the North Atlantic to diverge into the north-west Atlantic and Pacific lineages.

1.3. Fisheries and the importance of hake

Although the earliest documentation of hake catches dates back to the eighteenth century ([Casey and Pereiro, 1995](#)) and contrary to other gadoids such as cod and haddock which supported one of the world's great fisheries for centuries ([Boreman *et al.*, 1997](#)), the large-scale hake fishery only began during the first half of the twentieth century. This fishery developed because of two major events: (i) the technological development of fishing fleets and (ii) the collapse of major cod stocks ([Pitcher and Alheit, 1995](#)).

During the last half of the twentieth century and the beginning of the twenty-first century, hake were heavily exploited on a global basis. According to FAO statistics ([FAO, 2010](#)), the annual world catch of hake increased sharply from around an average of 400,000 tonnes at the beginning of 1960 up to levels of 700,000 and 1 million tonnes in 1963 and 1965, respectively. Catches continued to increase, with the exception of some years, to reach the maximum historic level of 2.2 million tonnes in 1973. Catches then steadily decreased to the levels observed in the mid-sixties and remained at that level of 1.1 million tonnes in the period of 1980–1984. More recently, annual total catches have fluctuated around 1 and 1.5 million tonnes, showing an increasing trend during some periods, whereas they showed a decreasing trend in others. For example, annual catches fluctuated around

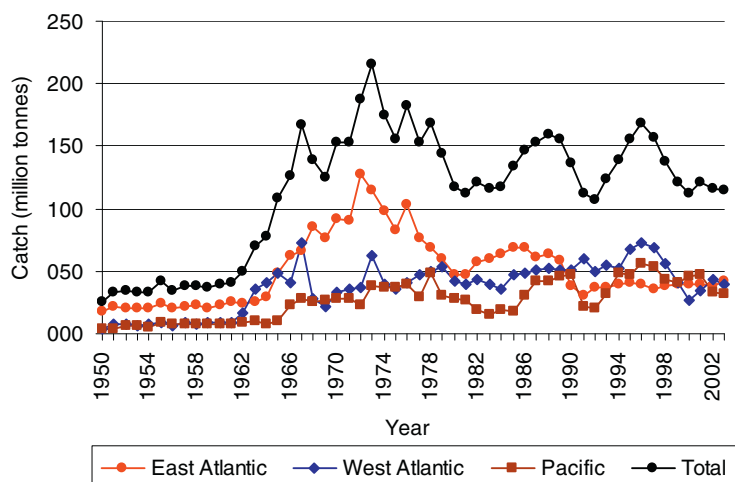


Figure 2.7 Total catches of *Merluccius* spp. and total catches by areas (source: FAO).

1.5 million tonnes in the periods of 1986–1990 and 1994–1999, to about 1.2 million tonnes in the period of 1991–1993 and of 2000–2003 (Fig. 2.7). In 2004 and 2005, catches were around 1.5 million tonnes and decreased again to around 1.2 million tonnes during the most recent period 2006–2008, although the catch figures for the last two years are still considered provisional.

The catch of hake in the Atlantic, especially the eastern Atlantic catches, have accounted for the major proportion of the total catch. However, there is an increasing trend in the percentage of hake caught in the Pacific in relation to the total catch, whereas the inverse trend can be observed in catches from eastern Atlantic (Fig. 2.8). The trend in the global hake catch follows a similar trend to that of the eastern Atlantic trend over most of this period; however, the contribution of the eastern Atlantic catch from 1990 onwards has decreased. During the last decade of the twentieth century, the western Atlantic catch contributed the most to the total catch, whereas during 1999–2008, the eastern Pacific hake contributed greatly to the global catch (Fig. 2.8). During the last few years, while the contribution to the total catch of the eastern Pacific was around 40%, the contribution from the eastern and western Atlantic stayed around 30%.

The contribution by each species of hake within each of the above-mentioned areas to the global catch is shown in Fig. 2.9. In the eastern Atlantic (Fig. 2.9A), from 1950 to 1965, most of the catches consisted of European hake. However, from 1966 onwards, Cape hake was dominant in captures from the eastern Atlantic due to the development of a large fishery for Cape hake (Payne and Punt, 1995). On the other side of the Atlantic (Fig. 9B), silver hake dominated the catches obtained up to 1966 when the

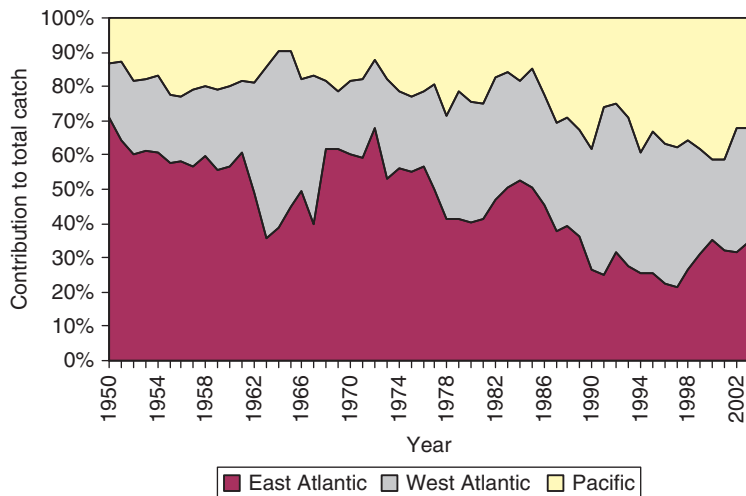


Figure 2.8 The contribution to total catches by area (source: FAO).

highest catches of this species were recorded (Helser *et al.*, 1995). Although Argentine hake catches were higher than silver hake in 1967 and 1968, most of the catches of hake in the western Atlantic were comprised of silver hake up until 1975. Argentine hake became increasingly more important from that year onwards with the development of a new offshore fishery (Bezzi *et al.*, 1995), and since the 1990s, more than 90% of the western Atlantic catch has comprised Argentine hake. Finally, in the Pacific (Fig. 2.9C), all catches consisted of Southern Pacific hake up to the development of the Northern Pacific and southern hake fisheries in 1966 and in 1979, respectively (Colman, 1995; Methot and Dorn, 1995). Since then, the contributions by Northern and Southern Pacific hake have fluctuated between 25 and 50% each, whereas the contribution by southern hake has stayed around 15–20%. From 2004 onwards, the contribution by Northern Pacific hake has been around 70%, whereas the contribution by Southern Pacific hake and southern hake has been around 20% and 10%, respectively.

Hake constitutes a high-quality fisheries product, although quality and price in the market vary depending upon the species. In the past, most of the hake catch outside of Europe was used for fishmeal production, or animal food; nowadays, most of the hake market is for human consumption (Pitcher and Alheit, 1995). For example, because of its excellent culinary characteristics, it is recommended that European hake and Austral hake are marketed as whole fresh or frozen fish (Lloris *et al.*, 2003). Europe, especially Spain, constitutes the major market for hake in the world, where they import around 700,000 tonnes annually.

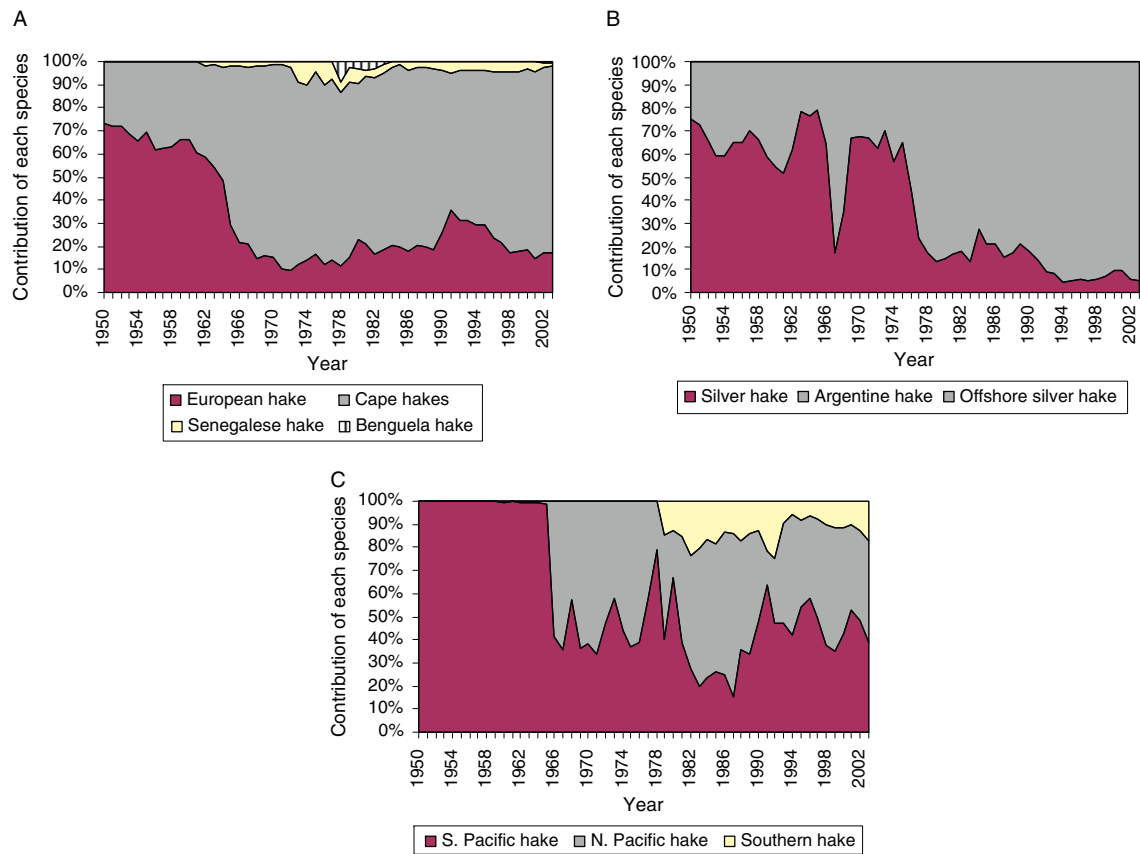


Figure 2.9 Contribution to each species to the total catch of the corresponding area: (A) East Atlantic area; (B) West Atlantic area and (C) Pacific area (source: FAO).

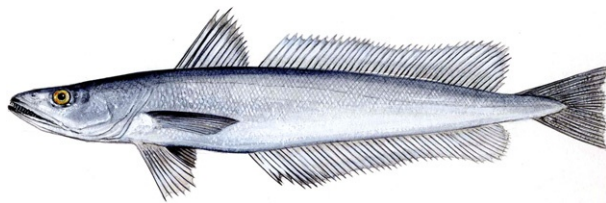


Figure 2.10 European hake, *Merluccius merluccius* (AZTI Tecnalia).

2. EUROPEAN HAKE, *MERLUCCIVS MERLUCCIVS*

2.1. Taxonomy and identification

In comparison to other *Merluccius* species, the European hake is characterised by a long slim body (Fig. 2.10). The head is large, being about 25–30% of the body length: the snout and upper jaw are about 30–35% and 48–54% of the head length, respectively (Inada, 1990). The ocular diameter is around 16–21% and the inter-orbital space 22–28% of the head length (Lloris *et al.*, 2003). The total number of grill rakers varies: on the first arch, it can be between 8 and 11 (mostly 9–11), ranging from 1 to 3 on the upper part and from 7 to 9 on the lower part. The first dorsal fin contains 1 spine and 7/10 rays, whilst the second dorsal and anal fins have 36–40 rays. The tip of the pectoral fins reaches the anal opening in fish below the 20 cm standard length, but not in adults. The margin of the caudal fin is normally truncated, but becomes forked with growth. The lateral line contains 127–156 small scales. The total number of vertebrae is 49–54. The colouration of the European hake is grey, in general, becoming lighter on the sides and silvery white on the belly (Cohen *et al.*, 1990).

2.2. Distribution and habitat

The European hake is widely distributed throughout the north-east Atlantic, from Norway in the north to the Guinea Gulf in the south, and throughout the Mediterranean and Black Sea, being more abundant from the British Isles to the south of Spain (Casey and Pereiro, 1995). European hake can be found together with other species of hake such as *M. senegalensis* and *M. cadenati* at the southern limit of its distribution (Fig. 2.11; Casey and Pereiro, 1995). The European hake is a demersal and benthopelagic species, found mainly between 70 and 370 m depth; however, it also occurs in inshore waters (30 m) and down to depths of 1000 m (Cohen *et al.*, 1990).

The maximum length and weight of this medium-large gadoid species are about 140 cm and 15 kg, respectively (ICES, 2009). Presently, it is



Figure 2.11 Distribution of European hake (*Merluccius merluccius*) (reproduced from FAO).

thought that the maximum age of the European hake is around 12 years. However, an important controversy exists with regard to its growth rates (see below) (De Pontual *et al.*, 2003, 2006). European hake lives close to the bottom during the daytime but at night they move up and down the water column (Cohen *et al.*, 1990). Juvenile and small European hake usually live on muddy beds on the continental shelf, whereas large adult individuals are found on the shelf slope, where the bottom is rough and associated with canyons and cliffs.

2.3. General hydrography of the area

The north-east Atlantic is affected by the North Atlantic current, which is a warm ocean current that carries the Gulf Stream north-east towards the European coast (OSPAR Commission, 2000). The North Atlantic current splits into two branches around west Ireland. While the Canary current takes a southerly direction, the other warm-water branch continues north along the coast of north-western Europe, heating the cold northern atmosphere. Other branches include the Irminger current and the Norwegian current, which sink to the depths of the Greenland and Labrador Seas to form the Labrador current. Most of the waters in the north-east Atlantic region originate from the North Atlantic, although waters found in the more southerly part have either a North Atlantic origin or are the result of a mixture between Atlantic and Mediterranean waters (OSPAR Commission, 2000).

The distribution of European hake in the north-east Atlantic comprises four different OSPAR Commission regions: the Atlantic Coast of the Iberian Peninsula, the Bay of Biscay, the Celtic Sea and the North Sea.

2.3.1. The Bay of Biscay and the Atlantic Coast of the Iberian Peninsula

This region comprises the area to the south of 48° N and to the north of 36° N and contains the Bay of Biscay, the European sector of the Gulf of Cadiz and the western Iberian margin (OSPAR Commission, 2000).

The Bay of Biscay can be defined as an open oceanic bay; geographically, it is located between France in the eastern part, oriented south–north, and Spain in the southern part, oriented west–east. The Bay consists of an area to the north of 43.5° N and to the south of 48° N, between $1^{\circ} 40'$ W and $9^{\circ} 20'$ W (Fig. 2.12). The northern boundary of the Bay of Biscay is approximately located between the Armorican shelf and the Celtic Sea, and can be considered as a natural element (OSPAR Commission, 2000). The southern limit is usually located at Cape Ortegal (Lavin *et al.*, 2004). There are two clearly different sectors, each of them with a different major gradient with regard to topography: longitudinally, there is a southern part with a narrow continental shelf of about 30–40 km, in general, but reaching as narrow as 12 km in parts (Cantabrian Coast); and latitudinally along the French coast with a extended continental shelf in terms of width (150–180 km on average) and length (Koutsikopoulos and Le Cann, 1996). These characteristics affect not only the general water circulation pattern but also the nature of the environmental and biological relationships of the different species inhabiting the Bay of Biscay.

One of the main characteristics of the Bay of Biscay is the relatively high amount of freshwater river runoff. Most of this runoff is related to two river systems: the Loire and the Gironde, which are only 220 km apart and contribute an annual mean outflow of about $900 \text{ m}^3 \text{ s}^{-1}$ (Lavin *et al.*, 2000). Seasonal variations in the runoff of both rivers show a maximum runoff exceeding $3,000 \text{ m}^3 \text{ s}^{-1}$ in winter or spring, and a minimum in summer, at around $200 \text{ m}^3 \text{ s}^{-1}$. In contrast, rivers on the Cantabrian coast are small in length, with pronounced slopes because of the orography of the region (Usabiaga *et al.*, 2004). As such, the contribution of these rivers to the total freshwater supply is only 30% in comparison to the Loire and Gironde (Lavin *et al.*, 2000). Due to their characteristics, the Cantabrian coastal rivers can be considered as torrential, with river discharge almost immediately following precipitation (Uriarte *et al.*, 2004). The maximum flow is in spring and autumn and the minimum during summer.

The Galician coastline is mountainous and extends 1,354 km first westwards and then southwards. This section of the Iberian Peninsula contains many ‘rias’, which are coastal inlets found around the north-western and northern Iberian Peninsula, and beaches covering 13.8% of the Galician coast. South of Galicia, but to the north of 41° N, the coastline is mostly rocky and shallow. To the south of 41° N, a sandy coast extends just north of Lisbon and further south it is replaced by cliffs which extend to Cape Raso, at the same latitude as Lisbon. Sandy beaches with dunes and marshes extend to 37° S and further east.

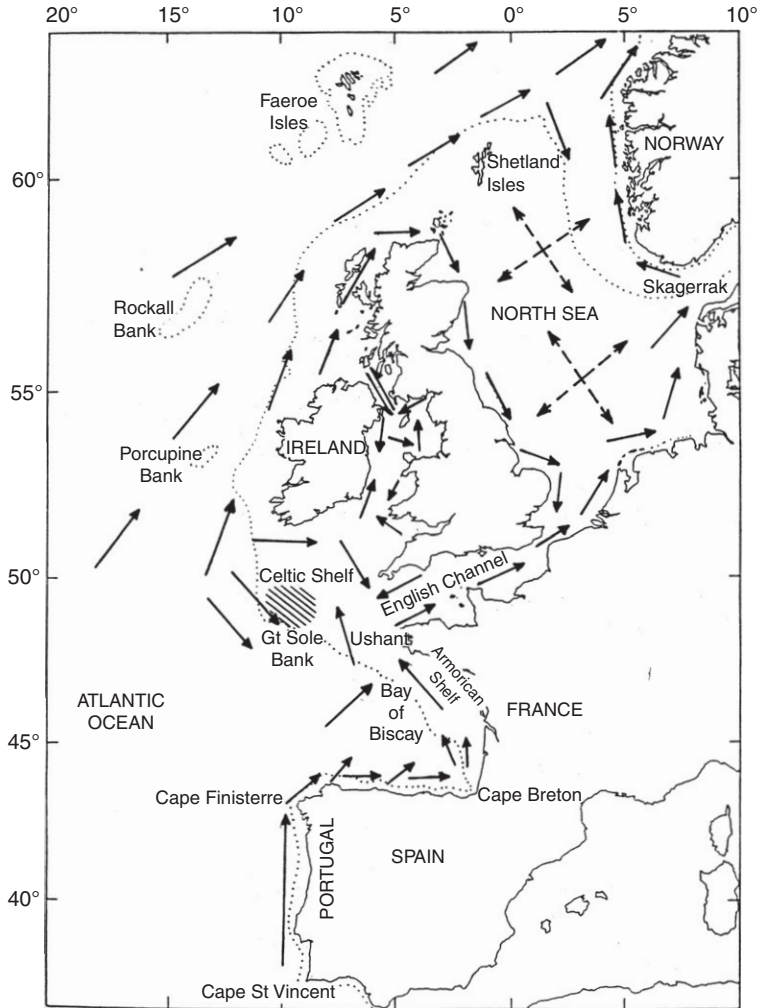


Figure 2.12 General circulation pattern in the North-east Atlantic (reproduced from [Casey and Pereiro, 1995](#)).

Most of the water masses of the Bay of Biscay and the Atlantic Coast of the Iberian Peninsula originate from North Atlantic water masses or are the result of a mixture of North Atlantic water masses and waters of Mediterranean origin ([OSPAR Commission, 2000](#)).

The main water masses for this area have been summarised by [Boucher \(1985\)](#), [Lavin *et al.* \(2004\)](#) and [Valencia *et al.* \(2004\)](#). In general, the water masses in the upper layer, which reaches depths less than 1,000 m, are characterised by north-east Atlantic central water (ENACW) with a

temperature ranging from 10.5 to 12 °C with a salinity of between 35.45 and 35.75 p.s.u. (Koutsikopoulos and Le Cann, 1996; Valencia *et al.*, 2004). Two sources of ENACW water masses can be identified in this area; a colder water mass with a sub-polar origin (ENACW_P) and warmer water of a subtropical origin (ENACW_T) (Ríos *et al.*, 1992). The upper ENACW waters, in addition to the surface waters, are mainly affected by seasonal variations in the atmospheric regime (see below). Below 1000 m, the waters are characterised by Mediterranean overflow water (MOV), which spreads into the north-east Atlantic from the Gibraltar Strait; it moves northwards from the Portuguese continental slope, entering into the Bay of Biscay (Lavin *et al.*, 2004). Between 1800 and 2500 m, the Labrador Sea waters appear (Lavin *et al.*, 2004), although some authors have included this water mass with the north-east Atlantic deep water (NEADW) (Koutsikopoulos and Le Cann, 1996; Valencia *et al.*, 2004). The NEADW appears at depths between 2500 and 3500 m and is characterised by a mixture of different water masses: Denmark Strait overflow water (DSOW) and Iceland–Scotland overflow water (ISOW).

Koutsikopoulos and Le Cann (1996) presented a synthesis of water circulation patterns in the Bay of Biscay and the seasonally more relevant hydrological features (Fig. 2.13), which can be extended into the eastern Atlantic Iberian coast (Fig. 2.12). The oceanic circulation in the Bay of Biscay is characterised by weak clockwise circulation, with a mean geostrophic current of about 1–2 cm s⁻¹ at depths of around 400 m. However, the mean flow could be stronger in the surface layers (Koutsikopoulos and Le Cann, 1996; Pingree and Le Cann, 1990). Wind forces, heating, rainfall and river runoff strongly influence the generally weak circulation, making the currents very variable spatially, seasonally and inter-annually (Lavin *et al.*, 2004).

In addition to the general clockwise circulation, and depending on the season, the circulation can become cyclonic along the Portuguese, Galician and northern Spanish and French continental slopes due to the slope current. The seasonality of the slope current is affected by wind. In winter, when the northerly wind component relaxes, a warm and saline polewards surface flow (ENACW_T) takes place at 20–30 cm s⁻¹ (Frouin *et al.*, 1990; Haynes and Barton, 1990) off the Iberian Peninsula; this moves eastwards along the Cantabrian coast to enter into the Bay of Biscay. As this warm water usually reaches the Bay of Biscay around Christmas, it has been referred to as the ‘Navidad’ current (Pingree and Le Cann, 1992). This event results in an anomalous situation: the warmest temperatures, below the seasonal thermocline, along the northern Spanish slope occur in mid-winter, whereas the coldest temperatures occur in mid-summer. This latter pattern is due to the intrusion of the polar ENACW and upwelling processes driven by the north/north-east winds in summer (Fig. 2.14).

Moreover, in winter, and linked to the slope current, one of the main characteristics of the regional oceanography is the presence of clockwise and

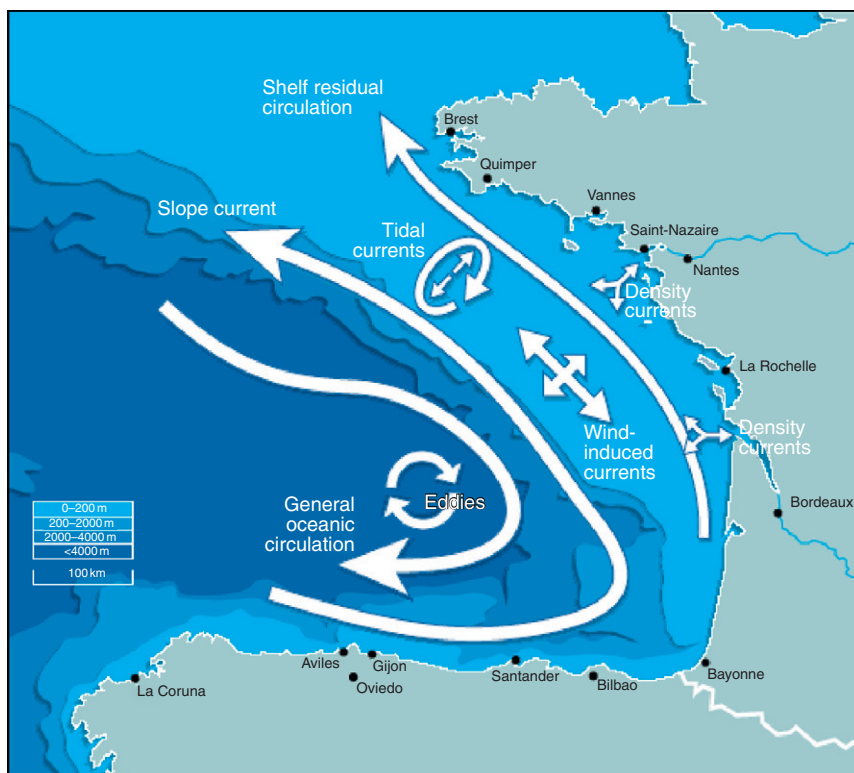


Figure 2.13 The main hydrographic features in the Bay of Biscay (reproduced from Koutsikopoulos and Le Cann, 1996 modified by OSPAR Commission, 2000).

anticlockwise eddies; these have been named ‘swoddies’ (slope water oceanic eddies), by Pingree and Le Cann (1992), because they are formed in the continental slope due to the interaction between the slope current and topography. Furthermore, because of their origin and westwards/northwards movement towards oceanic areas, these structures could be very important in relation to biological processes as they may transport biological material (plankton, eggs and larvae) from the continental shelf (Koutsikopoulos and Le Cann, 1996). This pattern could be very important for the life cycle of the European hake, since recruitment success has been associated with eddy structures in the Cantabrian Shelf (Sánchez and Gil, 2000). Another characteristic of winter is the presence of low salinity cold waters, with a river origin, on the continental shelf; this produces an inversion of vertical temperature profiles and strong vertical temperature gradients (Fig. 2.14) (Koutsikopoulos and Le Cann, 1996).

In spring, the low salinity cold waters are still present over the continental shelf, depending upon the intensity of river runoff and the wind regime

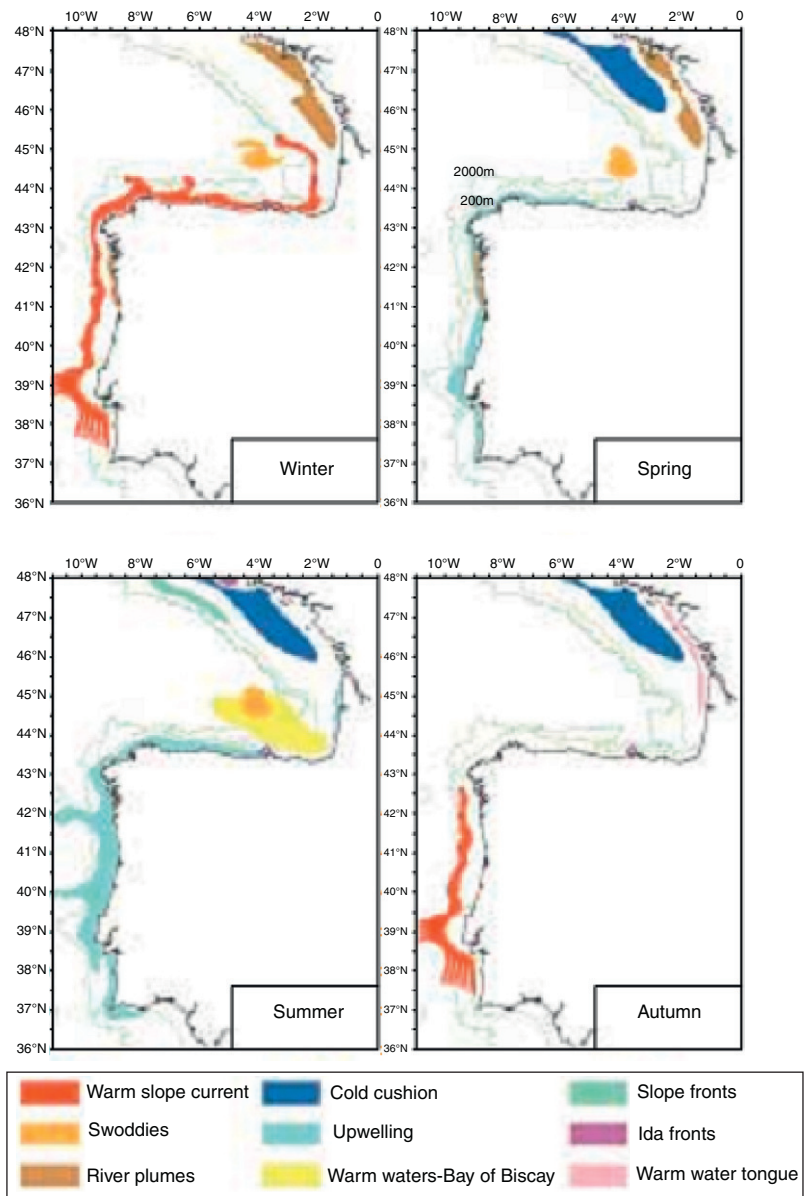


Figure 2.14 Seasonal variation in the main hydrographic structures in the Bay of Biscay and Atlantic coast of Iberian Peninsula (reproduced from [OSPAR Commission, 2000](#)).

(Lavin *et al.*, 2004). Moreover, a seasonal thermocline over the French shelf forms in April; this reaches the coastal region in May. Interestingly, a cold and relatively homogeneous ($< 12^{\circ}\text{C}$) water mass appears below the thermocline, centred around 100 m depth off the French coast from the south of the Brittany area to the Gironde estuary (Koutsikopoulos and Le Cann, 1996). This cold water mass forms because of the combined effect of ENACW_P water intrusion and upwellings once the southerly wind relaxes and northerly/north-easterly winds become predominant. Moreover, this cold water mass is observed all year round and is characterised by a low, less than 1°C , seasonal and inter-annual temperature difference (Valencia and Franco, 2004; Valencia *et al.*, 2004). This pattern could be very important for the European hake life cycle, since spawning of this species takes place at temperatures between 10.5 and 12°C (Ibaibarriaga *et al.*, 2007).

The coastal upwelling off the Galician/Portuguese coast starts to appear in late spring and reaches a maximum in summer. Summer coastal upwellings are also important hydrodynamic features within this area (Fig. 2.14). For example, in response to the prevailing northerly and north-westerly winds over the French continental slope, offshore surface water transportation towards the equator is replaced by colder deeper waters (Lavin *et al.*, 2004; Puillat *et al.*, 2003). Moreover, in summer and early autumn, tidal thermal fronts over the continental shelf are formed due to the interactions between tidal currents and bottom topography.

2.3.2. The Celtic Sea and the North Sea

The Celtic Sea consists of an area to the north of 48°N and to the south of 59°N , located between 11°W and 1°W , neighbouring the Bay of Biscay. The North Sea is situated on the continental shelf of north-west Europe and links to the Atlantic Ocean in the north and via the channel the south-west and to the Baltic Sea in the east.

The Celtic Sea shows oceanic conditions at the shelf break in the west of Ireland and in the relatively shallow semi-enclosed Irish Sea. The general salinity distribution pattern indicates that the water mass of the Celtic Sea has an Atlantic origin (OSPAR Commission, 2000). The sea surface temperatures on the western and southern Irish shelves are warmer than those of the shallow Irish Sea in winter. This is because the waters of the Irish Sea lose heat more rapidly as the influence of the warmer North Atlantic drift is more pronounced west of Ireland and Scotland. The circulation pattern can be described as an overall water movement from south to north. In general, North Atlantic water masses enter from the south and west of the region (i.e. the Bay of Biscay) and progress through the area to the north. The water masses then split into two branches, one entering Arctic waters and the other entering the North Sea.

The North Sea waters are a mixture of North Atlantic water and freshwater runoff. Heat exchange with the air and the supply of local

freshwater strongly affects the characteristics of waters from the different areas in terms of salinity and temperature (OSPAR Commission, 2000). Generally, the deeper water masses of the North Sea are of pure North Atlantic origin, whereas shallower and surface waters are modified by freshwater runoff and surface heat exchange.

2.4. Growth

Although a plethora of papers are available in the literature on European hake growth in the north-east Atlantic (Bagenal, 1954; Belloc, 1935; Descamps and Labastie, 1978; Goñi, 1983; Goñi and Piñeiro, 1988; Guichet, 1988; Hickling, 1933; Iglesias and Dery, 1981; Meriel-Busy, 1966; Morales-Nin *et al.*, 1998; Piñeiro and Hunt, 1989; Piñeiro and Pereiro, 1993; Robles *et al.*, 1975), it was not until recently that an 'internationally approved' ageing method from otoliths was accepted (Lucio *et al.*, 2000; Piñeiro and Sainza, 2003). However, this agreement was reached only to age fish up to 5 years old because ageing older fish is still problematic (de Pontual *et al.*, 2003). The lack of any previous conformity between otolith readers was because interpretation of the otolith ring structure, the definition of the otolith nucleus, the formation of annual or intermediary rings, the presence of false rings associated with changes in feeding or habitat and interpretation of the otolith edge is very difficult (Casey and Pereiro, 1995; Piñeiro and Sainza, 2003).

Regardless of the lack of an established protocol for European hake otolith readings, all authors concluded that males grow faster than females up to a specific age. Most of the authors agreed that this happens at around 3 years old and that the growth rate of males decreases, whereas females grow faster from that age onwards. This change in growth pattern, or growth rate, has been associated with the onset of maturity (Lucio *et al.*, 2000; Recasens *et al.*, 1998). Also, it is well known that females reach a larger size and grow older than males; in other words, the sex ratio is skewed towards females in the largest length classes. In fact, it has been found that all of the largest European hake are consistently female (Casey and Pereiro, 1995).

Such a sex ratio pattern may result in an accumulation of males in certain length classes, due to the larger decrease in growth than in females. In fact, the proportion of males in length classes of around 25–45 cm, following the male onset of maturation, is moderately higher than the proportion of females (Fariña and Fernández, 1986; Lucio *et al.*, 2000; Pérez and Pereiro, 1985; Piñeiro and Sainza, 2003). This pattern, coupled with the fact that males do not reach ages older than those of females (Piñeiro and Sainza, 2003), may suggest that the mortality rate for males is higher than for females.

As a result of the inconsistencies in age-reading methods, different authors have proposed very different growth models for European hake in

north-eastern Atlantic waters. Overall, there are two hypotheses concerning growth: the first classifies European hake as a slow-growing species and the second as a fast-growing species. Authors such as [Hickling \(1933\)](#), [Guichet et al. \(1973\)](#) and [Meriel-Busy \(1966\)](#) ([Table 2.2](#)) postulated a slow growth (of around 10 cm per year) for European hake and this has been the main accepted growth model for many years. Previous exceptions to this theory were those presented by [Belloc \(1935\)](#) and [Bagenal \(1954\)](#) who, with the recovery of a tagged fish from a pioneer tagging experiment and otolith readings, respectively, postulated that the European hake was a fast-growing species, with a growth rate of around 20 cm per year. Subsequent studies by [Lucio et al. \(2000\)](#) and [Piñeiro and Sainza \(2003\)](#) suggested that the growth rate of European hake is even faster than previously estimated 'slow-growth'; however, they presented a slower growth pattern than that proposed by the fast-growth hypothesis. However, recent tagging experiments in the Atlantic ([de Pontual et al., 2003, 2006](#); [Piñeiro et al., 2007](#)), based upon around 51 recoveries, have concluded that the European hake growth rate is twofold compared to previously published data; this provides direct evidence for European hake being a fast-growing species, as proposed by [Belloc \(1935\)](#) and [Bagenal \(1954\)](#). Interestingly, this latter result has recently been confirmed by studies undertaken on European hake larvae and juvenile growth rates using daily otolith growth increments ([Kacher and Amara, 2005](#); [Piñeiro et al., 2008](#)).

In summary, the latest investigations suggest that European hake grows much faster, by a factor of two, than previously considered. In the light of these new studies, there is a need to revise the internationally agreed otolith reading protocol for hake of up to 5 years old, since with the new growth model, this age would correspond to 2–3-year-old fish. The faster growth also affects the maturity-at-age pattern of hake and the agreed maturity ogive at age. This, in turn, would also have great implications for stock assessments, since this is evaluated using catch-at-age based methods, that is, virtual population analysis (VPA) ([ICES, 2009](#)).

2.5. Feeding

The European hake is a top predator of the demersal community in the north-east Atlantic area, preying on other fish species such as anchovies (*Engraulis encrasicolus*; [Linnaeus, 1758](#)), sardines (*Sardina pilchardus*; [Walbaum, 1792](#)), blue whiting (*Micromesistius poutassou*; [Risso, 1827](#)), horse mackerel (*Trachurus trachurus*; [Linnaeus, 1758](#)) and mackerel (*Scomber scombrus*; [Linnaeus, 1758](#); [Cabral and Murta, 2002](#); [Gonzalez et al., 1985](#); [Guichet, 1995](#); [Pereda and Olaso, 1990](#); [Velasco and Olaso, 1998](#)). A specific characteristic of European hake is that adult hake live and spawn at the shelf edge, whereas juvenile recruitment occurs in specific areas on the continental shelf ([Álvarez et al., 2004](#); [Ibaibarriaga et al., 2007](#)). Thus,

Table 2.2 Mean length (cm) at age for European estimated by different authors in different areas; (B) both sexes combined; (F) females and (M) males (modified from Piñeiro and Sainza, 2003)

Author	Area	Sex	Age											Ageing method
			0	1	2	3	4	5	6	7	8	9	10	
Hickling (1933)	Ireland	B			19.6	25.4	35.1	43.2	51.4	63.4	68	72.9		Otoliths and scales
Hickling (1933)	Scotland	B			20.9	25.6	34.6	42.1	50.9	59.8	67.9	74.1	81.2	Otoliths
Bagenal (1954)	Scotland	B		22.3	43.2	58.7	70							Otoliths-Petersen
Guichet <i>et al.</i> (1973)	Ireland	M			22.5	20.1	32.5	40.1	47.3	53	59.8	63.9	66	Otoliths
		F			19.1	27.9	33.8	42	49.6	56.5	62.2	69.9	76.9	Otoliths
Meriel-Busy (1966)	Bay of Biscay	B		11	19.6	28	36.6	43.5	51.2	58.7	65.1	69.6	80.1	Otoliths
Descamps and Labastie (1978)	Bay of Biscay	M		15.7	24.9	32.9	39.8	45.7	50.9	55.3	59.1	62.4	65.2	Otoliths
		F		15.9	25.2	33.7	41.4	48.4	54.7	60.4	65.6	70.3	74.5	Otoliths
Guichet (1988)	Bay of Biscay	B	16.3	24.1	32.3	39.1								NORMSEP Modal Progression
ICES (2000)	Bay of Biscay	B	11.2	20.7	26.9	34.3	41.8	50.4	59.3	63.7	90.3			Otoliths (ALK from 1999)
Lucio <i>et al.</i> (2000)	Bay of Biscay	B	13.1	17.8	24.7	33.1	42.6	51.6	60.9	67.7	72.7	85.1		Otoliths
Iglesias and Dery (1981)	N and NW Iberian waters	M		17.6	23.8	29.5	34.4	38.6	43.1	45.2	47.8	50.1		Otoliths
		F		19.6	24.7	29.4	33.8	38	41.9	45.5	49	52.2		Otoliths
		B		20.2	24.9	29.3	33.4	37.3	41	44.4	47.7	50.7		Otoliths
Robles <i>et al.</i> (1975)	NW Iberian waters	B		10.6	19.7	27.8	35.2	42.7						Otoliths
Goñi (1983)	Morocco	M		16	21.4	26.5	31.3	35.7	39.9	43.8	47.3	50.9		Backcalculated/ Otoliths
		F		15.4	21.4	26.9	32.2	37.1	41.7	46	50	53.8		Backcalculated/ Otoliths
		B		14.8	20.7	26.3	31.4	36.3	40.9	45.2	49.2	53		Backcalculated/ Otoliths

Goñi and Piñeiro (1988)	N and NW Iberian waters	B		15	23	28	32	36	40.5								Backcalculated/ Otoliths
ICES (1991)	N and NW Iberian waters	B	12	18	25	30	36	41	45	49	53	57	60				Kimura and Chikuni (1987)
ICES (1999a,b)	N and NW Iberian waters	B	14.9	21.5	29.4	36.8	43	48.6	54.4	58	63.6	67	77				Otoliths (ALK from 1998)
ICES (2000)	N and NW Iberian waters	B	12.6	21.4	28.7	33.8	41.8	48.7	53.4	58.1	63.7	69.9	79				Otoliths (ALK from 1999)
Piñeiro and Sainza (2003)	N and NW Iberian waters	M	17	21	29.5	36.4	42.7	45.7	49.7	54.2	60						Otoliths
		F	16.8	20.9	28.4	37	44.5	48.7	53.7	56.4	62.3	68.7	75				Otoliths
		B	11.9	20.6	29	36.7	43.8	50	55.4	58.3	63.1	67.1	75				Otoliths

the feeding spectrum of juvenile and adult hake is different. The main food items of juvenile hake (<20 cm) are decapod prawns and euphausiids, whereas the diet of hake between 20 and 40 cm is mainly composed of blue whiting, horse mackerel, mackerel and clupeids, and for hake larger than 40 cm, the main item is blue whiting (Velasco *et al.*, 2003). Velasco and Olaso (1998) also found differences in the diet of hake in relation to depth, with clupeids and horse mackerel being the main items at depths less than 100 m, whereas blue whiting appeared to be the main prey in the deepest strata. Based on previous work, it also seems that there are differences in hake diet between different areas. While Velasco and Olaso (1998) identified blue whiting as the main prey item of hake in the Cantabrian Sea, Guichet (1995) in the Celtic Sea observed that blue whiting only appeared in hake between 35 and 45 cm long, whereas anchovies and horse mackerel were the major prey items in smaller and larger hake, respectively. In this sense, the dependence of hake on blue whiting is especially significant in the Cantabrian Sea (Velasco and Olaso, 1998).

Moreover, Trenkel *et al.* (2005) found in the Celtic Sea that the feeding rate of European hake on horse mackerel and blue whiting was affected by prey density, that is, there was evidence for density-dependent feeding and spatial/seasonal prey-switching behaviours. These authors also found that the feeding habits of European hake followed a seasonal pattern, whereby they were focused upon blue whiting in the summer and mackerel and *Trisopterus* spp. in winter. The higher predation on blue whiting in summer was associated with the arrival of juveniles to the Celtic Sea.

Cannibalism is also observed in hake (Gonzalez *et al.*, 1985; Guichet, 1995; Hickling, 1927; Velasco and Olaso, 1998). However, the percentage of hake in the hake diet varied throughout the areas studied and also by length. For example, while Hickling (1927) found that cannibalism could account for between 15% and 20% of the diet of hake, Velasco and Olaso (1998) observed that it was less than 4% of the total volume of prey in the Cantabrian Sea.

2.6. Reproduction and recruitment

Understanding the relative importance of factors responsible for inter-annual variation in recruitment is a primary objective of fisheries science and management (Chambers and Trippel, 1997; Marshall *et al.*, 1998). Within this context, the relationship between population and recruitment is the central, and generally most difficult, outstanding problem in the study of population dynamics and the management of marine fish stocks (Hilborn and Walters, 1992).

Despite the ongoing discussion regarding the relationship between stock spawning biomass and recruitment (Gilbert, 1997; Marshall *et al.*, 2003; Myers, 1997), management of the majority of exploited fish populations is,

at present, based upon spawner-recruit models. Traditional recruitment models assume that the reproductive potential of a population is proportional to its spawning stock biomass (SSB; [Trippel *et al.*, 1997](#)); this is then commonly used to set biological reference points (BRPs) ([Fig. 2.15](#)). However, the standard spawner-recruit models developed by [Beverton and Holt \(1957\)](#), [Ricker \(1954\)](#) and [Sheperd \(1982\)](#) originally used the term fecundity ([Koslow, 1992](#); [Rothschild and Fogarty, 1989](#)), but afterwards used the term SSB instead as a proxy for fecundity. In such cases, it is assumed that a given weight of adult biomass has the same probability of generating the same level of recruitment. This implies that the survival rates of offspring are independent of parental age, body size or condition ([Cardinale and Arrhenius, 2000](#); [Murua *et al.*, 2003](#)) and that total relative fecundity and annual egg production, by length and between years, are invariable ([Marshall *et al.*, 2003](#)).

However, there is increasing evidence indicating that a direct proportionality between SSB and reproductive potential may not exist. [Trippel \(1999\)](#) introduced the new term, stock reproductive potential (SRP), as an alternative to SSB; this more accurately characterises the capacity of a population to annually produce viable eggs and larvae which may eventually recruit into the adult population or fishery. In this sense, the term SRP has the potential to include early life history stages related to recruitment

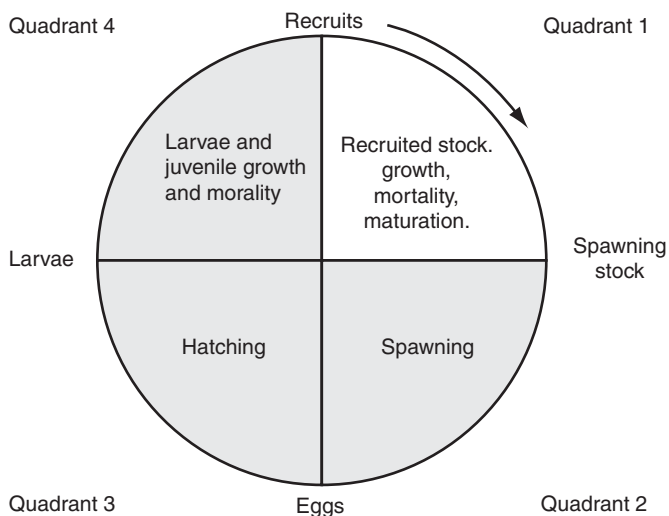


Figure 2.15 [Paulik \(1973\)](#) figure which showed that population assessment advice is normally limited to the un-shaded area (growth, mortality and maturation—quadrant 1) and traditionally does not include subsequent life history stages related to recruitment (quadrants 2–4) (sources: [Solemdal, 1997](#); [Ulltang, 1996](#); reproduced from [Trippel, 1999](#)).

processes (quadrant 2–4, Fig. 2.15). In particular, the reproductive potential of a population is affected by several factors, such as adult age structure and diversity (Marteinsdottir and Steinarsson, 1998), the proportion of first-time and repeat spawners (Evans *et al.*, 1996; Trippel, 1998) and nutritional condition (Hunter and Leong, 1981; Ma *et al.*, 1998); these are poorly reflected when using the SSB to represent the reproductive potential of the species. This limitation could even be more pronounced in the case of indeterminate fecundity species, where the production of eggs per unit SSB may vary substantially between years depending upon environmental conditions (temperature and food availability) during the spawning season (Hunter and Leong, 1981). In these species, feeding conditions greatly influence spawning activity and the rate of recruitment of pre-vitellogenic oocytes into the stock of yolked oocytes (Rinchard and Kestenmont, 2003). It has also been documented that fecundity within a stock varies annually and can undergo long-term changes (Kjesbu *et al.*, 1998; Murua *et al.*, 2006; Rijnsdorp, 1991).

In the light of these issues, there is a clear necessity to comprehensively study the inter-annual variations of fecundity and adult egg production; this, in turn, will enable the development of an understanding of the underlying mechanisms regulating annual variability in egg production, as well as improving the capacity to explain variability in recruitment. This component (quadrant 2, Fig. 2.15) represents the production processes which yield a number of potential zygotes, a quantity that becomes modified by mortality processes during early life stage dynamics to ultimately arrive at the number of recruits (quadrants 3 and 4, Fig. 2.15) (Marshall *et al.*, 1998; Ulltang, 1996).

Moreover, adult egg production information, in combination with concurrent estimates of egg production at sea (from ichthyoplankton surveys), would enable the estimation of SSB independently of commercial fishery data (Lasker, 1985; Parker, 1980; Saville, 1964). This approach would increase the knowledge with regard to the state of the population, improving the standard assessment of any commercially valuable fish species.

2.6.1. Reproductive biology

The quantification of fecundity and the understanding of reproductive strategies are fundamental topics in biology and in population dynamics studies of fish species (Hunter *et al.*, 1992; Murua and Saborido-Rey, 2003). In the case of commercial fish species, reproductive studies (including the assessment of size at maturity, duration of the reproductive season, daily spawning behaviour, spawning fraction and fecundity) permit basic data to be obtained for quantification of the reproductive capacity and also to assess the effects of fishing and other external factors on reproductive potential.

Despite its commercial importance, the information available on the reproductive biology of European hake in the North Atlantic is not extensive. In particular, little has been published on the seasonal variations in European hake fecundity and spawning activities. Some studies have presented the maturity ogives of European hake in Galician and Bay of Biscay waters (Domínguez-Petit *et al.*, 2008; Lucio *et al.*, 2000; Martin, 1991; Piñeiro and Sainza, 2003). According to these studies, males mature at around 35 cm, whereas females mature between 45 and 50 cm total lengths. In general, all the authors agreed that there is a sexual dimorphism with regard to maturation, with males maturing earlier than females. Domínguez-Petit *et al.*, 2008 showed that there was a decline of around 10 cm in the size at maturity observed in the Bay of Biscay from 1996 to 2004, which was related to fishing mortality and the age diversity of the stock. Similarly, they showed that size at maturity in the Galician shelf decreased around 15 cm from 1980 to 1988, increased again by about 14 cm until 1998 and decreased again in 1999, since when it has stayed relatively constant. These changes were related to different population biomass levels and environmental conditions in the area.

Previous studies into the reproductive biology of European hake have indicated that this species is a batch spawner (Murua *et al.*, 1998; Pérez and Pereiro, 1985; Sarano, 1986), spawning several batches within the reproductive season. This interpretation is consistent for other species of the genus *Merluccius*: Angelescu *et al.* (1958), Ciechomski (1967) and Christiansen and Cousseau (1971) for *M. hubbsi*; Balbotin and Fischer (1981) for *M. gayi gayi*; Alheit (1986) for *M. gayi peruanus* and Erkamov (1974) and Foucher and Beamish (1977) for *M. productus*. Moreover, the main spawning season of European hake was identified as lasting from December to July along the shelf edge of the Galician Coast and the Bay of Biscay to the south-west of Ireland (Lucio *et al.*, 2000; Martin, 1991). For example, Piñeiro and Sainza (2003) defined the hake spawning season from December to May in Iberian waters, with the spawning season in the Bay of Biscay from January to May and a defined spawning peak between February and March (Álvarez *et al.*, 2004; Lucio *et al.*, 2000). Recent investigations, however, have shown that the spawning season of European hake is very protracted on the Galician Coast and in the Bay of Biscay (i.e. spawning activity is observed all year round), although the main spawning season was observed between January and March in the Bay of Biscay and on the Galician shelf with a secondary peak in June–July for the Galician area (Domínguez-Petit, 2007; Korta *et al.*, 2010a; Murua and Motos, 2006, Murua *et al.*, 2006).

In this sense, the population asynchrony observed in spawning, as well as the extensive spawning season spanning the entire year, was also observed in European hake in the Mediterranean area (Recasens *et al.*, 1998). This protracted spawning season was the longest spawning period reported for species of this genus (*Merluccius*) (Table 2.3). The long spawning period was also found for *M. capensis* (Cadenat) (Bianchi *et al.*, 1993).

Table 2.3 Spawning period of different species of the genus *Merluccius*.

Species	Spawning period	Area	References
<i>M. albi</i>	April–August	Mexico–USA	Cohen <i>et al.</i> (1990)
<i>M. angustimanus</i>	April–June	Mexico	Mathews (1985)
<i>M. australis</i>	May–August	Argentina/Mexico	Cohen <i>et al.</i> (1990)
<i>M. bilinearis</i>	May–October	USA/Canada	Scotton <i>et al.</i> (1973)
<i>M. polli</i>	October–March	Mauritania/Guinean shelf	Garcia (1982)
<i>M. capensis</i>	January–December (peak spring and summer)	Namibia/South Africa	Bianchi <i>et al.</i> (1993)
<i>M. gayi</i>	August–November	Chile	Cohen <i>et al.</i> (1990)
<i>M. gayi peruanus</i>	August–March	Peru	Cohen <i>et al.</i> (1990)
<i>M. hubbsi</i>	November–April (peak January)	Argentina	Pájaro and Macchi (2001)
<i>M. productus</i>	January–June	Mexico/USA	Hart (1973)
<i>M. senegalensis</i>	September–March (peak November–February)	Southern Morocco, Northern Mauritania/Cape Verde	Wysokinski (1986)

European hake is characterised by asynchronous oocyte development, where oocytes of all stages are simultaneously present in reproductively active ovaries (Table 2.4 and Fig. 2.16). This has been interpreted as providing evidence for indeterminate annual fecundity (Murua *et al.*, 1998). The term ‘indeterminate’ refers to species in which the potential

Table 2.4 Summary of oocyte developmental stages in European hake ovaries (adapted from Murua and Motos, 2006)

Oocyte development stage	Characteristics	Oocyte diameter (µm)
Previtellogenic		
Cortical Alveoli	Appearance of cortical alveoli vesicles in the cytoplasm in preparatory of yolk development. Oil vesicles begin to accumulate in the cytoplasm. The chorion and follicle layers are apparent.	150–250
Vitellogenic (yolked)		
VIT 1	First stages of exogenous vitellogenesis. Yolked oocytes with eosinophilic yolk granules present in the cytoplasm. Oil droplets occupy more cytoplasmic area than yolk granules.	250–450
VIT 2	Exogenous vitellogenesis continues and oil droplets occupy a similar cytoplasmic area than yolk granules.	450–550
VIT 3	Exogenous vitellogenesis continues and oil droplets occupy less cytoplasmic area than yolk granules	550–650
Maturation		
Early migration	Oil droplets fuse into a unique oil globule and the nucleus start to migrate peripherally to the animal pole.	650–750
Late migration	Nuclear migration goes on, yolk granules start to fuse in plates starting in the centre and extending centrifugally.	750–950
Hydration	Once the nucleus migrated to the animal pole, it disintegrated. A rapid uptake of fluid by the oocyte through its follicle occurs and yolk fuses into a homogeneous mass. The cytoplasm and the cortical alveoli are restricted to a thin peripheral layer.	950–1150

The histological characteristics and the size ranges are given for each stage. Measures are made from histological sections.

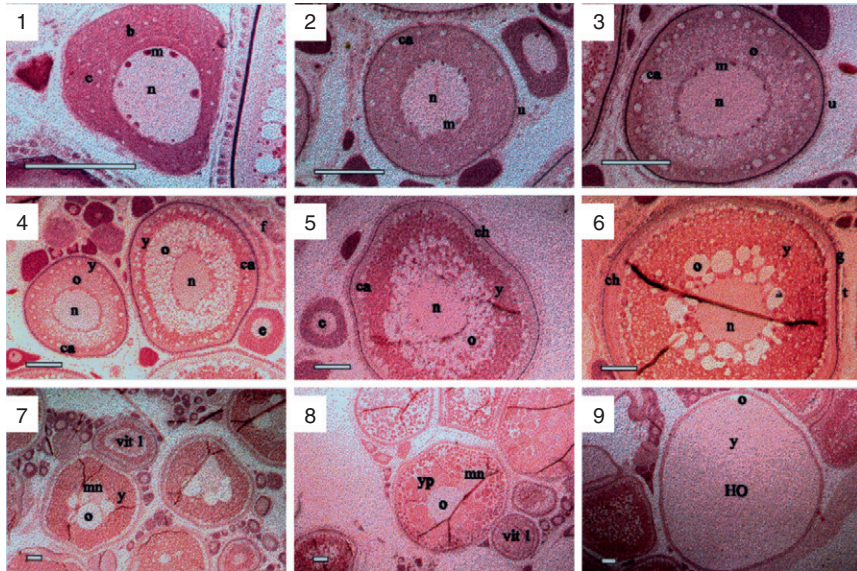


Figure 2.16 Oocyte development process (plates 1–9, see below) in European hake, *Merluccius merluccius*: (1) Primary growth stage oocyte; (2), (3) Cortical alveoli stage oocyte; (4) Cortical alveoli oocyte (left) and early vitellogenic oocyte (right); (5), (6) advanced vitellogenic oocytes; (7) early migration (maturation) stage; (8) migration stage (final maturation) and (9) hydrated oocyte (reproduced from [Murua and Motos, 2006](#)). n, nucleus; m, nucleolus; c, cytoplasm; ca, cortical alveoli; pg, primary growth; t, follicle layer; u, envelope of oocyte; y, yolk vesicles; o, oil droplets; mn, migratory nucleus; yp, yolk plates; HO, Hydrated oocyte; bar = 0.1 mm.

annual fecundity is not fixed prior to the onset of spawning ([Hunter *et al.*, 1992](#)). In such species, pre-vitellogenic oocytes can develop and be recruited into the yolked oocyte stock at any time during the season (*de novo* vitellogenesis) ([Hunter and Goldberg, 1980](#)). Estimation of total fecundity in the ovary, prior to the onset of spawning, is meaningless if during the spawning season oocytes are recruited to that stock. In these species, annual fecundity should be estimated from the number of oocytes released per spawning (batch fecundity), the percentage of females spawning per day (spawning frequency) and the duration of the spawning season ([Hunter and Macewicz, 2003](#); [Hunter *et al.*, 1985](#); [Hunter and Macewicz, 1985](#); [Murua *et al.*, 2003](#)). Further work by [Murua and Motos \(2006\)](#) on the histological examination of ovaries from hake in the Bay of Biscay, sampled on a monthly basis from December 1996 to October 1997, demonstrated that this species exhibits indeterminate fecundity. They showed that oocyte development is asynchronous with a continuous oocyte size–frequency distribution in pre-spawning, spawning and post-spawning females; there

was a gradual decrease in the mean diameter of advanced yolked oocytes as spawning proceeded, and a generalised atresia at the end of the spawning season was observed. These are considered characteristics of indeterminate fecundity species (Murua *et al.*, 2003). The use of a combination of modern stereological methods and the advanced oocyte packing density (OPD) theory (Kurita and Kjesbu, 2009) by Korta *et al.* (2010b) corroborated the theory that hake are an indeterminate fecundity species. The fecundity indeterminacy of hake can be explained through the energy allocation to gamete production during the breeding season (Domínguez-Petit and Saborido-Rey, 2010) or, in other words, because hake is considered as an income breeder (i.e. adjusts its food intake with breeding, with a minor reliance on energy stores).

Murua and Motos (2006) estimated that the spawning fraction, defined as the proportion of females spawning per day, ranged from 0.085 to 0.207 in the Bay of Biscay in 1996/1997, which is equivalent to a batch interval of 5–12 days; the spawning fraction was highest at the peak of spawning from January to March (5 days batch interval) and decreased afterwards as the spawning season progressed (batch interval of around 12 days). European hake in the Galician shelf was also found to spawn with a batch interval of around 5 days between January and March, with a decreasing batch interval afterwards to around 10 days (Domínguez-Petit, 2007). Argentine hake, *M. hubbsi*, were found to spawn once every 7 days during the peak of spawning and every 10 days at the end of the spawning season (Macchi *et al.*, 2004), showing a somewhat similar spawning activity to European hake in the Bay of Biscay.

Moreover, Murua *et al.* (2006) showed that relative batch fecundity varied significantly between months and years, but not between different areas within the Bay of Biscay. They presented two levels of relative batch fecundity for 1997: the highest between January and April (on average, 167 eggs per gram gutted females, $SD \pm 5$ eggs) and the lowest from May to October (on average, 112 eggs per gram gutted females, $SD \pm 3$ eggs). They also showed that the relative batch fecundity variation between years was 9% for 1996–1997 and 28% for 1997–1998, which in turn could be related to differences in productivity between years, and that both the intra- and inter-annual variations in relative batch fecundity may be due to the differing conditions of the fish. In fact, they illustrated that the difference between the gonado-somatic indexes was around 14% in 1996–1997 and 36% in 1997–1998.

The estimation of relative batch fecundity (Murua *et al.*, 2006) in conjunction with spawning fraction estimates and the percentage of active mature females in the adult population (Murua and Motos, 2006) were used to produce population-relative egg production figures. In this sense, they estimated that the relative egg production for this population varied from a high value in January to March (985 eggs per gram gutted female) to a low

egg production between April and October 1997 (445 eggs per gram gutted female). As such, the maximum egg production figures were for January–March and they were mainly as a consequence of the high spawning fraction and relative batch fecundity values. In their view, the subsequent decrease in relative daily egg production was due to the decline in the spawning fraction, relative batch fecundity and the percentage of mature active females. These results on adult egg production presented by [Murua *et al.* \(2006\)](#) were in agreement with ichthyoplankton data which showed that the peak of egg abundance occurred in March in the Bay of Biscay ([Álvarez *et al.*, 2001](#)). In summary, all of these works showed that the European hake has a protracted spawning season, with spawning females present all year round; however, there were different levels of egg production depending upon the month of the year in the Bay of Biscay (these were highest from January to March and subsequently decreased to low levels during the rest of the year). A similar situation was also observed in the Galician area where females in spawning condition were found all year round, and the spawning fraction and batch fecundity were also highest between January and March with a second smaller peak observed in June and July ([Domínguez-Petit, 2007](#)).

2.6.2. Recruitment

As suggested by egg/larvae and spawning adult distribution studies, the main spawning areas of European hake are concentrated over the shelf break off the French coast in the Bay of Biscay and in the Celtic Sea to the west of Ireland ([Álvarez *et al.*, 2004](#); [Kacher and Amara, 2005](#)). There is also another main spawning area located over the shelf off the north-west coast of the Iberian Peninsula ([Casey and Pereiro, 1995](#)). The eggs of European hake are pelagic and their major densities are mainly found in the upper 200 m of the water column over the shelf break ([Álvarez *et al.*, 2001](#); [Ibaibarriaga *et al.*, 2007](#)); although, depending upon environmental conditions (upwelling, temperature), the depth distribution throughout the water column can be different. The optimum temperature range for the spawning of European hake appears to be between 10 and 12.5 °C ([Fig. 2.17](#)), as European hake eggs are mainly distributed in water at such temperatures, although they can be found in temperatures of up to 15 °C ([Álvarez *et al.*, 2001](#); [Ibaibarriaga *et al.*, 2007](#)).

The main nursery areas have been identified in the north-east Atlantic as located over the shelf along the French coast (*Le Grand Vasière*), the shelf in the Celtic Sea and off the west coast of Ireland ([Casey and Pereiro, 1995](#)). After hatching, early European hake larvae are still found over the shelf break ([Álvarez *et al.*, 2004](#); [Ibaibarriaga *et al.*, 2007](#)). However, shortly after this, hake larvae appear to undergo a coastward displacement over the continental shelf, towards the main nursery areas. For example, [Álvarez *et al.* \(2001\)](#) found that smaller hake larvae (<8 mm total length) were distributed around the spawning area over the shelf break, whereas larger

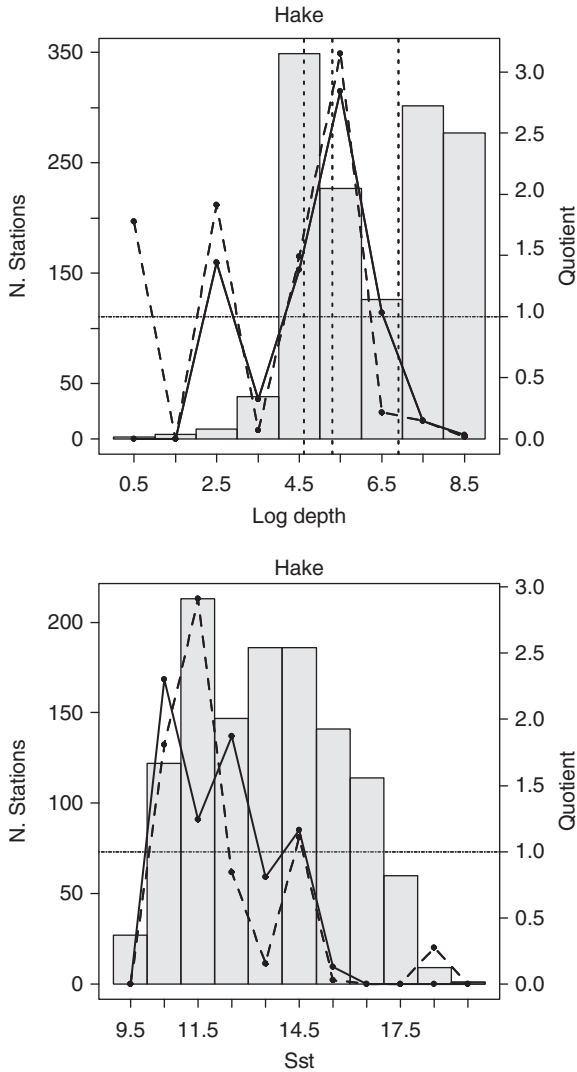


Figure 2.17 Quotient lines of European hake egg (solid line) and larval abundance (dashed line) with respect to the logarithm of bottom depth (left) and to sea surface temperature (right). The vertical bars indicated the number of samples taken in each class (reproduced from [Ibaibarriaga et al., 2007](#)).

larvae (> 8 mm in total length) appeared in shallower waters over the inner part of the continental shelf. Interestingly, [Kacher and Amara \(2005\)](#) found that more 0-group European hake were distributed inshore than in the areas of major larval densities. As the spawning grounds over the shelf are far from the main nursery areas, it is evident that the retention and transportation of

eggs and larvae, from the spawning grounds towards the nursery areas, are critical processes in the early life history of European hake, as for other fish species, that is, the migration triangle hypothesis (Cowan and Shaw, 2002; Harden Jones, 1968; Miller, 2002; Secor, 2002). In this sense, fish species have adapted their reproductive strategies to match the principal environmental and oceanic events; this leads to retention and transportation towards the main nursery areas (Pianka, 2000; Wootton, 1998). In the case of European hake, the transportation of early life stages from the Bay of Biscay and Celtic Sea spawning grounds coastwards to juvenile recruitment areas can be foreseen in relation to the general water mass circulation, as postulated by Koutsikopoulos and Le Cann (1996). In fact, Álvarez *et al.* (2004) inferred a north and north-east dispersion of eggs and larvae due to the main pattern of oceanic processes such as wind-induced currents and geostrophic flow in the Bay of Biscay (Fig. 2.18). Similarly, in the other main spawning nursery area (which corresponds with the southern hake stock) identified over the north and west Iberian Peninsula coast, the transportation of larvae to the open ocean has a negative impact on recruitment, whereas transportation and retention to the nursery area have a positive impact on recruitment (Sánchez and Gil, 2000).

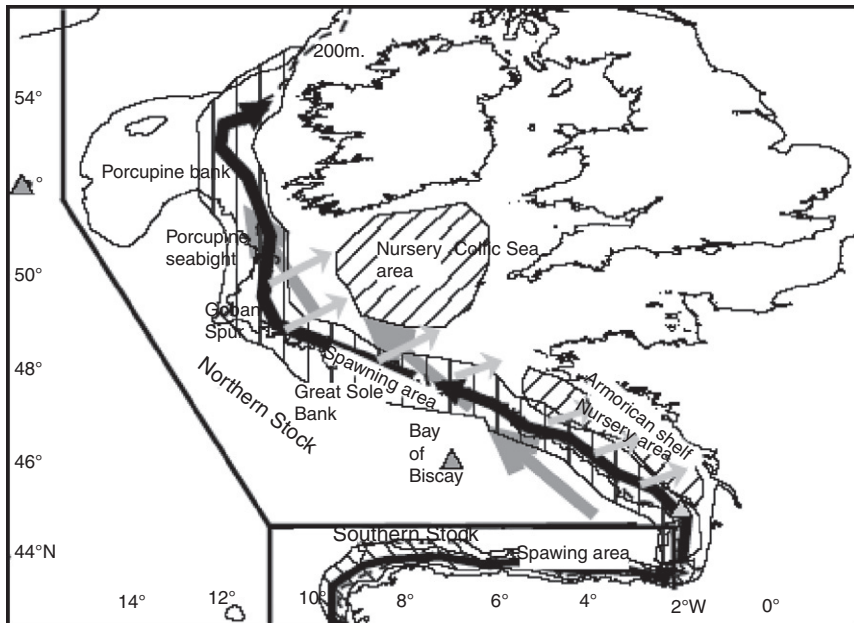


Figure 2.18 Main spawning and nursery areas for European hake in North-east Atlantic waters. Δ , NOAA winds recorded station; solid black line, the slope current; big grey arrows, geostrophic flow; small grey arrows, residual flow and dotted line, 200 m isobath (reproduced from Álvarez *et al.*, 2004).

European hake larvae are mainly found in water temperatures of between 10.5 and 13 °C (Álvarez *et al.*, 2001; Ibaibarriaga *et al.*, 2007), and have a pelagic existence until they settle on the seabed, around 40 days after hatching in the Bay of Biscay (Álvarez and Cotano, 2005; Kacher and Amara, 2005) and around 50 days in the north-west Iberian region (Piñeiro *et al.*, 2008). The 0-group European hake are found in muddy bottoms, between depths of 70 and 200 m, with the highest densities at a depth of 100 m (Kacher and Amara, 2005) on the continental shelf of the main two nursery areas mentioned earlier. In autumn, the 0-group European hake are recruited into the population (Pereiro *et al.*, 1991).

The population spawning asynchrony, as well as the protracted spawning season spanning the entire year for European hake, confront the hypotheses of a critical first-feeding period (Hjort, 1914) and larval match-mismatch (Cushing, 1975, 1990); which state that stocks adapt their spawning season to the peak of plankton production in the area to avoid starvation during the critical first-feeding critical. In the case of European hake, it seems that this could be true for the peak spawning season identified. However, the observation of spawning all year round could be related to the higher probability of hake larvae locating food than the larvae of other species, as mentioned by Bailey (1981). Bailey (1981) suggested that for Pacific hake (*M. productus*), the first-feeding period may not be as important as for other fish species due to their longer period for locating food based on (1) slow growth, slow metabolic rates and the low daily rations of Pacific hake larvae; (2) the large mouth of first-feeding hake larvae and therefore, larger food items in the diet and (3) the relatively longer starvation time for Pacific hake larvae. In the case of European hake, although it seems that the larvae exhibit fast growth rates (Kacher and Amara, 2005; Piñeiro *et al.*, 2008), it has also large mouths at first feeding and a relatively high starvation endurance (Álvarez and Cotano, 2005). In addition, Albaina and Irigoien (2004) found that the shelf edge in the Bay of Biscay is an area of relatively high zooplankton biomass and that larger copepods are found off the shelf edge in the Bay of Biscay where European hake larvae inhabit. Thus, spawning to match peaks in food concentration might not be a limiting factor for first-feeding European hake larvae.



3. FISHERIES AND THE STATE OF THE POPULATION

3.1. Population structure in the north-east Atlantic

In the north-east Atlantic, ICES (International Council for the Exploration of the Sea) recognises the existence of two stocks: the northern stock (ICES Division IIIa, Sub-areas II, IV, VI and VII and Divisions VIIIa, b, d) and the southern stock (ICES Divisions VIIc and IXa) (ICES, 2009). The northern

limit for the northern stock is located on the Norwegian coast in the north-east Atlantic, whereas the southern limit for the southern stock is the Gibraltar Strait. The geographical boundary between these stocks was established as lying at the Cap Breton Canyon (close to the border between the French and Spanish coasts), which was considered as a geographical barrier limiting the exchange between both populations. According to [Lundy *et al.* \(1999\)](#) and [Castillo *et al.* \(2004\)](#), there were subtle geographical genetic differences between Atlantic hake populations; however, genetic studies did not reveal any evidence for multiple populations in the north-east Atlantic ([Pla and Roldán, 1994](#); [Roldán *et al.*, 1998](#)). Moreover, [Castillo *et al.* \(2005\)](#) found that there were no genetic differences between European hake in Divisions VIIIc and VIIIa, b, d, that is, the boundary between northern and southern stocks (see above). A similar conclusion was reached by [Mattiucci *et al.* \(2004\)](#), who concluded that there were no genetic differences between European hake in the Celtic Sea and in the southern Bay of Biscay. In this sense, it seems that management-focused administrative criteria were preferred when establishing stock boundaries rather than a biologically grounded basis.

3.2. The northern stock

3.2.1. Fisheries

The northern stock of European hake supports a major commercial fishery in Atlantic European waters, which has been commercially exploited since the eighteenth century ([Casey and Pereiro, 1995](#)). It is especially important for Spanish and French fishing fleets. The annual catch of this stock ranged from 40,400 to 96,000 tonnes, during the 1961–2006 ([ICES, 2009](#)) period. Specifically, from 1961 onwards, the catch decreased continuously from its highest level of 96,000 tonnes in 1961 to 51,000 tonnes in 1971. It increased again to reach a second peak of around 78,000 tonnes in 1973, being on average around 70,000 tonnes during the period of 1972–1976. However, it decreased to levels of around 55,000 tonnes in 1977 and remained at around 60,000 tonnes, on average, until 1995. From 1995 onwards, the catch steadily decreased to reach the lowest value in the time series of 35,800 tonnes in 1998; since then it has remained at low levels between 40,000 and 45,000 tonnes ([Fig. 2.19](#)). The catch in 2008 was 47,800 tonnes and the provisional catch in 2009 was 42,800 tonnes.

Hake are mainly caught in Sub-areas VII and VIII with a relatively low catch level in Sub-areas IV and VI. During the beginning of the time series, the catch was slightly higher in Sub-area VIII than in VII. However, between 1995 and 2001, the decrease in total landings was mainly due to the decline of the total catch in Sub-area VIII, which diminished from around 25,000 to 10,000 tonnes. Since 2002, the catch in Sub-area VIII increased and has remained stable at around 15,000 tonnes, whereas the catch in VII has also remained constant at around 25,000 tonnes.

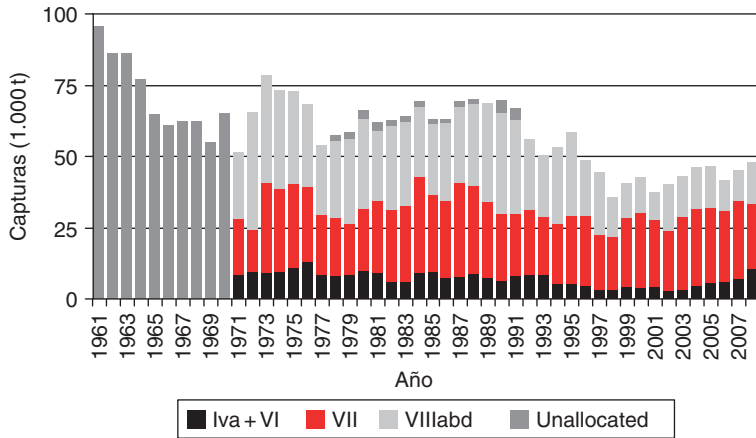


Figure 2.19 Total catches of the northern stock of European hake in the North-east Atlantic (source: ICES, 2009).

Historically, Spain, France and the United Kingdom have been the main countries involved in this fishery; however, the relative importance of these contributors, in relation to total landings, has changed during the catch history. In more recent years, Spain has accounted for around 65% of the total catch, France around 25%, the United Kingdom about 7% and Denmark and Ireland 3% each (ICES, 2009).

Several fleet segments focus their activities on the northern stock of European hake and most of them catch hake in mixed fisheries. Amongst the other species, megrim, monkfish, nephrops, blue whiting and horse mackerel can be found in the catch of these mixed fisheries. In this sense, various fishery units have been associated with the northern hake fishery in order to investigate the fishing activity in relation to demersal species (ICES, 1991). These fishing units use a combination of fishing areas and mixed gear to harvest European hake and are defined to allow a precise monitoring of hake catches by fleet. Most of the catch is taken by six fishery units (around 90% of the total landings), which comprise three fishing units in Sub-area VII (medium to deep water long lines, gillnets and trawls); two in Sub-area VIII (shallow to medium water gillnets and medium to deep water trawls) and one in Sub-areas IIIa, IV, V and VI (ICES, 2009).

3.2.2. Status of the stock and management

The size of the northern hake population declined sharply during the late 1990s; the present level appears to be only 50% of the level in the 1970s. The ICES Working Group on the assessment of southern shelf stocks of hake, monk and megrim, based upon the most recent estimates of SSB and fishing mortality, considers that the northern stock has a full reproductive

capacity and that it is harvested sustainably (ICES, 2009). The SSB was estimated in 2009 to be just above the precautionary approach BRP ($B_{PA} = 140,000$ tonnes) and the fishing mortality was estimated to be around the precautionary approach fishing mortality reference point (F_{PA}) since 2001 (Fig. 2.20). Although the stock currently lies within the safe biological limits, at the beginning of the 1990s, the spawning biomass had decreased below the B_{PA} to around the B_{lim} until 2001. However, since 2001, the SSB increased and is presently estimated to be just above the B_{pa} (ICES, 2009). Due to the critical state of the population during the most recent years of the twentieth century, and in order to assist in its recovery, an emergency plan was introduced in June 2001 (Council Regulation No. 1162/2001). Finally, a recovery plan was implemented for the northern stock of European hake in 2004, under EC Reg. No. 811/2004.

Therefore, the present management objectives of this stock are those explicitly established in EC Reg. No. 811/2004. The objective of the European hake recovery plan for the northern stock is to increase the level of spawning biomass to levels equal to or greater than 140,000 tonnes (B_{pa}) in two consecutive years (EC No. 811/2004). Once the target level has been achieved, the Commission will introduce follow-up management measures to replace the recovery plan. The agreed fishing mortality in the recovery plan was set at lower than or equal to the F_{PA} (0.25), which will

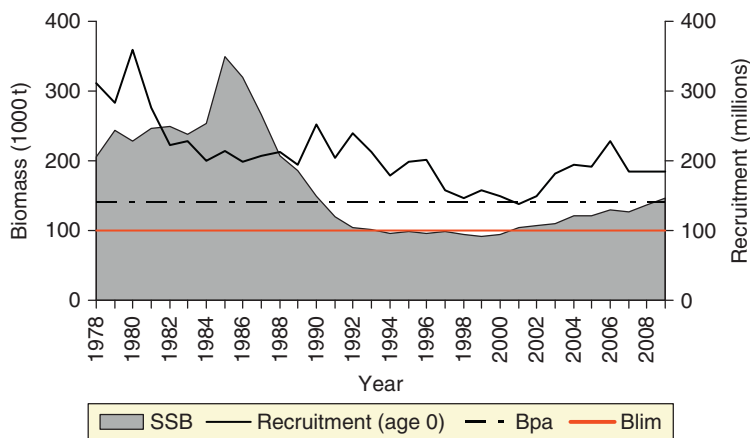


Figure 2.20 Spawning stock biomass and recruitment (age 0) as well as the biological reference points of the northern stock of European hake. B_{pa} is the biomass below which the stock would be regarded as potentially depleted or over-fished and it is judged to give a reasonable certainty that, in spite of year-to-year fluctuations, the stock will stay above B_{lim} . B_{lim} is the limit spawning stock biomass, below which recruitment is impaired or the dynamics of the stock are unknown. In the case of northern hake population, B_{pa} and B_{lim} are set at 140,000 and 100,000 tonnes, respectively (ICES, 2009).

produce the total allowable catch (TAC). The change in TAC from year-to-year is constrained so that it does not exceed 15% unless the SSB is below 100,000 tonnes. In this case, a lower TAC than implied by the 15% constraint is applied. The northern hake SSB has been estimated to be above the recovery plan target (140,000 tonnes) for the last two years and thus a management plan prescribed in the recovery plan should be implemented soon.

The northern hake population, as with the majority of the EU stocks, is managed by TAC and quota regulations. In addition, the following technical measures are in place: minimum length at a landing of 27 cm (30 cm in Division IIIA), minimum mesh size of 70 mm in the Bay of Biscay and minimum mesh size of 100 mm for otter trawls when European hake comprises more than 20% of the total catch (EC No. 811/2004). In specific areas, the minimum mesh size of 100 mm is required for all otter trawls.

3.3. The southern stock

3.3.1. Fisheries

The southern stock of European hake supports an important coastal commercial fishery on the Atlantic coast of the Iberian Peninsula, which has been commercially exploited since the eighteenth century (Casey and Pereiro, 1995). It is especially important for Spanish and Portuguese fishing fleets. The annual catch of this stock increased from 26,000 tonnes to the highest level in the time series of 35,000 tonnes in 1973 and then decreased again to 26,000 tonnes in 1976. Since then, the catch has fluctuated between 10,000 and 23,000 tonnes (ICES, 2009). Specifically, from 1976 onwards, the catch decreased continuously from 26,000 to 17,000 tonnes in 1981 and increased again to reach a level of around 23,000 tonnes in 1984, being on average around 19,000 tonnes in the period of 1983–1988. However, it decreased continuously to levels of around 12,000 tonnes in 1995 and again to the lowest level observed, of around 7000 tonnes in 2004. From 2004 onwards, the catch slightly increased to reach levels similar to those in the beginning of the 1980s. The catch in 2008 was 19,200 tonnes and the provisional catch in 2009 was 22,400 tonnes.

The southern hake stock is fished by Spanish and Portuguese fleets in a mixed fishery (Fig. 2.21). An industrial and semi-industrial trawler fleet and a very heterogeneous artisanal fleet, using various types of gear (traps, large and small gillnets and long lines, for example), have been identified in both countries (ICES, 2009). The Spanish fleet was responsible for between 60% and 75% of the catch during the 1972–2005 period, whereas it was responsible for more than 80% in 2006 and 85% in 2007 and 2008. The Spanish trawler fleet mainly uses two types of gear, that is, a pair trawl and a bottom trawl, and has been responsible for 67% of the total southern hake Spanish catch during recent times. The percentage of hake present in the landings of the mixed trawl fishery has become smaller during recent years, as the trawl

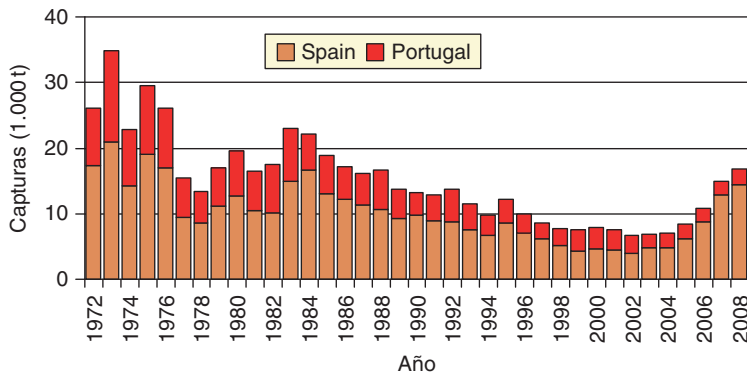


Figure 2.21 Total catches of the southern stock of European hake in the Atlantic Iberian Peninsula coast (source: ICES, 2009).

activity has been focused on various other important target species such as anglerfish, megrim, Norway lobster, blue whiting, horse mackerel and mackerel (ICES, 2009). On the contrary, the contribution of the Spanish artisanal fleet to the total Spanish catch has significantly decreased to around 15% of the total catch during recent years, although it reached 43% in 1987. In 2007 and 2008, the contribution of the Spanish artisanal fishery increased again up to 25% and 30%, respectively.

Similarly, hake is caught by the Portuguese trawler and artisanal fleets in a mixed fishery together with other fish species and crustaceans. The contribution of the Portuguese catch to the total catch was between 30% and 40% between 1972 and 2004. This contribution decreased to 25% in 2005 and further to around 15% in 2007 and 2008. In this case, however, the contribution of the artisanal fleet was higher in comparison to the trawler fleet, that is, around 60% of the Portuguese catch was made by the artisanal fleet in comparison to 40% by the trawler fleet.

3.3.2. Status of the stock and management

The SSB of the southern hake population declined sharply and continuously since 1983 to the lowest observed level of 7,300 tonnes in 1998. The SSB remained relatively stable around 10,000 tonnes from 1999 to 2005 and it increased to around 20,000 tonnes and 25,000 tonnes in 2008 and 2009, respectively (Fig. 2.22). Based on the most recent assessment of this species, the southern hake stock is suffering reduced reproductive capacity and is at risk of being harvested unsustainably (ICES, 2009). The stock is outside the safe biological limits and the spawning biomass had decreased below the precautionary approach level ($B_{PA} = 35,000$ tonnes) in 1985, and it has remained at that level ever since. Moreover, fishing mortality has increased in recent years and is well above the precautionary fishing mortality level

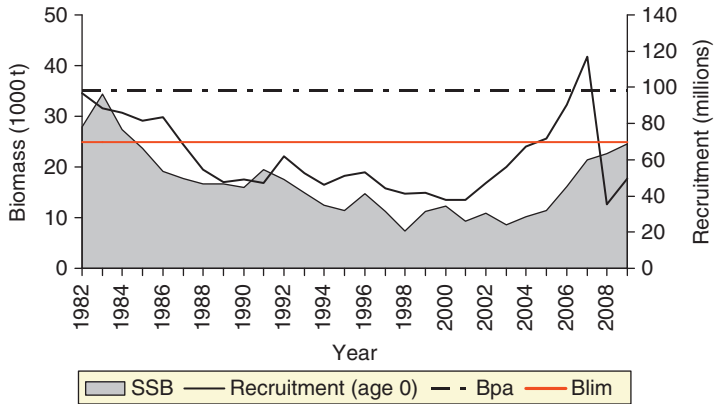


Figure 2.22 Spawning stock biomass and recruitment (age 0) as well as the biological reference points of the southern stock of European hake. B_{PA} is the biomass below which the stock would be regarded as potentially depleted or over-fished and it is judged to give a reasonable certainty that, in spite of year-to-year fluctuations, the stock will stay above B_{LIM} . B_{LIM} is the limit spawning stock biomass, below which recruitment is impaired or the dynamics of the stock are unknown. In the case of southern hake population, B_{PA} and B_{LIM} are set at 35,000 and 25,000 tonnes, respectively (ICES, 2009).

($F_{PA} = 0.4$) and is near the limit of the fishing mortality reference point ($F_{LIM} = 0.55$). Due to the critical state of the population and in order to recover the population, a recovery plan was introduced in December 2005 (see Council Regulation No. 2166/2005).

Therefore, the present management objectives of this stock are those explicitly established in EC Reg. No. 2166/2005. The objective of the European hake recovery plan for the southern stock is to increase the level of spawning biomass to levels equal to or greater than 35,000 tonnes (B_{PA}) in two consecutive years within a period of 10 years (i.e. by 2016) and to reduce the fishing mortality to 0.27 (F_{target}). Once the biomass target level has been achieved, the Commission will introduce follow-up management measures to replace the recovery plan, as proposed for the northern hake stock. The procedure for setting the TACs will include a 10% annual reduction in fishing mortality and a 15% constraint on TAC changes between years. Although a formal evaluation of the recovery plan has not been attempted yet, it seems that in recent years, the increase in SSB has been mainly due to an improvement in recruitment since recent fishing mortality has been increasing and the TAC has been exceeded throughout the recovery period.

The southern hake population is also managed by TAC and quota regulations. In addition, the following technical measures are in place: minimum length at landing of 27 cm, minimum mesh size, effort limitation, seasonal restrictions and closed area (EC No. 850/98).



4. FUTURE PERSPECTIVES

Although European hake in the north-east Atlantic is an important fishery resource, knowledge of the biology and ecology of this species is still quite scarce. In contrast to most gadoids and demersal species, European hake appear to exhibit a high growth rate (De Pontual *et al.*, 2003, 2006), indeterminate fecundity (Korta *et al.*, 2010b; Murua and Motos, 1996), a protracted spawning season (Domínguez-Petit, 2007; Murua *et al.*, 2006) and energy allocations to reproduction during the spawning season (Domínguez-Petit and Saborido-Rey, 2010). This pattern could be interpreted as European hake having adopted a more opportunistic life strategy, which is unusual for a gadoid and a demersal species. In this context, the new findings in relation to European hake growth patterns are of especial importance, because the uncertainties of age determination have hindered the use of catch-based assessment methods and have great implications for correct assessment and hence management of the species. Bertignac and De Pontual (2007) investigated the consequences of growth underestimation in the northern hake stock assessment and concluded that this bias has an effect on the absolute level of fishing mortality and stock biomass, as well as on the SSB trend. Nevertheless, they also showed that the trends in fishing mortality and recruitment are comparable and more importantly, that the population status in relation to precautionary reference points is generally the same. Therefore, the ICES Working Group is still using the 'old' growth pattern to carry out assessment of this stock until a new ageing protocol based on a new, validated growth pattern from tagging studies is agreed upon. Therefore, it can be expected that tagging studies will continue into the future to answer the pending questions concerning the growth patterns of hake.

Similarly, it is clear that this species is not as 'simple' as other gadoids when studying the reproductive biology (Kjesbu *et al.*, 2010). In the case of species of indeterminate fecundity, such as hake, fecundity should be estimated based on batch fecundity and spawning fraction estimations. While the first parameter can be obtained, it is more difficult to carry out the necessary extensive sampling of mature females for spawning fraction estimation due to the high cost of the fish in the market. However, as mentioned earlier, the combination of stereological methods (to estimate volume fractions) and the advanced OPD theory (Kurita and Kjesbu, 2009) make it possible to successfully establish hake oocyte packing densities and oocyte diameter relationships (Korta *et al.*, 2010b) which could be used with 'next generation' OPD formulae to predict the total annual fecundity in indeterminate spawners, as done today for determinate spawners such as cod, amongst other species. In any case, it is necessary to continue further studies of the reproductive biology of hake to estimate batch fecundity and

the spawning fraction because this information, in addition to providing a very useful knowledge of the hake reproductive strategy, can be used to estimate the SSB in combination with egg production estimation at sea. In contrast to normal assessment methods, one advantage of egg production estimation methods is that estimation of SSB is independent of any commercial fishery data (Gunderson, 1993; Somarakis *et al.*, 2004). These methods estimate the SSB based upon concurrent estimates of fecundity and population egg production at sea (Gunderson, 1993; Stratoudakis *et al.*, 2006). Moreover, fishery independent methods, whether using an egg production method (EPM) or any other suitable direct method, allow for contrasting and fine-tuning the estimates of SSB obtained using VPA-based traditional assessment methods (Armstrong *et al.*, 2001). In addition, the application of population egg production estimation methods provides further information about the reproductive biology and reproductive behaviour of a population and about its distribution, mortality and development of early life stages, which are of particular importance in studying the underlying mechanisms of recruitment (Alheit, 1993). In this sense, Murua *et al.* (2010a) presented, for the first time, an application of the daily egg production method (DEPM) to hake. Despite limitations in the estimation of various parameters, these authors concluded that DEPM can potentially be applied to European hake. However, as European hake was not a target species of the triennial egg research surveys used in this study, they concluded that the egg sampling strategy at sea should be adapted to the spawning behaviour of hake. In any case, it would be convenient to continue with this type of work because an independent estimation may be obtained that would be very useful for comparing with VPA-based assessments, especially considering the problems of age uncertainties which are associated with this species.

In the case of European hake, environmental and biological factors may lead to large inter-annual variations in egg production per unit of SSB due to the reproductive strategy described earlier, which could have implications in the assessment of this population, as for other indeterminate species (for northern anchovy, Hunter and Leong, 1981; for European anchovy *Engraulis encrasicolus* L., Somarakis *et al.*, 2004). As mentioned before, this could also affect the stock-recruitment relationship used in the assessment, as normally, the SSB is estimated without accounting for various reproductive and population characteristics which can influence egg production. In this context, Murua *et al.* (2010b), using the management strategy evaluation (MSE), concluded that the inclusion of improved biological and fecundity information affected the perception of population dynamics, the BRPs and also the perception of the stock in relation to these BRPs. Similarly, the management performance, that is, the capacity of maintaining the population above BRPs, was different between the SSB estimated in the working group and in the population when realistic reproductive

characteristics were included. Murua *et al.* (2010b) concluded that the probability of a wrong perception, that is, the working group population (using the SSB) perception in relation to the BRP was contrary to the perception using alternative reproductive indices, could be different for the different reproductive potential indices studied. They also showed that use of the MSE simulation framework can be regarded as a valuable tool for testing the suitability of including a greater biological reproductive 'realism' into assessment strategies, which can be easily extended to investigate the different sources of uncertainty in the data and models during the assessment and management processes of European hake (e.g. growth).

In summary, further work in all aspects of European hake biology, ecology and assessment are necessary to address the many questions about this 'peculiar' gadoid species, which is a commercially important species that has been harvested since ancient times and was first described as a sea pike in the sixteenth century.

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