Influence of the northeastern Atlantic oceano-meteorological variability on the northern hake (*Merluccius merluccius*). Analysis of the 1978-2006 period

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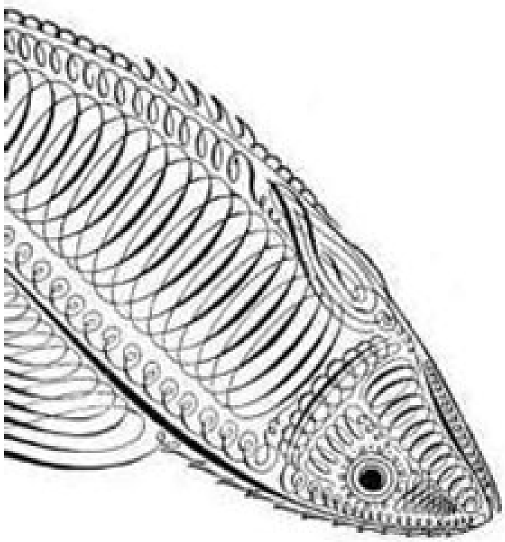

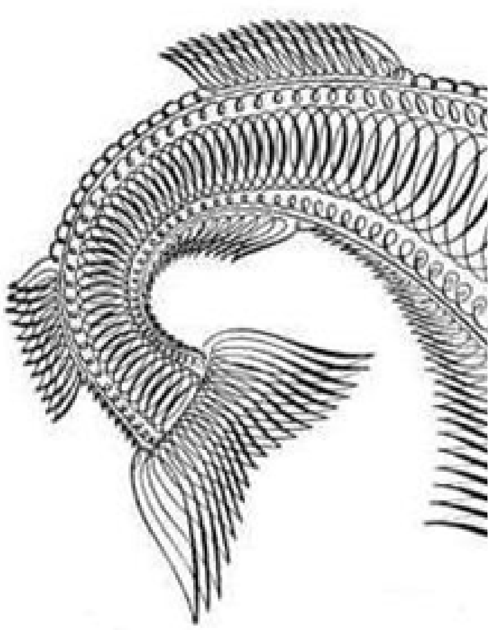

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Influence of the northeastern Atlantic oceano-meteorological variability on the northern hake (*Merluccius merluccius*).
Analysis of the 1978-2006 period

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Eskerrik beroenak…

Zuoi guztioi. Baten bat ahazteko arriskuarekin ere (izan ere makinatxo bat zarete ibilbide profesional honetan modu batean edo bestean nire alboan egon zarienok) ezin ditut aipatu gabe utzi hurrengo hauek.

Eskerrik beroenak tesi honen tutoreari. Xabier, beti agertu zara prest edozein duda, komentario, galdera erantzuteko eta beti ere modurik zuzen eta praktikoenean. Asko lagundu didate zure gomendioek, batez ere azken txanpan, gauzak oso argi ikusten ez nituen momentuetan.

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Aztiko langileei. Behin edo behin laguntza eske joan naizenean prest agertu diralako. Eskerrik asko nigan konfidantza izan dutenei ere. Baita animoak eman dizkidazuen guztiei ere. Ainho empezamos juntas en esto, ¿te acuerdas? Aitor, Nat, vaya isleta. Iratxe, Irati E., Irati L., Stefani, Eneko, Maialen, Iker, Maitane, Josean (por tanto machine learning…), Ganix, Izaro, Maria, Luci, Manel, Julien, Luis, Imanol, Nikolas, Flo, Leire, eta abar luze bat. Zuentzat ere tesi hau. Jon, zuri ere, Aztin sartu ditudan ordu luzeetan konpañia egin didazu eta. Baita kotxea zaindu ere. Mila esker. Mike, I am very grateful for your support and readiness whenever I needed help. Leire, Oihane, Iñigo, mila esker azken momentuko animoekaitik! Igor zeuri be eskerrak, neugan izanzun konfiantzigaitxik eta azken hilabete honetan emonstazuzen erreztasunekaitxik tesidxe ahalik eta arinen amaitxuteko.

Naro, orain badakit zer sentitu duzun. Zenbat negar eta barre egin ditugun ibilibide honetan! Zati luze batean fisikoki, eta azken partean interaktiboki, baina beti alboan. Skype-eri ere eskerrak emon beharko dizkiot ba, gure arteko komunikazioa eten ez duelako. Asko eskertzen dizkizut gomendioak eta batez ere animoak. Horiek barik nekeza da aurrera egitea. Eta gogoratu: together we don’t have limits!

Nat, orain zuri tokatzen zaizu. Lasai, zu nire alboan egon zaran moduan ni ere hor eukiko nauzu. Asko lagundu didazu bide luze honetan, eta ez naiz maleta gorriari buruz ari. Asteburu honetan Barakaldora zoaz? Etxekoak informatzearren…☺

Haimara, ya he terminado la tesis. Fran, ¡espero que se lo hayas dicho ya! ☺ Larissa, complimenti! Si yo he llegado a este punto, tú también estarás coronando la cima. Casualidades de la vida, siempre hemos ido a la par en este último año. Un placer compartir despacho contigo. A los compañeros del IEO de Santander, Pablo, Alberto, Izaskun, Marian, Antonio… Mi estancia fue más corta de lo esperado, pero lo suficiente para conoceros y haber aprendido de vosotros. Me he sentido como en casa. Os debo una lasaña de amatxu…

To you, Adam. And to your family. I thank you for welcoming me so warmly. You were very important at the beginning of this adventure. To Katie. She will be always in our hearts.

Family, ailega da egune. Zelako deskantsue hartungu danok ezta? Batez be zeuek. Eskerrik asko okinzuien pazentzidxegaitxik eta bueno, noiz edo noiz, zelan due tesidxe galdetute arpi zantarren bat imini badoten be parkatute nau ezta? Amatxu, laster batungot kuartoko desastrie.

Bidxotz, tesi honen momentorik garrantzitsuenan atrapa nozu, eta igual gatzenan be bai. Baie haur egon zara beti eta badaitz auntxerik aurrera be egongo zarala. San Martin-ek be neugaz batera amaitxuko daue beran tesi pertsonala. Etapa barri bat daku itxaroten alkarregaz hasteko. Zeuk guzunien.

Baten bat lerro hauetatik kanpo utzi baldin badut, jakin dezala ez dala nahita izan. Bide honetan gurutzatu baldin bagara, seguru nire bihotzean bere txokotxoa duela.

maite ditudan guztiei

maite nauten guztiei

Bagoaz mendian gora…

CONTENTS

Laburpena

LABURPENA

Arrain-populazioen gorabeherak ozeanografia eta klima-dinamikarekin lotuta daude mundu-mailan. Inguruneko kondizio ozeanografikoek, era berean, baldintza klimatikoen araberakoak direnak, bertako itsas-ekosistemetan dute eragina. Bestalde, arrantza-jarduerak presio handia ezartzen du garrantzi komertziala duten espeziengan (legatz europarra, kasurako), stockaren murrizketa eraginez. Ustiaketak itsas espezieak klimaren aurrean sentikorragoak izatera eramaten ditu. Beraz, garrantzi handikoa da klimaren aldaketa naturalek itsas ekosistemetan ze punturaino eragiten duten aztertzea. Gainera, informazio hori itsas baliabideen azterketan eta kudeaketan nola erabili ulertu beharra dago. Honenbestez, tesi honen xede nagusia izan da iparraldeko legatz europarraren populazio-dinamika ikertzea, eta inguruneko parametroen eragina aztertzea 1978-2006 artean. Gainera, bizitzako lehen faseetan legatzaren kalteberatasunaren atzean dauden kausak zeintzuk diren ere identifikatu izan dira.

Legatz europarraren banaketa-eremuko inguruneko aldaketak hobeto ulertzeko asmoz, tesi honen lehenengo pausoa izan da Atlantikoko ipar-ekialdeko plataforma kontinentalaren karakterizazio ozeano-klimatikoa egitea (**lehenengo kapitulua**). Globalki, 80ko hamarkadaren amaieratik 90eko hamarkadaren erdialderako denbora-tartean, NAO indizeak (Ipar-Atlantikoko Oszilazio indizea) balio positiboak izan zituen. Aldi berean, Golkoko itsaslasterra eta Ipar-Atlantikoko korrontea indartu egin ziren, eta, honek, ipar-ekialderanzko ur beroaren garraioa handitu zuen. 1995etik aurrera, tesi honetako ikerketa eremua EA (Atlantiko Ekialdeko indizea) positibo batean murgildu zen. Honen ondorioz, Ipar Hemisferioko tenperaturan bigarren beroketa bizi bat nabarmendu zen. Beroketa global honek eskualde-mailan ere izan zuen eragina; ipar-ekialdeko Atlantikoko plataforma kontinentalean, hain zuzen ere. Hala ere, beroketa-tasa desberdina izan zen latitudinalki: ur-azaleko tenperaturaren beroketa nabarmenagoa izan zen Bizkaiko Golkoan; aitzitik, iparralderago beroketa ahulagoa izan zen. Latitudinalki desberdintasuna erakutsi zuen beste parametro bat haizeak eragindako Ekman garraioa izan zen. Nahiz eta orokorrean ekialderanzko eta hegoalderanzko norabidea erakutsi, indarrari dagokionez, garraioa ahulagoa izan zen Bizkaiko Golkoan; eta, alderantziz, baliorik altuenak Rockall Trough-an neurtu ziren. Urtaroak kontuan izanda, Bizkaiko Golkoko eta Zelta Itsasoko errute-eremuetan beroketarik handiena uda hasieran gertatu zen (maiatzean eta ekainean). Bestalde, Bizkaiko Golkoan, Ekman garraioak kostatik urruntzeko (ahulki, mendebalderantz eta iparralderantz) joera izan zuen udaberri eta udan, baina kostaranzko norabidea (gogorrago, ekialderantz eta hegoalderantz) erakutsi zuen neguan. Ikerketa-zonako klima eta ozeanografia aztertzeaz gain, lehenengo kapitulu honetan, kopepodoen ugaritasunak jasotako aldaketak aztertu ziren; izan ere, kopepodoak legatz-larben eta gazteen janaria dira. Orokorrean, beheranzko joera izan zuen ikerketa-eremu osoan. Hala ere, urtean zehar aldaketa nabarmenak erakutsi zituen kopepodo-kopuruak eta baliorik altuenak udaberri eta udan ikusi ziren. Beheranzko joera hori nabarmenagoa izan zen Zelta itsasoko errute-eremuan, non kopepodo kopuru handiena maiatzean gertatu zen.

Legatz europarraren populazioak erauzte-arrantza handia jasaten du Atlantikoko ur europarretan. 80ko hamarkadako bigarren erdialdean, arrantzak eragindako heriotza izugarri handitu zen, eta, ondorioz, stockaren biomasa asko jaitsi zen (**bigarren kapitulua**). 90eko hamarkadan, stocka etengabe ustiatu zen, nahiz eta biomasa oso maila txikian egon eta erreklutamenduaren porroterako arriskua handia izan. Aitzitik, gurasoen biomasarekiko erreklutamenduaren arrakasta handitu egin zen sasoi horretan, eta horrek stockaren murrizketa konpentsatuko zuen ziurrenik eta kolapsorik ez gertatzea ahalbidetu. Errreklutamendua eta ugaltzaileen biomasa suspertu egin dira oraintsu, maila baxuetan denbora luze bat egon ostean. Ondorioz, iparraldeko legatzaren stocka egoera lasaigarriago batean dagoela esan dezakegu. Ikertutako denbora-tartean legatz populazioak izandako gorabeherek, legatzaren erreklutamenduak stockaren dentsitatearenganako duen menpekotasuna azpimarratzen dute. Hala ere, datu-eskasiak ezinezko egiten du stock ugaltzailearen biomasaren erreklutamendu-dinamika aztertzea stockaren tamaina guztietarako. Erabilgarri dauden datuek Ricker formako stock-erreklutamendu erlazioa iradokitzen dute, non gehiengo erreklutamendua stockaren tamaina hobezin baterako ematen den. Stock-tamaina handiagoetarako erreklutamendua jaisten hasten da, ziurrenik, espezie-barneko lehiaketa dela eta (kanibalismoa). Stock txikietarako, ordea, erreklutamenduaren jokaera ziurgabea da, batez ere, datu faltagatik; hori dela eta, ezin izan dira aztertu “Allee effect” moduko mekanismoak.

Muturreko egoeretan, arrantzaren eraginez populazioaren dinamika erreklutamenduaren gorabeheren menpe gelditzen da, nagusiki; eta, horrela, litekeena da stockaren klimarekiko sentikortasuna areagotzea. 90eko hamarkadan, stock ugaltzaileen biomasa oso txikia izanik, inguruneko kondizio ezegokiek stockaren egoera okerragotu zezaketen. Hala eta guztiz ere, erreklutamenduaren porrota gertatzetik urruti, stockak pixkanakako hobekuntza erakutsi zuen, erreklutamendu-arrakastak 80ko bukaeran izandako igoera markatuaren ostean. **Hirugarren kapituluan**, inguruneak legatzaren erreklutamendu-arrakastaren aldaketa horretan izan lezakeen eragina azaldu da. Horretarako, erregimen-aldaketak detektatzeko metodoa (Rodionov, 2004) aplikatu zen, eta horrela ikusi zen ea aldaketa ozeano-klimatikorik gertatu zen erreklutamendu-arrakastaren aldaketaren sasoi berean. Ikerketa honen emaitzek iradokitzen dute erregimen-aldaketa ekologiko bat gertatu zela Atlantikoko ipar-ekialdeko plataforma kontinentalean 1988/89 urteetan. Erregimen-aldaketa hau eskala globalean ez ezezik (NAO, Golkoko korronte indizea eta Ipar Hemisferioko tenperaturen anomaliak), eskualde-mailan ere gertatu zen (Atlantikoko ipar-ekialdeko klimatologia eta Zelta itsasoko kopepodoen aldakortasuna). Tenperatura freskoko eta haize ahuleko sasoi batetik (1978-1989) tenperatura epelagoko eta mendebaldeko haize gogorragoko sasoi batera (1990-2006) pasatu zen ikerketa-eremua. Legatzaren erreklutamendu-arrakastan gertatutako aldibereko aldaketa kontuan izanik, ondorioztatu zen sasoi horretako ingurunea legatzarentzat onuragarria zela. Ikusi zen legatzaren bizitzako lehen faseetan tenperatura epelagoak izatea mesedegarri izan daitekeela legatzarentzat (bai kondizio egokien eremua/sasoia zabaltzen delako, edo/eta hazkuntza-tasa altuagoengatik). Gainera, kostaranzko garraioak fase sentikorren dispertsioa saihestuko zuen, eta errute-eremuetatik hazkuntza-eremuetarako garraioa lagunduko zuen. Atlantikoko ipar-ekialdeko plataforma kontinentalean deskribatutako erregimen-aldaketa hau eskala handiago batean gertatutako aldaketa baten barnean sartzen da. Aldaketa horrek inguruko beste itsaso batzuetan ere eragin zuen, esaterako, Ipar Itsasoan, Baltiar Itsasoan eta Mediterraneoan.

Azkenik, **laugarren kapituluan** legatzaren erreklutamenduaren gorabeherak modelizatzeko saiakera egin da. Horretarako, kontuan hartu dira gurasoen biomasa eta aldakortasun klimatikoa. Lehen pausoan, erreklutamendu-arrakasta azaltzeko baliagarriak diren parametroen azpitalde bat eratzeko asmoz, ikuskatutako sailkapen metodologia aplikatu zitzaion hasierako datu-baseari (1. kapitulua). Hurrengo pauso batean, modeloak eraikitzeko inguruneko parametroen talde murriztua eta stock ugaltzailearen biomasa erabili ziren. Alde batetik, bigarren kapituluan definitutako Ricker modeloa aldatu zen inguruneari buruzko informazioa modeloari gehituz (Ipar Hemisferioko tenperatura-anomalia eta kopepodokopurua legatzaren errute-aldirako). Stock-erreklutamendu erlazio berri honek erreklutamenduaren aldakortasunaren portzentai altuagoa azaldu zuen. Bestalde, GAM (generalised additive model) bezala ezagutzen diren modeloak erabili ziren stockaren eta erreklutamenduaren arteko erlazio motari buruzko inolako usterik ez jartzeko. Nahiz eta aldagai berdinak aukeratu, GAMak hobeto azaldu zuen erreklutamenduaren aldakortasuna. Hori horrela izanik, legatz europarraren erreklutamenduaren gorabeherak ulertzeko gurasoen biomasa parametro garrantzitsua dela ondorioztatu zen; baina, ezin esan daiteke dentsitatearekiko menpekotasun horrek Ricker itxura hartzen duenik iparraldeko legatz europarraren kasuan, behinik behin.

Summary

SUMMARY

Worldwide fish population variability is linked to oceanography and climate dynamics. Marine ecosystems are affected by the oceanographic characteristics of their environment, which are in turn driven by changes in climatic conditions. In addition, fishing activity exerts a large pressure on commercially relevant fish stocks (e.g. European hake), leading to the decline of the stocks; exploitation increases the sensitivity of marine species to climate variability. Hence, it is critical to investigate to which extent the climatic natural variability influences marine ecosystems and understand how this information can be used in the assessment and management of marine resources. To this end, the principal objective of this thesis was to investigate the northern European hake population dynamics and assess the influence of diverse environmental parameters during the period 1978-2006. Further, environmental mechanisms underlying hake early life stages vulnerability were identified.

In order to better understand the environmental variability within the distribution range of northern European hake, the present thesis starts with the oceano-climatic characterisation of the Northeast Atlantic continental shelf (**Chapter I**). In global terms, the study period of this work was characterised by a positive NAO (North Atlantic Oscillation) phase from late 1980s to mid-1990s. Synchronously, the Gulf Stream and the North Atlantic Current strengthened, with the subsequent increase in warm water transport northeastward. From 1995 onwards, the study area was under the influence of a positive EA (East Atlantic) pattern; consequently, a second intense warming in Northern Hemisphere temperature was observed. This global warming also affected regional waters over the continental shelf of northeastern Atlantic. However, the warming rate showed latitudinal differences: SST (sea surface temperature) warming was more pronounced in the Bay of Biscay, whereas northwards the increase in SST was lower. Another parameter that differed latitudinally was the wind-induced Ekman transport: although the general direction was eastward and southward, the transport was weaker in the Bay of Biscay, whereas the strongest values were found at the Rockall Trough. In seasonal terms, the warming was more pronounced in the spawning grounds of the Bay of Biscay and the Celtic Sea in early summer (May and June). Further, Ekman transport in the Bay of Biscay was offshore (weak westward and northward) in spring and summer but coastward (stronger eastward and southward) in winter. In addition

to climate and oceanography of the area, Chapter I also analysed copepod abundance variations, as hake larvae and juvenile main prey. A general decreasing trend was observed in copepod abundance over the whole of the study area. Seasonality was clear in copepod abundance, with higher copepod abundances in spring and summer. The decreasing trend was more pronounced in the spawning ground of the Celtic Sea, where the highest copepod abundance was observed in May.

The European hake population supports a major commercial fishery in Atlantic European waters. In the second half of the 1980s, fishing mortality increased dramatically leading to the sharp fall in hake SSB (spawning stock biomass) (**Chapter II**). In the 1990s, the stock was being continuously overexploited despite its critically low biomass, and the risk of recruitment failure was high. By contrast, hake recruitment success per parental biomass did increase at this period which probably allowed the stock to compensate for the depletion without collapsing. Recruitment and SSB have recently registered a recovery after a relatively long period at low levels, and therefore northern hake stock is found to be in a safer situation. Hake population fluctuations registered over the study period pointed out the density-dependence of hake recruitment. However, the poor range of data made impossible the comparison of the dynamics of recruitment to SSB across the full range of stock sizes. The available hake data suggested a Ricker-like SR (stock-recruitment) relationship, where the maximum recruitment occurred at an optimum stock size. At higher stock sizes, recruitment began to decrease probably due to intra-specific competition (cannibalism). Recruitment response at low stock levels, though, remains unknown due to the lack of observations; as such, mechanisms such as “Allee effect” could not be studied.

In extreme cases, fishing makes the population dynamics almost exclusively driven by recruitment fluctuations, which is likely to increase stock sensitivity to climate variability. In the 1990s, at such low SSB values, unfavourable environmental conditions could have worsened the stock situation. However, far from recruitment failure hake stock showed a progressive recovery after the stepwise increase in hake recruitment success in late 1980s. In **Chapter III** the likely environmental influence on the sharp change in hake recruitment success was studied; a regime shift detection method (Rodionov, 2004) was applied to investigate whether an oceano-climatic shift occurred in synchrony with the stepwise increase in hake recruitment success. The results of this study suggest that an ecological regime shift occurred in the Northeast Atlantic shelf system in 1988/89. This regime shift was detected at global scale (NAO, Gulf Stream index and Northern Hemisphere temperature anomaly) as well as regionally (climatology of the Northeast Atlantic and copepod variability in the Celtic Sea). The region went from a period of cool temperatures and relatively weak winds (1978-1989) to a period of warmer temperatures and stronger westerly winds (1990-2006). Given the synchronous stepwise increase in hake recruitment success, it was concluded that the environment shifted to a regime that was favourable for northern hake. Early life stages of hake were found to benefit from a warming trend (either through the widening of the optimal environmental window or/and higher growth rates). In addition, coastward transport avoided vulnerable stages from their dispersion to oceanic areas and helped in their transport from spawning areas to nursery grounds. The regime shift described in the Northeast Atlantic shelf system is part of a wider-scale change that also affected other neighbouring basins, such as the North Sea, the Baltic Sea and the Mediterranean Sea.

In a further study, C**hapter IV** attempted to model hake recruitment fluctuations considering both, SSB and environmental variability. As a first step, a supervised classification methodology was applied to the initial dataset (Chapter I) in order to select a subset of recruitment success explanatory parameters. Afterwards, the reduced group of environmental parameters, together with the SSB, was used to build the models. On one hand, the Ricker approach defined in chapter II was modified by introducing environmental information (Northern Hemisphere temperature anomaly and copepod abundance for hake spawning season) to the model. This environmentally modified SR relationship explained a higher percentage of recruitment variability than the Ricker SR itself. On the other hand, generalised additive models (GAMs) were used to build a model with no prior assumption regarding the form of the relationship between the stock and recruitment. Despite selecting same explanatory variables, the GAM succeeded in explaining better the recruitment variability. Thus, even if parental biomass is an important factor to understand northern hake recruitment variations, it was not possible to assume that this density-dependence takes a Ricker form in the case of northern European hake.

General introduction

GENERAL INTRODUCTION

Climate relevance

Climate has an important effect on ecosystem functioning. In marine ecosystems a wide number of studies have been published showing the influence of environmental parameters on different levels of the trophic web (Beaugrand and Reid, 2003; Beaugrand, 2004; Alheit *et al*., 2005; Alheit, 2009; Möllmann *et al*., 2009; Pörtner and Peck, 2010). Concerning fish populations, climate effects have been studied in pelagic species like anchovy (Junquera, 1988; Ruiz *et al*., 2006; Borja *et al*., 2008), sardine (Guisande *et al*., 2001, 2004; Santos *et al*., 2007), mackerel (Borja *et al*., 2002; Hannesson, 2007) and horse mackerel (Lavín *et al*., 2007; Santos *et al*., 2007; Rijnsdorp *et al*., 2009), as well as in demersal species such as blue whiting (Hátún *et al*., 2009a) and cod (Drinkwater, 2005; Vikebo *et al*., 2005; Stige *et al*., 2006; Mieszkowska *et al*., 2007; Brander, 2010) amongst others. Given the influence that climate exerts on marine ecosystems, variations in environmental conditions suppose fluctuations in fish stocks.

Climate can influence marine fish populations at different age stages. However, early life history has been observed to be more vulnerable to environmental changes (Pörtner and Peck, 2010). Indeed, the relative year-class strength of a population is determined at the early stages; this period is the major cause of marine fish production variability (Cushing, 1971). As an example, recruitment failure of Eastern Baltic cod was mainly caused by high egg and larval mortalities as a result of climate –induced hydrographic change (Köster *et al*., 2005; Möllmann *et al*., 2008).

Changes in climate can occur as an environmental long-term progressive trend. For instance, the ongoing warming of the climate is reflected on the 100-year linear trend of 0.74 ºC of the global average surface temperature. Besides, the continuous sea level rise and the observed decrease in snow and ice extend are also consistent with the global warming (IPCC, 2007). On the other hand, decadal changes are often described as regime shifts in which a rapid reorganisation of the ecosystem takes place from one relatively stable state to another (Scheffer *et al*., 2001; Rodionov and Overland, 2005). Climatic regime shifts have been identified in the sea surface temperature of the Northern Hemisphere in the last century

(Yasunaka and Hanawa, 2002). Further, climate driven ecological regime shifts have been observed in both Pacific and Atlantic oceans (Alheit and Bakun, 2010; Overland *et al*., 2010). Actually, ecosystems seem to answer non-linearly with strong regime shifts to small changes in the physical variables (Hsieh *et al*., 2005).

Hake relevance

The role of hake is relevant within the marine ecosystem. As a top predator, they prey on small pelagic species placed in lower trophic levels, but they also play the role of food for sharks and other larger predators (ICES, 2010). Further, they are widely distributed occupying marine ecosystems worldwide. In the Northeast Atlantic, European hake distribution extends from the tropical western coast of North Africa to the cold waters of the western coast of Norway (Casey and Pereiro, 1995).

Aside from the ecological importance, there is no doubt about the economical significance of hake. Hake fishery has a long history. The earliest documentation of the European hake fishery was during the 18th century (Casey and Pereiro, 1995). However, it was not until the first half of the 20th century when a large-scale hake fishery began; this was mainly related to the technological development of fleets and the collapse of major cod stocks (Pitcher and Alheit, 1995).

Showing such a wide spatial distribution, hake is exploited by fleets from several countries. The European hake population supports a major commercial fishery in Atlantic European waters. This species has been a very important economical resource for many demersal fisheries in the area but it is especially important for Spanish and French fleets (ICES, 2010). Europe, especially Spain, constitutes the major market for hake in the world, where they import around 700,000 tonnes annually (Murua, 2010).

Hake belong to a very extended and diverse community of commercial species and it is caught in mixed fisheries. Amongst others, megrim, monkfish, nephrops, blue whiting, and horse mackerel can be found in the catch of these mixed fisheries. Several fishing units focus their activities on the northern stock of European hake and thus hake is harvested using various gears such as longlines, gillnets and medium to deep water trawls (Murua, 2010).

Assessment and management of the northern European hake

Within ICES (International Council for the Exploration of the Sea), the Working Group on the Assessment of Southern Shelf Stocks of Hake, Monk and Megrim (WGHMM) meets annually in order to collate, review and, when needed, revise working documents on data and/or assessments of the status and forecasts of stocks (ICES, 2008). As a result, this institution provides annual reports with the review of the stock.

The assessment is based on the age structure of the population (XSA: age-based assessment), taking into account commercial CPUE (catch per unit effort) series. This method gives annual estimates of spawning biomass, recruitment and fishing mortality derived from an analysis of biological samples of landings and research vessel abundance indices (ICES, 2009a).

Considering the biological reference points B_{lim} and B_{pa} (limit and precautionary approach spawning biomass, respectively) and taking into account the agreed fishing mortality, hake population is managed by TAC (Total Allowance Catch) and quota regulations. In addition, there are other technical measures that have been implemented: a minimum legal size of 27 cm total length (30 cm in Division IIIa), a 100 mm minimum mesh size for otter-trawlers when hake comprises more than 20% of the total catch, excluding vessels less than 12 m in length and which return to port within 24 hours of their most recent departure. In specific areas, a 100 mm minimum mesh size is required for all otter-trawlers. Further, fishing mortality has been limited to 0.25 and a maximum change in TAC of 15% between years has been set (ICES, 2010).

Northern hake population has been overfished for decades, leading to a pronounced decrease in the spawning stock biomass. Consequently, all the above-mentioned measurements have been implemented under an emergency plan in 2001 (Council Regulations EC 1162/2001, EC 2602/2001 and EC 494/2002) and a recovery plan in 2004 (EC Reg. No 811/2004). However, none of the plans considered that the northern hake population dynamic might be also affected by climatic variability. At present, a new management plan is under development by the European Commission (ICES, 2010).

Overfishing is most often the principal reason for strong reductions of fish stocks. Nevertheless, the effects of overexplotation could be augmented by the influence of adverse environmental conditions (Brodziak and O'Brien, 2005), since overfishing leads to increased sensitivity of fish populations to climate fluctuations (Worm and Myers, 2004; Perry *et al.*, 2010). Climate and exploitation interact in their effects (Planque *et al.*, 2010) and thus, models of fish populations that do not take into account the systematic changes in environmental indicators may provide misleading information for developing fisheries management strategies (Brander, 2005).

Both hake and cod are emblematic gadoid species for European fisheries. Studies concerning North Atlantic climate influence on cod stocks are numerous (Saetersdal and Loeng, 1987; Rodionov, 1995; Ottersen and Sundby, 1995; Planque and Fox, 1998; Planque and Frédou, 1999; Ottersen and Loeng, 2000; Sundby, 2000; Parsons and Lear, 2001; Buch *et al.*, 2003; Planque *et al.*, 2003; Brander and Mohn, 2004; Stein and Borovkov, 2004; Brodziak and O'Brien, 2005; Köster *et al.*, 2005; Vikebo *et al.*, 2005; Drinkwater, 2005, 2006; Brunel and Boucher, 2006; Stige *et al.*, 2006; Sundby and Nakken, 2008; Rijnsdorp *et al.*, 2009). But works on climate effect on hake stocks are very scarce; only some studies have been undertaken regarding environmental preferences (Sánchez and Gil, 2000; Motos *et al.*, 2000; Sánchez *et al.*, 2003; Álvarez *et al.*, 2004; Ibaibarriaga *et al.*, 2007; Persohn *et al.*, 2009). Further, in the case of cod, the synergistic effects of climate and fishing activity have been investigated (O'Brien *et al.*, 2000; Brander, 2005; Ottersen *et al.*, 2006; Mieszkowska *et al.*, 2007; Möllmann *et al.*, 2008; Brander, 2010), and such information has even been introduced in models in order to evaluate its implications in cod fisheries management (Cook and Heath, 2005; Kell *et al.*, 2005; Lindergreen *et al.*, 2009). This is not the case for hake where environmental effects have not been considered yet.

Modern fisheries research and management must take into account the interaction between climate and fishing (Perry *et al.*, 2010). Nevertheless, the ecological factors or environmental conditions impacting on hake population dynamics are not taken into account at present in the assessment and in the management of the northern European hake. According to ICES, this is because our knowledge on these issues is still very limited (ICES, 2010).

Hypothesis

If we are asked to list the most critical factors that could be affecting the population dynamics of northern European hake, two main causes come first to mind. Considering its commercial importance, fishing pressure seems to be the main cause for the stock decline. Fishing mortality directly affects the parental stock, leading to variations in spawning stock biomass; the progeny would be also affected indirectly. However, the offspring population could also be influenced by other density-independent agents. In fact, the early life stages of a marine population are more sensitive in comparison to adult stages, and thus they have to face the environmental conditions in order to survive and come to recruit to the adult population. The recruitment success is critical since the early life history of a population is believed to determine the strength of an incoming year-class.

In this regard, we pose the following hypothesis as a basis for this study: Northern European hake population dynamic, aside from the parental influence, is affected by environmental conditions that occur at the early life stages of individuals.

Objectives

In order to test the above presented hypothesis, the principal aim of this thesis is to investigate the northern European hake population dynamics and assess the influence of diverse environmental parameters during the period 1978-2006.

With that aim, several operative objectives have been determined and are listed below:

- To **describe the general oceano-climatic characteristics of the Northeast Atlantic Ocean** for the study period, in terms of both spatial and temporal variability.

- To **analyse northern European hake population dynamics** based on spawning stock biomass and recruitment fluctuations:
    - To study the recruitment success variations of the stock.
    - To assess the sustainability of the stock and the effect of fishing activity over the study period.

- To **determine whether a regime shift occurred** in the distribution range of northern hake over the study period, that could have affected hake recruitment success.

- To analyse whether a density-dependent factor, such as **stock-recruitment relationship** or a density-independent factor such as an environmental factor, is more important in recruitment dynamic:
  - To search for a stock-recruitment relationship that best fits northern European hake data and try to improve it incorporating one or more environmental variables to the model.
  - To explore the dependence of hake recruitment on spawning stock biomass and environmental variables, with no assumption of any type of stock-recruitment relationship.

- To provide a better understanding of the **environmental mechanisms underlying hake early life stages** vulnerability.

Structure of the thesis

STRUCTURE OF THE THESIS

With the purpose of achieving the objectives above stated, this thesis conforms to the following structure:

Initially, a brief summary of hake ecology and fishery is presented. This section summarises the classification and biogeography of hakes, and it gives some notions concerning the distribution and biology of European hake. Further, the worldwide importance of hake fishery is reviewed, highlighting the economical relevance of European hake.

Afterwards, the results of the thesis are presented. This section constitutes the main body of the thesis and it is arranged in four chapters. Each chapter starts with an introduction presenting the context of the chapter, followed by the methodology used and the results observed, and it finishes with the discussion of the main findings. The main theme of each chapter is stated below:

As a first step, the hydro-climatic characterisation of the distribution range of the northern European hake is carried out (CHAPTER I). In this section the main trends and the seasonal patterns of several hydrological and climatic variables covering the Northeast Atlantic continental shelf are evaluated. Further, anomalies recorded over the study period are identified. Such study is undertaken based on global, regional and local parameters and both spatial and temporal variability are assessed.

Northern European hake population dynamics are described in CHAPTER II. This part of the thesis focuses mainly on SSB and recruitment variations; it also studies the recruitment success of the stock along the study period. In addition, taking into consideration the evolution of the fishing mortality, the exploitation level of the stock is assessed and hake population sustainability over the three-decadal period is described. To finish, the density-dependence of hake recruitment is explored by means of a stock-recruitment model that best fits to hake data.

CHAPTER III explores the environmental variability over the study period, and its potential influence on northern hake recruitment success. On one hand, it investigates to which extent the recruitment success fluctuations are driven by changes in NE Atlantic continental shelf environment, considering the likely occurrence of a regime shift. On the other hand, it studies how the relationship between hake and environment distributes spatially; in this regard, the influence of sea surface temperature anomaly and Ekman transport (east-west and north-south) on hake recruitment success is analysed over the whole of the study area and particularly, over the main spawning grounds (Celtic Sea and French shelf of the Bay of Biscay).

In a further study, hake recruitment dynamics are studied in relation to parental stock biomass and previously selected environmental parameters (CHAPTER IV). For that purpose, a machine-learning framework is built and the optimal parameters to explain recruitment success variability are selected. Additionally, based on the selected variables, hake recruitment dynamic is modelled following two procedures: firstly, an environmentally modified stock-recruitment model (GLM) is built with the aim of improving the SR relationship described in Chapter I; secondly, a generalised additive model (GAM) is used in order to explain recruitment fluctuations under no assumption of any determined SR relationship.

In the final section, the major findings observed in this thesis are discussed as a whole, and the main conclusions drawn from the general discussion are enumerated.

Brief summary of hake fishery and ecology

BRIEF SUMMARY OF THE HAKE FISHERY AND ECOLOGY

Taxonomic classification and biogeography of hakes

Hakes are marine fish populations that belong to the following taxonomic classification (Cohen *et al*., 1990):

Order Gadiformes
    Family Merlucciidae
        Genus Merluccius

The generous *Merluccius* shows a wide geographical distribution (Figure 1), with some discontinuities around the equatorial latitudes and its proximities. It is found in both, the north and south hemisphere: in both sides of the Atlantic Ocean, along the whole American eastern Pacific, and New Zeeland; it shows also a punctual distribution in the western Pacific (Japan) and the Indian Ocean (south and southeast of Madagascar) (Lloris *et al*., 2003).

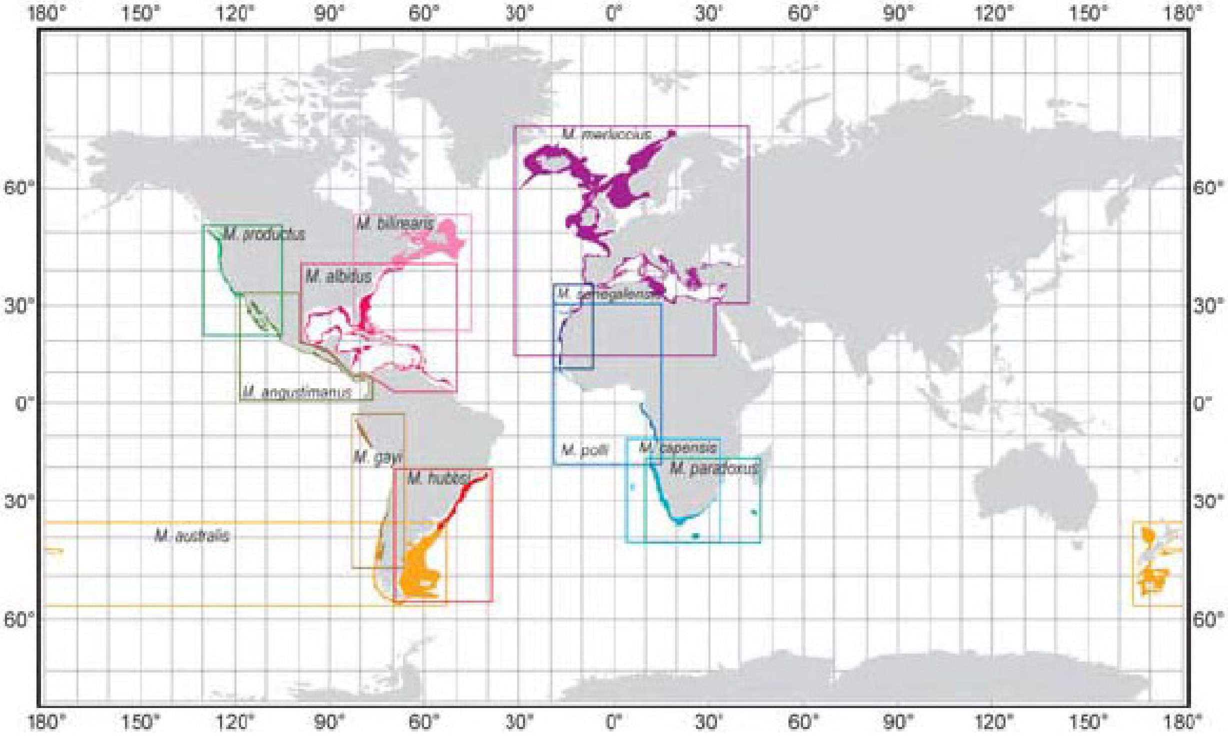


Figure 1: Worldwide geographical distribution of the generous Merluccius (source: Lloris et al., 2003).

The importance of hake fishery

The Merlucciidae family in general, and *Merluccius* generous in particular, has a great fishing interest, and some of the species belonging to this generous, are target species of an important industrial exploitation (Lloris *et al*., 2003).

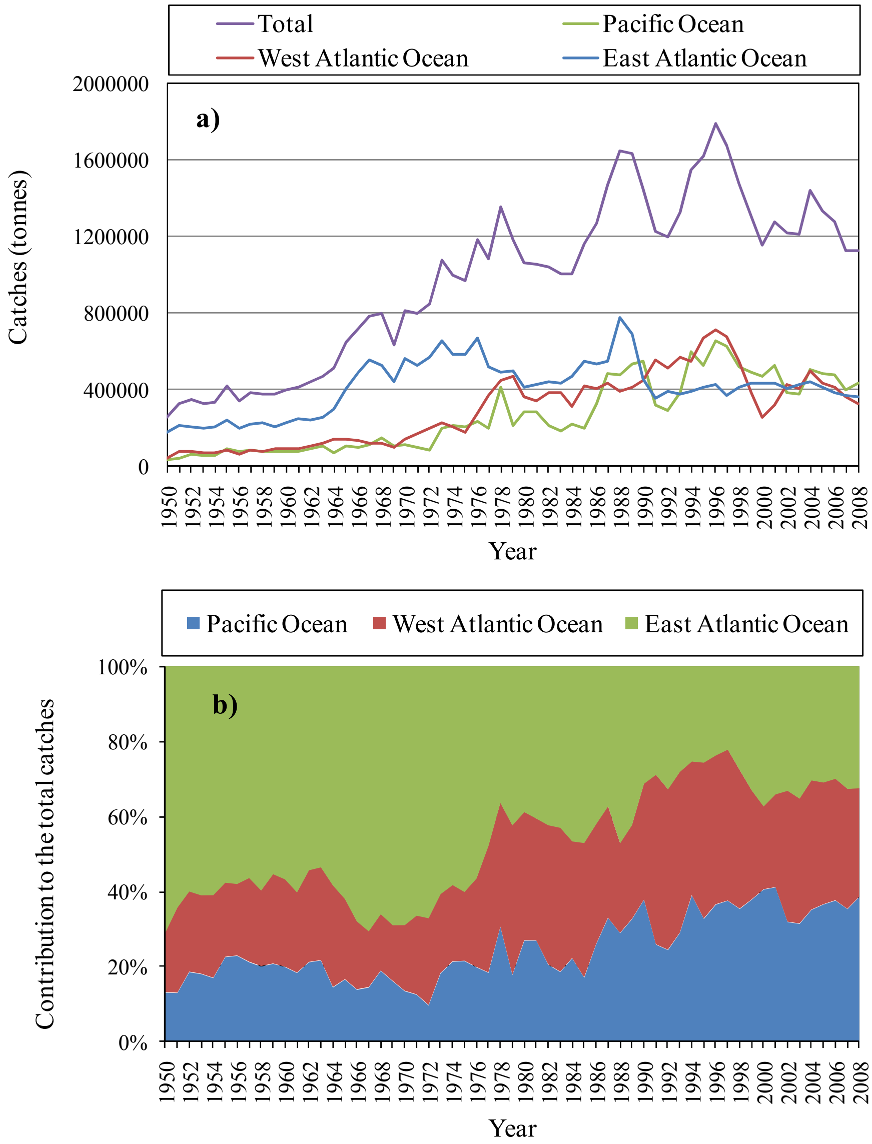


Figure 2: a) Time-series of total catches and catches per area of Merluccius sp.; b) Contribution of each area catches to the total world catches (source: FAO).

As reported by FAO statistics (FAO, www.fao.org/fishery/statistics), world annual hake catches suffered a sharp increase in the mid-60s and it continued increasing until late 70s (Figure 2a). In the recent two decades, total catches has shown high fluctuations with a general downward trend. The same graph illustrates hake catch fluctuations for East and West Atlantic Oceans and for Pacific Ocean. Focusing on different area catches, during the first two decades, the greatest part of the total catches has been taken in the East Atlantic Ocean, particularly at the end of the 1960s, when East Atlantic Ocean catches accounted for almost 70% of the total catches (Figure 2b). At the second mid of the 70s, Pacific and West Atlantic catches importance increased in the world hake fishery and catches belonging to these two fisheries rose significantly during the period 1975-1995 (Figure 2a, b). Over the last two decades, the three areas have contributed similarly to the total catches, fluctuating around 400,000 tonnes.

Figure 3 shows the contribution of each species catches to the total catches within the East Atlantic Ocean. European hake (*Merluccius merluccius*) and Cape hakes (*Merluccius capensis* and *Merluccius paradoxus*) were the mostly exploited hake species for the first decade of the series. In the 1960s, Cape hakes catches proportion increased substantially, and from that time onwards, mainly cape hakes and secondly European hake were the most important species of the East Atlantic Ocean hake fisheries. Other species such as Senegalese hake (*Merluccius senegalensis*), Argentine hake (*Merluccius hubbsi*) and Silver hake (*Merluccius bilinearis*) contributed in a lower extent.

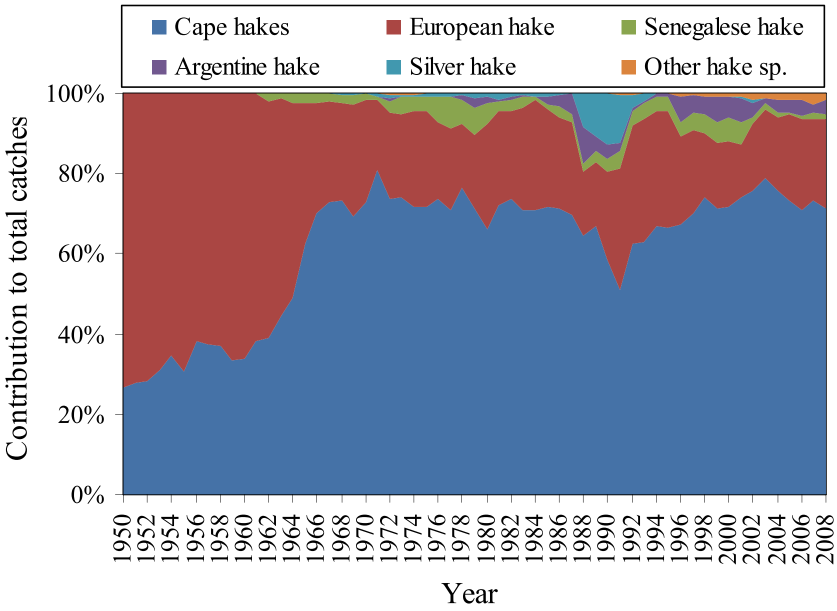


Figure 3: The contribution of different species to the total catches of Merluccius in the East Atlantic Ocean (source: FAO).

With reference to the European hake (*Merluccius merluccius*), it is widely distributed over the Northeast Atlantic shelf (Figure 4). Its range extends from Mauritania to off the western coast of Norway (between 21ºN and 62ºN) and the waters south of Iceland (Casey and Pereiro, 1995), with a larger density from the British Islands to the south of Spain (ICES, 2008). It also extends eastwards into the North Sea, Skagerrak and Kattegat, and into the Mediterranean (Casey and Pereiro, 1995). It is also found in the Black Sea (ICES, 2008).

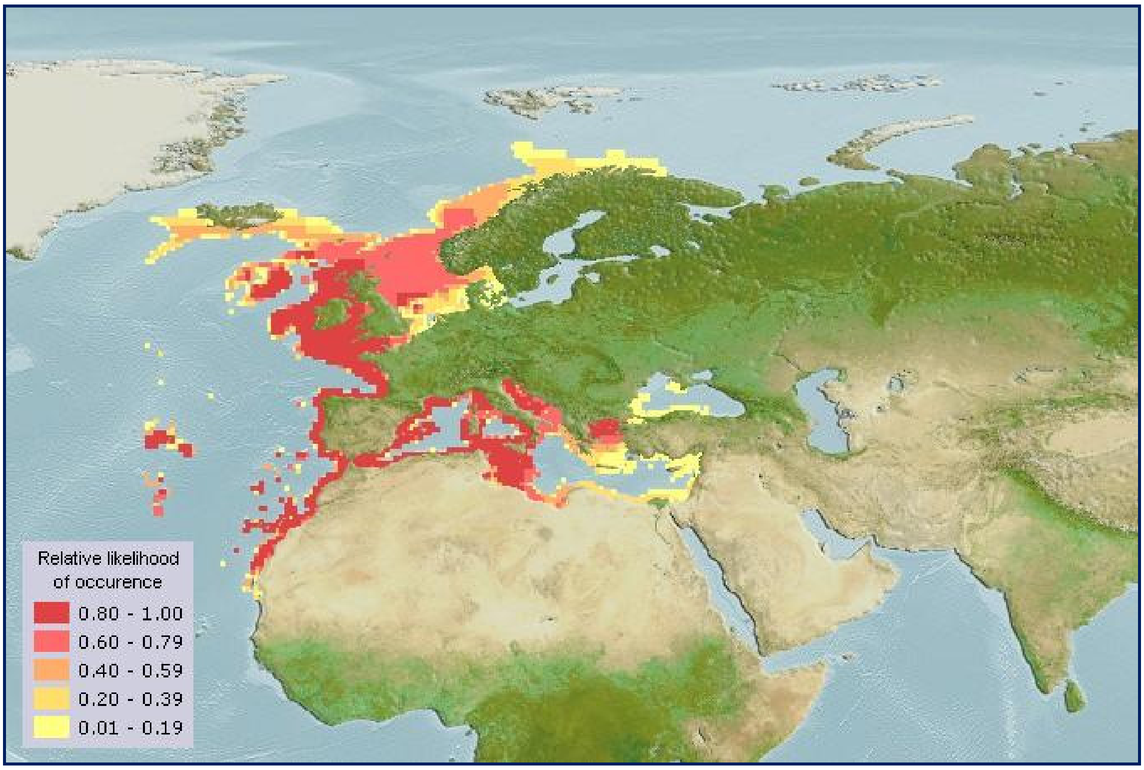


Figure 4: European hake distribution over the northeastern Atlantic shelf, Mediterranean Sea and the Black Sea (source: http://www.fishbase.org.cn).

Hake is exploited all along the western European shelf from the Strait of Gibraltar in the south to about 61ºN in the vicinity of the Shetland Isles (Casey and Pereira, 1995). For assessment purposes, the International Council for the Exploration of the Sea (ICES) assumes since the end of the 70s the existence of two stocks: the so called Northern stock, which is found in Division IIIa, Subareas II, IV, VI and VII and Divisions VIIIa,b,d; and, the so called Southern stock, distributed along the Spanish and Portuguese coasts, in Divisions VIIIc and IXa (Figure 5). Despite genetic studies have shown that there is no evidence of multiple populations in the Northeast Atlantic (Mattiuci *et al*., 2004; Castillo *et al*., 2005), the main reason for this choice was that the Cap Breton canyon could be considered as a geographical bound, limiting exchanges between the two populations (ICES, 2008). This barrier is located close to the border between the southern part of Division VIIIb and the more eastern part of Division VIIIc, adjacent to the discontinuity between the Spanish and French coastlines.

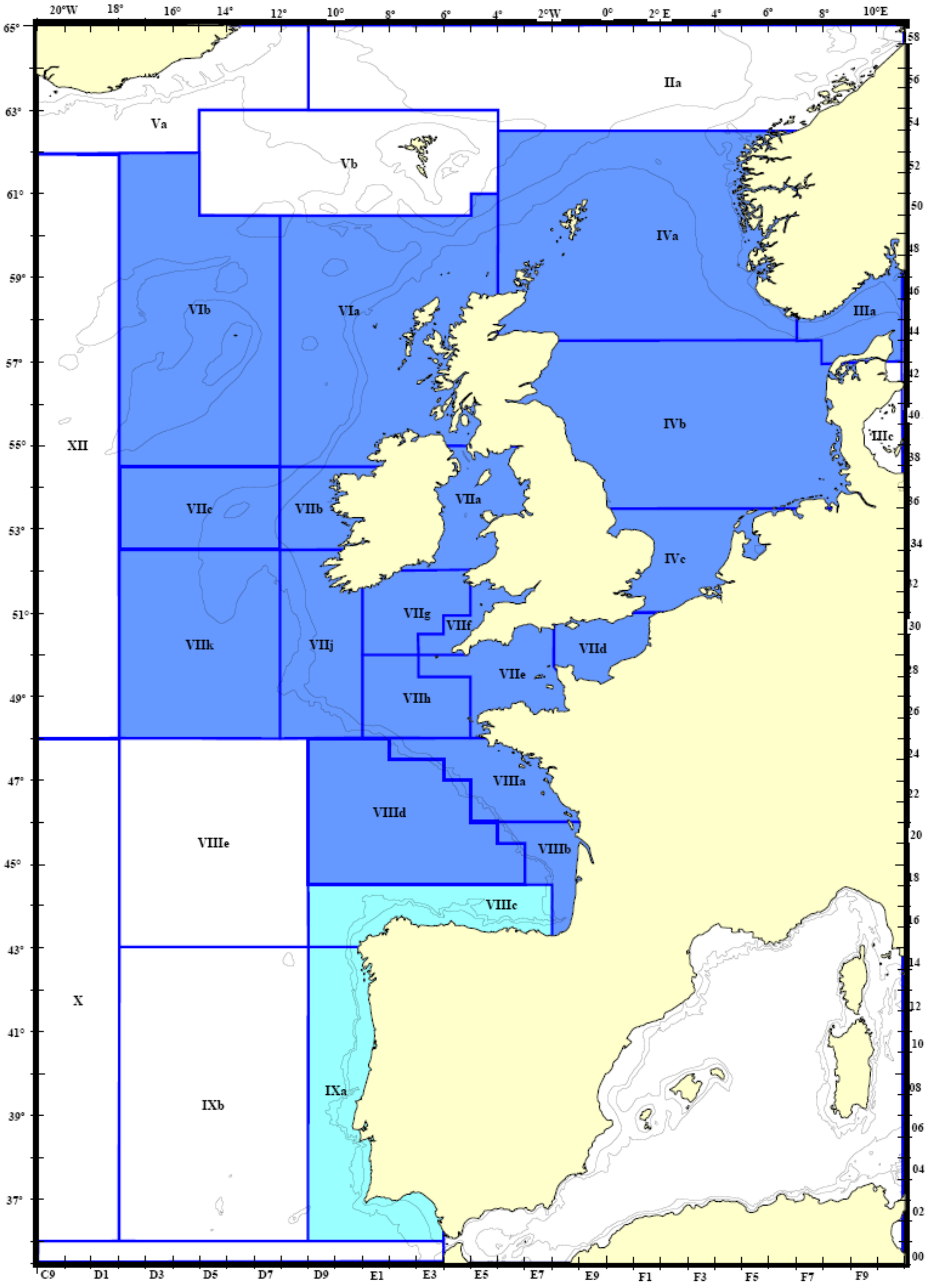
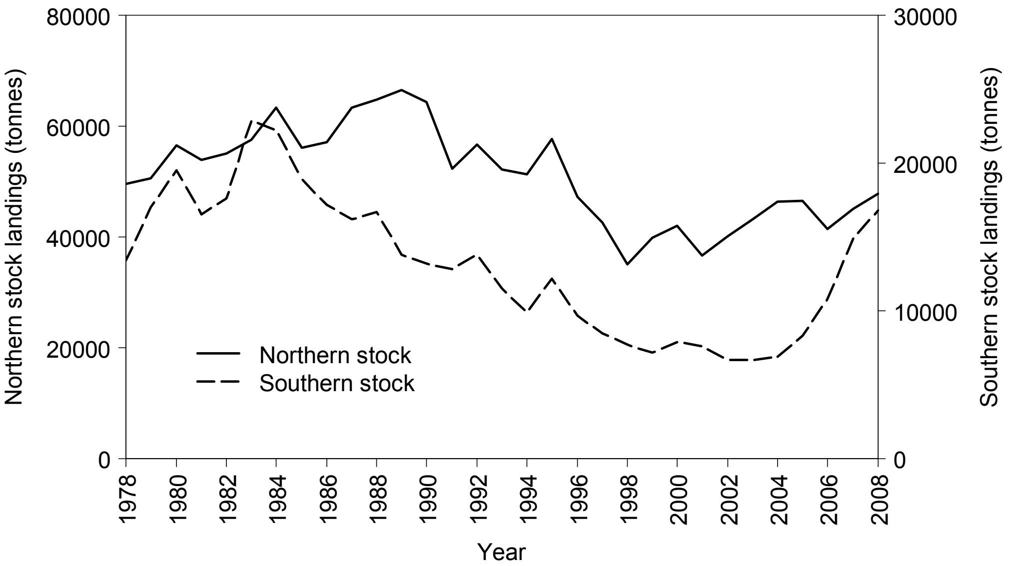


Figure 5: Map of ICES divisions. In dark blue, northern hake distribution areas, where hake data used in this study belongs to. In light blue, southern stock distribution around the Iberian coast (source: ICES, 2010).

So far, the assessment and management of the mentioned stocks has been done separately. However, it is highlighted the need for further studies (e.g. tagging experiments and genetic studies) (ICES, 2008) in order to clarify whether European hake is divided in two different stocks or a unique population exists for the whole northeastern Atlantic area. Further, Roldán *et al.* (1998) concluded that the present management of Atlantic populations based on two distinct "northern" and "southern" stocks, requires modification, since the population structure within the Atlantic is more complex.

Landings of both northern and southern stocks are plotted on Figure 6. Southern stock reached the catches peak (above 20,000 t) at the beginning of the 1980s decade, whereas northern stock catches registered circa 70,000 tonnes at the end of the 1980s decade. Although they both showed a general decreasing trend in the 1990s, recently both fisheries seem to be recovering initial landing values.



<u>Figure 6</u>: Hake landings fluctuations over the period 1978-2008, for both the northern and the southern stock (source: ICES, 2010).

The present thesis will focus on the northern stock of European hake. For many decades, this species has been a very important resource for many demersal fisheries of the region, being especially important resource for the Spanish and French fishing fleets but also for Irish and English fleets. It is landed as targeted or incidental catch by a wide variety of gears (bottom trawls, nets, and longlines) (ICES, 2008).

Figure 7 focuses only on our target species and it summarises northern stock landings over a longer time period. The annual landings fluctuated between 30,000 and 90,000 tonnes during the period 1962-2008. The highest landings were recorded at the beginning of this period and afterwards total landings decreased progressively until 1971. For the last three decades, the information on annual mean landings is divided by ICES areas. The importance of hake fishery has been highly more important in the Celtic Sea (VII) and the Bay of Biscay (VIIIa,b) comparing to the landings off the Scottish (VI) and Norway coasts (IVa). Celtic Sea and Bay of Biscay fishery showed the greatest landings at the 1970 decade, decreasing steadily until the end of the 1990s, when they reached their lowest values for the whole 1962-2008 period.

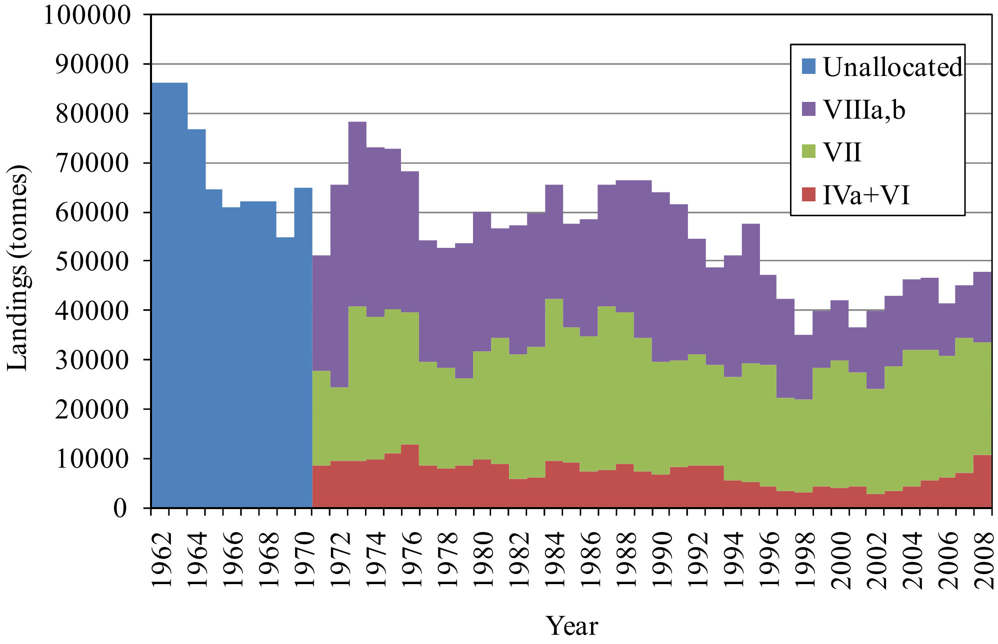


Figure 7: Northern stock annual total catches for the different ICES defined areas in the Northeast Atlantic (source: ICES, 2010).

Northern European hake, Merluccius merluccius (Linnaeus, 1758)

Habitat

The European hake is a demersal and benthopelagic species; it lives mostly between 70 and 370 m, although it is found in both shallower and deeper waters, from coastal waters (30 m) to 1000 m (Lloris *et al.*, 2003; Meiners, 2007). Usually it is close to the bottom during daytime and then moves vertically in the water column during the night.

Although European hake distributes widely over the northeastern Atlantic continental shelf, the distribution pattern changes as a result of the seasonal migrations. Hake movements have been studied from the seasonal distribution of reported catches: from the beginning of the year until March-April adult hake are present in the north of the Bay of Biscay; they appear on the shelf edge in the Celtic Sea in June and July.; between August and December a large hake fishery is centred to the west and southwest of Ireland, with a decline in catch rates in shallower waters (ICES, 2008). Migrations have been found to be mainly linked to reproduction (Persohn *et al*., 2009).

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 (Murua, 2010).

Biology: growth, feeding and reproduction

Hake has a medium-large size with a maximum size and weight of about 140 cm and 15 kg, respectively (Figure 8). However, it rarely exceeds from 100 cm and 10 kg (Lloris *et al*., 2003). At present it is believed that is has a medium lifespan, with a maximum age of about 12 years.

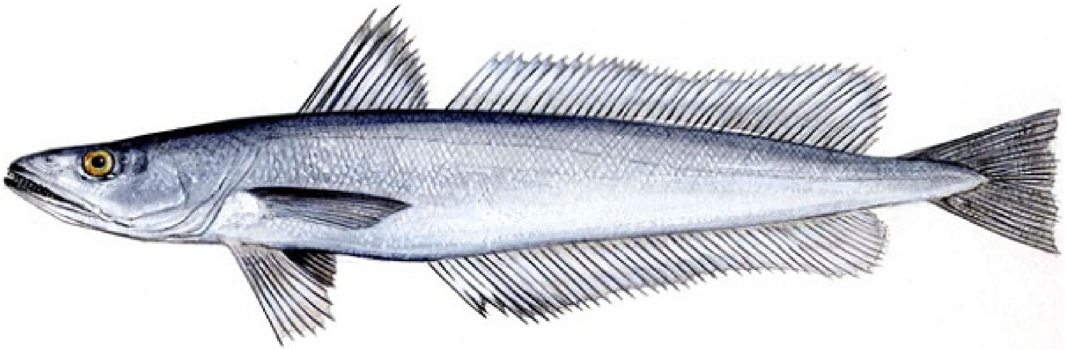


Figure 8: Illustration of the European hake, Merluccius merluccius (Murua, 2010).

Growth

Otoliths have been used as an internationally approved ageing tool for many years. However, the lack of conformity between otolith readers led to inconsistencies in age-reading methods. Consequently, different authors proposed different growth models for European hake (Murua, 2010). Generally speaking there are two hypotheses regarding the European hake growth rate. For many years, European hake was believed to be a slow-growing species, growing about 10 cm per year. However, recent tagging experiments have reported that the European hake exhibit a twofold faster growth rate compared to previously published data, information that classifies the European hake as a fast-growing species (dePontual *et al.*, 2003, 2006; Piñeiro *et al.*, 2007). This is an issue of critical importance since the annual assessment of European hake has been based on the age structure of the population (XSA: age-based assessment) for many years (ICES, 2009b).

Males grow faster than females up to around 3 years old and from that age onwards the growth rate of males decreases and females grow faster. Further, females reach a larger size and grow older than males; consequently, the sex ratio is skewed towards females in the largest length classes (Murua, 2010).

Feeding

European hake feed on crustaceans and fishes (Cabral and Murta, 2002; Lloris *et al.*, 2003). Larvae and juvenile hake prey mainly upon planktonic crustaceans (above all euphausids, copepods and amphipods) (Reiss *et al.*, 2005; ICES, 2008). As hake grow, fish become more prevalent in their diet (Velasco and Olaso, 1998; Mahe *et al.*, 2007); in hakes longer than 50 cm fish occurs in all stomachs (Lloris *et al.*, 2003). Adults are top predators that feed mainly on blue whiting; however, other gadoid species and small pelagic fish such as, sardine, anchovy, mackerel and horse mackerel are also present in their diet (Guichet, 1995; Du Buit, 1996; Velasco and Olaso, 1998; Cabral and Murta, 2002; Pinnegar *et al.*, 2003; ICES, 2008).

Cannibalism on juveniles by adults is also observed in European hake (Guichet, 1995; Velasco and Olaso, 1998); however the degree of cannibalism differs among areas. Cannibalism in the diet of hake was found to be relatively rare in the western (Cabral and Murta, 2002) and northern Iberian coasts (Velasco and Olaso, 1998) but was found to be significant in the northern Bay of Biscay and the Celtic Sea (Mahe *et al.*, 2007). These geographical differences were attributed to the width of the continental shelf: in areas with a steep continental shelf, like off Portugal and Cantabrian Sea, different length groups tend to live at different depths; whereas, in areas with a broad continental shelf, such as the Celtic Sea and off the northern French coast in the Bay of Biscay, there may be a coexistence of hakes of different lengths (Velasco and Olaso, 1998; Cabral and Murta, 2002; Mahe *et al.*, 2007).

Indeed, Figure 9 shows the overlap between hake juvenile and adult distribution for a study undertaken between 1992 and 2006 (Pershon *et al*., 2009).

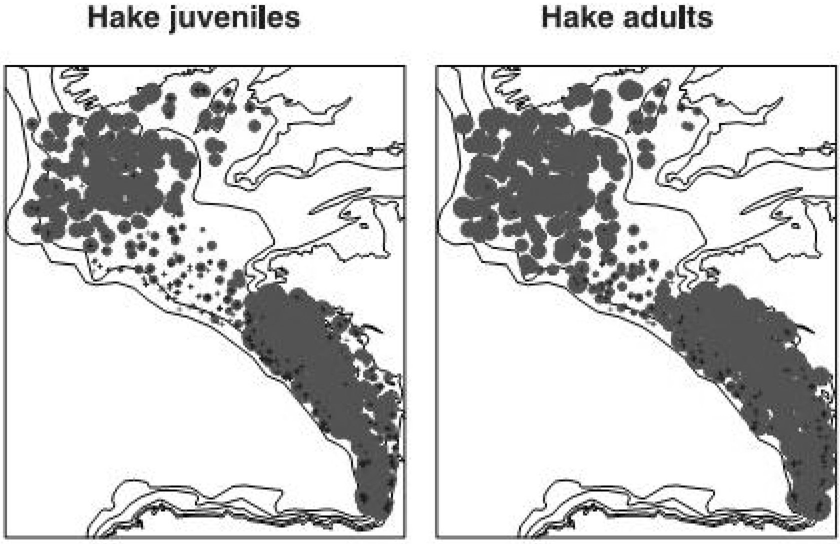


Figure 9: Spatial distribution of European hake juveniles (on the left) and adults (on the right) over the French continental shelf and the Celtic Sea for the period 1992-2006 (source: Pershon et al., 2009).

Reproduction

Males reach the first maturity at about 39 cm and 3.4 years whereas females become mature with 47 cm and 4.2 years (ICES, 2008).

European hake exhibits indeterminate fecundity, which means that the potential annual fecundity is not fixed prior to the onset of the spawning. Oocytes of all stages are simultaneously present in reproductively active ovaries (asynchronous oocyte development) (Murua, 2010). European hake shows a protracted spawning season, with spawning females present all year round (Murua and Motos, 2006).

Hake spawning is linked to the shelf break area, extending from the north of the Bay of Biscay to the south and west of Ireland (Figure 10). The maximum egg abundance takes place close to the 200 m isobath (Motos *et al*., 2000). However, northwestern Celtic Sea and the north of the Bay of Biscay are the spawning concentration areas (Poulard, 2001). Although spawning occurs all year round, the egg production differs depending on the season; European hake eggs have been mainly found in temperatures from 10 ºC to 12.5 ºC (Ibaibarriaga *et al*., 2007) but they can be found in higher water temperatures of up to 15 ºC

(Álvarez *et al*., 2004; Ibaibarriaga *et al*., 2007). Generally speaking, hake spawn mainly from February through July along the shelf edge (ICES, 2008), but there are temporal differences depending on the latitude, since hake larvae show a northern displacement as the season progresses (Álvarez *et al*., 2004). The peak spawning time of hake is earlier in southern waters, whereas it takes place later as the latitude increases (Casey and Pereiro, 1995): in the Bay of Biscay, it ranges from January to May (Sarano, 1983; Martin, 1991), with the highest levels of egg production from January to March (Murua and Motos, 2006). Other authors have documented February-March as the peak spawning season (Lucio *et al.*, 2000; Álvarez *et al*., 2001) with March showing the highest peaks. In the Celtic Sea, Lannin (2006) defined January to August as the peak spawning season. Other studies reported that peak spawning occurs from April to June (Coombs and Mitchell, 1982; Fives *et al.*, 2001). In western Ireland, spawning takes place from April to July and in the west of Scotland, from May to August (Hickling, 1930; O'Brien, 1986). Northward, spawning has been recorded in the West Coast of Norway in August (Kvenseth *et al*., 1996).

The eggs of European hake are pelagic. In spite of the fact that their major densities are found mainly in the upper 200 m of the water column over the shelf break (Álvarez *et al*., 2004; Ibaibarriaga *et al*., 2007), the depth distribution through the water column can be different depending on the environmental conditions such as water temperature.

After hatching, early European hake larvae are still found over the shelf break (Álvarez *et al*., 2004; Ibaibarriaga *et al*., 2007). Afterwards, hake larvae appear to undergo a coastward displacement as the spawning season progresses, heading to the main nursery areas over the continental shelf. Larvae remain in the plankton until they metamorphose to the juvenile stage and thus, the drift of larvae from spawning areas to nursery grounds depends on the physical characteristics of the area. By late June the majority of the larvae are located over the shelf (Fives *et al*., 2001). This theory is supported by the particular spatial pattern of larval distribution that has been described in the literature: small larvae (2-4 mm) close to the spawning grounds at the shelf break; mid-size larvae (4-8 mm) widely distributed from the continental shelf and to areas well beyond the shelf break; the biggest larvae sampled (>8 mm) only on the continental shelf (Álvarez *et al*., 2004). European hake larvae are found mainly in water temperatures of between 10.5 ºC and 13 ºC (Álvarez *et al*., 2001; Ibaibarriaga *et al*., 2007).

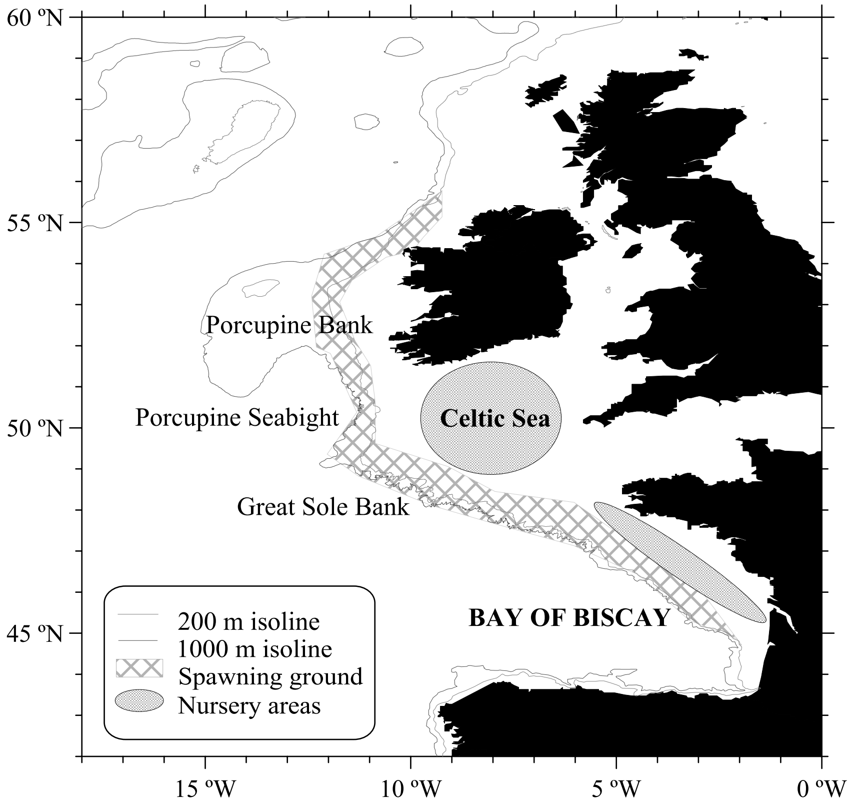


Figure 10: Northeast Atlantic area with the main spawning grounds and nursery areas for the northern stock of European hake.

After a pelagic life, 0-group hakes reach the bottom in depths of more than 200 m, around 40 days after hatching (Álvarez and Cotano, 2005; Kacher and Amara, 2005). Although they are found between depths of 70 and 200 m, the highest density is recorded at a depth of 100 m (Kacher and Amara, 2005) on the nursery areas. There are two major nursery areas (Figure 10): one is located over the shelf along the French coast (Le Gran Vasiére), in the Bay of Biscay and the other is situated over the shelf in the Celtic Sea, off southern Ireland (Casey and Pereiro, 1995; Kacher and Amara, 2005). This distribution pattern has been recently confirmed by Persohn *et al.*, (2009) (Figure 9). In autumn, the 0-group European hake are recruited into the population and the fishery of the area (Pereiro *et al.*, 1991).

NOTES OF INCERTITUDE

Hake SSB and recruitment estimations are derived from an assessment based on the age structure of the population (XSA: age-based assessment), taking into account commercial CPUE series. However, there has been a recent discussion regarding hake growth rate; dePontual *et al*. (2003) suggested and Kacher and Amara (2005) and dePontual *et al*. (2006) concluded that there has been an underestimation in European hake growth in the Bay of Biscay, and thus age estimation was believed to be biased (ICES, 2009b). Consequently, in the last ICES Report of the working group on the assessment of southern shelf stocks of hake, monk and megrim (WGHMM) the Stock Synthesis 3 (SS3) assessment model was used in biological parameters estimation (ICES, 2010). The use of a different model resulted in different recruitment and SSB time-series. Despite that, for the time that the analysis of this thesis were made, the last time-series available was that published in 2009 (ICES, 2009a) and thus all the analysis are based on the previous age-based assessment estimations. However, Bertignac and dePontual (2007) studied the consequences of growth underestimation in the northern stock assessment and reported that despite absolute values being affected, the trends in recruitment are comparable.

Regarding the hake-environment analysis of the thesis (chapters III and IV), another source of uncertainty should be signalled. There is only one time-series (for each biological parameter) which is representative of such a wide area as the whole northeastern Atlantic Ocean. In this perspective, problems may arise when relating environmental parameters to hake recruitment success fluctuations in terms of their reliability. However, this problem is somehow solved by working with recruitment data. Indeed, early life stages seem to be mainly distributed in a restricted area; they are mainly found in the Celtic Sea and the French shelf of the Bay of Biscay. Therefore, environmental conditions occurring in those two areas would be more influential for hake recruitment dynamics; even more if average values for spawning periods are considered. As stated by MacKenzie and Schiedek (2007), "*interpreting and predicting how individual populations and species in a local ecosystem respond to temperature variations is, therefore, more likely to be reliable when data are scaled closely to their perceived environments and life histories (e.g. regional average by season)*"

Results

Chapter I

Oceano-climatic characterisation of northern European hake distribution range

INTRODUCTION

According to the European Environment Agency, the Northeast Atlantic Ocean is limited to the south by the 36ºN parallel, to the west by the 42ºW, to the north by the 62ºN and to the east by the Atlantic coast of Europe, up to the British Channel and further along the west coast of England and Scotland. Based on this definition, the study area of the present work covers the continental shelf of the Northeast Atlantic Ocean with the French continental shelf and the west coast of Scotland as the southern and northern limits, respectively. Therefore, marginal seas such as the North Sea are excluded, when referring to the Northeast Atlantic continental shelf.

In the southern limit, the French continental shelf broadens with latitude and is divided into the Aquitaine shelf (50-150 km) and the Armorican shelf (180 km). Northwards, the Celtic Sea is bounded to the south and west by an extensive, 1000-km shelf edge, which descends rapidly to depths greater than 1000 m. In the west of the Celtic Sea, the shelf edge is interrupted by the Porcupine Seabight, north of which is located the Pocupine Bank. Further north, Rockall Trough lies to the west of Scotland (Mason *et al.*, 2006) (Figure 11).

In the Bay of Biscay, while the deep regions of the bay may be affected primarily by general oceanic circulation, the shelf is characterised by the dominance of mesoscale structures which are strongly influenced by regional or local hydroclimatic conditions (Planque *et al.*, 2003). Slope currents in the Bay of Biscay show a consistent poleward transport (Pingree and Le Cann, 1990). Instead, the currents over the shelf are mainly driven by the wind, by buoyancy and by tides. The general northerly wind circulation of the shelf produces upwelling on the French coast (Mason *et al.*, 2006). This results in the enrichment of the surrounding waters due to the upwelled cool and nutrient-rich waters.

In the Celtic Sea, a persistent poleward-flowing slope current is present along the entire length of the ocean-boundary. At the surface, along the length of the shelf break, a region of cooler water occurs. It is though to be a consequence of an internal tide, generated at the 200-m contour, which propagates both onto the shelf and into the ocean. This results in the mixing of cooler, nutrient-rich waters to the sea surface, leading to the potential enhancement of phytoplankton production (Mason *et al.*, 2006).

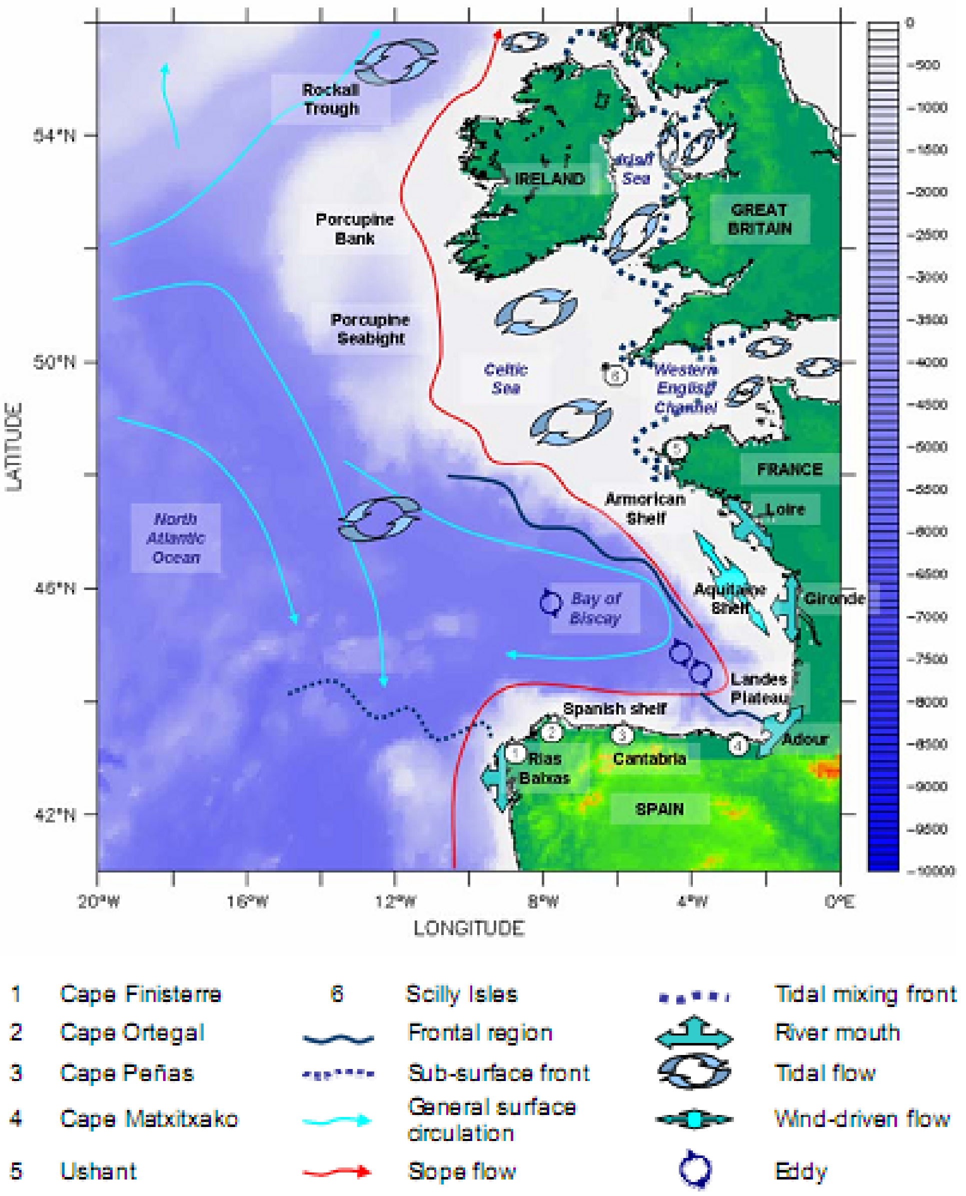


Figure 11: Map covering the main study area of the present thesis. The principal physical features of the Celtic Sea and the Bay of Biscay are shown on the map (source: Mason et al., 2006).

The poleward shelf edge current flows all along the European continental shelf break bringing warm and saline upper water with Eastern North Atlantic upper water (ENAW) characteristics though the Rockall Trough. Rockall Trough is one pathway and provides a route for warm Atlantic Water to flow northwards into the Nordic Seas (Holliday, 2003).

Large-scale events should be taken into account in order to understand variability at smaller scales (Beaugrand *et al.*, 2000). Apart from local hydrographical parameters, low frequency teleconnection indexes are believed to influence biological factors through their effect on sea surface temperature, storms and precipitation (Hurrell *et al.*, 2003). Global indexes influencing the Northern Hemisphere, and particularly the North Atlantic, are believed to affect the climate and oceanography of the study area of this thesis (Hurrell *et al.*, 2003).

The North Atlantic Oscillation (NAO) exerts a dominant influence on climate, fisheries and ecosystems of the Atlantic Ocean and surrounding continents (Marshall *et al.*, 2001). Decadal NAO variability influences regional temperatures, precipitation and wind speed and directions throughout Europe, as well as ocean heat content, ocean currents and their related heat transport (Hurrell, 1995; Hurrell and Deser, 2009). However, Barnston and Livezey (1987) identified other teleconnection patterns in the Northern Hemisphere such as the Eastern Atlantic Pattern (EA). Although, EA is the second main pattern in the Atlantic basin, it has been found to be more influential than NAO in some areas of the Northeast Atlantic, such as the Bay of Biscay (Borja *et al.*, 2008).

In the Northwest Atlantic, the Gulf Stream separates from the US coast near Cape Hatteras (33ºN, 75ºW) and then travels eastwards across the North Atlantic, becoming the North Atlantic Current at about 55ºW. The Gulf Stream position changes interannually and it is believed to influence the climate of the European continental shelf (Taylor, 1996). Further, the main North Atlantic current is driven by the gradient of potential energy anomaly across the mutual boundary between the subtropical and subpolar gyres (Curry and McCartney, 2001). The Northeast Atlantic is located at the influential area of both subtropical and subpolar gyre and thus, the transport resulting from the potential energy difference at the boundary of both gyres may influence the oceanography of the study area. As such, an intense warm anomaly in the subtropical gyre in 1988-94 resulted in the greatest temperature anomalies in the North Atlantic during the period of 1950-94 (Grey *et al.*, 2000). Further, the weakening of the subpolar after 1995 resulted in the increasing northward penetration of the warm and saline waters leading to a rapid warming and salinification of the northeastern Atlantic (Hátún *et al.*, 2005).

Ocean temperatures have shown a progressive increase in the last decades and are expected to continue to rise in the future. Since the sun's radiation is the principal driving force for global climate, it is natural to suspect that solar irradiance variations could be a possible source of climate variability (Reid, 1991). Anomalous heat from changing solar irradiance is stored in the upper layer of the ocean (White *et al*., 1997). However, the complex interaction between the ocean and atmosphere involves exchange of turbulent fluxes of heat and momentum, by which the ocean vents the heat absorbed from solar radiation (Cayan, 1992b).

Anomalous temperatures in Northern Hemisphere may result in changes in the North Atlantic ecosystem, such as the increase/decrease in some marine populations. Further, the reorganisation of some ecosystems could be related to the migration or redistribution of marine populations given the increase in the sea water temperature.

At a more regional and local scale, environmental parameters could be more related to different physiological aspects of fish. For instance, temperature has a direct effect on metabolism (Neill *et al*., 1994). The environmental influence has been demonstrated to be more pronounced during early life stages, since larvae and juveniles are more sensitive to changes in their habitat. A rise in temperature has been found to increase the development rate of early life stages, with the subsequent faster growth of individuals (Ottersen and Sundby, 1995; Fiksen and Slotte, 2002). As a consequence, individuals would spend less time in such vulnerable stages, increasing larvae and juveniles' survival. Shorter larval development time also implies a limited dispersal with potential consequence for species relying in the colonisation of new habitats (O'Connor *et al*., 2007).

The optimal development of the individuals requires a minimum quantity and quality of food. In this regard, in shelf waters such as off the French coast, upwelling of deeper cool and nutrient-rich waters results in the enrichment of the habitat, with sufficient food for larvae and juveniles' growth. However, on one hand the French coast is more dependent on river input than on the upwelling for nutrients. And on the other hand, strong upwelling episodes could result in offshore transport of eggs and larvae transporting them away from the nursery areas. Dynamical factors such as turbulence and wind-induced Ekman transport are additional critical factors during early life stages in terms of the stability of the water column and the retention or dispersion of eggs, larvae or even hake juveniles' main food (copepods).

Given the complexity of the Northeast Atlantic Ocean and the unknown interaction between the northern hake and its habitat, this chapter aims at having a general look at the environmental changes that occurred in the area occupied by the northern European hake. For that purpose, the objectives are as follows: (i) to study the general oceano-climatic variability of the northeastern Atlantic area for the study period, and (ii) to analyse the behaviour of hake influencing potential parameters concerning both temporal and spatial variability.

METHODOLOGY

1. Data source and parameter estimation

Briefly, the environmental parameters considered within this thesis were selected because of their direct and/or indirect likely influence on either northern hake population itself or its habitat. This information will be extended in the following chapters of the present thesis. Instead, this section describes the large data set used for this work. It gives information about the source, and it also provides a description with regard to the type of variable, duration of the time-series and the location of the measurement points.

A) Oceano-meteorological data

Global indices were used to check whether regional modifications of hake population are directly or indirectly triggered by large-scale hydroclimatic processes. Further, regional parameters were selected representing the main distribution area of hake. Particularly, the two main spawning grounds of the Celtic Sea and the Bay of Biscay were represented by means of environmental indices estimated for each of the spawning areas. Finally, local variables were also selected. The position of measurement points were chosen taking into account hake's main spawning grounds, off the French coast and in the Celtic Sea.

A.1) Global and climatic indices

Two key modes of large-scale atmospheric circulation over the Northern Hemisphere were selected for analysis: the North Atlantic Oscillation (NAO) and the East Atlantic pattern (EA). The NAO index consists of a north-south dipole of anomalies; one centre is located over Greenland and the other centre with the opposite sign covers the North Atlantic from east to west. The anomaly centres of the EA pattern are displaced southeastward to the approximate nodal lines of the NAO index (Barnston and Livezey, 1987). NAO and EA pattern data were available in a monthly basis at the NOAA website (ftp://ftp.cpc.ncep.noaa.gov/wd52dg/data/indices/tele_index.nh). In addition to the annual mean of the NAO index, winter (December-March) mean values for each year were also estimated since this index shows its maximum fluctuations in this season (Marshall *et al.*, 2001).

Another mode of variability occurring in the North Atlantic Ocean is the Atlantic Multidecadal Oscillation (AMO). It is defined as sea surface temperature anomaly from detrended mean global warming value. Monthly means of this parameter were provided by the Physical Science Division belonging to NOAA (www.esrl.noaa.gov). The Northern Oscillation Index (NOI) is a climate index for the North Pacific and it is available online at www.pfeg.noaa.gov, on a monthly basis. Both global indices are associated with upper ocean temperature anomalies.

TPEA is a transport index defined by Curry and McCartney (2001) and it is calculated from the difference of the potential energy anomalies (PEA) near Bermuda and in the Labrador Basin. This index estimates the strength of the Gulf Stream and North Atlantic Current System.

The Gulf Stream index (GSNW) used in this study is the annual mean of the first principal component of the position of the North Wall of the Gulf Stream (NWGS). The Gulf Stream index is a measure of the latitudinal position of the north wall of the Gulf Stream where it breaks away from the east coast of North America. Positive values of this index are indicative of a displacement to the north of the long-term mean location of the NWGS, while negative values indicate a southward movement (Taylor, 1995, 1996; Nunn *et al.*, 2007). Data were downloaded from the website of the Plymouth Marine Laboratory, U.K (www.pml-gulfstream.org.uk).

Two solar indices, the annual number of sunspots and sun geomagnetic activity (AA index), were provided by the National Geophysical Data Center from NOAA (www.ngdc.noaa.gov). These parameters are likely to influence the marine environment and, particularly, the sea surface temperature.

Apart from the annual means of EA, AMO, NOI, GSNW, sunspot number and AA indices, February-July average values (hake main spawning period for the study area; ICES, 2009a) were also estimated.

Table 1: Summary of the global indices utilised, including area of influence, sampling rate and mean value calculated for each of the indices.

Index	***Influence area***	***Sampling***	***Average studied***
NAO	North Atlantic	Monthly	Annual December-March
EA	North Atlantic	Monthly	Annual February-July
AMO	North Atlantic	Monthly	Annual February-July
NOI	North Pacific	Monthly	Annual February-July
TPEA	North Atlantic	Annual	Annual
GSNW	North Atlantic	Monthly	Annual February-July
Sunspot number	Global	Monthly	Annual February-July
AA index	Global	Monthly	Annual February-July
NHT	Northern Hemisphere	Monthly	Annual February-July

Monthly sea surface temperature anomalies (from the base period 1961-1990) for the Northern Hemisphere (NHT) were provided by the Hadley Centre for Climate Prediction and Research, Meteorological Office, London, UK (Rayner *et al*., 2006). Similarly to the other global parameters, annual and February-July means were performed.

Table 1 lists the global indices considered in this study, as well as the influence area, sampling rate and average period studied for each of the indices.

In addition, climatic variability was represented by the first three principal components (CLI1, CLI2 and CLI3) of a principal component analysis (PCA) of six climate variables (NAO –North Atlantic Oscillation-, EA –East Atlantic pattern-, EA/WR –East Atlantic/Western Russia pattern-, SCA –Scandinavia pattern-, TNH –Tropical/Northern Hemisphere pattern-, POL –Polar/Eurasia pattern-) which represent the atmospheric circulation over the Northern Hemisphere (for detailed information refer to Bode *et al.*, 2006; Fernandes *et al.*, 2009).

A.2) Regional parameters

Regional environmental parameters representing the main distribution area of hake early life stages were selected. Annual and spawning season (February-July) sea surface temperature (SST) anomalies (from the base period 1961-1990) were obtained from the hadSST2 dataset (Rayner *et al.*, 2006), on a 5º×5º grid-box basis (Figure 12).

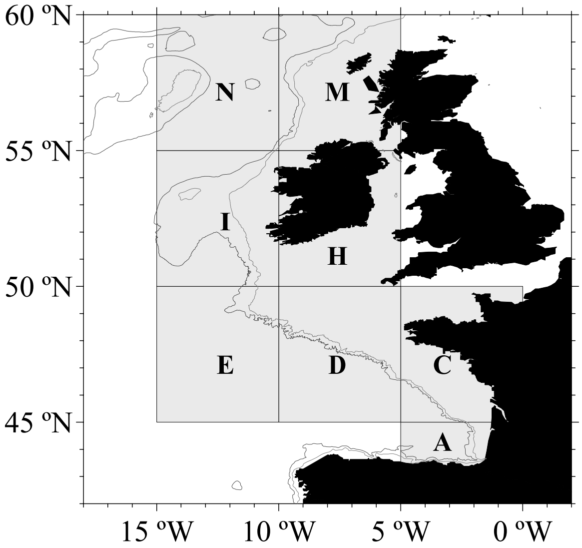


Figure 12: 5º x 5º grid showing the SST anomaly measurement boxes for the Northeast Atlantic.

Additionally, and with the aim of studying spatial variability (this chapter and Chapter III), temperature anomaly and Ekman transport grids were built covering the northeastern Atlantic continental shelf. Spatial changes in temperature anomaly were assessed using data set ERSST.v3. Both in situ and satellite (AVHRR) SST data were used as inputs for the extended reconstruction of SST and the anomalies are computed taking 1971-2000 as a reference period (Xue *et al*., 2003). The processing is described in Smith *et al*. (2008) and the series was available at www.ncdc.noaa.gov, on a 2ºx2º grid basis (Figure 13a). Further, Ekman transport in both directions (north-south and east-west) was available on a 1ºx1º grid basis (Figure 13b) at www.las.pfeg.noaa.gov. These datasets were available at daily intervals.

The two main hake spawning grounds of the Celtic Sea and the Bay of Biscay were represented by means of environmental indices estimated for each of the spawning areas. According to literature (Álvarez *et al*., 2001, 2004; Fives *et al*., 2001; Ibaibarriaga *et al*., 2007; ICES, 2009a), the spawning ground off the French coast is limited to the continental shelf between 44-48ºN and 1-8ºW, whereas the spawning area of the Celtic Sea is located between 48-52ºN and 5-12ºW (Figure 13c, d). A principal component analysis (PCA) was used to estimate representative indices for temperature anomaly and Ekman transport for each of the spawning ground. This analysis was based on a 2º×2º grid (Figure 13c) for temperature anomaly (dataset ERSST.v3, www.esrl.noaa.gov) and on a 1º×1º grid (Figure 13d) for both north-south and east-west Ekman transport (www.las.pfeg.noaa.gov). For this particular analysis, in addition to annual mean values, January-May and April-June means were selected for the Bay of Biscay and the Celtic Sea respectively, which correspond to the spawning periods in these areas (Sarano, 1983; Martin, 1991; Fives *et al*., 2001). As a result, 12 PCAs were carried out. The component explaining the highest percentage of variability was taken as the representative index for the given area, period and parameter. The first principal components of the PCA carried out per parameter and spawning area explained a high percentage (between 83% and 97%) of the observed variability (Table 2); therefore, we considered them to be good representatives of the temperature anomaly and Ekman transport patterns of each of the spawning areas for the considered spawning seasons.

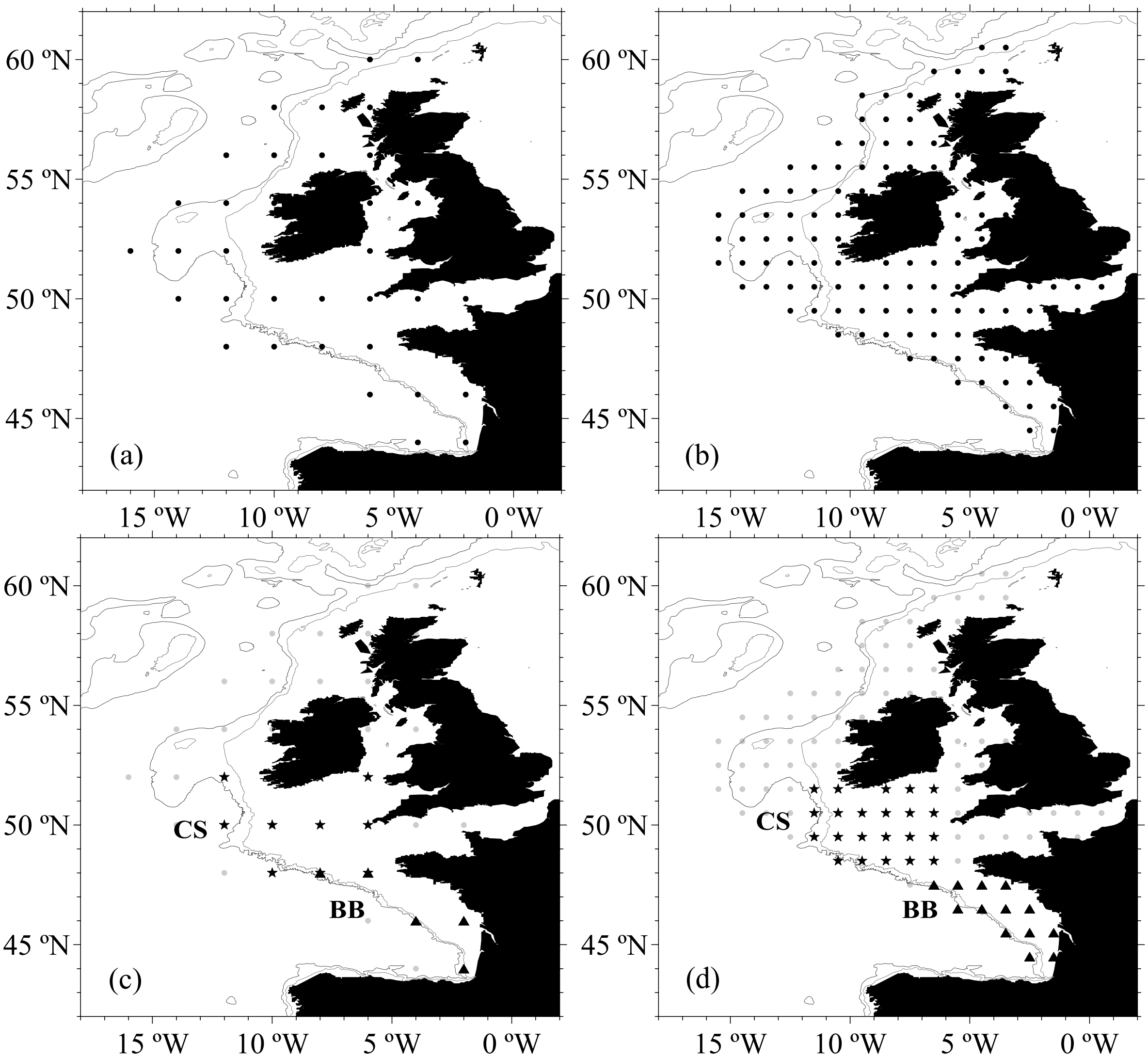


Figure 13: Location of the measurement points selected for the spatial variability analysis of (a) temperature anomaly (2ºx2º grid) and (b) Ekman transport (1ºx1º grid) over the continental shelf of the northeastern Atlantic; (c) Temperature index (2ºx2º grid), and (d) Ekman transport index (1ºx1º grid) for the Bay of Biscay (BB) spawning area (triangles) and the Celtic Sea (CS) spawning area (stars), measurement points selected for the PCA analysis to estimate regional environmental parameters.

Table 2: Percentage of the variability explained by the first component of each of the PCA analyses carried out per spawning area, variable and period. Note that each line represents the result for a different PCA.

Spawning area	*Variable*	*Period*	*Variability explained*
Bay of Biscay	Temperature anomaly	Annual mean	93.01%
		January-May	93.73%
	E-W Ekman transport	Annual mean	83.81%
		January-May	83.62%
	N-S Ekman transport	Annual mean	86.45%
		January-May	89.35%
Celtic Sea	Temperature anomaly	Annual mean	97.54%
		April-June	95.96%
	E-W Ekman transport	Annual mean	90.87%
		April-June	92.47%
	N-S Ekman transport	Annual mean	93.94%
		April-June	91.19%

A.3) Local parameters

In addition to sea surface temperature, monthly water temperature data at depths of 50, 75 and 100 m was downloaded from www.las.pfeg.noaa.gov based on the same 1ºx1º grid as in Figure 13b. However, such time-series was only available for the period 1978-2001, not covering the last part of the study period (2002-2006). Additionally, subtemperature data time-series was not complete for any of the 104 measurement points at any of the considered depths. Figure 14 shows the number of months with available subtemperature data at each of the locations, for the period 1978-2001. The shelf break at around 46-48ºN and the northern part of the study area showed a better temporal coverage, while measurement points at the west and south of Ireland and the continental shelf within the Bay of Biscay had less than 60 months sampled out of 288 months (24 years).

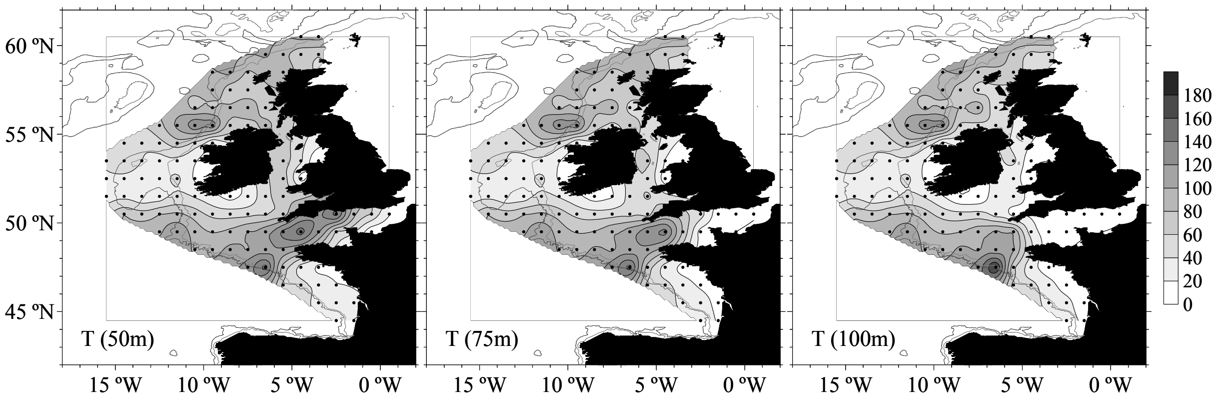


Figure 14: Subsurface temperature data coverage at depths of 50, 75 and 100 m. The darker the grey scale, the higher the number of monthly measurements for that particular location.

In view of this problem, time-series lacking the lowest number of months were selected and the interpolation method by Colebrook (1975) was used to estimate the temperature values for the missing months. In this case, only the time-series located at 100 m depth, at the position of 47.5N; 6.5W was selected for being the series with the highest number of recorded subtemperature data (Figure 14). The missing values within this series were estimated following the equation by Colebrook (1975):

$$\overline{M} \times \frac{\mathrm{Y}}{\overline{\mathrm{Y}}} \qquad (1)$$

where $\overline{M}$ is the long-term mean of that month, Y is the annual mean of the particular year, and $\overline{\mathrm{Y}}$ is the long-term annual mean.

This measurement point is located at the Bay of Biscay shelf break, off the French coast (Figure 15), where hake spawning takes place. Further, hake larvae and pre-recruits are found to remain in depths of between 50 to 150 m before they recruit to the juvenile stage (Motos *et al.*, 2000; Sánchez and Gil, 2000). Therefore, temperature at the sampling location at 47.5N; 6.5W, at a depth of 100 m, being biologically crucial for hake early stages, was considered as a slope temperature indicator, and consequently added to the oceanographic data set of this study. Apart from annual mean of slope temperature, average values for February-July and January-May (ICES and Bay of Biscay spawning seasons, respectively) were also estimated.

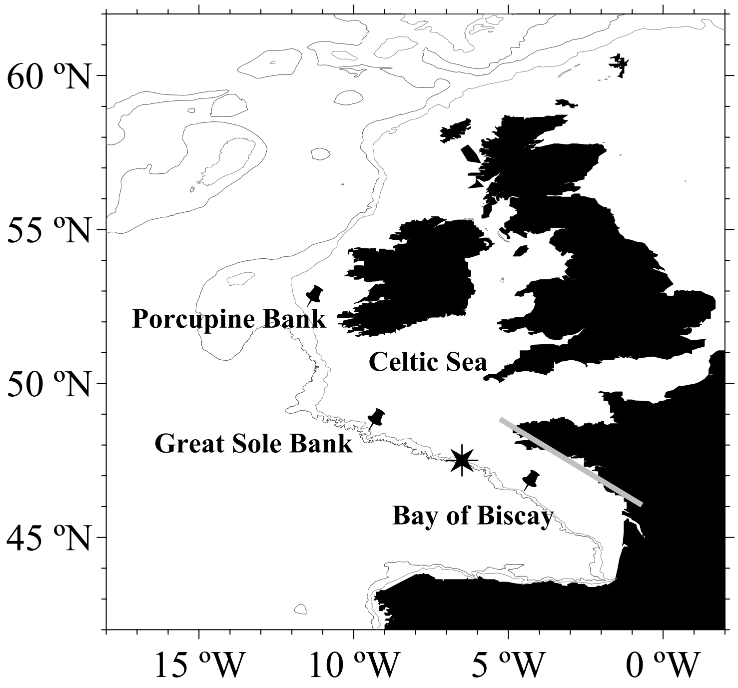


Figure 15: Location of the measurement points of local parameters in the Bay of Biscay, Great Sole Bank and Porcupine: the star represents the location of the slope temperature data series, whereas the drawing pins show the measurement points for upwelling index, turbulence, Ekman transport and heat and momentum fluxes. The grey line represents the coastline (Brest-La Rochelle) considered for the computation of the upwelling index.

Upwelling values for every 6 hours were available at the Environmental Research Division's Live Access Server (http://las.pfeg.noaa.gov/las6_5/servlets/dataset), at the shelf break off the French coast (46.5ºN; 4.5ºW) (Figure 15). For the computation of the upwelling index, the coastline orientation of the French Brittany was provided; Brest-La Rochelle line was taken as a reference when computing the coast angle. Taking into account the coast angle definition given by NOAA (the "coast angle" is the angle the landward side of the coastline makes with a vector pointing north (http://las.pfeg.noaa.gov/las6_5/doc/upwell_custom.htm)) an angle of 120º was chosen for the computation of the upwelling index, i.e. the angle between the coastline Brest-La Rochelle and northward point vector (see Figure 15). Once 6 hourly upwelling data were downloaded, daily and monthly mean values were estimated. An upwelling index was calculated defined as the sum of monthly positive values for the selected periods (the whole of the year; February-July: ICES spawning period; January-May: Bay of Biscay spawning season, and December-March; months with highest upwelling values).

For the rest of the local parameters (see below), and after reviewing several papers regarding egg and larvae distribution for the northern stock European hake (data from surveys undertaken in 1983, 1986, 1989, 1992-1995, 1998, 2001, 2002) (Álvarez *et al*., 2001, 2004; Álvarez and Cotano, 2005; Fives *et al*., 2001; Poulard, 2001; Dransfeld *et al*., 2004; Ibaibarriaga *et al*., 2007; ICES, 2008), three points were selected close to the continental shelf-edge, over the spawning area of hake: 46.5ºN; 4.5ºW (Bay of Biscay), 48.5ºN; 9.5ºW (Great Sole Bank) and 52.5ºN; 11.5ºW (Porcupine Bank) (Figure 15).

A turbulence index (defined as the cube of the wind speed) and north-south and east-west Ekman transport data were downloaded from the same Live Access Server. In addition, meridional and zonal momentum fluxes (hereafter MMF and ZMF, respectively) and sensible and latent heat flux data (hereafter SHF and LHF, respectively) were available as part of the NCEP/NCAR Reanalysis Project (www.esrl.noaa.gov). Annual and February-July means for turbulence index, Ekman transports in both directions and flux variables were calculated for the three measurement points. Moreover, January-May (Bay of Biscay), April-June (Great Sole Bank) and April-July (Porcupine) mean values were calculated taking into account the temporal variability of the spawning season depending on the spawning ground, i.e. the peak spawning period of hake is earlier in southern waters, and it takes place later as the latitude increases (Casey and Pereiro, 1995).

B) Biological data

Apart from oceano-climatic parameters, biological data on hake larvae and juvenile main prey was included in the analysis. In this context, copepod abundance data was obtained for waters around UK and Ireland, specifically the area corresponding to the CPR Standard Areas C3, C4, D3 and D4 (Johns, 2009, SAHFOS) (Figure 16).

Zooplankton data used in this study was collected by the continuous plankton recorder (CPR) survey. It was provided by the Sir Alister Hardy Foundation for Ocean Science (SAHFOS).

The continuous plankton recorder (CPR) survey is the largest multi-decadal plankton monitoring programme in the world. The survey was initiated in 1931 and since then, it has been collecting data from the North Atlantic and the North Sea. Over this period, the survey has aimed at minimising changes in the counting procedures to maintain a consistent long-term time-series. In this context, it provides the scientific community with the best long-term measure of the state of oceanic plankton (Richardson *et al*., 2006).

In spite of the effort to maintain the time-series consistency, there are two factors to consider when using CPR data. The first is the sampling bias (both temporal and spatial); the use of ships of opportunity in the methodology makes difficult the sampling of each of the standard area on a regular basis. The second is the semi-quantitative nature of CPR data (they are semi-quantitative estimates of plankton abundance and not absolute measures). However, in spite of the semi-quantitative nature of CPR sampling, inter-annual changes and seasonal cycles are well captured by the CPR and thus, it reflects the major patterns observed in the plankton. Additionally, because of the longevity of the survey (more than 70 years), CPR database is one of the longest and most geographically extensive biological time-series in the world (Batten *et al*., 2003; Richardson *et al*., 2006).

The self-contained automatic plankton recorder collects plankton continuously from a standard depth of about 7 m. Water enters the CPR through a square aperture and flows down an expanding tunnel and exists through the rear of the device. Plankton in the water is filtered onto a constantly moving band of silk (270 µm mesh size). The filtering silk meets a second band of covering silk, effectively sandwiching the plankton, and is then wound onto a spool in a storage tank containing formalin. In the laboratory, the full length of the silk is marked and divided into samples representing 10 nautical miles of tow. Zooplankton identification is carried out in two steps: firstly, in the stepped traverse of the CPR silk (at 54x magnification), all zooplankton organisms < 2 mm total length are counted; secondly, all zooplankton individuals > 2 mm are identified and enumerated (zooplankton eyecount) (Batten *et al*., 2003; Reid *et al*., 2003a; Richardson *et al*., 2006).

The water volume filtered for each 10 nautical mile sample is ~3 m^3. Therefore, SAHFOS provides monthly total copepod data expressed as abundance per sample, that is, numbers per ~3 m^3. CPR samples provide relative estimates of abundance that are useful for assessing relative patterns, and thus, abundance estimates are seldom converted to per m^3 estimates in practice (Richardson *et al*., 2006). However, in this work it was decided to divide by 3 the abundance estimates in order to obtain copepod abundance estimates per m^3.

The whole information describing CPR methodology can be found in Colebrook, (1975), Batten *et al*. (2003), Reid *et al*. (2003a) and Richardson *et al*. (2006).

CPR data are averaged spatially in geographic areas known as CPR standard areas. The positioning and size of these areas have been determined taking into account some characteristics. The edges of many standard areas follow the edge of the continental shelf (200 m isobath). Further, the size of the boxes on the shelf is smaller than those in the oceanic area in order to reflect the more dynamic physical environment, larger biological variability and greater CPR sampling.

Monthly total copepod abundance data was obtained from Sir Alister Hardy Foundation for Ocean Science (SAHFOS). Data corresponds to C3, C4, D3 and D4 CPR boxes (Figure 16), covering a great part of hake egg, larvae and juvenile distribution area over the northeastern Atlantic continental shelf (Álvarez *et al*., 2001, 2004; Ibaibarriaga *et al*., 2007; ICES, 2008).

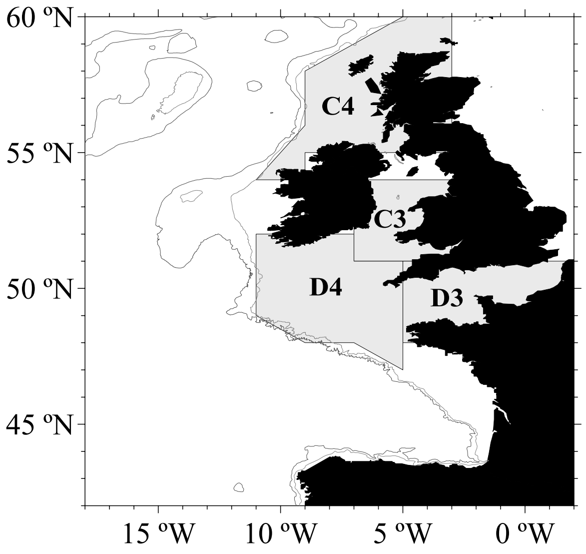


Figure 16: CPR (Continuous Plankton Recorder) Standard Areas considered in the present study covering waters around the UK and Ireland, for the copepod abundance analysis.

For the study period corresponding to this thesis, some months were not sampled due to the sampling bias aforementioned. Highly seasonal plankton data is problematic when some month data are lacking, and thus, averaging over months would not be a good estimator in order to calculate the annual mean copepod abundance. In this context, a more robust annual estimate is obtained by first estimating the abundance of plankton for months where there are no data. For that purpose, interpolation method by Colebrook (1975) was chosen following the equation 1 above (similarly to the estimation of SST anomaly data). At least, eight months need to be sampled in a year to have an adequate estimate of the seasonal cycle in order to estimate the annual abundance, rule that has been fulfilled by all CPR standard areas considered for such study.

2. Data analysis

- **Temporal variability**
  - Trend analysis: Fluctuations over the three-decadal period (1978-2006) were graphically studied by means of linear plots. As such, graphical representation of global, regional and local oceano-meteorological variables was undertaken.
  - Seasonal pattern: In the case of those parameters for which monthly values were available, seasonal variability was studied. As such, monthly average values over the period 1978 to 2006 were plotted by means of linear graphs.

The plots were produced with the R statistical software available from the Comprehensive R Archive Network (http://cran.r-project.org).

- **Spatial variability**
  - With the aim of studying SST, SST anomaly, E-W and N-S Ekman transport spatial distribution over the study area, average values for the period 1978-2006 were plotted. Contour plots were used to illustrate maps, based on a 2º×2º grid (Figure 13a) for SST and temperature anomaly and on a 1º×1º grid (Figure 13b) in the case of both north-south and east-west Ekman transport.
  - Seasonal pattern: The seasonal variations of SST, temperature anomaly, E-W and N-S Ekman transport were represented by monthly contour plots.

Maps were produced using interpolation by krigging with Surfer software (Golden software Inc.).

RESULTS

A) Oceano-meteorological data

Temporal variability

A.1) Global and climatic indices

Both, NAO and EA indices showed high variability over the study period, alternating between positive and negative phases. However, NAO index showed a prolonged positive period from late 1980s to mid-1990s (Figure 17a), whereas EA index was positive during the last decade of the study period (Figure 17c). NAO time-series for December-March mean registered more extreme values (mostly positive) than the NAO index itself, since it shows higher values during winter months (Figure 17b). Concerning EA, no seasonal pattern was observed (Figure 17d) and thus annual and February-July time-series showed similar variability (Figure 17c).

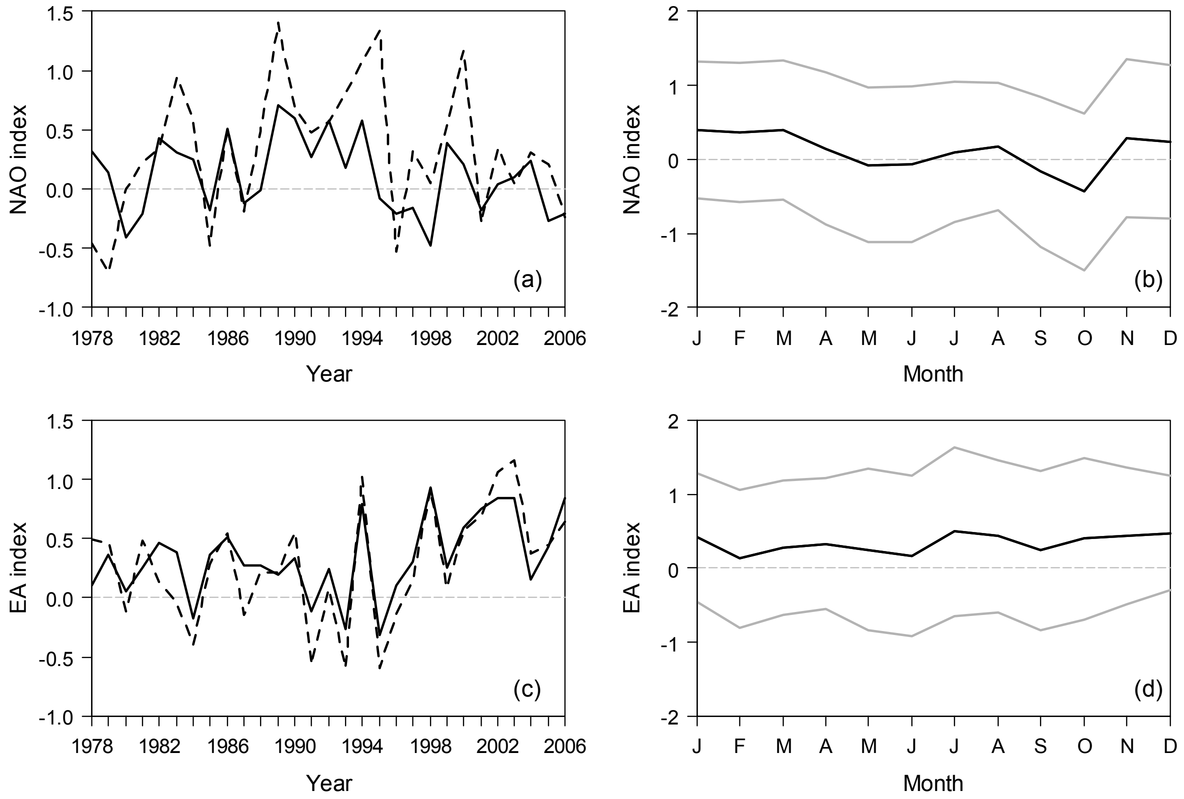


Figure 17: Above, (a) NAO index time-series temporal trend and (b) seasonal variability for the study period; below, (c) EA index time-series temporal trend and (d) seasonal variability for the study period. Note that the black line represents the annual mean, dashed line December-March mean (for NAO) or February-July mean (for EA) and grey lines the mean ± SD value.

In the mid-1990s, AMO index changed from a mostly negative to a highly positive period, with a sharp increase in the last decade of the study period (Figure 18a). By contrast, NOI was mainly negative, apart from the last decade when alternation of positive and negative years was seen (Figure 18c). Given the unclear seasonal pattern for both indices (Figure 18b, d), the annual and February-July time-series did not highly differ.

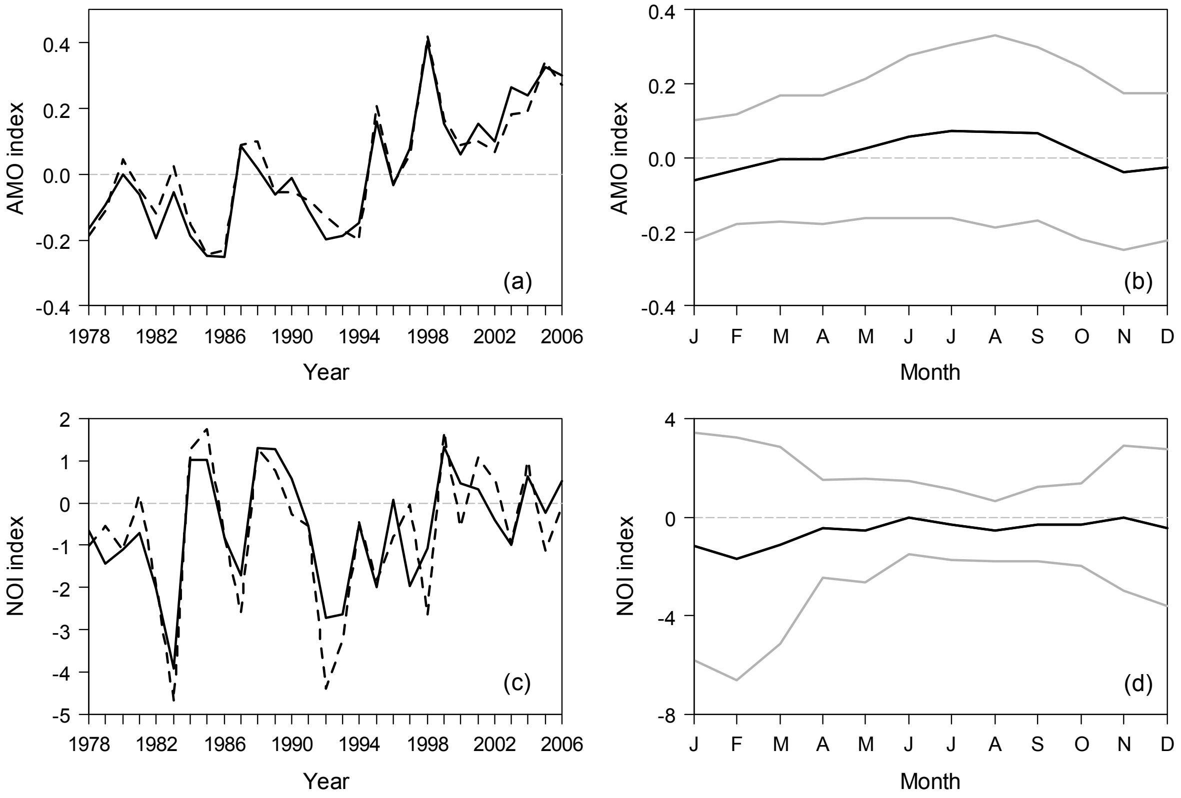


Figure 18: Above, (a) AMO index time-series temporal trend and (b) seasonal variability for the study period; below, (c) NOI index time-series temporal trend and (d) seasonal variability for the study period. Note that the black line represents the annual mean, dashed line February-July mean and grey lines the mean ± SD value.

Despite pronounced fluctuations over the study period, GSNW index was found to be positive from late 1980s to mid-1990s (Figure 19a). February-July time-series followed a similar pattern. Concerning seasonality, GSNW index was positive from July to March, in contrast to the negative phase in April-May-June (Figure 19b). Although TPEA series was not complete for the study period of this work, a period of higher transport can be appreciated from late 1980s to mid-1990s (Figure 19c).

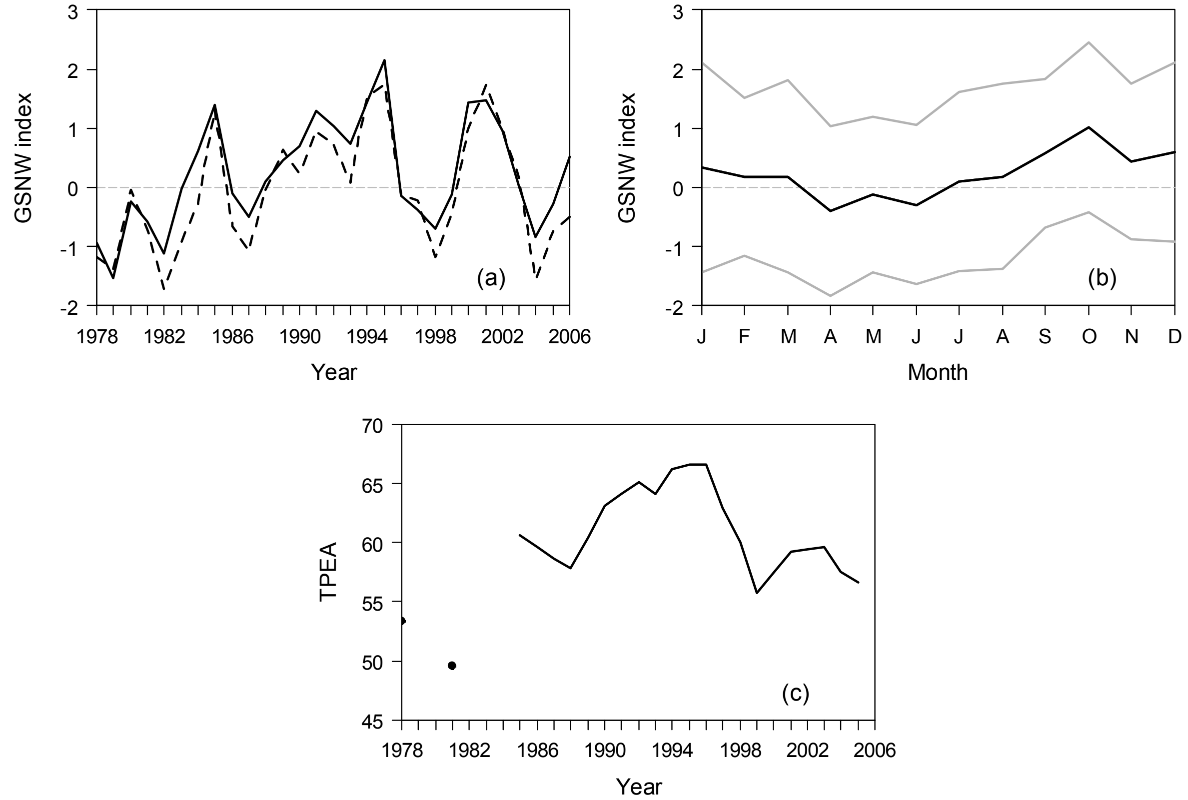


Figure 19: Above, (a) GSNW index time-series temporal trend and (b) seasonal variability for the study period; below, (c) TPEA (Megatons/sec) time-series temporal trend for the study period. Note that the black line represents the annual mean, dashed line February-July mean and grey lines the mean ± SD value.

Sunspot number showed a cyclic inter-annual variability of about 10 years but no intra-annual seasonal pattern (Figure 20a, b). The sunspot cycle maximums were registered in 1978, 1988 and 2000, while the minimums were in 1986 and 1996. AA index was high from late 1980s to mid-1990s, with high peaks also in 1982 and 2003 (Figure 20c). Monthly mean values were slightly higher in February-April and September-October in contrast to the lower values of winter and summer (Figure 20d). Northern Hemisphere temperature anomaly increased almost continuously from mid-1980s to mid-2000s. In spite of the negative values in 1984-86, anomalously positive temperatures were recorded for the rest of the time-series with a pronounced increase after 1987 (Figure 20e). In Figure 20f, the seasonal pattern of NH temperature anomaly variable can be observed, with higher positive anomalies in summer months. However, all months showed higher than average temperatures comparing with the reference period (1961-1990). Annual mean and February-July time-series showed very similar trend for the three global variables plotted in Figure 20.

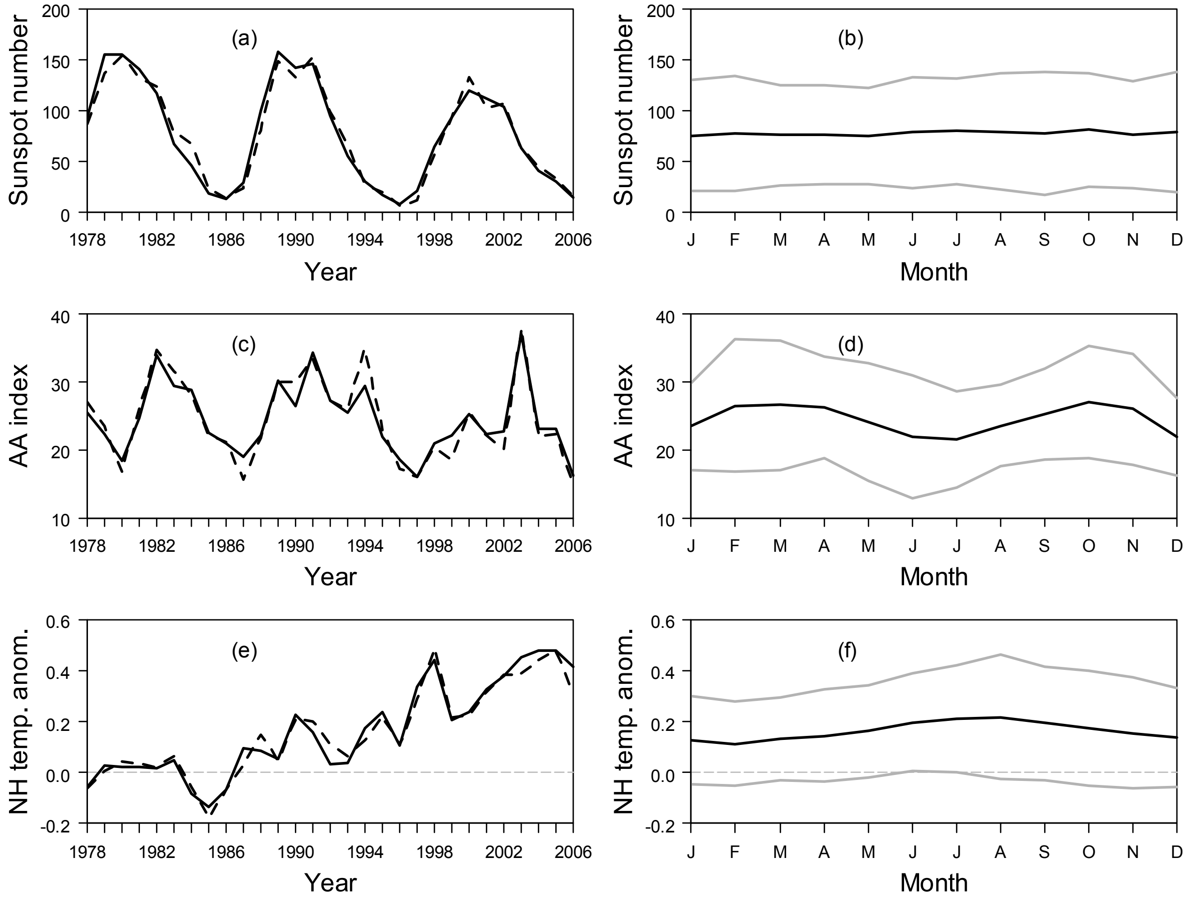


Figure 20: (a) Sunspot number time-series temporal trend and (b) seasonal variability for the study period; (c) AA index time-series temporal trend and (d) seasonal variability for the study period; and, (e) Northern Hemisphere temporal anomaly (ºC) temporal trend and (f) seasonal variability for the study period. Note that the black line represents the annual mean, dashed line February-July mean and grey lines the mean ± SD value.

With reference to the composite climatic indices no clear trend can be observed in Figure 21; the three indices fluctuated much along the study period, shifting between positive and negative phases.

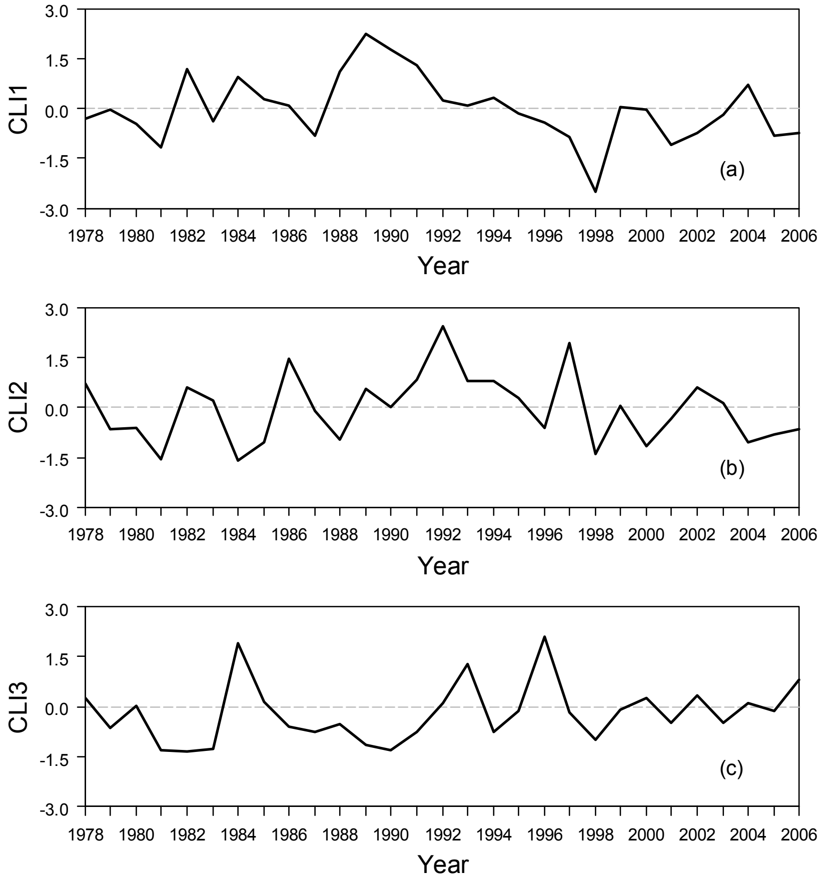
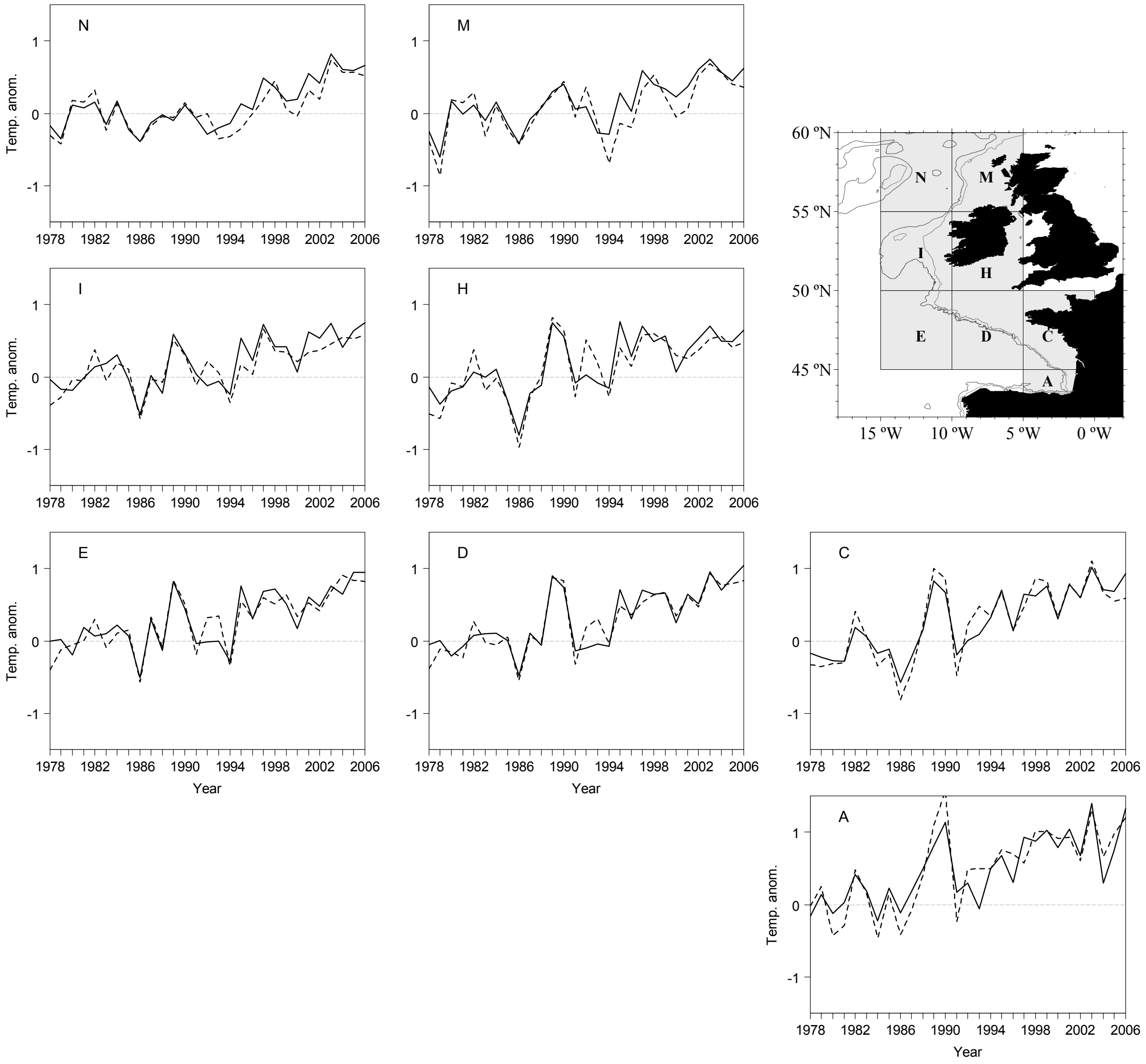


Figure 21: Temporal trend of annual values for the climatic indices (a) CLI1, (b) CLI2 and (c) CLI3.

A.2) Regional parameters

Generally speaking, after some years of average temperatures, a general warming trend was observed in all regions (Figure 22). However, the increase in temperature anomalies was more pronounced in regions A, C, D and E; these areas also showed a high positive peak in 1989. In addition, regions A, C, D, E and H registered higher than average temperatures in 1992-93 for the period February-July, event that was not noticeable in the annual means of those years.



<u>Figure 22</u>: Temperature anomaly (ºC) trend over the study period, at the 5ºx5º regional scale. Note that the black line represents the annual mean and the dashed line the February-July period.

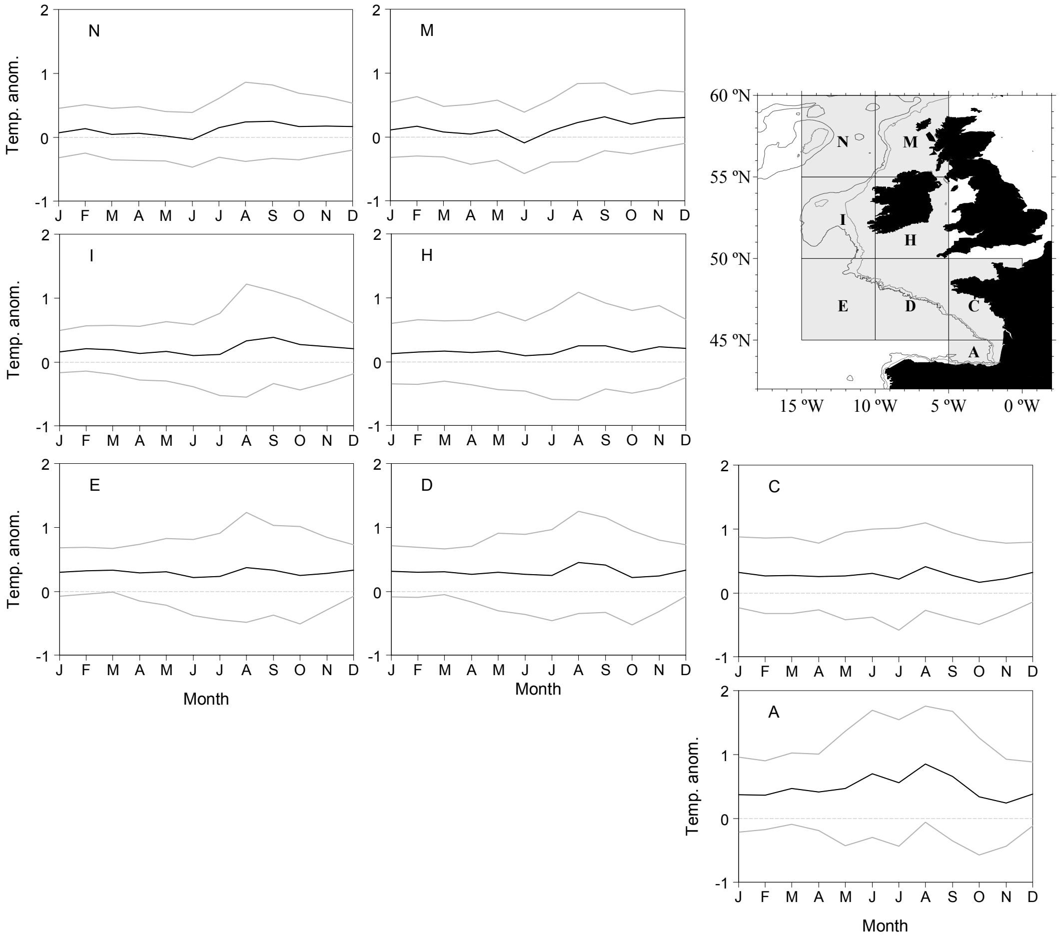


Figure 23: Temperature anomaly (ºC) seasonal pattern over the study period, at the 5ºx5º regional scale. Note that the black line represents the monthly mean values and the grey lines the mean ± SD value.

No clear seasonal pattern was found regarding temperature anomalies (Figure 23). Only region A showed higher temperature anomalies during summer months in comparison with the rest of the year.

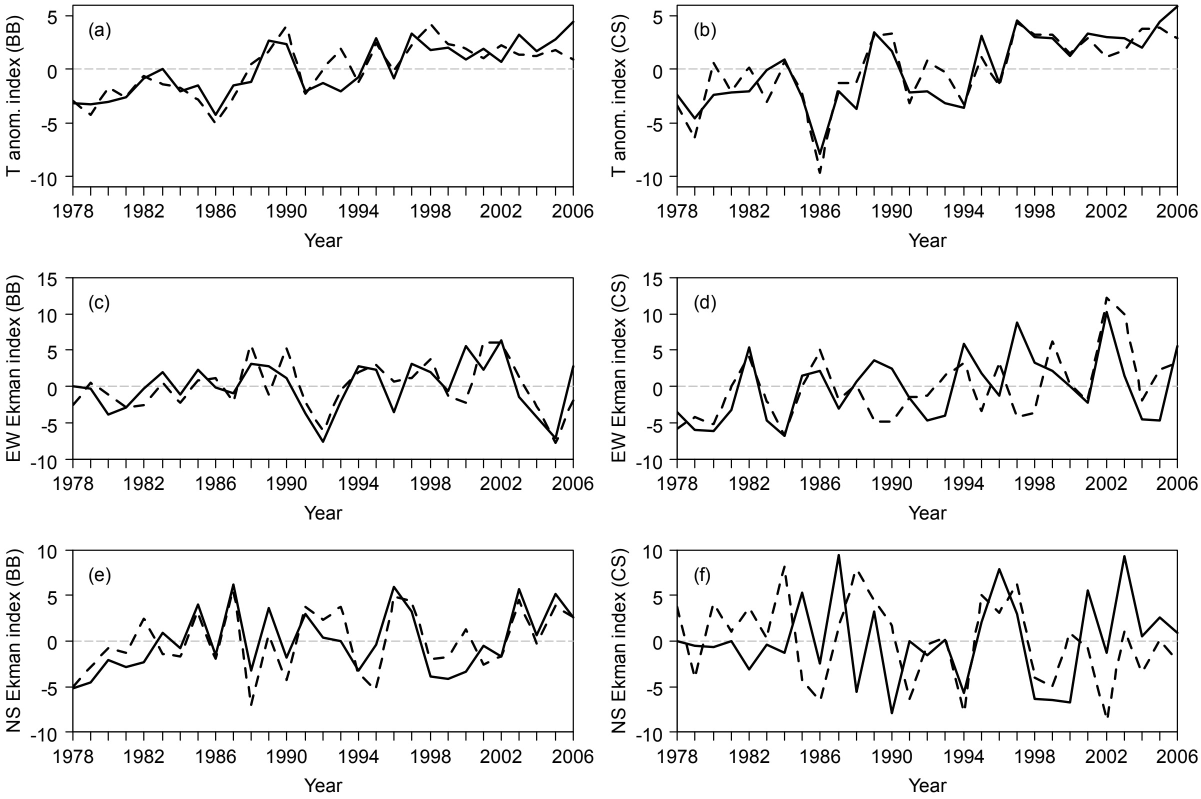


Figure 24: Time-series of environmental indices: (a) temperature anomaly (ºC) index for the Bay of Biscay and (b) the Celtic Sea; (c) East-West Ekman transport (kg·m^{-1}·s^{-1}) for the Bay of Biscay and (d) the Celtic Se; and, (e) North-South Ekman transport (kg·m^{-1}·s^{-1}) for the Bay of Biscay and (f) Celtic Sea. Note that the black line represents the annual mean and the dashed line the January-May and April-June periods for the Bay of Biscay and the Celtic Sea, respectively.

Concerning the environmental indices for the spawning grounds, a general increasing trend in temperature anomaly was observed in both areas (BB and CS) with mainly negative anomalies until 1995 and positive anomalies in the last decade of the study period (Figure 24a, b). Both areas underwent a sharp increase in temperature from 1986 to 1989, although it was more pronounced in the Celtic Sea. Further, both areas have in common the absence of negative temperature anomalies in February-July time-series in 1992 and 1993, in comparison to the annual mean time-series. Zonal Ekman transport shifted between eastward and westward directions in the Bay of Biscay as well as in the Celtic Sea. In the Bay of Biscay two peaks (1992 and 2005) of stronger westward transport are evident (Figure 24c). Celtic Sea changed from mostly westward transports in the first years to a period of eastward transports in the second mid of 1990s (Figure 24d). In the Bay of Biscay, the first mid of 1990s and the last decade of the study period registered mostly northward transports, whereas the rest of the study period was characterised by peaks in both directions (Figure 24e). Meridional Ekman transport was particularly strong in Celtic Sea with peaks in both northward and southward directions (Figure 24f). It should be noted that annual and February-July time-series showed highly different values in the case of NS Ekman transport. Generally speaking, it could be said that transport was stronger in the Celtic Sea comparing to the Bay of Biscay.

A.3) Local parameters

Annual slope temperature ranged between 11.5 ºC and 12.6 ºC, with higher variability from late 1980s onwards. February-July and January-May periods followed the same pattern as the annual mean time-series but registered lower temperature values (Figure 25a). In fact, the seasonal pattern in Figure 25b shows the lowest temperature values in February-April and maximum temperatures in October-November.

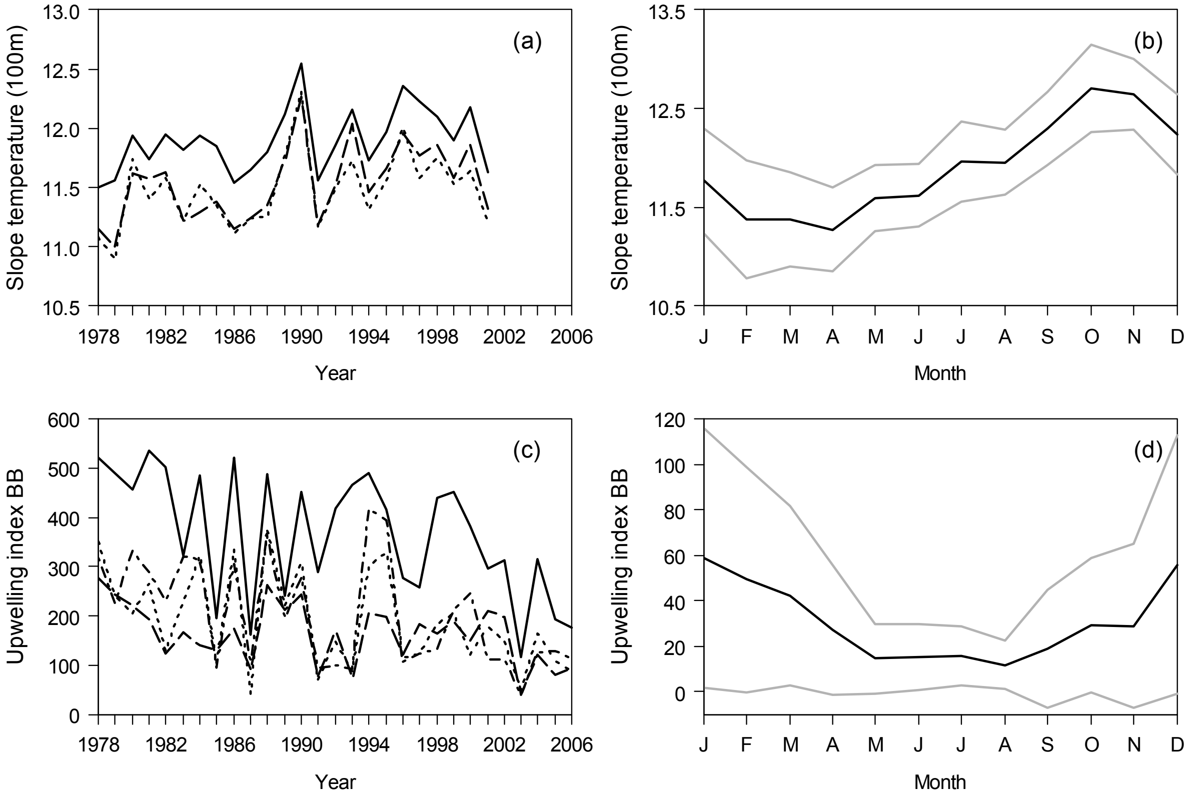


Figure 25: Above, (a) slope temperature (ºC) (100 m depth, at 47.5N; 6.5W) temporal trend and (b) seasonal variability for the study period. Below, (c) temporal trend and (d) seasonal pattern of the upwelling index in the Bay of Biscay (46.5ºN 4.5ºW). Note that the black solid line represents the annual mean, the dashed line February-July period, the dotted line January-May period and the dotdash line December-March period.

On the other hand, upwelling index in the Bay of Biscay registered high fluctuations with a slightly decreasing trend towards the end of the study period (Figure 25c). A seasonal pattern is clearly observed in Figure 25d, with low upwelling episodes from May to August, and higher upwelling values from December to March.

Figure 26 shows turbulence, E-W and N-S Ekman transport time-series for the three local measurement points concerning three different periods. Annual and February-July (ICES spawning period) turbulence showed latitudinal differences; Porcupine registered the highest turbulence values, followed by Great Sole Bank and Bay of Biscay (Figure 26a, b). The time-series for the regional spawning periods, instead, did not show differences among the three locations (Figure 26c). This same pattern was found in the case of E-W Ekman transport (Figure 26e, f, g). By contrast, in the case of N-S Ekman transport the latitudinal differences were not so clear; slightly lower transport values were observed in the Bay of Biscay for annual and February-July time-series (Figure 26i, j). By comparing mean N-S Ekman transport for regional spawning periods the Bay of Biscay showed higher fluctuations (more extreme peaks) whereas Great Sole Bank and Pocupine registered a similar range (Figure 26k). Concerning intra-annual variability, a clear seasonal pattern is evident for the three parameters, with lower turbulence and transport values during summer and maximum values in winter (Figure 26d, h, l). The three locations had in common transport direction; the mean transport was eastward (positive E-W transport values) and southward (negative N-S transport values).

Both SHF and LHF recorded high variability for annual and February-July time-series over the study period (Figure 27a, b, e, f). Considering regional spawning periods, Bay of Biscay showed greatly higher SHF values (Figure 27c); in the case of LHF, latitudinal differences were found with Bay of Biscay showing the highest values followed by Great Sole Bank and Porcupine (Figure 27g). The seasonal differences were evident in both cases, with low fluxes in summer and high fluxes in winter (Figure 27d, h).

MMF varied latitudinally with higher negative fluxes in Great Sole Bank and Porcupine for annual and February-July time-series (Figure 28a, b). However, considering regional spawning periods no latitudinal differences were found (Figure 28c). Bay of Biscay registered slightly higher flux values (positive fluxes) in February-July comparing to the rest of the mean periods (Figure 28b). There is a seasonal pattern with null (Great Sole Bank and Porcupine) or positive (Bay of Biscay) meridional momentum fluxes in spring-summer and negative fluxes in winter (Figure 28d). ZMF fluctuated similarly in the three locations for annual and February-July mean periods (Figure 28e, f). It should be highlighted that Bay of Biscay ZMF fluctuated sharply for the regional spawning period (January-May mean) time-series, with relevant negative peaks in 1990, 1995 and 1999 (Figure 28g). The three locations showed lower ZMF fluxes in spring-summer and higher negative fluxes in winter (Figure 28h).

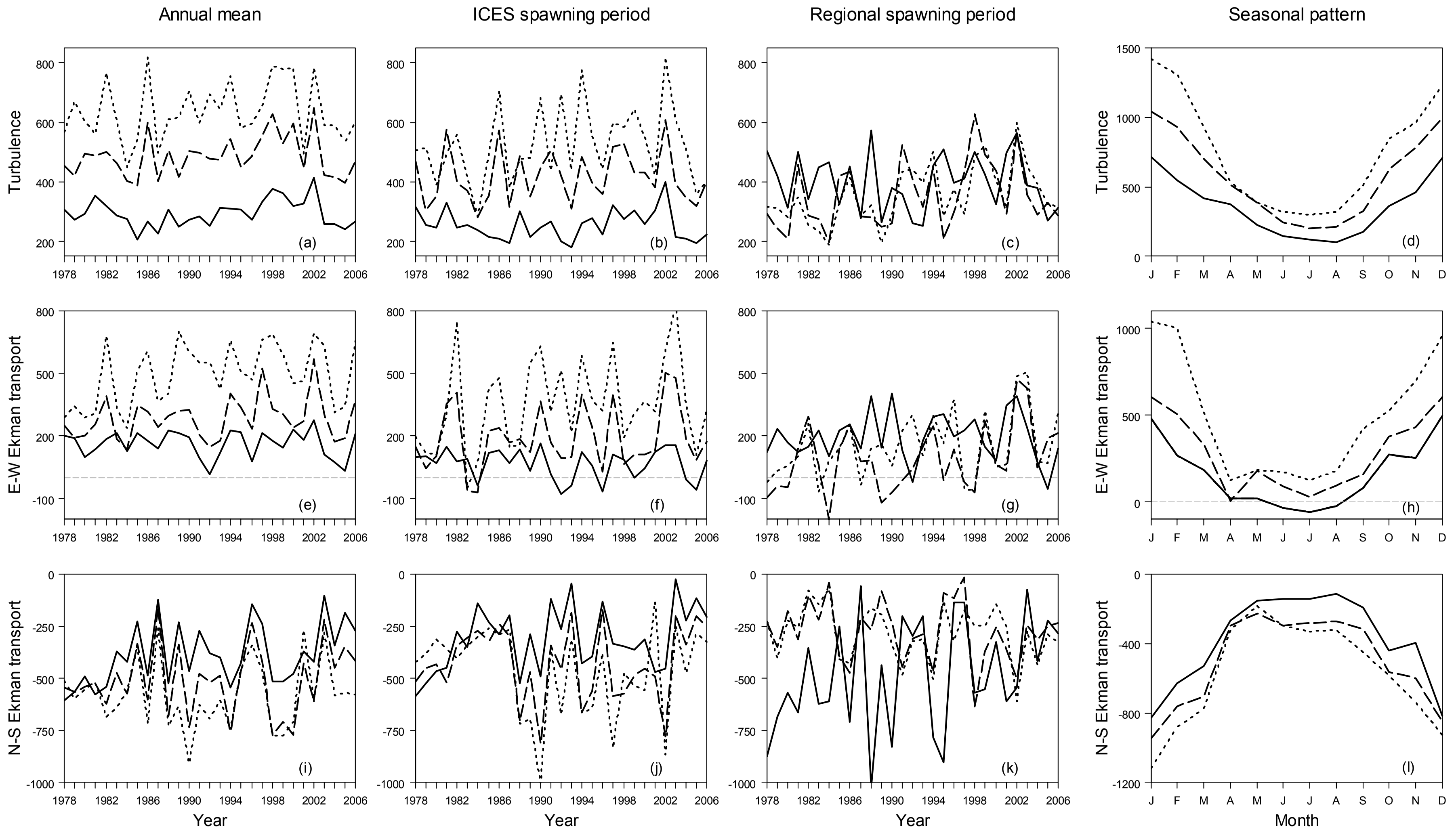


Figure 26: Turbulence ($m^3 \cdot s^{-3}$) (first row), EW ($kg \cdot m^{-1} \cdot s^{-1}$) (second row) and NS ($kg \cdot m^{-1} \cdot s^{-1}$) (third row) Ekman transport time-series, for annual mean (first column), ICES spawning period (second column) and regional spawning period (third column), at the local measurement points of the Bay of Biscay (solid line), Great Sole Bank (dashed line) and Porcupine (dotted line). The fourth column represents the seasonal pattern of the local parameters for the study period 1978-2006. Note that the magnitude of the transport is given by the absolute value whereas the positive/negative sign represents the direction of the transport.

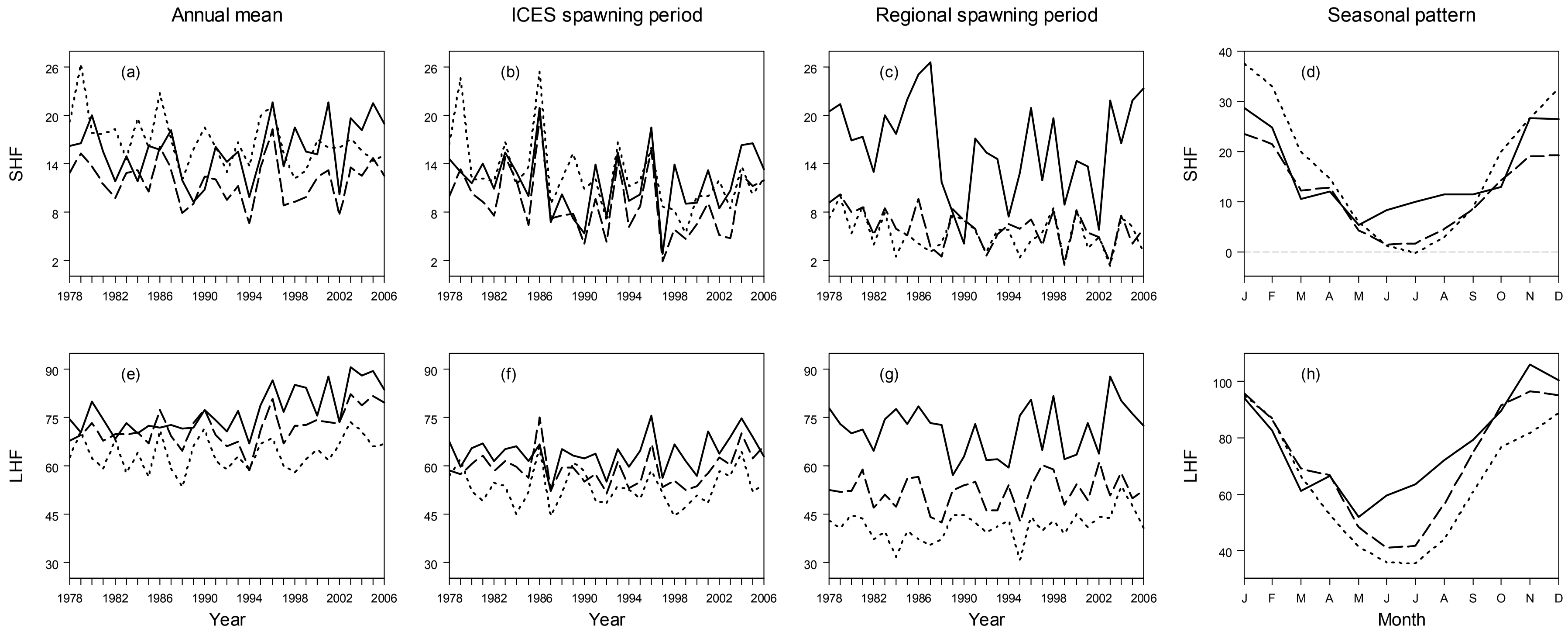


Figure 27: Sensible heat flux ($W \cdot m^{-2}$) (first row) and latent heat flux ($W \cdot m^{-2}$) (second row) time-series, for annual mean (first column), ICES spawning period (second column) and regional spawning period (third column), at the local measurement points of the Bay of Biscay (solid line), Great Sole Bank (dashed line) and Porcupine (dotted line). The fourth column represents the seasonal pattern of the local parameters for the study period 1978-2006. Note that the magnitude of the flux is given by the absolute value whereas the positive/negative sign represents the direction of the flux.

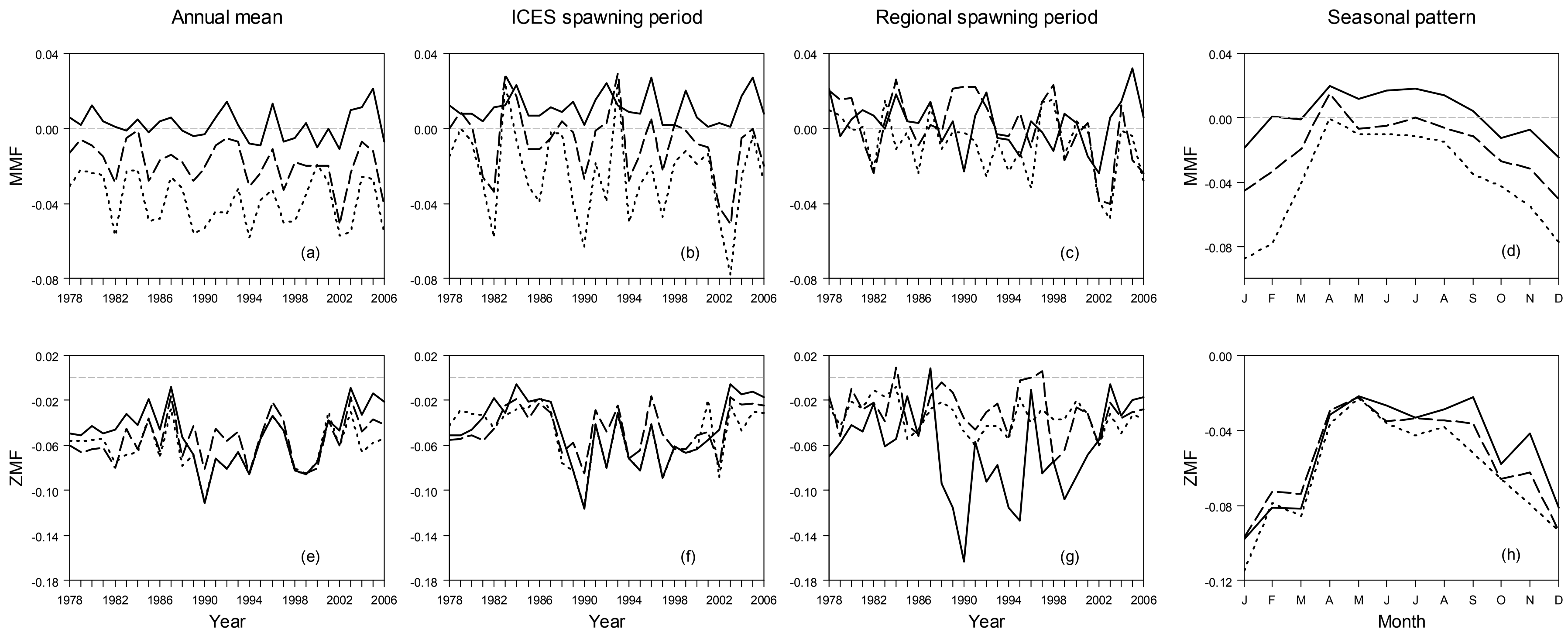


Figure 28: Meridional momentum flux ($N \cdot m^{-2}$) (first row) and zonal momentum flux ($N \cdot m^{-2}$) (second row) time-series, for annual mean (first column), ICES spawning period (second column) and regional spawning period (third column), at the local measurement points of the Bay of Biscay (solid line), Great Sole Bank (dashed line) and Porcupine (dotted line). The fourth column represents the seasonal pattern of the local parameters for the study period 1978-2006. Note that the magnitude of the flux is given by the absolute value whereas the positive/negative sign represents the direction of the flux.

Spatial variability

The average temperature for the study period shows a clear latitudinal pattern, ranging from temperatures of 9.5 ºC in the north of Scotland to 16 ºC in the warmer waters of the Bay of Biscay (Figure 29a). Comparing with the reference period of 1971-2000, sea surface water warmed over the whole of the area (positive temperature anomalies); this warming was more pronounced in the South (up to 0.3 ºC) in comparison to the North (0.1-0.15 ºC) (Figure 29b).

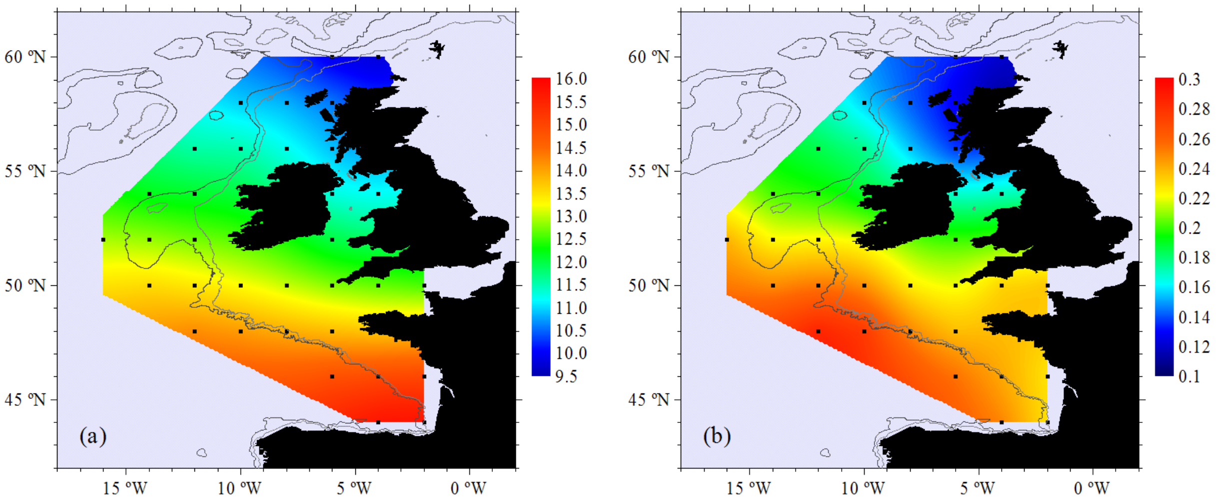


Figure 29: Spatial distribution of (a) temperature (ºC) and (b) temperature anomaly (ºC), averaged over the study period (1978-2006). Black dots represent the measurement points over the Northeast Atlantic continental shelf.

From January to March a similar distribution of temperature was observed with values ranging from 7.2 ºC on the shelf to 12.7 ºC at the southern shelf break (Figure 30). In April, a continuous warming of the waters started, reaching maximum values in August (about 21 ºC in the Bay of Biscay and more than 12 ºC in waters around Scotland). Afterwards, a progressive cooling of waters took place to reach winter low temperatures.

Generally speaking, the study area registered warmer-than-average temperatures for all months, except for waters around UK from January to March and waters west of Scotland in November (Figure 31). The most pronounced warming was registered in the area between 44ºN and 52ºN, in the months of May and June.

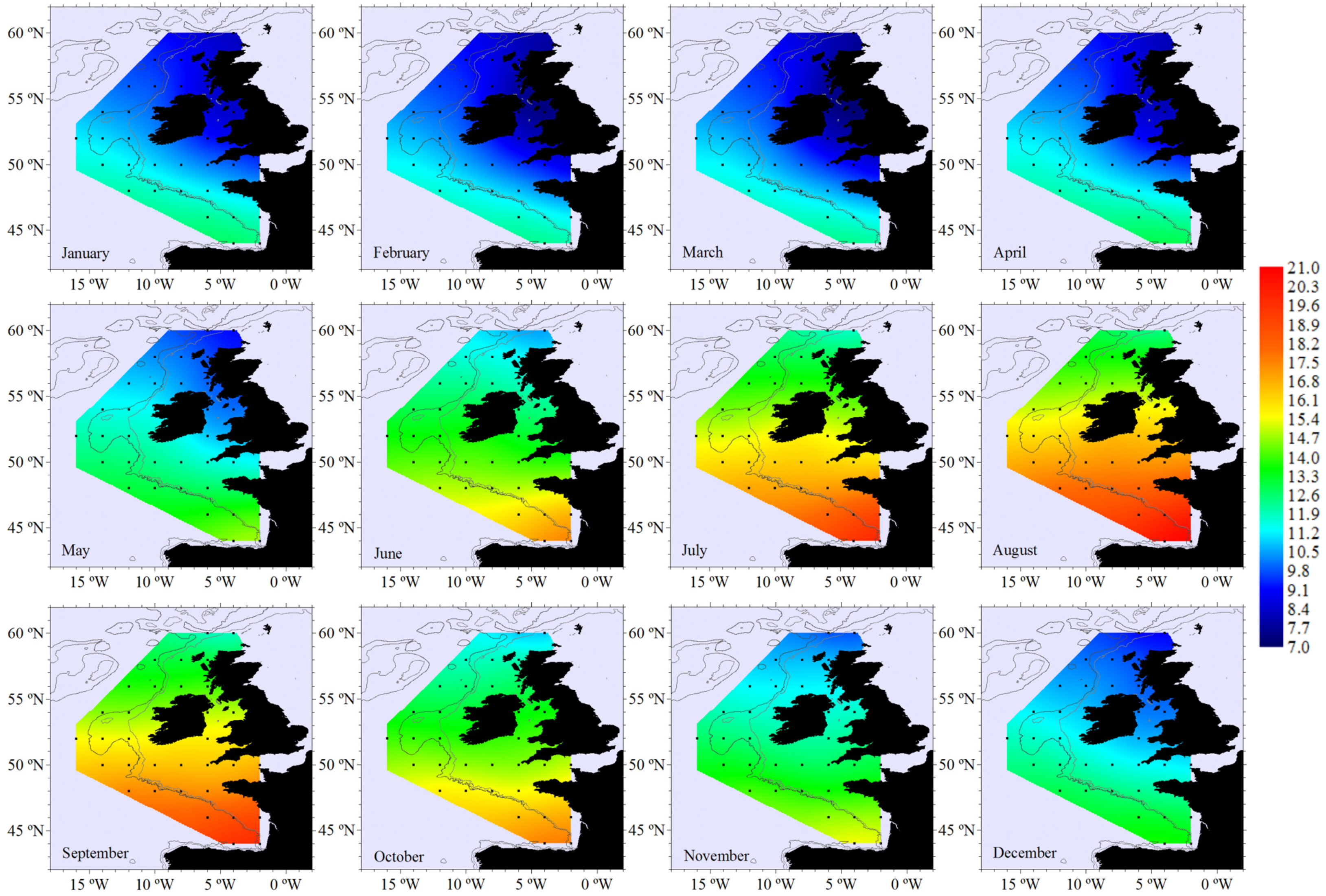


Figure 30: Spatial distribution of monthly temperature (ºC), averaged over the study period (1978-2006). Black dots represent the measurement points over the Northeast Atlantic continental shelf.

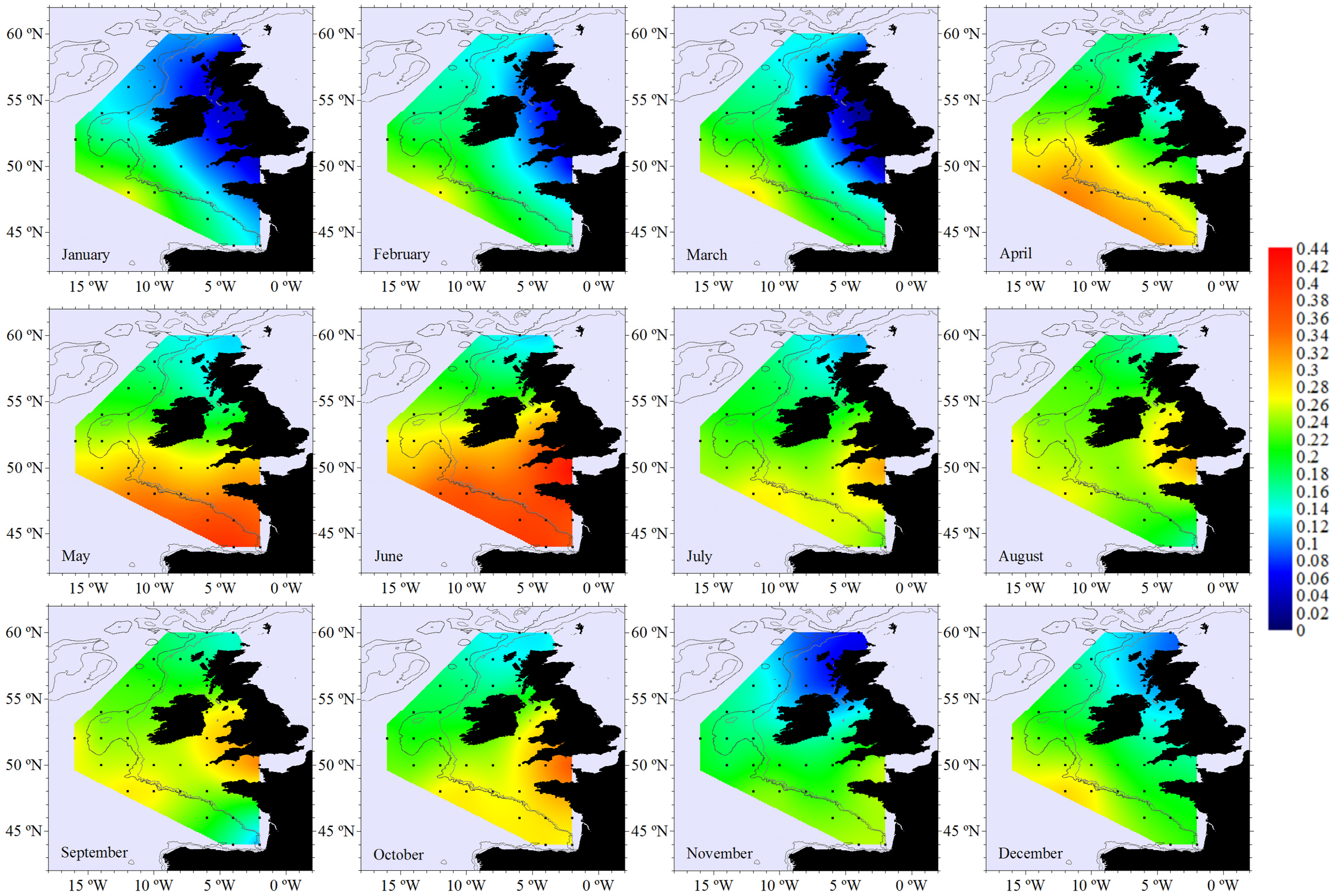


Figure 31: Spatial distribution of monthly temperature anomaly (ºC), averaged over the study period (1978-2006). Black dots represent the measurement points over the Northeast Atlantic continental shelf.

The average Ekman transport for the study period showed eastward (positive E-W Ekman transport) and southward (negative N-S Ekman transport) direction (Figure 32). The spatial pattern was similar for both zonal and meridional transports: the weakest transport was registered in the Bay of Biscay, whereas the strongest transport was observed north and west of Ireland.

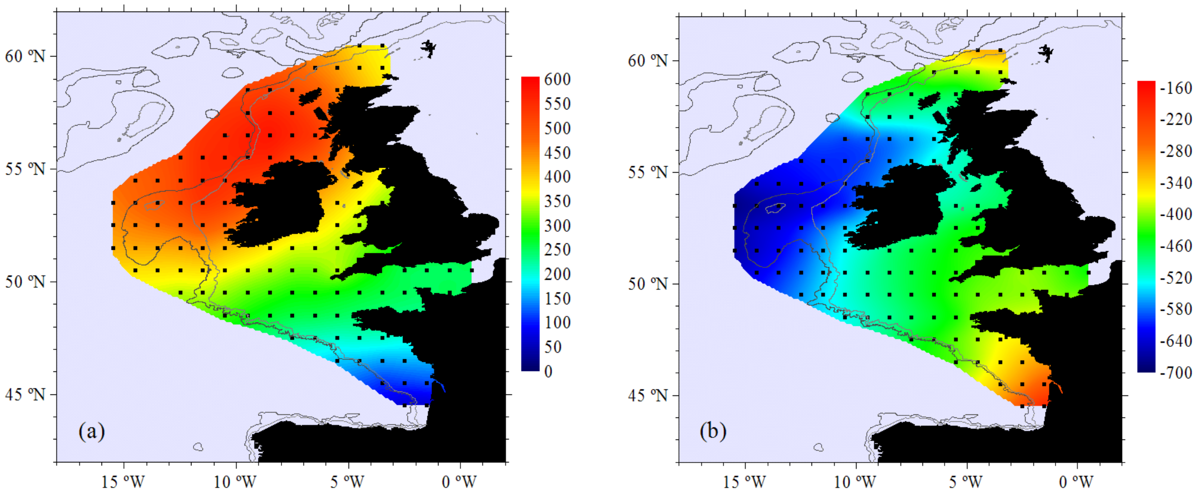


Figure 32: Spatial distribution of (a) East-West and (b) North-South Ekman transport (kg·m-1·s-1), averaged over the study period (1978-2006). Black dots represent the measurement points over the Northeast Atlantic continental shelf.

The seasonal pattern for E-W Ekman transport can be seen in Figure 33. From September to March the whole of the study area registered eastward Ekman transport, with the strongest transport values (> 800 kg·m^{-1}·s^{-1}) recorded at the north and west of Ireland (December to February). By contrast, transport decreased considerably from April to August in the whole of the study area: in the Bay of Biscay, westward transport can be found, reaching values up to 150 kg·m^{-1}·s^{-1} in July.

Regarding N-S Ekman transport, in general a southward direction (negative N-S transport) was found for the whole of the study area (Figure 34): the strongest values were registered in January, being maxima at the latitudinal range of 53ºN-58ºN. From February to May, transport weakened progressively. From May onwards a slight increase in southward transport was registered for most of the study area; however, southern Bay of Biscay showed weak northward (positive) N-S Ekman transport during summer months (June to August). In autumn, the continuous strengthening of southward transport was observed up to the maximum values of January.

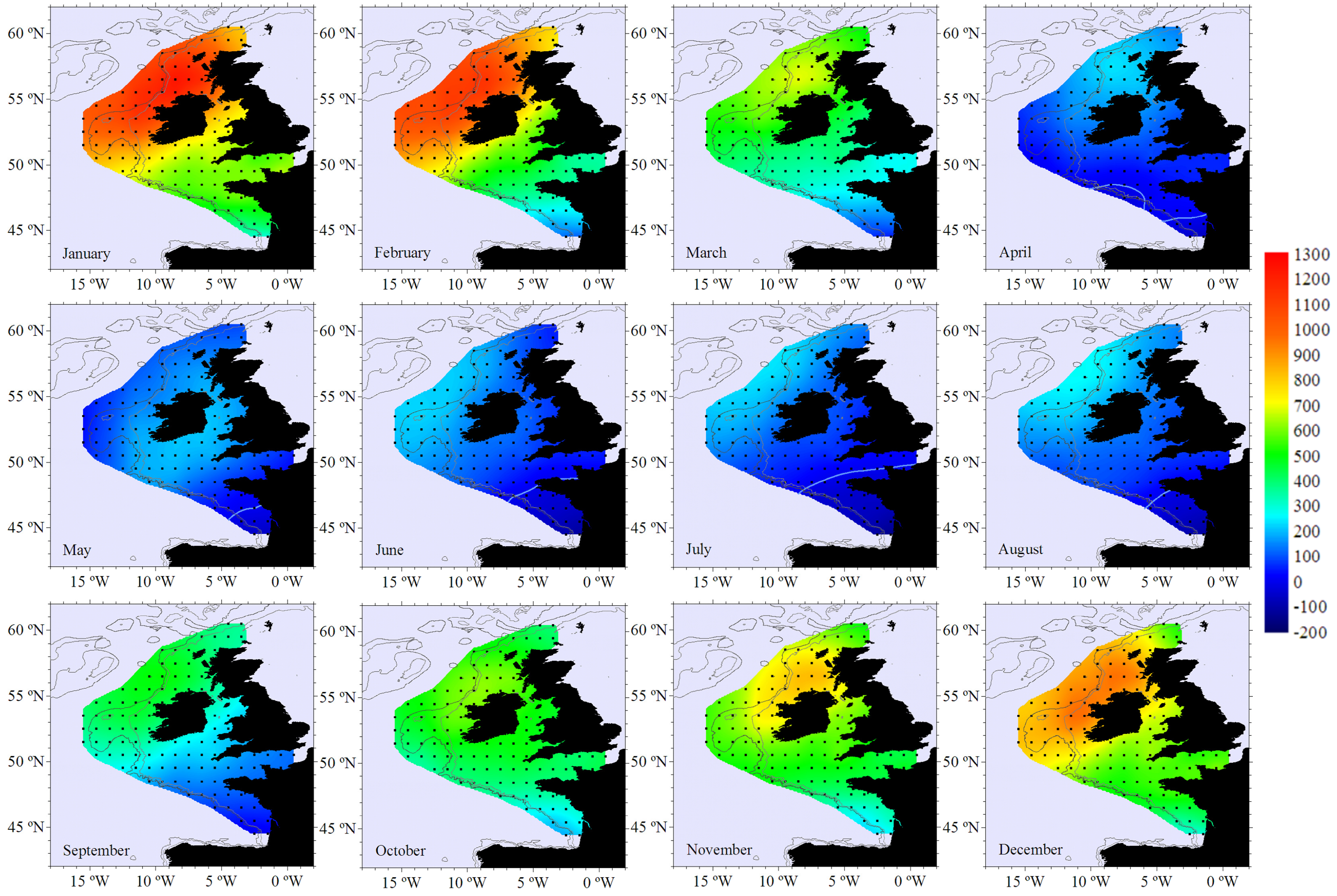


Figure 33: Spatial distribution of monthly East-West Ekman transport (kg·m^{-1}·s^{-1}), averaged over the study period (1978-2006). Black dots represent the measurement points over the Northeast Atlantic shelf. The light blue line indicates the limit between eastward and westward transport (null Ekman transport).

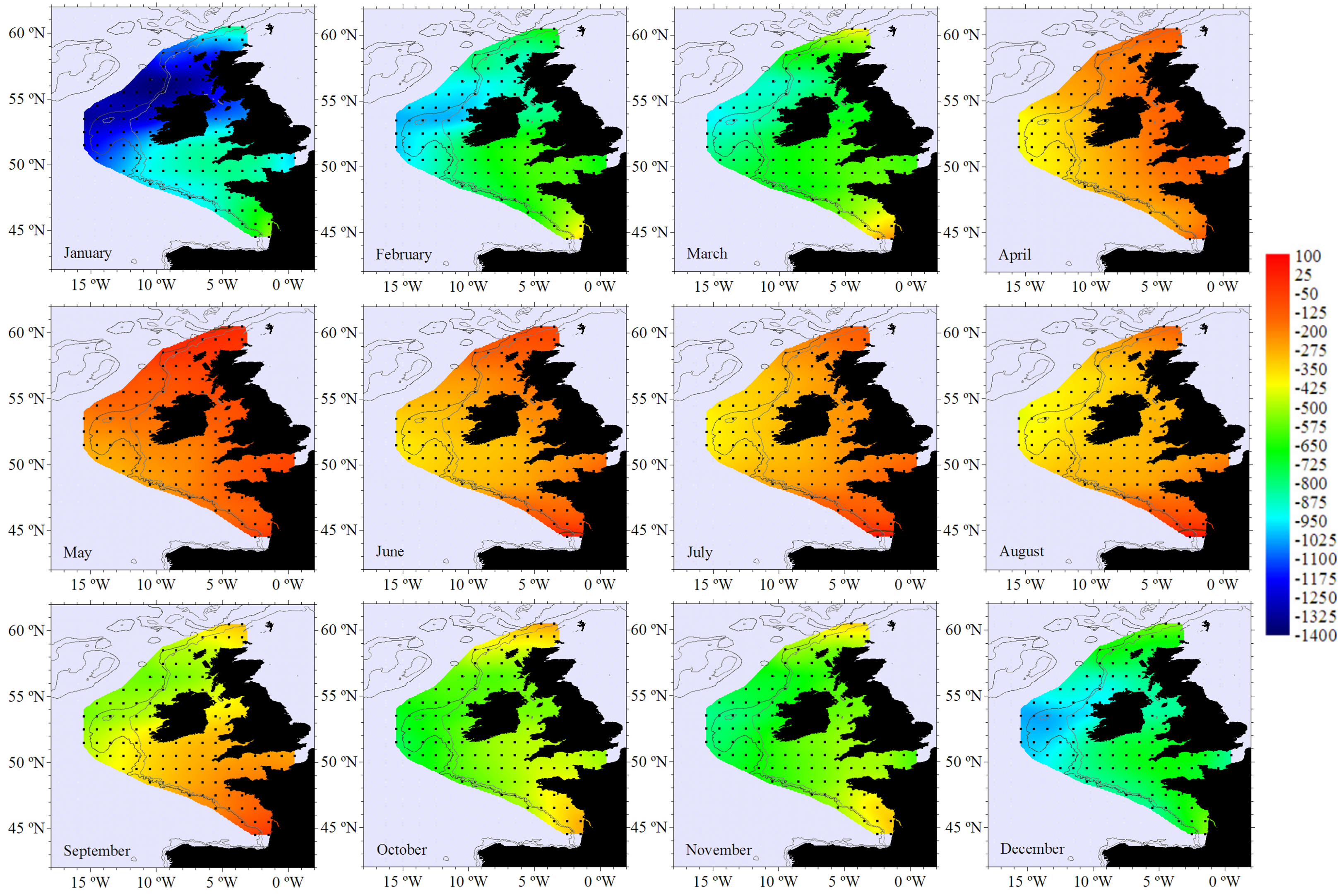


Figure 34: Spatial distribution of monthly North-South Ekman transport (kg·m^{-1}·s^{-1}), averaged over the study period (1978-2006). Black dots represent the measurement points over the Northeast Atlantic continental shelf. The red line indicates the limit between northward and southward transport (null Ekman transport).

B) Biological data

Undertaking the whole of the study area, copepod abundance showed a general decreasing trend from late 1980s onwards (Figure 35a). However, studying each Standard area separately, different trends were evident (Figure 35b):

- C3 (East of Ireland): it showed the lowest copepod abundance, with a peak in 1995.
- C4 (North of Ireland, West of Scotland): high inter-annual variability with relevant maximum abundances in 1985 and 1994.
- D3 (English Channel): high variability over the study period reaching minimum abundances in 2000s.
- D4 (Celtic Sea): after high fluctuations at the beginning of the series, a decreasing trend was found from late 1980s onwards.

February-July mean time-series showed similar trends concerning both the whole of the study area (Figure 35c) and each of the Standard Areas (Figure 35d).

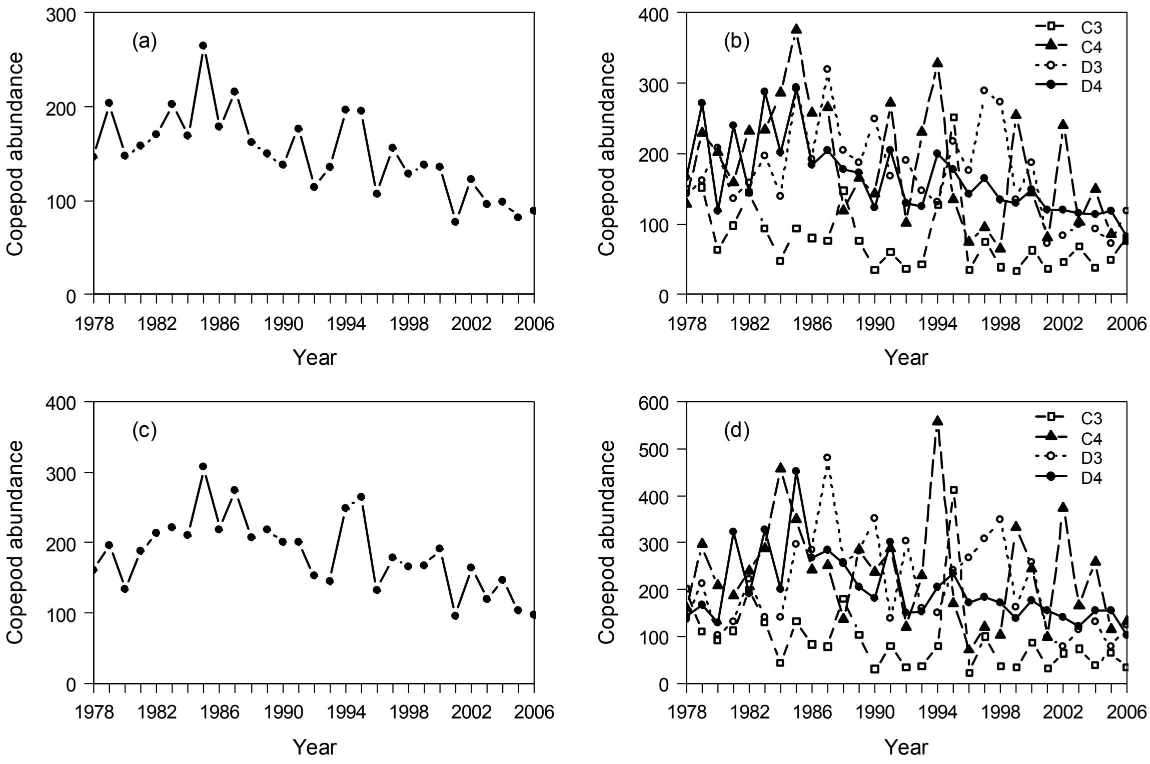


Figure 35: Above, copepod annual mean abundance (number·m^{-3}) time-series for (a) the whole of the study area and, (b) for each of the CPR Standard Areas considered in this study; below, copepod February-July mean abundance time-series for (c) the whole of the study area and, (d) for each of the CPR Standard Areas considered in this study.

Considering mean copepod abundance for the four Standard Areas, seasonality was clear with higher copepod abundances from April to October. The peak abundance was registered in May-June (Figure 36).

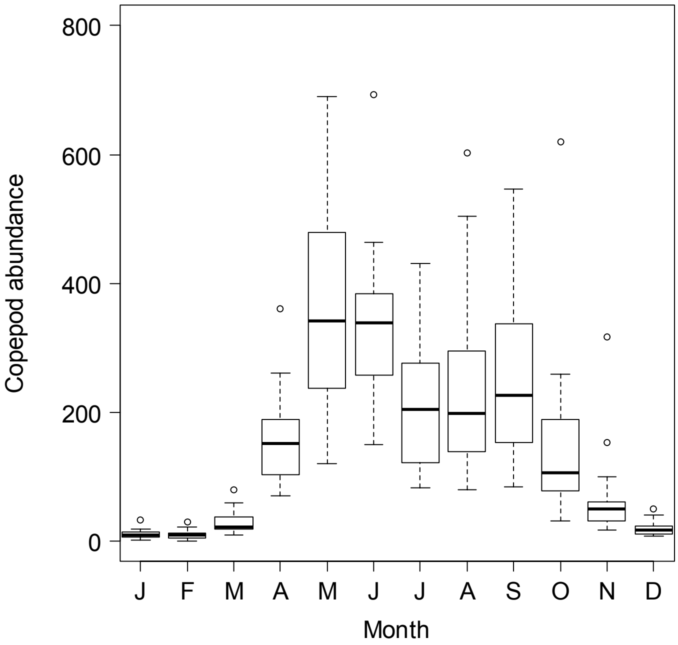


Figure 36: Boxplot of monthly mean copepod abundance (number·m^{-3}) for the study period. The boxes represent the range between the 75th and the 25th percentiles and the horizontal line within the box indicates the median value.

If each Standard area is analysed separately regional evidences arise (Figure 37):

- C3 (East of Ireland): slightly higher copepod abundances in May-August.
- C4 (North of Ireland, West of Scotland): higher abundances from May to September with peak abundance in June.
- D3 (English Channel): slightly higher values from May to September, with a maximum in June.
- D4 (Celtic Sea): Increase in copepod abundance from April to October, with a clear peak abundance in May.

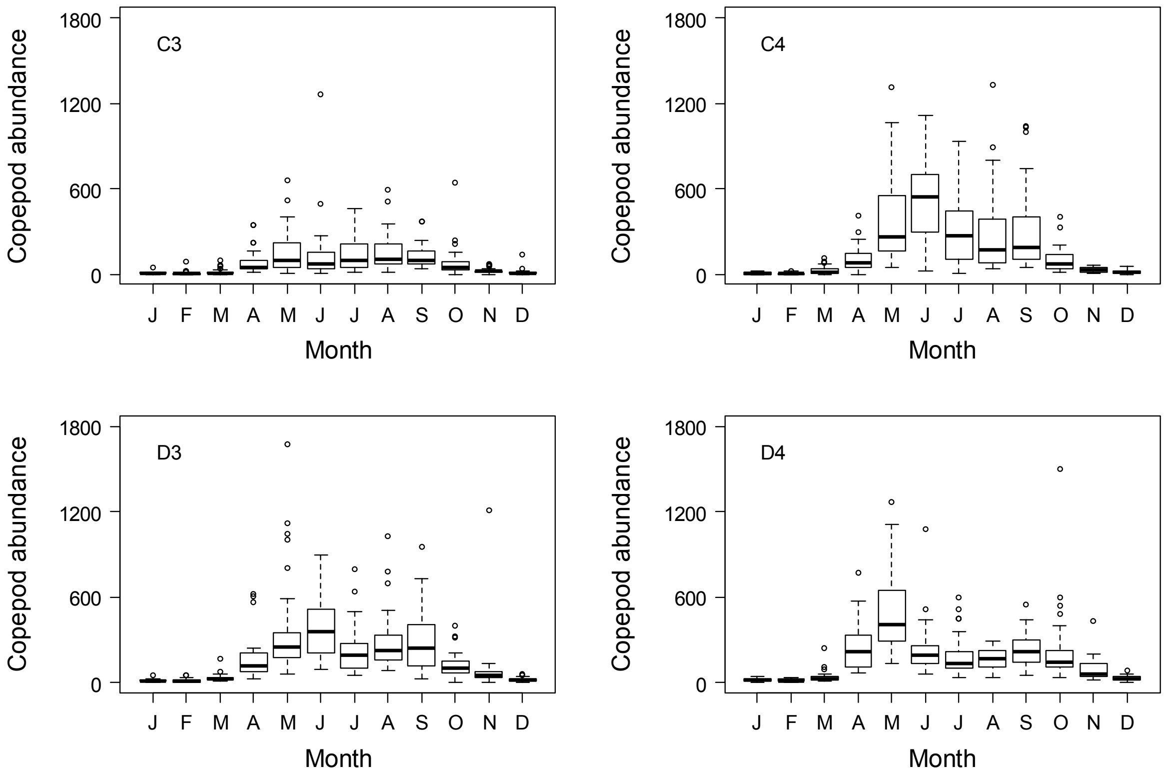


Figure 37: Boxplots of monthly copepod abundance (number·m^{-3}) for the study period, for each of the CPR Standard Areas. The boxes represent the range between the 75th and the 25th percentiles and the horizontal line within the box indicates the median value.

DISCUSSION

Northern Hemisphere

The North Atlantic Oscillation is a leading pattern of weather and climate variability over the Northern Hemisphere. The NAO is most pronounced in amplitude and areal coverage during winter (December-March) (Marshall *et al.*, 2001), as demonstrated also in our results. There are different procedures for the estimation of the NAO index, but most modern NAO indices are derived either from the simple difference in surface pressure anomalies between various northern and southern locations, or from the principal component time series of the leading empirically-determined orthogonal functions (EOFs) of sea level pressure (Hurrell and Deser, 2009). Although the NAO index selected for the present study and the widely used Hurrell's index differ on the selection of the pressure centres, they both showed a similar temporal variability with a period of highly positive phase from late 1980s to mid-1990s. Further, both indices coincided in the extreme negative value in winter NAO index for 1996. Relative to previous decades, the study period of this thesis was characterised by positive NAO period, in comparison to the negative NAO phase from mid-1950s to mid-1970s (Hurrell and Deser, 2009).

Coinciding with the period of positive NAO index, GSNW index also showed positive values from late 1980s to mid-1990s. Positive values of this index are indicative of a displacement to the north of the long-term mean location of the North Wall of the Gulf Stream (NWGS), while negative values indicate a southward movement. In fact, the position of the GSNW moves northward during positive NAO phases (Taylor and Stephens, 1998; Taylor *et al.*, 1998; Hurrell and Deser, 2009). Further, greater transport (higher TPEA values) was found from late 1980s to mid-1990s. Curry and McCartney (2001) observed that the Gulf Stream and the North Atlantic Current gradually weakened during low NAO period of the 1960s and then intensified in the subsequent 25 years of persistently high NAO to a record peak in the 1990s. Grey *et al.* (2000) identified an intense warm anomaly in the subtropical gyre in 1988-94, together with the greatest temperature anomalies in the North Atlantic during the period of their study (1950-94). During the warm period 1988-94, a stronger Gulf Stream with greater northward heat transport by near-surface waters was observed.

The NAO exerts a dominant influence on winter time temperatures across much of the Northern Hemisphere. Indeed, the positive state in the NAO index contributed much to the observed warming in Northern Hemisphere surface temperatures over the past decades (Marshall *et al.*, 2001; Hurrell *et al.*, 2003). Concerning the study period of the present thesis, during the positive phase of the NAO, the Northern hemisphere temperature clearly changed from negative to positive temperature anomalies from 1987 onwards. This change was also evident for the Atlantic Multidecadal Oscillation index, which showed a stepwise change in late 1980s.

The Eastern Atlantic pattern is the second prominent mode that influences northeastern Atlantic hydro-climatology. Above average temperatures can be found in Western Europe during positive EA (NOAA, 2008). This global index fluctuated until 1995, shifting between negative and positive values, and then remained in the positive state from

1995 onwards. In addition, AMO changed dramatically from negative values until 1995 to positive values from 1995 onwards. This increase in temperatures is again evident in the Northern Hemisphere temperature time-series, which showed a second stepwise increase in 1995.

Long-term variations in Earth's temperature are closely associated with variations in the solar cycle length (Friss-Christensen and Lassen, 1991). Solar activity influences terrestrial climate (Benner, 1999) but also ocean's temperature. Indeed, the record of globally averaged sea-surface temperatures over the past 130 years has been shown to have a closely similar variation to that of solar activity (Reid, 1991). In the Northern Hemisphere, irradiance values have been related to temperature (Lean *et al.*, 1995).

Sunspot numbers are often used as a convenient proxy for solar activity. Sunspot numbers fluctuate regularly with cycles of 11 years (Tsiropoula, 2003). Within the study period, three peaks in sunspot number were registered, in late 1970s, 1980s and 1990s. From late 1980s to mid-1990s, both the solar and geomagnetic activity showed high values, represented by sunspot numbers and AA index, respectively.

Lastly, the climatic indices defined from the low-frequency climatological modes, did not show any clear pattern during the study period. Only CLI2 showed positive values from late 1980s to mid-1990s coinciding with the positive phase in NAO index. Actually, the second component of the PCA on climate indices (CLI2) reflects mainly the variability in the North Atlantic Oscillation (NAO) (Bode *et al.*, 2006; Fernandes *et al.*, 2010).

The North Oscillation index, being a North Pacific climatic index, did not show similarities on temporal fluctuations with the above described North Atlantic indices.

Table 3 summarises the global indices that showed clear trends over the study period. Most of the global indices coincided in the timing of the change in trend and/or sign; during late 1980s or/and mid-1990s.

Table 3: Summarising information of the general trends and signs of the global indices for the study period.

Index	**Trend**			**Sign**		
		late 80s	**mid-90s**		**late 80s**	**mid-90s**
NAO	—	∧	—	±	+	±
GSNW	—	∧	—	±	+	±
TPEA	(no data)	∧	—	(no sign)		
EA	—		/	±		+
AMO	—	∧	/	-	±	+
NH temp anom.	/	/	/	±	+	+
Sunspot number	Cyclic			(no sign)		
AA index	Cyclic			(no sign)		

Northeastern Atlantic

The general warming observed for the Northern Hemisphere also affected regional waters over the continental shelf of northeastern Atlantic. Rapid increases in Northeast Atlantic SST have been observed in recent decades as part of larger-scale global warming of the ocean surface (Rayner *et al*., 2006). However, the warming rate showed latitudinal differences. Relative to the base period of 1971-2000, the increase in SST was more pronounced over the shelf edge of the Bay of Biscay and the Celtic Sea, where the mean annual temperature ranged from 13.5 ºC to 16 ºC. Northwards, the increase in SST was lower; the minimum increase was registered northwest of Scotland where the SST registered the coldest annual mean values of the study area (9.5 ºC-10.5 ºC).

The temporal variability of SST anomalies also showed geographical differences over the study period. The Bay of Biscay (5ºx5º boxes A, C and D in Figure 12) underwent the greatest warming with differences of up to 1 ºC in recent years (relative to the period 1961-

1990). This increase was more pronounced in the southeastern corner of the Bay of Biscay. This is in accordance with Planque *et al*. (2003), who observed that the rate of temperature increase was greatest in the southeastern part of the bay. Northwards the increase rate was slower. These geographical differences were also observed by Planque *et al*. (2003) who highlighted a rapid warming of warmer waters in the South and slower warming of colder waters in the North. 1992 and 1993 can be mentioned as exceptional years since they showed higher than average February-July mean values in comparison to the annual means of those years.

Analysing the annual cycle of SST over the northeastern Atlantic continental shelf, a seasonal pattern was evident: the coldest temperatures were registered from January to March; in April, with the stratifications of the water column, a continuous warming started, leading to maximum values in August; then, due to the wind-mixing, the stratification broke and a progressive decrease in SST took place to reach winter low temperatures. Comparing to preceding decades, the Bay of Biscay and the Celtic Sea registered a pronounced warming in May and June.

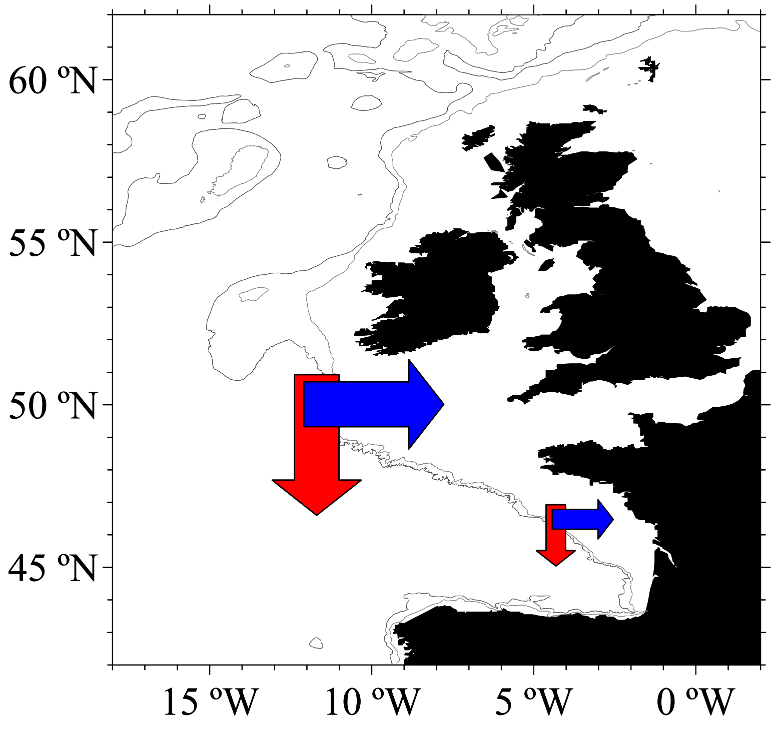


Figure 38: General pattern of the annual wind-driven Ekman transport over the continental shelf for the period 1978-2006. Note that the blue arrows represent zonal transport and red arrows represent meridional transport. The size of the arrows is proportional to the strength of the transport.

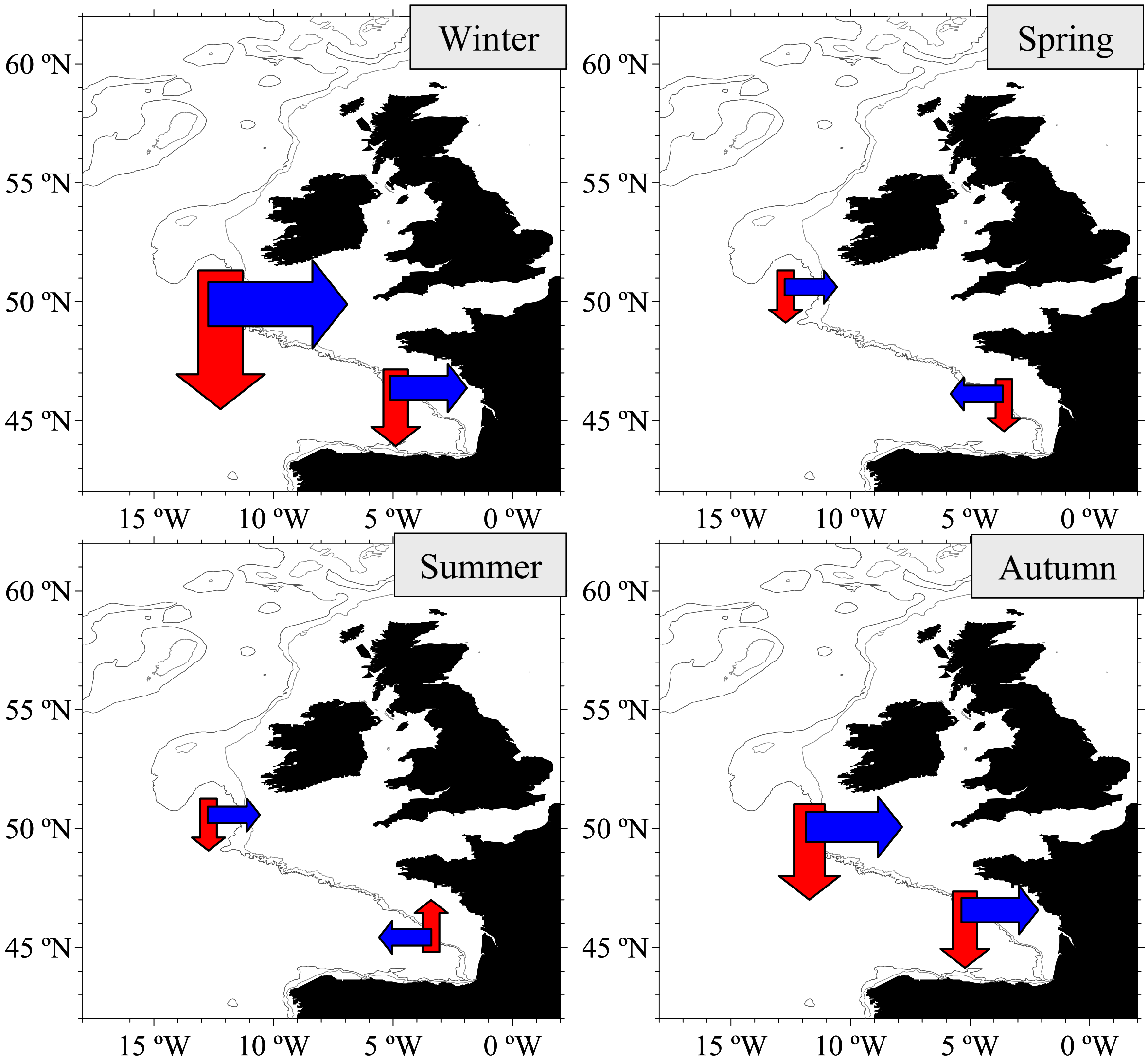


Figure 39: General pattern of the seasonal wind-driven Ekman transport over the continental shelf for the period 1978-2006. Note that the blue arrows represent zonal transport and red arrows represent meridional transport. The size of the arrows is proportional to the strength of the transport. Winter considered as J-F-M, spring as A-M-J, summer as J-A-S and autumn as O-N-D.

The annual picture of wind-driven Ekman transport over the study area, was formed by mean eastward and southward transport over the whole of the continental shelf (Figure 38). However, in general terms, transport was weaker in the Bay of Biscay whereas the strongest transports were observed at the Rockall Trough. If monthly Ekman transport is analysed, seasonal variability can be found in both zonal and meridional transports (Figure 39). Eastward transport is clearly stronger in January and February at the Rockall Trough. However, in spring and summer zonal transport weakened dramatically; what is more, Ekman transport changed direction to show offshore transport in the Bay of Biscay from April to August. With reference to North-South Ekman transport, in autumn and winter a general southward transport was registered over the study area; it should be noted that the Rockall Trough underwent the strongest values in January. Dominant winds over the Bay of Biscay are westerlies and result in wind-driven coastal currents being oriented principally to the south (Planque *et al*., 2003). However, in the southeasternmost part of the Bay of Biscay wind pattern changed in summer showing weak northward Ekman transport.

Generally speaking, the total copepod abundance underwent a decreasing trend in both annual and hake spawning period time-series over the whole of the study area. However, this decrease was more pronounced from late 1980s onwards in the Celtic Sea. Copepod abundance showed clear seasonality with higher abundance from April to October; the peak abundance was registered in May-June after the spring phytoplankton bloom. More locally, May showed the highest values of copepod abundance for the D4 CPR box, within the spawning area of the Celtic Sea; 20% of the annual copepod abundance was observed in May. It should be noted that May and June registered the most pronounced warming in the Bay of Biscay, English Channel and the Celtic Sea. This warming could have been the cause for the decreasing trend registered from late 1980s onwards, due to either a decrease in copepod number of the area or even a northward shift of local copepods (Beaugrand *et al*., 2002; Beaugrand and Reid, 2003).

Hake spawning grounds

The main spawning areas described for northern hake are located off the French coast in the Bay of Biscay and in the Celtic Sea, south of Ireland; some spawning takes place also in waters west or Ireland (Porcupine area). Given the importance of these areas as hake spawning grounds, their hydro-physical characterisation is described in the following lines and summarised in the comparative Table 4.

As described for the Northern Hemisphere and for the northeastern Atlantic continental shelf, both Bay of Biscay and Celtic Sea registered an increasing trend in temperature with negative anomalies until mid-1990s and warmer-than-average temperatures from 1995 onwards. This pattern was not reflected in slope temperature of the Bay of Biscay at 100 m depth. Besides, slope temperature reached the peak value two months later (October) than sea surface temperature (August).

The upwelling index off the French coast showed great fluctuations, with a general decreasing trend towards the end of the study period. This weakening in the upwelling index could be associated to the positive period of EA, as shown in Borja *et al.* (2008). Such authors reported that during positive EA phases, wind circulation (mainly from the NW and SW) was unfavourable for upwelling episodes; this is supported by our study where the decrease in upwelling index has been confirmed during hake spawning periods (February-July and January-May) and even in upwelling peak months (December-March). Upwelling index is significantly higher in winter (December-March) than in spring or summer (May to August).

Concerning Ekman transport, interannual variability was great, with fluctuations between eastward-westward and northward-southward directions, and thus no clear inter-annual trend was found in the spawning grounds.

Comparing Bay of Biscay, Great Sole Bank and Porcupine measurement points, latitudinal differences were observed. In the Bay of Biscay turbulence and E-W Ekman transport were weaker in comparison to the other two areas; Porcupine showed the greatest turbulence and E-W Ekman transport values. Porcupine is an open area located close to the Rockall Trough, which is a pathway by which warm Eastern North Atlantic upper water (ENAW) travels northward. The upper layers of the trough have two sources: water from the North Atlantic Current, which follows the boundary between the subpolar and subtropical gyres, and water from more southern areas west of and over the continental shelf (Hátún *et al.*, 2005). It is therefore a very dynamic area in comparison to the more protected Bay of Biscay.

The only clear pattern was found in terms of seasonal variability with summer months characterised by low turbulence, zonal and meridional Ekman transports, and winter months of high turbulence and transport values. This duality of water column stability in summer against winter mixing was repeated in both spawning grounds.

Interannual SST variability is governed by the response of the oceanic mixed layer to the local exchange of heat with the atmosphere (Kushnir, 1994). Latent and sensible heat exchanges at the ocean surface are an important mechanism for transferring heat from ocean to atmosphere. For example, northerly winds advect cooler, drier air and produce higher latent and sensible fluxes (Cayan, 1992a). In this regard, winter months registered higher ocean-atmosphere fluxes due to the frequent northerly wind pattern found during this season. Latitudinal differences were found when studying regional spawning period time-series. As such, Bay of Biscay showed consistently higher fluxes during regional spawning season, in comparison to Great Sole Bank and Porcupine time-series. This difference may be due to the windier conditions found in the Bay of Biscay during January-May.

Another mode of interaction between the ocean and atmosphere is the sea-air momentum flux, which is mainly dependant on the wind speed and ocean currents. Given the importance of meridional transport in the Pocupine area, it is understandable the higher meridional momentum fluxes registered during the study period. The lowest fluxes were found in the Bay of Biscay. As expected, summer months showed lower momentum fluxes given the more stable state of the ocean at this season.

Table 4: Comparison table of the hydro-dynamical conditions in Porcupine (Porcup.), Celtic Sea (CS) and Bay of Biscay (BB).

Parameter		**Comparison**
Turbulence	Dynamics-related	Porcup. > CS > BB
Ekman transport		
Momentum fluxes		
Temperature anomaly	Hydrography-related	Porcup. < CS < BB
Heat fluxes		

Chapter II

Northern European hake population: Stock-recruitment analysis

INTRODUCTION

In spite of being an economically important fishing species, there are hardly any studies regarding northern hake fluctuations over time and the causes related to such variations. The majority of the research focuses upon egg and larvae distribution (Álvarez *et al*., 2001, 2004), hake growth (de Pontual *et al*., 2003, 2006; Álvarez and Cotano, 2005; Kacher and Amara, 2005), reproduction (Murua, 2006; Murua and Motos, 2006; Murua *et al*., 2006) or feeding ecology (Mahe *et al*., 2007); all of them based on particular survey data. The only works regarding recruitment and spawning stock biomass fluctuations along time are those published annually by the Working Group on the Assessment of Southern Shelf Stocks of Hake, Monk and Megrim. However, such reports focus mainly on the estimation of the biological parameters with the aim of setting management criteria.

Understanding the recruitment dynamics of marine fish stocks is crucial in selecting fisheries management strategies. It is critical to understand the recruitment patterns of marine fish and the importance of factors responsible for interannual variations in recruitment, and so, it is a primary objective of fisheries science and management (Chambers and Trippel, 1997; Marshall *et al*., 1998). In this context, it is critical to investigate whether and to what extent recruitment depends on spawning stock biomass. The relationship between the stock and recruitment is a central, generally most difficult, outstanding problem in the study of the population dynamics and the management of marine fish stocks (Hilborn and Walters, 1992).

There is a wide range of papers regarding the stock-recruitment (S-R) relationship (Ricker, 1954; Beverton and Holt, 1957; Cushing, 1971; Shepherd, 1982; Fargo, 1994; Iles, 1994; Jacobson and MacCall, 1995; Myers and Barrowman, 1996; Myers, 1997; Zheng, 1996; Zheng and Kruse, 2003) due to its importance for fisheries resource management. The majority of these papers assume that a density-dependent stock-recruitment relationship exists, and they discuss how the parameters of the S-R relationship can be estimated or how the degree of bias due to natural perturbations or measurement errors can be evaluated. However, it has also been questioned whether stock and recruitment can be related, and few papers doubt about the existence of the so well-known Ricker or Beverton and Holt type density-dependent S-R relationships (Walters and Ludwig, 1981; Walters, 1985; Amstrong and Shelton, 1988; Koslow, 1992; Gilbert, 1997; Sakuramoto, 2005). Generally speaking, the precise identification of a stock-recruitment model or the selection between different given models is difficult (or impossible), in cases where the observed recruitment is too variable (Koslow, 1992; Maury, 1996).

Bias in stock-recruitment relationships is a subject that has been widely studied (Walters and Ludwig, 1981; Walters, 1985; Amstrong and Shelton, 1988; Koslow, 1992; Myers and Barrowman, 1995) and several difficulties for establishing stock-recruitment models have been noted: firstly, stock-recruitment analysis is often difficult because of the lack of independence between the spawning stock and recruitment, that is to say that, under favourable conditions for recruitment an increase in spawning stock biomass will occur, and as a consequence a positive correlation with time lag may emerge (Sparholt, 1996; Myers and Barrowman, 1995, 1996); secondly, there is often lack of data over some parts of the whole range of SSB values, above all at low SSB values (Koslow, 1992); thirdly, errors in recruitment and SSB estimations can affect S-R model parameter estimations (Walters and Ludwig, 1981; Myers and Barrowman, 1995); lastly, the relationship between spawning stock and recruitment can be hidden by other external factors such as predation, competition and physical environmental variability (Walters and Korman, 1999).

Despite the ongoing discussion regarding the relationship between stock spawning biomass and recruitment (Myers, 1997; Gilbert, 1997), the 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 (Chambers and Trippel, 1997); fact that is used commonly to set biological reference points.

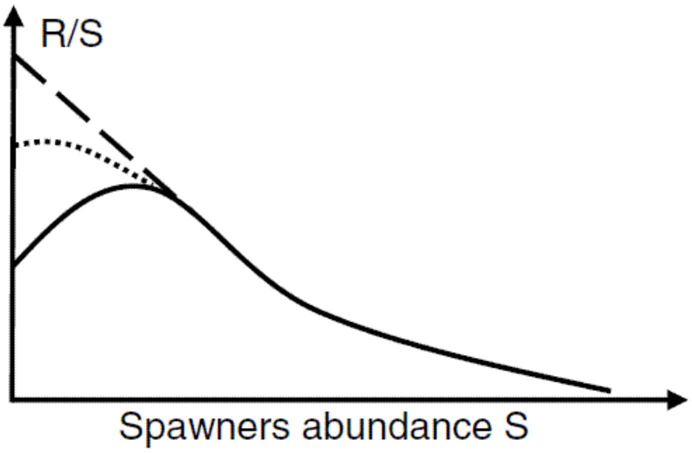
A stock-recruitment relationship describes a probable recruitment level of progeny from a given reproductive stock size (Zheng and Kruse, 2003). Underlying model that is generally assumed in fisheries assessment is that recruitment success (recruitment per unit spawner biomass) decreases with increasing SSB (Shelton and Healey, 1999; Gascoigne and Lipcius, 2004). As population decreases, food and habitat availability increases resulting in elevated growth rates, which can in turn, result in increased productivity and thus increased recruitment success (Frank and Brickman, 2000; Walters and Kitchell, 2001). Therefore, increasing pre-recruit survival compensates for reductions in egg production associated with decreasing SSB (Frank and Brickman, 2000). This is termed the "compensatory" response of the stock to the decrease in population size.

In contrast, reproductive success could decline with decreasing population size. This "depensatory" response is believed to happen due to the increasing predation on pre-recruit fish (Shelton and Healey, 1999). Beyond this type of response is the hypothesis known as the "cultivation effect". It states that dominants may be species that are fortuitously capable of being especially good at capturing the particular smaller forage fishes that are, in turn, potential competitors/predators of their own juveniles and could cause worst effects on them (Walters and Kitchell, 2001). With the decline of larger predator population, small forage species would increase in abundance; consequently, they can predate on the juveniles causing higher juvenile mortality rate, or they will compete for food with the pre-recruits of their larger predators, diminishing recruitment success at low stock levels (Persson *et al*., 2007; Vergnon *et al*., 2008). Actually, this "cultivation effect" is equivalent to the "intraguild predation" effect considered in ecology (Polis *et al*., 1989).

In general, compensatory mechanisms are thought to be prevalent in fish stocks (Frank and Brickman, 2000). Contrarily, despite depensation being difficult to detect due to the limited and variable data associated to low spawning stock levels, this kind of dynamics have been observed in species such as northern cod (Frank and Brickman, 2000). Myers *et al.* (1995) found little empirical evidences for depensation in assessed fish stocks.

More widespread ecological phenomena are the so-called Allee effects. While both compensatory and depensatory responses assume that stock-recruitment curve passes through the origin, models showing Allee effects have a non-zero intercept. Similar to depensation, there is also a production decrease in low population levels but in this case, a SSB limit is defined under which no recruitment takes place. The mechanisms underlying Allee effects are physiological and behavioural; difficulty in finding a mate, a breakdown in social structure and migration patterns, difficulty in fending off predators and competitors, and a requirement for exceeding a critical population size before food resources can be properly exploited (Frank and Brickman, 2000).

With the aim of identifying compensatory/depensatory responses of a fish stock, recruitment per unit spawner biomass is plotted against spawner biomass (Figure 40). R/S measures the ability of depleted populations to recover at very low population size where, according to Vergnon *et al*. (2008), three types of response can be found: in some cases, the compensatory dynamics assume a better reproductive success at low population size (classic compensation); in other situations, compensation occurs but increasing forage species biomass decreases the reproductive success (component Allee effect); in the third case, R/S declines at low SSB values when cultivation effects take place due to the negative influence of forage predation on pre-recruits (demographic Allee effect). The last case is the equivalent to depensatory mortality in populations (Gascoigne and Lipcius, 2004).



<u>Figure 40</u>: Recruitment success against spawner abundance, representing three types of response to low abundance levels: compensation (dashed line), component Allee effect (dotted line) and depensation or demographic Allee effect (solid line) (source: Vergnon et al., 2008).

Depending on the biological processes affecting S-R dynamics of various species, such as density-independence, compensation and depensation, S-R curves can adopt different shapes (Hilborn and Walters, 1992). Several functional forms have been proposed for the S-R relationship, but commonly the Ricker and Beverton & Holt models are considered. Their approaches assume the following functional form:

$$R = f(SSB;\alpha) \qquad (2)$$

where R is the recruitment, SSB is the stock spawning biomass and α is a vector of parameters. Thus, it is a parametric S-R model where recruitment is assumed to be a function of spawning stock biomass (O'Brien, 1999). There are certain constraints that have to be imposed in order to be the stock-recruitment relationship consistent with reality (Iles, 1994): clearly, the function should give positive recruitment values for all positive SSB values (obviously negative stock or recruitment values do not make sense); further, the function should not return a positive recruitment value for zero SSB, since if the stock disappears so will recruitment; lastly, the function should not give infinite recruitment values, except possibly for infinite SSB values.

The main difference between Ricker and Beverton and Holt models is their behaviour at high SSB values. In S-R relationship models, when the stock level is low, the recruitment increases as stock increases. However, when the stock exceeds a certain level, the recruitment begins to decrease in Ricker type models, or becomes saturated in Beverton and Holt type models, as the stock increases (Figure 41). In such context, Beverton and Holt curve is asymptotic of recruitment on stock, whereas the Ricker curve yields a dome-shaped curve because a stock-dependent mortality is used (Harris, 1975).

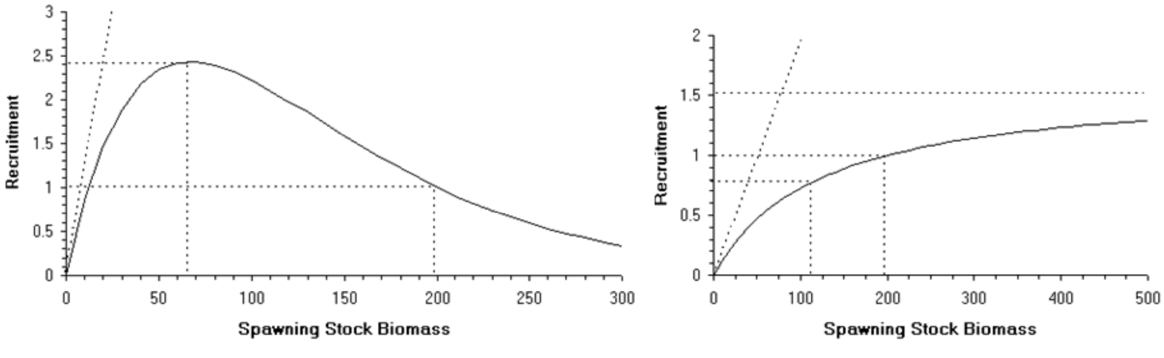


Figure 41: Graphical examples of a Ricker stock-recruitment curve (on the left) and Beverton & Holt stock-recruitment curve (on the right) (source: http://www.fao.org/docrep/w7219e/w7219e00.htm).

The stock-recruitment relationship determines the sustainability of a particular harvest at varying levels of fishing mortality (Sparholt, 1996). Actually, the variations in spawning stock biomass over time, for different fishing mortality levels along the study period, makes possible the study of the stock situation in terms of sustainability or overfishing. In such case, biological reference points such as limit and precautionary spawning stock biomass, or limit and precautionary fishing mortality levels, are used as reference points when analysing the exploitation level of a stock. For instance, in the case of stocks that are under a high risk of recruitment failure, poor climatic conditions could drive the stock and fishery to collapse. Temporary moratorium would be an immediate corrective action.

Therefore, this chapter aims at analysing European northern hake recruitment and SSB fluctuations over the period 1978-2006 and comparing them to variations in recruitment success. Additionally, this chapter builds a stock-recruitment relationship for such stock and it studies the trajectory of the stock in terms of sustainability and the influence of fishing upon the stock.

METHODOLOGY

1. Data source

The biological data regarding the northern stock of the European hake has been taken from the ICES annual stock assessment report (ICES, 2009a). The last two years estimations of the time-series (2007 and 2008) have not been included in this study due to their retrospective pattern, and thus for not being fully reliable estimations. Hence, the time-series under study covers the period 1978-2006 and it broadly represents the northeastern continental shelf of Europe, including the ICES areas IIIa, IV, VI, VII and VIIIa,b, shown in Figure 5 (ICES, 2009a).

Table 5 states a glossary of the biological variables used in this study; the biological data taken from the ICES report (ICES, 2009a) and a short definition regarding each parameter.

Table 5: Glossary of the terms used in this work (sources: Cardinale and Hjelm, 2006; ICES, 2009a; www.cefas.co.uk)

Recruitment	number of 0-year hake at the end of the year
SSB	total biomass of fully reproductive individuals in the population
Total biomass	total weight of both mature and immature fish in the population, that is, biomass of the whole of the population
B_{lim}	the limit reference point for biomass, below which there is a serious risk of stock collapse
B_{pa}	the precautionary reference point for biomass, below which there is an increased risk of low number of recruits
Recruitment success	Number of recruits produced per biomass of adult individuals
Landings	weight of the fish landed (catches minus discards)
F_{bar2-6}	Average fishing mortality of the most representative ages of the catches (2-6 years old)
F_{lim}	the level of fishing mortality at which there is an unacceptably high risk that stock will collapse
F_{pa}	a lower level of fishing mortality which offers a high probability that F_{lim} will never be reached

2. Data analysis

a. Trend analysis

Firstly, recruitment and SSB series over time were plotted in order to study hake fluctuations along the study period (1978-2006). Further, recruitment success time-series has been estimated dividing recruit numbers by spawning stock biomass. Recruitment success variations have been compared to both recruitment and SSB fluctuations.

Additionally, hake fishery data has been studied by analysing landings and fishing mortality of 2-to-6-aged population. Except for studying their evolution over time, a simple bivariate system has been used in order to represent what Garcia and De Leiva Moreno (2005) called a sustainability indicator framework. In this context, several zones have been defined with limit and precautionary reference points of both fishing mortality and biomass as borderlines: a “safe zone” where both fishing mortality and biomass appear to be better than the precautionary levels (F_{pa} and B_{pa}); a “buffer zone” where both fishing mortality and biomass are between the threshold and limit reference points; an “unsafe zone” (or also called a high-risk zone) where whether fishing mortality is above the established limit reference point (F_{lim}) or the biomass is below the established limit reference point (B_{lim}). In the case of above-limit fishing mortalities and below-limit biomass values, the stock is being continuously depleted despite its biomass being critically low.

b. Stock-recruitment relationship

Initially a LOWESS (locally weighted regression scatter plot smoothing) smoother was performed in order to see the shape of the line which best fits the data and reveal the shape of the stock-recruitment relationship (Figure 42). The fitted lowess smoother suggested a dome-shaped relationship between stock and recruitment, shape typically described by Ricker S-R model (Ricker, 1954; Cushing, 1971; Harris, 1975; Iles, 1994).

Therefore, a modest level of density-dependence at high stock sizes indicated that a Ricker curve would be the ideal model to be applied to recruitment and SSB data. The following function describes the relationship between recruitment and spawning stock biomass proposed by Ricker (1954):

$$R = \alpha SSB e^{-\beta SSB + \varepsilon} \qquad (3)$$

The parameter α represents the slope of the curve at the origin, it measures the fish stock reproductive performance at low stock size and has the dimensions of recruits-per-unit-biomass, whereas β expresses the magnitude of biomass above which density-dependent effects dominate and has the dimensions of a biomass. ε is a normally distributed error term with mean 0 and standard deviation σ.

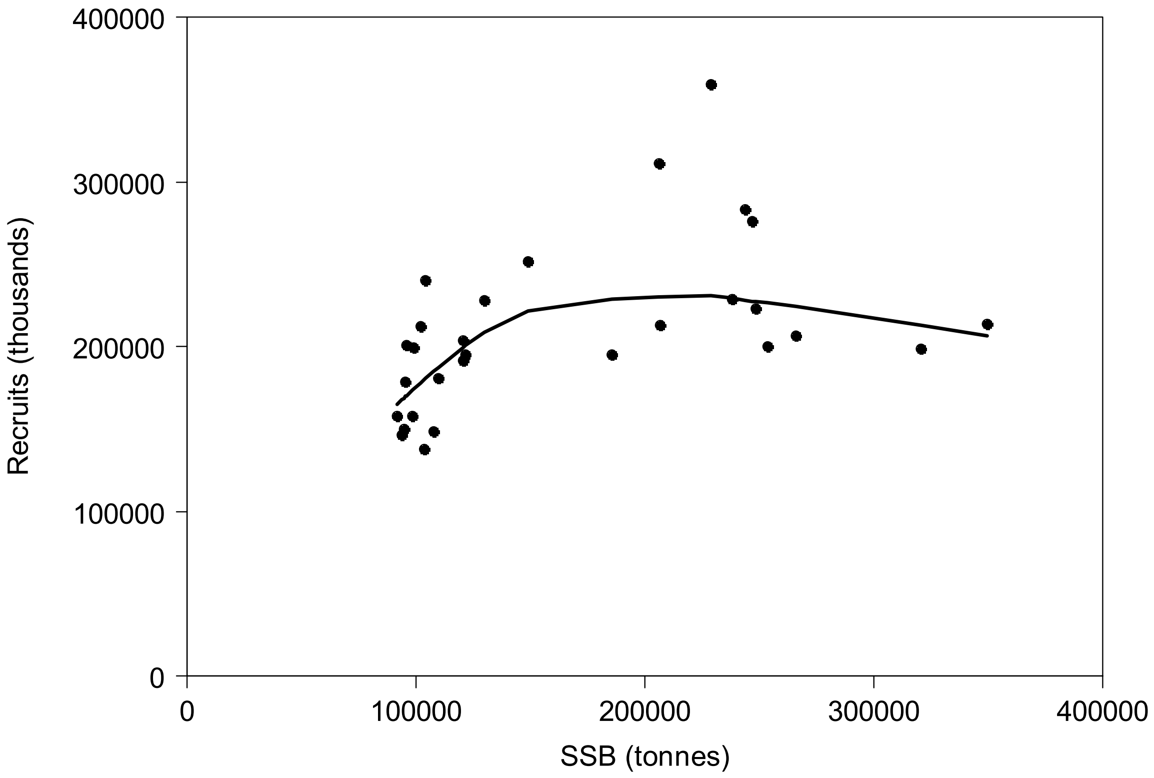


Figure 42: A LOWESS smoother fitting, suggesting the shape of relationship between stock and recruitment.

A Ricker stock-recruitment model was fitted by means of Generalized Linear Models, following O'Brien (1999). A flexible and reliable way to fit such parametric models is rewriting the S-R model as a generalized linear model (GLM). Reparametrization of the model gives the following transformed form:

$$LnR = Ln\alpha + LnSSB - \beta SSB \qquad (4)$$

$$LnR = \alpha_2 + LnSSB - \beta_2 SSB \qquad (5)$$

where α_2 and β_2 are functions of α and β, respectively:

$$\alpha_2 = Ln\alpha \qquad (6)$$

$$\beta_2 = -\beta \qquad (7)$$

The Ricker curve has logarithmic link function when expressed as GLM and so it could be fitted by the approach of least squares regression with lnR as the dependent variable. The call of the model used is as follows:

```
glm(formula = Recruitment ~ offset(LogSSB) + SSB,
                  family = quasi(link = log, variance = "mu"),
                  data = data.SR, na.action = na.exclude ,
                  control = list(epsilon = 1e-04,
                  maxit = 50, trace = F))
```

Residuals from the fitted model were tested by means of graphical representation. Residuals have been plotted against predicted values to test their homogeneity. Besides, the normality has been tested checking the Normal-QQ plot. Finally, Cook's distance has been used to detect the presence of outliers.

The analyses presented here were performed using the R statistical software available from the Comprehensive R Archive Network http://cran.r-project.org.

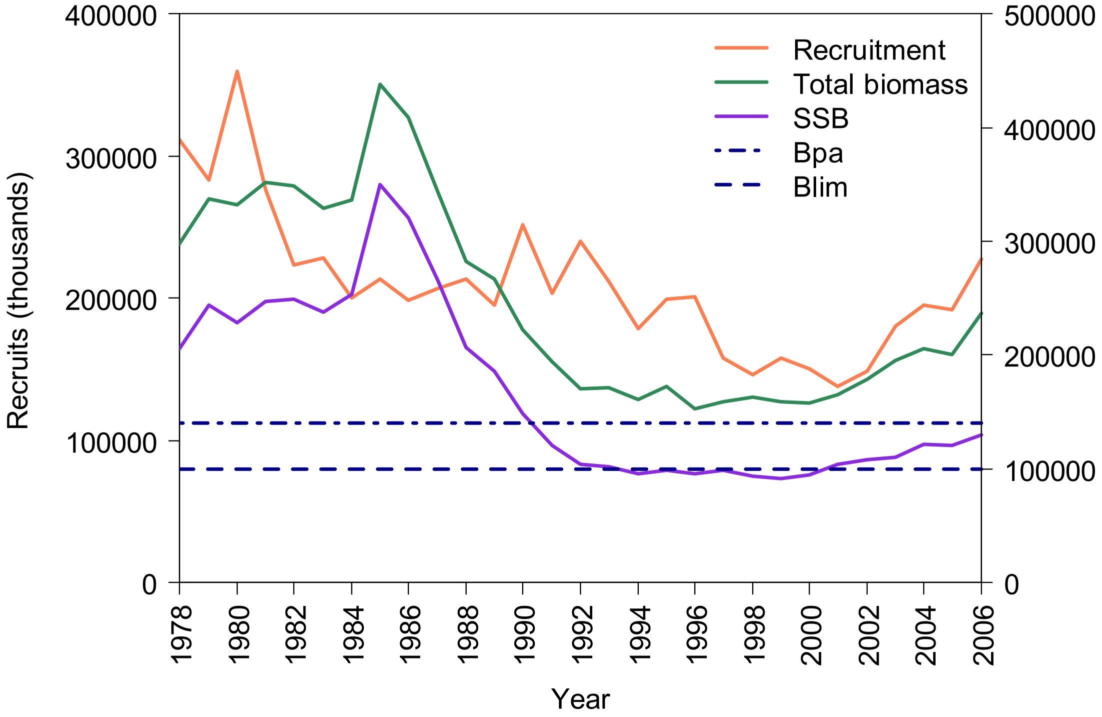
RESULTS

a. Trend analysis

SSB and recruitment

Hake spawning stock biomass ranged between 90,000 and 350,000 tonnes. At the beginning of the series, the spawning stock biomass showed a solid and constant increase, reaching the maximum of about 350,000 tonnes in 1985. After such peak, hake SSB underwent a sudden change and it decreased progressively until the 1990s. During that period, SSB remained below the limit biomass (Blim). In the last decade, it has showed a slight recovery but still remaining below the precautionary level of 140,000 tonnes for SSB (Bpa) (Figure 43).

With reference to recruitment time-series (Figure 43), 0-aged hake individuals ranged from the maximum of 360,000 up to the minimum of about 138,000 thousands of recruits. After the peak in 1980, recruitment decreased sharply in three years, reaching values of around 200,000 thousands of recruits per year in the 80s decade. In the 1990s, recruitment interannual fluctuations were higher than in the previous decade but showing a general decreasing trend towards the beginning of the next decade. In 2001, hake stock showed the worst recruitment level (137,925 thousands) recorded for the whole study period. Recently, recruitment time-series has showed a continuous increase, similarly to the biomass.



<u>Figure 43</u>: Time-series of northern European hake recruitment, total biomass and spawning stock biomass (SSB) time-series (in tonnes), for the study period 1978-2006. Precautionary biomass level (140,000 t) and biomass limit level (100,000 t) are also plotted.

On the other hand, Figure 44 represents recruitment success (R/SSB) time-series in comparison to recruitment and SSB variables. It should be highlighted the low recruitment success in the mid-1980s, due to the low recruitment values despite the peak in SSB. Further, in contrast to the recruitment series, the decade of the 90s showed the highest values of recruitment success; although recruitment values were not the highest ones registered over the series, the low SSB values made the recruitment success to be high at this period of time. It should be emphasised the sharp increase in recruitment success from the minimum value registered in 1985 up to the peak recorded in 1992.

Figure 45 shows recruitment success changes for the whole of the hake SSB range. It can be clearly seen that they are related negatively since, for high SSB values the recruitment success decreases and *vice versa*. When the spawning stock biomass fluctuated around 100,000 tonnes, the recruitment success showed its maximum values for the whole study period. However, due to the lack of data at low SSB values, recruitment success behaviour for SSB values lower than 90,000 tonnes remains unknown.

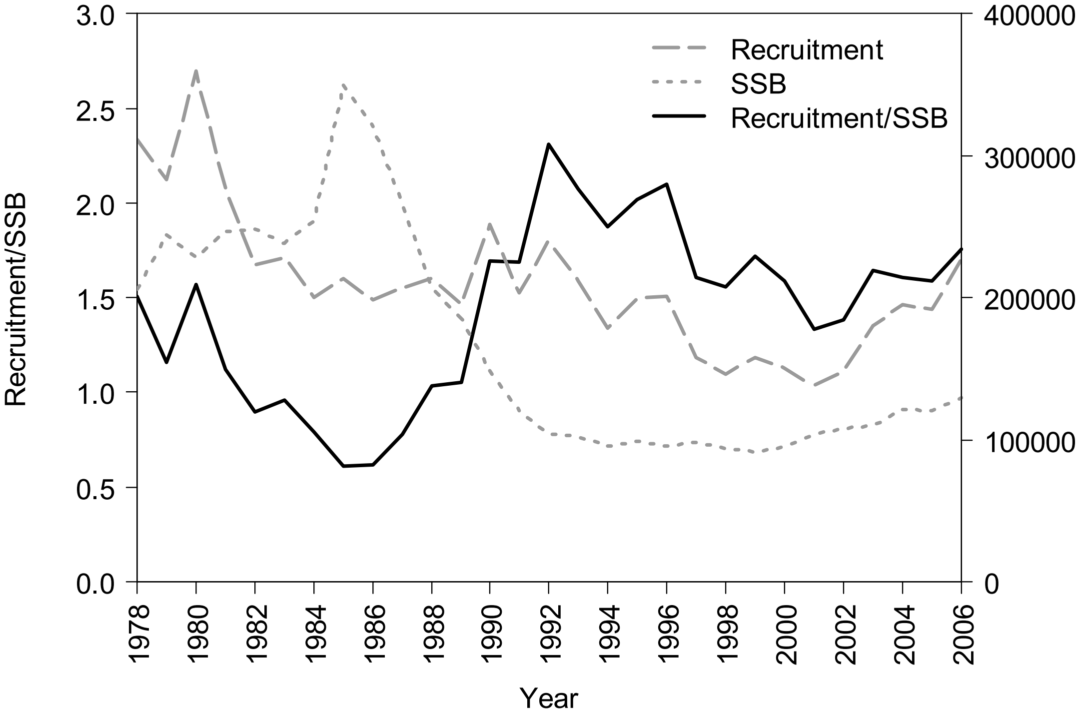


Figure 44: Recruitment and SSB time-series in grey and recruitment success (Recruitment/SSB rate) in black.

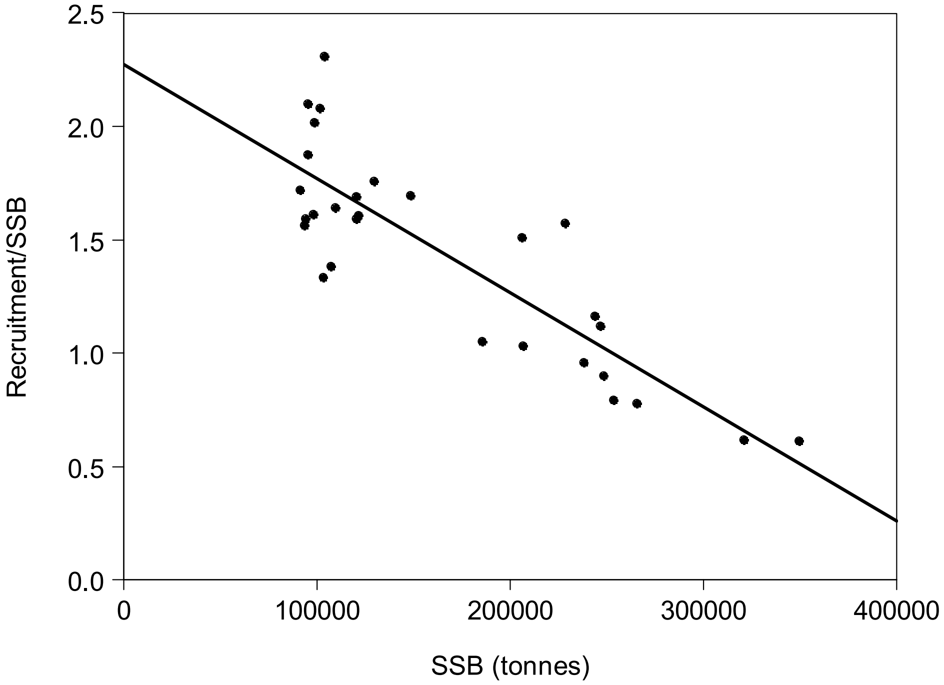


Figure 45: Relationship between spawning stock biomass (SSB) and recruitment success (Recruitment/SSB).

Landings and fishing mortality

Regarding hake fishery, landings over time are plotted on Figure 46. From the beginning of the series till 1996, landings have fluctuated between 50,000 and 70,000 tonnes, showing the highest captures in 1989 (66,472 t). However, at the end of the ninetieth decade, hake has undergone the highest fall in landings, from values of 57,619 tonnes (1995) to 35,010 tonnes (1998). At the end of the series landings have fluctuated without reaching the high values of the beginning. With reference to fishing mortality, the values were around 0.2 till the end of 1980s. Then, fishing mortality has sharply increased until 1995, when fishing mortality has been the greatest of the whole series, even exceeding the limit level (Flim=0.35). From then on, fishing mortality has fallen, reaching precautionary levels for fishing mortality (Fpa=0.25).

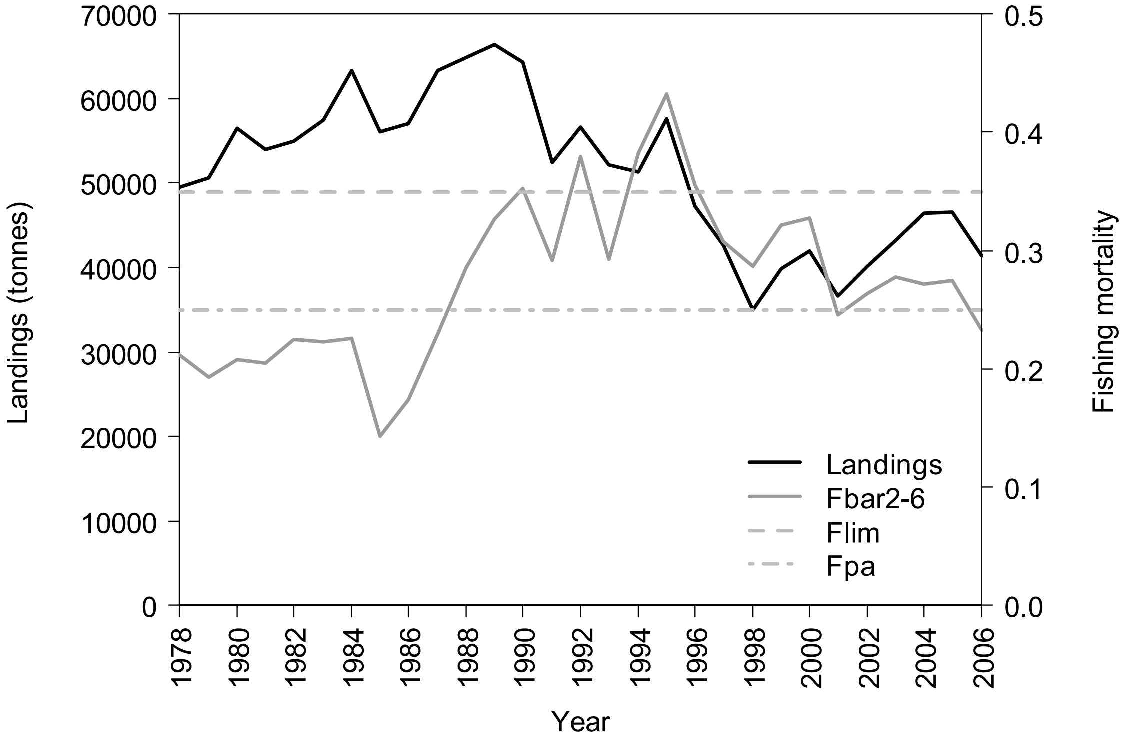


Figure 46: Landings and fishing mortality (Fbar2-6) time-series representation. Precautionary (Fpa=0.25) and limit levels (Flim=0.35) for fishing mortality are also plotted.

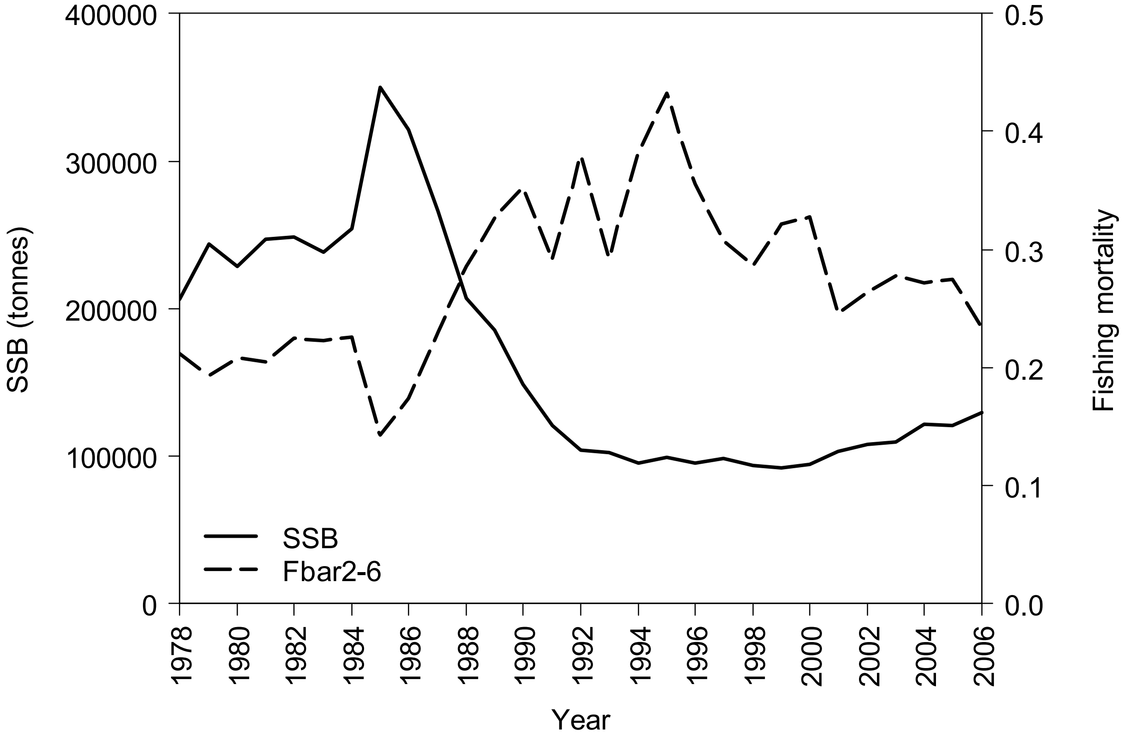


Figure 47: Spawning stock biomass (SSB) and fishing mortality (Fbar2-6) time-series.

Plotting SSB and fishing mortality on the same graph, the opposing trend of these parameters can be seen (Figure 47). After the increasing fishing mortality in the second half of the 80s, SSB decreased sharply reaching the historically lowest values.

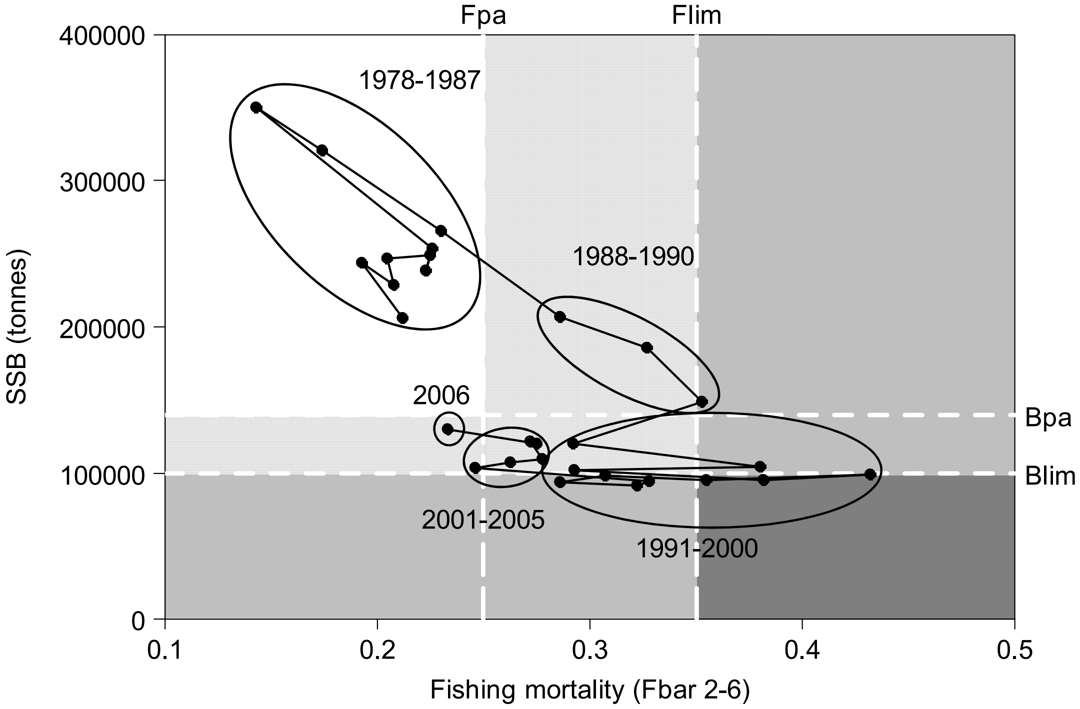


Figure 48: Relationship between SSB and fishing mortality. Precautionary and limit reference points for both variables are also plotted. Note that the safe zone (in white), the buffer zone (in light grey), the high-risk zone (in grey) and the unsustainable zone (in dark grey) are also marked.

Figure 48 shows a system of representation of fishing mortality and SSB, with precautionary and limit reference points proposed by ICES. Further, the chronological trajectory of the stock is plotted within the bivariate system. Hake stock state has moved among different safety situations (represented with different intensities of grey) along the study period:

- 1978-1987: within the safe zone. 1985 and 1986 showed good levels of biomass and low fishing mortality which gave rise to sustainable years.
- 1988-1990: within the buffer zone. Year 1990 in the borderline with the high-risk zone due to high fishing mortality values.

- 1991-2000: shifts between the buffer zone (1991, 1993 and 1997-2000) and the high-risk zone (1992 and 1994-1996). Years within the unsafe zone (high-risk zone) showed high levels of fishing mortality and thus, the stock has been overfished during this time.
- 2001-2005: improvement in the stock state, maintaining it in the buffer zone.
- 2006: still in the buffer zone but getting closer to the safe zone.

b. Stock-recruitment relationship

The shape of the line relating SSB and recruitment suggested a Ricker S-R relationship, since maximum recruitment occurs at intermediate SSB levels and for high SSB values recruitment seems to fall, with the result of a dome-shaped curve (Figure 49). Hence, a Ricker S-R curve has been fitted to hake data (Table 6).

Table 6: Coefficients estimation for the Ricker S-R model.

	Estimate	***Std. Error***	***t value***	***p value***
α_2	1.014	832.6	12.1841	<0.001
β_2	-4.162e-06	4.352e-07	-9.563	<0.001

Since,

$\alpha_2 = Ln\alpha$

$\beta_2 = -\beta$

then,

$\alpha = 2.76$ and $\beta = 4.16 \cdot 10^{-6}$ are estimated from Table 6.

In the resulting model SSB explained 78.71% of the total variability in recruitment (Figure 49). The model showed that the maximum values of recruitment are achieved with 210,000-230,000 SSB levels; however, the dispersion level at this point of the curve is high with recruitment values between 200,000 and 380,000 for the same spawning stock biomass.

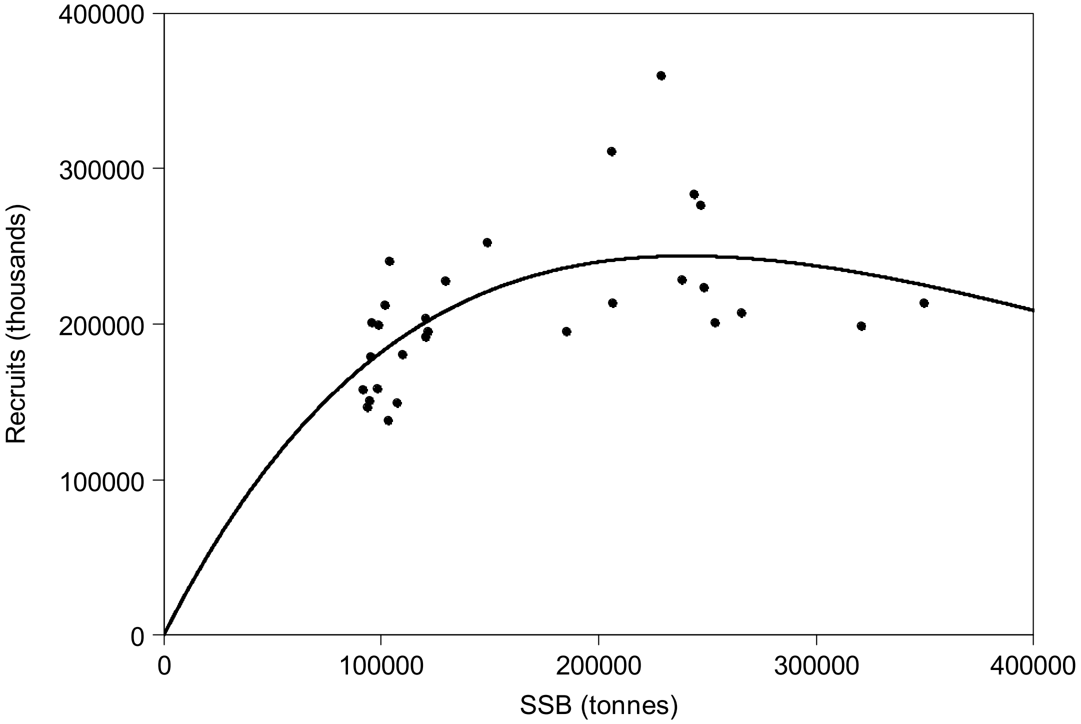


Figure 49: Ricker stock-recruitment model fitted to northern hake data. The model is described by the following Ricker relationship: $R = 2.76 \cdot SSB \cdot e^{(-SSB \cdot 4.16 \cdot 10^{-6})}$

In order to validate the Ricker model, residual plots have been performed. Residuals versus fitted values confirmed the homogeneous distribution of the residuals (homogeneity), whereas normality has been validated on the QQplot. Further, no clear outliers were found checking the Cook's distance (Figure 50).

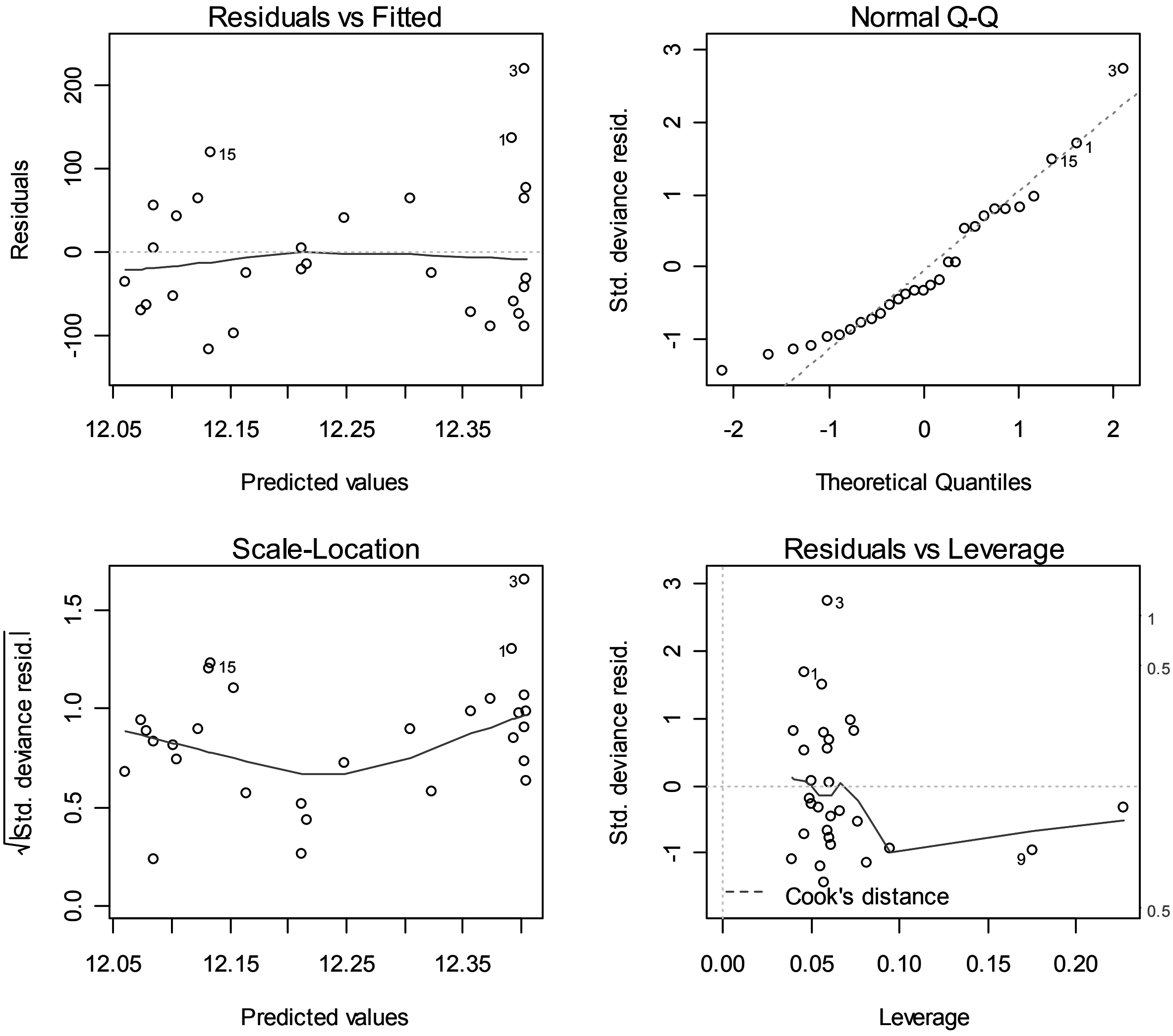


Figure 50: Graphical representation of the residuals of the Ricker stock-recruitment relationship.

On Figure 51 the chronological trajectory of the stock has been added to the stock-recruitment relationship representation. The plot shows that, at the beginning of the series, variability around S-R curve was high with years like 1978 and 1980 showing higher than expected recruitments. 1985 and 1986 are situated on the density-dependent zone of the S-R curve, due to high SSB values and moderate recruitment values registered in both years. However, in the last two decades of the series, the relationship between SSB and recruitment has been seen to be positive.

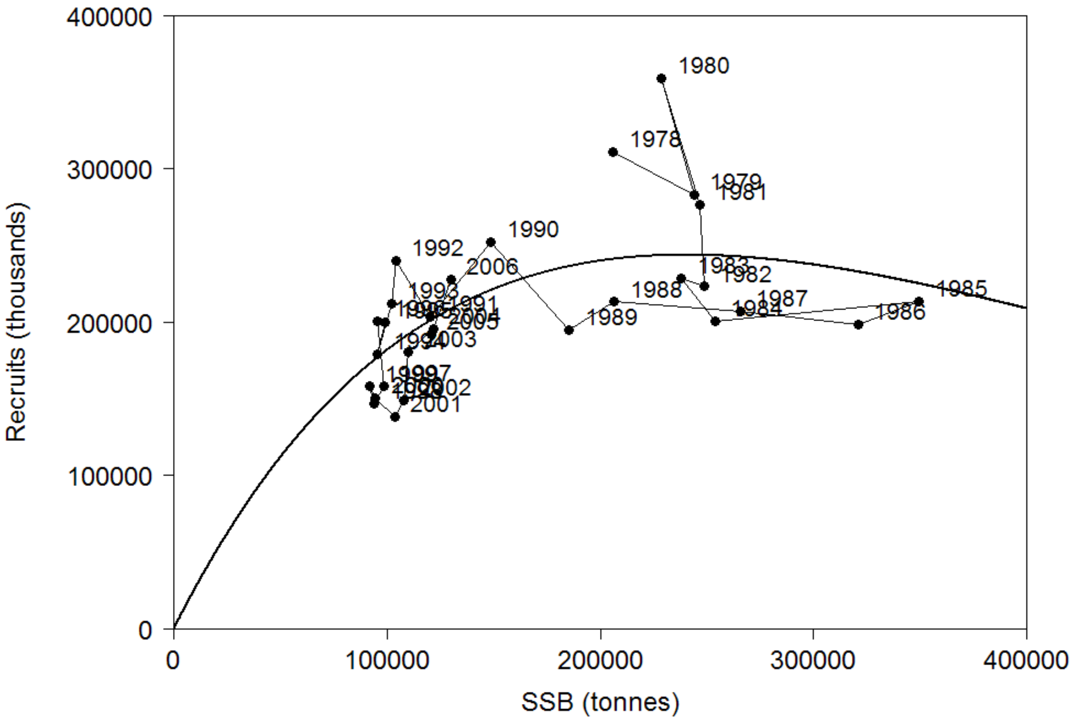


Figure 51: Ricker stock-recruitment model fitted to hake data. Data points have been labelled with the corresponding year.

Taking into account the sustainability indicator framework represented in Figure 48, data can be grouped into two periods: 1978-1987 period, when the stock was in safety conditions (within the safe zone); and 1988-2006 period, when the stock was under a risky situation (buffer and high-risk zones). Following this division, new stock-recruitment curves were fitted for each of the periods (Figure 52a). The Ricker curve for the period 1978-1987, accounted for the 75.15% of the variability, whereas the Ricker curve corresponding to the period 1988-2006, explained the 56.88% of the variability.

In contrast, the data points represented around the stock-recruitment curve in Figure 51, suggest that they could be grouped into two different periods: one from 1978 to 1989 and the other one from 1990 to 2006. Thus, if two stock-recruitment curves were fitted following this division, one of them (1978-1989) would explain the 60.57% of the variability, whilst the other (1990-2006) would only explain 2.96% of the variability (Figure 52b).

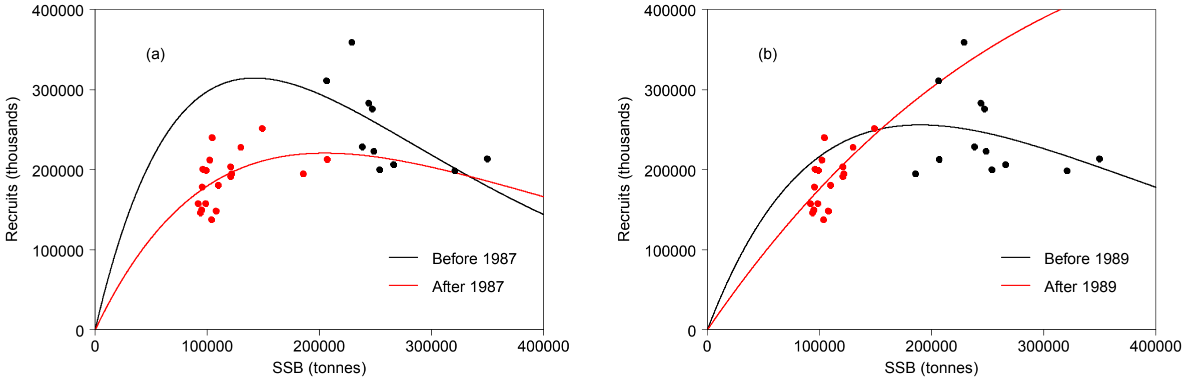


Figure 52: Ricker stock-recruitment relationships for the periods before (in black) and after (in red) 1987 (a) and 1989 (b).

DISCUSSION

a. Trend analysis

SSB and recruitment

After the peak of 1985, hake spawning stock biomass, and consequently also the total biomass, did undergo a sharp decrease until the 1990s. In such period, SSB reached values below the limit reference point of 100,000 tonnes and thus, an emergency plan has been implemented in 2001 and 2002 (EC 1162/2001, EC 2602/2001 and EC 494/2002). SSB showed a slight increase in the following years bringing the stock to a safer situation above the limit SSB level. In 2004 a recovery plan has been implemented under EC Reg. No 811/2004, with the aim of achieving a SSB of 140,000 tonnes (Bpa). To do so, the plan states that fishing mortality should have been limited to F=0.25. After the implementation of the plan, fishing mortality has only been below this limit in 2006, when it reached the value of F=0.23.

According to the article 3 of the recovery plan, a management plan should be implemented when the northern hake stock meets the SSB target in the recovery plan of 140,000 tonnes. Although, at the end of the study period of this work, SSB has not reached the precautionary reference point, it has shown a regular increase recently which let us believe that in 2007 or 2008 it could have reached the SSB target level (years not considered in this study).

Northern hake stock went down and stayed down over a long period. However, the reproductive rate did increase (Figure 44) which made possible to compensate the stock for the depletion. At the present, taking into account the last estimates of SSB and fishing mortality, ICES considers that the stock is at full reproductive capacity and harvested sustainability (ICES, 2009a).

Landings and fishing mortality

In the second half of the 1980s, fishing mortality increased dramatically and consequently the greatest landings of the last three-decadal period have been registered in 1989. Overfishing is believed to be a critical factor in the decrease, and sometimes collapse, of a stock (Myers *et al.*, 1996, 1997; Pauly *et al.*, 2002; Hutchings and Reynolds, 2004). Hence, the high level of fishing pressure suffered by the northern hake population is proposed to be behind the dramatic decrease of the ninetieth decade. Similarly, exceeding fishing has been reported as the main reason of the worldwide known fishery collapses of the Peruvian anchoveta in 1971-1972 and cod stocks off New England and eastern Canada in the late 1980s and early 1990s (Pauly *et al.*, 2002).

Garcia and De Leiva Moreno (2005) described a synoptic representation of sustainability indicators to summarise simplistically the state of stocks in the ICES area. Based on such representation, hake stock state and trajectory has been analysed using biomass and fishing mortality precautionary and limit reference points as thresholds.

At the beginning of the study period, the situation was fully satisfactory in terms of sustainability, and the fishery was in the long-term safe zone. Since the farther the stock from the threshold reference point the better, 1985 and 1986 were the years that showed smaller risk for the resource. However, at the end of the decade, fishing mortality increased rapidly which resulted in the stock being located between the precautionary and limit reference points; thus, the risk of recruitment failure was higher, particularly in 1990 when the stock was very close to being overfished. For the following years, hake biomass fluctuated around the limit reference point for biomass, and fishing mortality ranged between 0.38 and 0.44. Consequently, in years like 1992, 1994, 1995 and 1996 excessive fishing mortality was applied and overfishing was ongoing; the stock was being continuously depleted despite its critically low biomass. In such situation, the stock is considered to be under a high risk of recruitment failure. In the last decade, fishing mortality has decreased considerably which took the stock to slightly better biomass levels but still below the precautionary biomass level.

Although Garcia and De Leiva Moreno (2005) stated as a particular constraint the possible changes in reference points across time, such synoptical representation is a good tool in order to study the state of one or more stocks and to follow their trajectory over time.

To sum up, in spite of the good levels on biomass at the beginning of the series, the increasing fishing activity took the stock to high-risk zone where it has been overfished. According to Zhen (1996), after the stock collapse, many years are required for a spawning stock to produce sufficiently strong recruitment to recover. This seems to be the case of the northern hake, since the recovery of the stock is taking longer than the fall; despite the decrease in fishing mortality, the biomass seems to stay the same or increase slightly. Indeed, the time required for population recovery in many marine fishes appears to be considerably longer than previously believed (Hutchings, 2000; Hutchings and Reynolds, 2004).

b. Stock-recruitment relationship

The stock-recruitment relationship paradigm involves the hypothesis that recruitment is dependant on spawner abundance (Myers, 1997); particularly, it states that recruitment is positively related to spawning stock biomass (SSB) of the stock, at least at low SSB values. Such paradigm is widely assumed in the fisheries science literature and in fisheries management policies worldwide (Gilbert, 1997).

It goes without saying that recruitment is related to its spawning stock, at least at low spawning stock levels, since recruits are the survivors from the eggs that have been spawned by the spawning stock; according to Zheng (1996), without eggs there will be no recruits in a closed population. However, not all the stock data fits well to the relationship described by stock-recruitment models (Walters and Ludwig, 1981; Walters, 1985; Amstrong and Shelton, 1988; Koslow, 1992; Hilborn and Walters, 1992; Gilbert, 1997), suggesting that SSB and the subsequent recruitment are independent (Gilbert, 1997) or are not related following the stock-recruitment relationships (Koslow, 1992) described by the worldwide well-known models such as Ricker (1975), Beverton and Holt (1957), Shepherd (1982) and Cushing (1971).

In the case of the northern hake, Ricker SR model fitted quite well to data. Actually, spawning stock biomass alone explained 78.71% of hake recruitment variability. Although not common, more than half of recruitment variability could have also been explained by spawning biomass alone, in the case of other stocks such as, North Sea herring and ICES district VIa north stocks (Zheng, 1996). Further, the graphical analysis of the residuals of the model, confirms the validity of the model in terms of homogeneity, normality and the absence of outliers.

In spite of the high percentage of the variability explained by the model, possible error sources have to be taken into account when analysing the stock-recruitment relationship. Biases in S-R models have been widely studied in literature (Walters and Ludwig, 1981; Walters, 1985; Amstrong and Shelton, 1988; Koslow, 1992; Myers and Barrowman, 1995). Among the mostly studied biases (see Introduction), there are two types of errors that could be misleading the S-R relationship in the case of hake:

- Lack of data over the whole range of SSB values (Koslow, 1992):
  In the case of hake, we have to be aware of the lack of low SSB values (no data has been recorded between 0 and 90,000 tonnes of SSB). Thus, the model has carried out an interpolation based only in two points, one of them being a non-real point (0,0) since recruitment is bound to be zero at zero stock size. Stock-recruitment models include implicitly the assumption that the stock will fail to reproduce itself if it becomes very small, thus, the (0, 0) point is an essential feature of a stock-recruitment relationship (Shepherd, 1982). However, care should be taken when there is no availability of the full range of SSB data, that is to say that care has to be taken in extrapolating beyond the limits of the data, as it is the case of the northern hake for low SSB values. In this perspective, Koslow (1992) noted that most data in fishery stock-recruitment data sets are on the relatively flat right-hand limb of the SR curve, where density-dependent processes affect recruitment. He concluded that the concept of a simple deterministic S-R relationship appears to be of limited applicability when applied to organisms characterised by high fecundities (Koslow, 1992).

- Errors in recruitment and SSB estimations (Walters and Ludwig, 1981):
  Recruitment and SSB data have implicitly the assumption of the existence of errors, since they are estimated from catch data coming from different fleets (they are not direct measurements of the population). Further, in the case of hake, aging errors could affect recruitment and SSB estimations. De Pontual *et al.* (2006) referred to the age estimation error in northern hake and they evidenced an underestimation of European hake growth. In this context, given the need for validated age-reading criteria, ICES has recently published a report explicitly regarding hake age estimation (Piñeiro *et al.*, 2009). Therefore, bias in age estimation is an additional impact for stock parameters estimation and consequently for stock assessment results.

Myers and Barrowman (1995) concluded that in the case of species with low α (initial slope of the S-R curve), such as hakes, time series bias can be assumed to be important. But they also stated that natural mortality for this genus is assumed to be high, which would substantially reduce the bias.

Myers and Barrowman (1996) analysed 364 spawner-recruitment time series (including the genus *Merluccius*) to determine whether recruitment is related to spawner abundance. In the case of the hake studied by such researchers, strong year classes resulted from relatively high spawner abundance and they found fair evidence that the mean recruitment was greater for larger abundances. However, they did not find any evidence for the smallest recruitment occurring when spawner abundance was low, except if there was a wide range of spawner abundance. This is in accordance with our results, since high recruitment episodes took place with relatively high SSB values; however, we could not determine the relationship between stock and recruitment at the lowest SSB values due to the lack of observations at these low biomass levels.

There is an ongoing discussion regarding the recruitment behaviour at low stock levels. While some populations show compensation dynamics (Zheng, 1996), depensatory response has been found in the case of species such as, the northern cod (Frank and Brickman, 2000). An additional debate is whether the stock-recruitment curve should pass through the origin or the intercept should be defined for a determined value of SSB. Actually, the high standard error of α_2 coefficient estimation (1.014 ± 832.6) makes evident the unclear reproductive performance at low stock size.

- What could be happening at low stock levels?

Compensation?

At low stock levels, competition is believed to be reduced due to higher food and habitat availability, which in turn, results in higher productivity and greater survival. This is the case when, recruitment success shows its maximum values at low SSB values. The great majority of the populations show evidence of increased survival at lower population levels (Myers and Cadigan, 1993) and this could be the case for northern hake. Data suggest compensatory response at the lowest SSB values registered during the study period. However, the lack of data at the very low SSB values, keeps uncertainty in stock behaviour at these levels and thus, the compensatory dynamic of the northern hake remains unconfirmed.

Depensation? Cultivation effect?

Additionally, recruitment success can show a depensatory response at low biomass levels. These could happen, for instance, with populations showing “cultivation effects” (see introduction). In these populations, when adult abundance is severely reduced by fishing, forage species would increase, with the subsequent lagged reduction in juvenile survival (Walters and Kitchell, 2001). Such theory has been hypothesised for the shallow water hake. Distributions of adults of shallow water hake and their potential preys (for instance, anchovy and sardine) overlap. Such small pelagic fish are also potential predators and competitors of shallow water hake pre-recruits. Hence, they are liable to undergo an increase in their biomass as a result of the hake depletion and thus, they may induce a high mortality of shallow water hake pre-recruits (Vergnon *et al*., 2008).

Additionally, predation on pre-recruits is the mechanism proposed to explain the slow-down of the recovery of depleted populations of large demersal fishes (Vergnon *et al*., 2008). Actually, they carried out a simulation where the depletion of the shallow water hake population triggers a major increase of the biomass of forage species and consequently their model predicted an increasingly negative effect of small pelagics on the recovery of shallow water hake; their simulation demonstrated that shallow water hake recovered later and slower when the level of piscivory in the diet of forage species increased. This statement is a hypothesis that could be the explanation for the slow recovery of the northern hake stock during the last years.

European hake is a large piscivorous predator which is placed at the top of the foodweb (Du Buit, 1996; Velasco and Olaso, 1998; Cabral and Murta, 2002). Studies regarding European hake feeding ecology in the Bay of Biscay and the Celtic Sea, reported that small individuals feed on small pelagic fish, such as mackerel, horse mackerel, anchovy and sardine whereas larger hake prey upon larger demersal prey, such as blue whiting (Du Buit, 1996; Pinnegar *et al*., 2003; Mahe *et al*., 2007). Regarding hake prey diet, anchovy, sardine, mackerel and horse mackerel, feed upon different zooplankton groups, particularly copepods (Plounevez and Champalbert, 1999; Ferreira-Garrido, 2007), whereas adult mackerel and horse mackerel also prey upon larger preys such as euphausiids, decapods and fish larvae (Olaso *et al*., 1999, 2005); further, blue whiting prey on copepods when juveniles and crustaceans when adult (Sorbe, 1980, Cabral and Murta, 2002). Although they do not seem to prey on hake pre-recruits, they feed on the main feeding species for hake pre-recruits such as copepods and thus, this competition for the same food could have a detrimental effect on hake pre-recruits with the subsequent decrease in recruitment success (depensation response). However, Myers *et al*. (1995) analysed population dynamics of exploited fish stocks at low population levels, and they concluded that those stocks, including hakes, did not display depensatory dynamics in reproduction.

Allee effect?

There is indirect evidence for Allee effects in some exploited gadoid populations (Hutchings, 2000). In particular, Marshall *et al*. (1998) have demonstrated that Northeast Atlantic cod shows a critical population biomass threshold below which no recruits are produced. The existence of an Allee effect has been suggested as one explanation for the relatively slow recovery of Atlantic cod and other marine species (Shelton and Healey, 1999; Frank and Brickman, 2000; Hutching and Reynolds, 2004). In addition, increases in fishing mortality interact very strongly with Allee effects, and thus exploitation has the potential to render populations very vulnerable to collapse when Allee effects are present (Gascoigne and Lipcius, 2004).

In this context, and taking into account the lack of data in low biomass levels, we cannot reject the possibility where the relationship does not pass through the origin because of Allee effects affecting hake stock. Actually, two cases could take place: positive recruitment values when SSB=0, only possible when due to migration new recruits enter the local stock; no recruitment below a positive critical SSB value, in which case it would refer to as Allee effect. However, such hypothesis remains unproven because we ignore the behaviour of recruitment success at low stock levels due to the lack of data at low SSB values, (there are no observations for SSB values lower than 90,000 t). Indeed, Shelton and Healey (1999) concluded that depensatory effects are likely to be difficult to detect in typical data sets that have few observations at very low stock size.

- What happens at high stock levels?

On the other hand, hake stock-recruitment relationship at high biomass levels seems to show clear evidences of density-dependence.

Density-dependent mortality during juvenile stage has been studied and demonstrated in species such as North Sea plaice (Iles and Beverton, 1998; Beverton and Iles, 1992a; Beverton and Iles, 1992b), Northeast Atlantic cod (Sundby *et al.*, 1989), North Sea-Skagerrak-Kattegat system cod (Chen *et al.*, 2005), herring stocks in the North Atlantic and Northeast Pacific oceans (Zheng, 1996) and Japanese sardine (Wada and Jacobson, 1998). Most of the marine demersal fish populations examined by Myers and Cadigan (1993) showed significant density-dependent juvenile mortality.

Among the mechanisms to explain density-dependent mortality, competition for food, habitat limitation and predation are mentioned by Myers and Cadigan (1993). Further, cannibalism is the mechanism that is often used in order to explain the Ricker curve behaviour at high stock levels (Harris, 1975; Ricker, 1975). That is to say that, the major predator is the adult stock itself. Cannibalism has been suggested as a regulatory mechanism for recruitment and thus population size. Hake is a species where cannibalism may be significant; actually, cannibalism has been found to be rare off the Portuguese coast (Cabral and Murta, 2002), in the southern Bay of Biscay (Mahe *et al.*, 2007) and in particular in the Cantabrian Sea (Velasco and Olaso, 1998). However, in the case of the northern Bay of Biscay and Celtic Sea, large hake (>30 cm) prey on 0-group juveniles of the same species

(Mahe *et al*., 2007). The reason that has been hypothesised for this different behaviour in such neighbouring areas is the difference in the continental shelf bathymetry (Velasco and Olaso, 1998; Cabral and Murta, 2002; Mahe *et al*., 2007). The Portuguese and the Cantabrian continental shelves are narrower and an abrupt change in depth occurs relatively close to the coast, and thus, juvenile and adult hake are distributed in different depths based on their preferences. In contrast, the northern Bay of Biscay and the Celtic sea continental shelves are broader. Further, the main nursery areas are placed in these areas, so adult and juvenile groups are believed to overlap their distributions and thus, cannibalism is more probable to take place (Mahe *et al*., 2007). Species such as silver hake, Chilean hake and cape hake, all of them belonging to the genus *Merluccius*, are also reported to have a cannibalistic behaviour between individuals of the same species (Garrison and Link, 2000).

Beverton described the effects of either fishing pressure or environmental impacts on the shape of the stock-recruitment curves (Beverton, 2002). According to his study, hake stock-recruitment relationship suggests a fishing generated event, where both recruitment and stock size decreases steadily whereas the reproductive rate (recruitment rate per parent or Recruitment/SSB) increases as the stock falls. Such event can be clearly seen during the second half of the 80s and at the beginning of the 90s (Figure 44) when the fishing pressure increased; fishing mortality of the 2-6 aged population increased during this period (Figure 46). However, from the decade of the 90s onwards, when fishing pressure stays the same or decreases steadily, the survival curve gradually decreases resulting in fewer recruits for a given stock. In such case, both the stock and recruitment declines at the same rate but the recruitment success rate, instead of going up all the time, either stays constant or declines slightly as the population attempts to stabilize itself on the way down. Such event would be an environmentally mediated event (Beverton, 2002).

Because the dynamics of fish stocks could change in time, particularly due to fishing pressure but possibly also because of pollution and other environmental effects, it may be the case that a particular stock will exhibit different stock-recruitment relationships over different periods of time (Iles, 1994). For instance, North Sea herring displayed stronger compensation behaviour after the stock collapse in 1976, than before the collapse, and thus, the relationship between stock and recruitment drew a different curve for pre- and post-collapse periods (Nash *et al*., 2009). Chen (2001) also demonstrated that herring stock-recruitment relationships varied significantly during different regimes. With reference to hake data, two different divisions were undertaken: the former (1978-1987 and 1988-2006), taking into account the sustainability indicator framework, whereas the latter (1978-1989 and 1990-2006) was based on the grouping suggested by the S-R representation of the data. Clearly, stock-recruitment relationships changed depending on the considered time of period.

Considering the first division, S-R curve for years within the safe zone showed a higher reproductive performance at low stock size (higher initial slope) and the maximum recruitment was situated beyond 300,000 thousand recruits. In contrast, for the period under risk, the expected maximum recruitment was 100,000 thousand recruits lower. The stock showed stronger density-dependency before rather than after 1987. Such division reflects the different situation and the exploitation level of the stock during the two periods under consideration.

In contrast, the second division groups years with higher SSB values (before 1989) against years when the spawning stock biomass recorded lower values (after 1989). The former period showed a typical SR Ricker curve whereas for observations after 1989 Figure 52 only shows the first part of the curve, where the relationship between the stock and recruitment is still positive. Despite the smaller stock size during 1990-2006, recruitment success was higher and consequently the maximum recruitment is expected to be incredibly high (it falls out of the plot). The possible reasons for such abrupt change in recruitment success before and after 1989 are believed to be shifts in environmental parameters and they will be taken into consideration in Chapter III.

Chapter III

Links between the recruitment success of northern European hake and NE Atlantic environment: identification of a regime shift

INTRODUCTION

Understanding the recruitment dynamics of marine fish stocks is crucial for fisheries management. To do so, the first step is to determine the recruitment patterns of the stocks and study the possible reasons for recruitment fluctuations over time. In addition to density-dependent effects on recruitment (Chapter II), environmental factors may play an important role in modulating such variations. Although there have been many studies published that describe the effects of environmental factors on recruitment to fish stocks (Borja *et al*., 1998, 2008; Planque and Frédou, 1999; Maynou *et al*., 2003; Brander and Mohn, 2004; Planque and Buffaz, 2008), few of these studies concerned hake in general, or hake recruitment success in particular.

During the period 1982 to 1988, there was a stepwise change in the North Sea ecosystem that was linked to large scale hydroclimatic forcing (Beaugrand, 2004). At the same time, the reproductive stock of cod (*Gadus morhua*) decreased sharply after the peak in 1981 (Figure 53). Coinciding with this stepwise change in the North Sea, the spawning stock biomass of the northeastern European hake began to decline (Figure 53). Large-scale hydro-climatic forcing also modified local hydro-meteorological factors around the North Sea after 1987, which influenced different components of the North Sea ecosystem, such as gadoid recruitment (Beaugrand, 2004). Therefore, although they inhabit different areas, these two species underwent changes at very similar times: in the case of the North Sea cod the change has been linked to the climatic shift around 1988-1989 (Reid *et al*., 2001a; Beaugrand, 2004; Alheit *et al*., 2005), whereas for the northern hake stock, the cause of the change is still unknown.

Climate driven large-scale decadal fluctuations affect marine ecosystems worldwide (Stenseth *et al*., 2002; deYoung *et al*., 2004). A wide range of studies have investigated the North Pacific climate variability and its long-term influence on different trophic levels of marine ecosystems (Beamish, 1995; Hare and Mantua, 2000). Likewise, the North Sea and the Baltic systems have also been widely researched: there is literature that refers to climate driven decadal fluctuations that affect phytoplankton (Edwards *et al*., 2001; Reid *et al*., 2001a; Beaugrand and Reid, 2003), zooplankton (Fromentin and Planque, 1996; Reid *et al*., 2001a; Beaugrand and Ibañez, 2002; Beaugrand *et al*., 2002; Beaugrand, 2003, 2004) and fish populations (Alheit and Hagen, 1997; Reid *et al*., 2001a; Beaugrand *et al*., 2003; Hofstede *et al*., 2010). In addition, some studies have analysed the influence of the climate on the entire marine food web, from primary production up to top predators (Beaugrand and Reid, 2003; Beaugrand, 2004; Alheit *et al*., 2005; Alheit, 2009; Möllmann *et al*., 2009).

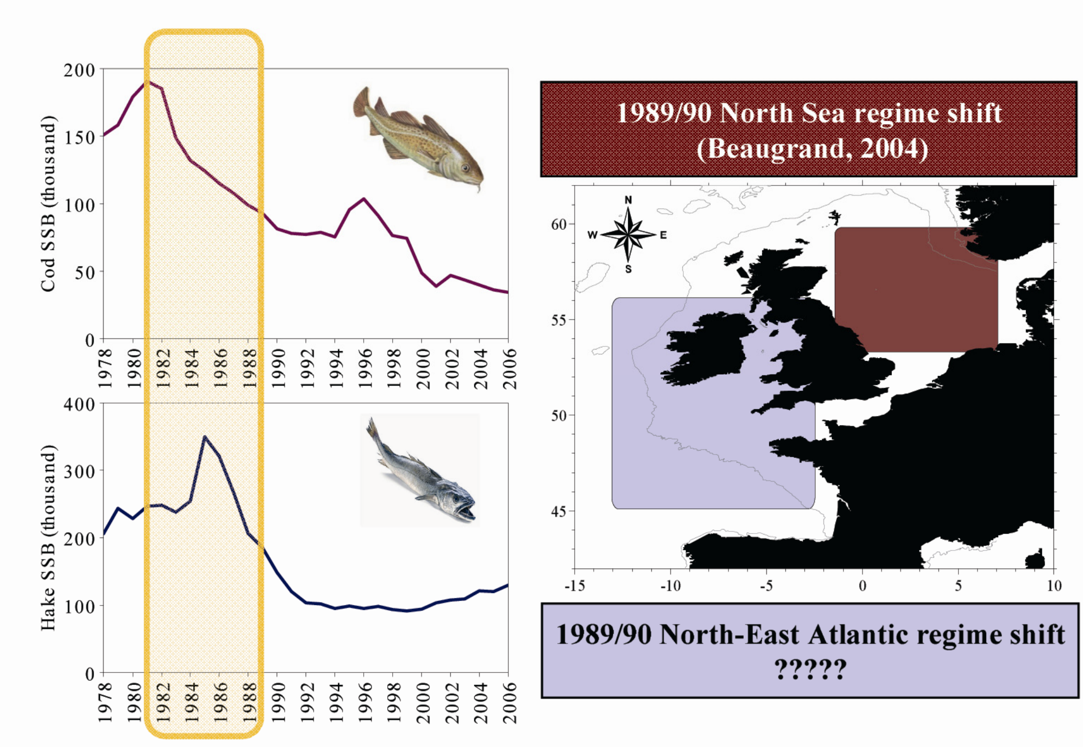


Figure 53: Diagram comparing the evolution of the SSB (in tonnes) over time of North Sea cod and northern European hake. The main distributions of cod in the North Sea (in maroon) and European hake in the NE Atlantic continental shelf (in blue) are shown on the map.

These decadal changes are often presented as regime shifts in which a rapid reorganisation of the ecosystem takes place from one relatively stable state to another (Scheffer *et al*., 2001; Rodionov and Overland, 2005). In the marine environment, regimes may last for several decades and the transition time is much shorter than the lifespan of these regimes. Shifts often appear to be driven by changes in the climate system (Rodionov and Overland, 2005), and in turn, regime shifts often correspond to changes in production of different marine species (McFarlane, *et al*., 2000; Beaugrand and Reid, 2003; Beaugrand, 2004; Cury and Shannon, 2004; Alheit *et al*., 2005; Litzow, 2006; Alheit and Bakun, 2010).

Although six climatic regime shifts have been identified in the sea surface temperature (SST) of the Northern Hemisphere in the last century (Yasunaka and Hanawa, 2002), the 1976/1977 and 1988/1989 regime shifts are considered to have been the largest because they also affected the Pacific Ocean (Hare and Mantua, 2000; Alheit and Bakun, 2010). Regime shifts have also been documented in the North Atlantic area (Drinkwater, 2006).

Since 1989, the temperature regime of the Baltic Sea has showed an increase in the winter temperature which has been linked directly to heat fluxes associated with the positive phase of the North Atlantic Oscillation (NAO) (Alheit *et al*., 2005). This change in winter SST is believed to have caused large changes in the ecosystem, such as, a sharp increase in phytoplankton, pronounced changes in zooplankton species like *Acartia* (increase) and *Pseudocalanus* sp. (decrease), and an increase in sprat (*Sprattus sprattus*) after low abundances in the 1980s (Alheit *et al*., 2005; Alheit and Bakun, 2010). Möllmann *et al*. (2009) identified a reorganisation of the marine ecosystem of the Central Baltic Sea after a discontinuous regime shift in the period from 1988 to 1993.

At the end of the 1980s, the Mediterranean Sea underwent a major change that encompassed marine circulation as well as hydrological and biological properties. This regime shift has been suggested to be linked to the Northern Hemisphere climate through large scale indices such as the North Atlantic Oscillation and the Northern Hemisphere Temperature index (Conversi *et al*., 2010).

The North Sea is one of the areas that has been most extensively studied and referenced in relation to the regime shift that occurred in the late 1980s. This shift has been related to the NAO index changing to a positive phase (Reid and Edwards, 2001; Alheit, *et al*., 2005), which in turn coincided with an increased incursion of warm Atlantic ocean water into the northern North Sea (Edwards *et al*., 2001, 2002; Reid *et al*., 2001a, 2001b, 2003b; Beaugrand, 2003). This ecological regime shift affected all trophic levels, ranging from an increase in phytoplankton biomass to changes in zooplankton community structure to variations in fish populations (Reid and Edwards, 2001). After 1987, catches of the western stock of horse mackerel (*Trachurus trachurus*) increased greatly in the northern North Sea (Reid *et al*., 2001a). After the period of high cod biomass called the “gadoid outburst”, in

1987 cod entered a period of low recruitment (Alheit *et al*., 2005), possibly due to a reduction in both the quantity and quality of *Calanus finmarchicus* (Beaugrand *et al*., 2003; Beaugrand, 2005). Parsons and Lear (2001) concluded that the gadoid outburst was linked to temperature, which in turn was linked to the long-term changes in the NAO index.

Several studies in the Northeast Atlantic have reported changes in the hydro-meteorological factors. The subtropical gyre became warmer and the subpolar gyre became cooler over the period from 1955 to 2003, which is consistent with a predominantly positive NAO phase (IPCC, 2007). In particular, the temperature of the upper 300 m of the North Atlantic increased by about 0.57 ºC between 1984 and 1999, with a stepwise increase after 1987 in both water and air temperature (Brander *et al*., 2003). There has also been an increase in the surface heat flux over the last decade (Michel *et al*., 2009). Environmental variations have led to changes in the biota at different trophic levels: an increase in phytoplankton (Edwards *et al*., 2001), with a stepwise change after the mid-1980s (Reid *et al*., 1998; Reid, 2005); a biogegraphical shift of zooplankton assemblages (Beaugrand *et al*., 2002; Beaugrand, 2009); and changes in fish distribution (Brander *et al*., 2003; Rijnsdorp *et al*., 2009; Dufour *et al*., 2010), biodiversity (Hutchings and Baum, 2005; Hofstede *et al*., 2010), recruitment (Beaugrand, 2004; Brunel and Boucher, 2007) and abundance (Rijnsdorp *et al*., 2009) in the Northeast Atlantic. As a consequence, it is hypothesised that the variability in the hake population may have been caused by changes in the NE Atlantic environment.

The main objective of this chapter is to provide a better understanding of the environmental mechanisms underlying the fluctuations in the northern European hake stock over time. Therefore, our aim was to determine whether an environmental regime shift occurred in the distribution range of northern hake in the period from 1978 to 2006 that could have affected its recruitment success.

METHODOLOGY

1. Temporal trend: Regime shift analysis.

a. Environmental data

A regime shift detection method was applied to environmental data presented in Chapter I, in order to detect the possible regime changes that could have been occurred during the study period. TPEA and slope temperature were not considered in this analysis for not being available for the whole time period. In the case of copepod abundance, in addition to annual and February-July mean values for each CPR box, May-June mean values (copepod peak abundance for the whole area, see Chapter I) were also considered for the averaged whole area. More locally, May copepod abundance for the D4 CPR box was included because this the month with the highest values within the spawning area of the Celtic Sea (see Chapter I). Appendix 1 (global indices), Appendix 2 (regional parameters), Appendix 3 (local parameters) and Appendix 4 (biological regional parameters) list the whole of the parameters that have been considered in the environmental regime shift analysis.

A wide range of methods have been proposed to detect unhomogeneities in time series. These methods typically employ standard statistical techniques, such as the Student's or Mann-Kendall tests (Easterling and Peterson, 1995). Some of these techniques are automated, whereas others require a preliminary visual inspection of the time-series. Further, they have different sensitivity to trends, outliers, and other forms of non-normality (Rodionov and Overland, 2005). However, all these techniques have in common a problem: they need to accumulate enough data (at least 10 or more years) in order to detect a discontinuity with a certain degree of confidence; consequently, the regime shifts are usually detected long time after they actually occurred and the performance of these standard methods decreases drastically at the ends of the series (Rodionov, 2004). With the aim of solving this problem, Rodionov (2004) proposed a new data processing technique, based on sequential t-test analysis of regime shifts (STARS). This new tool gives the possibility to estimate the probability of the occurrence of a regime shift with a minimum delay and it also allows for monitoring how this probability changes over time. In addition, the user can adjust the setting parameters (cut-off length l and probability level p) so that the method will detect those shifts that have meaningful environmental and biological implications (Rodionov, 2004).

In contrast to hypothesis-driven analysis, data-driven analysis, such as the one employed in this study, does not require an *a priori* hypothesis on the timing of the regimes shifts. This is an advantage for automatic computation with unlimited number of variables. Additionally, this sequential analysis obtains consistent results even if a trend is present in the time-series (Rodionov, 2004), as can be the case with many environmental parameters.

- **Regime detection method**

Given a time-series $x_1, x_2, \ldots, x_i, \ldots$, with new data arriving regularly, each time a new observation arrives, a Student's t-test is performed to determine if there has been a regime shift. This test determines whether the new observation represents a statistically significant deviation from the mean value of the current regime ($\bar{x}_{cur}$), and then checks for likely regime shifts between different periods by means of a sequential t-test analysis (Rodionov, 2004). According to the Student's t-test, the difference between the mean value of the current regime ($\bar{x}_{cur}$) and the mean value of the new regime ($\bar{x}_{new}$) to be statistically significant at the level *p* should satisfy the following condition:

$$diff = \bar{x}_{new} - \bar{x}_{cur} = t\sqrt{2\sigma_l^2 / l} \qquad (8)$$

where *t* is the value of the t-distribution with *2l-2* degrees of freedom at the given probability level *p*. It is assumed that the variances for both regimes are the same and equal to the average variance σ_l^2 for running *l*-year intervals in the time series $\{x_i\}$. It means that *diff* remains constant for the entire session with the given time series.

The mean value of the new regime ($\bar{x}_{new}$) is unknown at the current time, but it is known that it should be equal or greater than the critical level ($\bar{x}_{crit}$) that should be reached in the subsequent *l* years to qualify for a shift to the new regime.

$$\bar{x}_{crit} = \bar{x}_{cur} \pm diff \qquad (9)$$

If the new observation represents a statistically significant deviation from the mean value of the current regime, that year is marked as a potential change point *c*, and subsequent observations are used to confirm or reject this hypothesis. The hypothesis is tested using the regime shift index (RSI), which is calculated for each *c*:

$$RSI_c = \sum_{i=c}^{c+m} \frac{x_i^*}{l\sigma_1} \tag{10}$$

where m = 0, …, *l*-1 (i.e. number of years since the start of a new regime), *l* being the cut-off length of the regimes to be tested, and σ_l is the average standard deviation for all one-year intervals in the time-series. Here, $x_i^* = x_i - \overline{x}_{crit}$ if the shift is up, or $x_i^* = \overline{x}_{crit} - x_i$ if the shift is down.

RSI represents a cumulative sum of normalised deviations x_i^* from the hypothetical mean level for the new regime ($\overline{x}_{new}$), for which the difference, *diff*, from the mean level for the current regime ($\overline{x}_{cur}$) is statistically significant according to a Student's t-test. If, at any time from the start of the new regime, RSI becomes negative, the test fails and a zero value is assigned. If RSI remains positive throughout *l*-1, then *c* is declared to be the time of a regime shift at the level ≤*p*. The search for the next regime shift starts with *c*+1 to ensure that its timing is detected correctly even if the actual duration of the new regime is <1 year.

The existence of a strong autocorrelation in the time-series can lead to regime shifts being identified incorrectly; therefore, before the method is applied, the red noise component needs to be removed from the autocorrelated time-series by means of a prewhitening procedure (Rodionov, 2006). Thus, all parameters were graphically checked for autocorrelation by means of lagged autocorrelation estimation (ACF: autocorrelation function) (see Appendix 5 to 8).

For the environmental parameters that showed serial correlations (see Appendix 9), red noise was modelled with the first order autoregressive model (AR1). The AR1 coefficient was estimated by means of the Ordinary Least Square method (OLS). After the prewhitening procedure was implemented, the regime shift detection method was applied (in the case of autocorrelated parameters the filtered time-series was used).

The regime shift detection method was easily applied by means of STARS, which is a Visual Basic Application (VBA) for Excel. STARS can be tuned to detect the regimes of certain time scales and magnitude and the results will be determined by the cut-off length (L), probability level (p) and the Huber weight parameter (H). The time scale to be detected is controlled primarily by the cut-off length for proposed regimes. The probability level is the level at which the null hypothesis that the mean values of the two regimes are equal is tested. Both the cut-off length and probability level affect the statistically significant difference between regimes, and hence the magnitude of the shifts to be detected. The Huber weight parameter defines the range of departure from the observed mean (in standard deviations) beyond which observations are considered as outliers (Rodionov, 2004; Litzow, 2006). In accordance with the review by deYoung *et al.* (2004), in which the persistence time-scale of regime shifts for the North Sea and Northwest Atlantic was estimated to be more than ten years, the cut-off length for detecting the Northeast Atlantic regime shift was set at 10 years. In addition, the Huber parameter (factor for weighing the influence of potential outliers) was defined as 1 and the target significance level set at 0.05.

More details on the regime detection method can be found in literature (Rodionov, 2004, 2005, 2006; Rodionov and Overland, 2005) and also online (www.beringclimate.noaa.gov/regimes/index.htm).

b. Recruitment success

Among the studies concerning the effects of environmental variability on a given species, the biological parameter used most as a recruitment proxy is the observed number of recruits (Cardinale and Hjelm, 2006). However, many of the works that investigate the environmental influence on recruitment have ignored the effects of SSB (Planque and Frédou, 1999; Brander, 2005; Drinkwater, 2005; Megrey *et al.*, 2005), and instead analysed the relation between the observed number of recruits and the various climate variables without taking into account the variability that could have been caused by changes in adult biomass. Therefore, it is not possible to distinguish the effects of the physical environment from those of variations in SSB due to fishing pressure. However, several studies on other fish stocks have used recruitment success to analyse the influence of the environment (Jacobson and MacCall, 1995; Wada and Jacobson, 1998; Brodziak and O'Brien, 2005). To avoid confusing maternal and environmental effects Brodziak and O'Brien (2005) used recruits per spawner to evaluate the influence of environmental factors on recruitment success independently from the parental influence. Similarly, Wada and Jacobson (1998) justified the use of recruitment success, stating that it is an important part of biological production and can change more quickly in response to environmental variability. In this context, what Cardinale and Hjelm (2006) called the "recruitment success approach" accounts for the effect of the SSB on recruitment by relating recruitment success, i.e. the number of recruits produced per biomass of adult individuals, to various climate variables. Therefore, the effect of the SSB on recruitment is reduced by using recruitment success as the recruitment proxy. This is justified only if there is a significant relationship between recruitment and SSB. Furthermore, Beverton (2002) suggested that recruitment success should increase as SSB decreases.

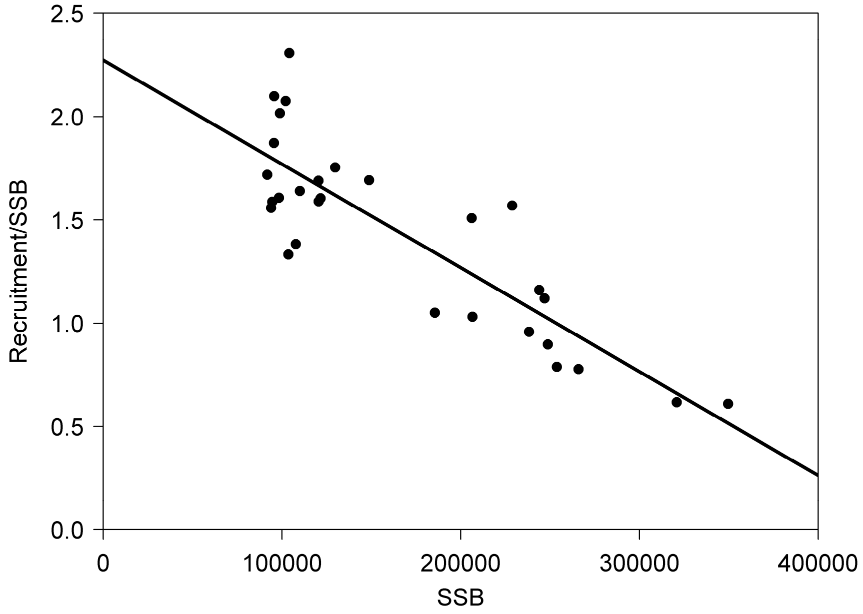


Figure 54: Dispersion plot showing the negative relationship between spawning stock biomass (SSB; in tonnes) and recruitment success (Recruitment/SSB).

According to the graphical representation of Cardinale and Hjelm (2006), data on the northern European hake stock indicate that there is a significant relation between SSB and recruitment (Figure 54). Consequently, recruitment success is a good proxy for a recruitment-climate analysis in the case of European hake.

The recruitment success before and after an environmental regime shift was compared using a two sample t-test. The significant difference between the means of the two periods was tested based on the null hypothesis of the two sample means being the same. The analysis was performed with the R statistical software available from the Comprehensive R Archive Network (http://cran.r-project.org).

2. Spatial pattern analysis.

a. North-East Atlantic. Correlation maps.

With the aim of studying how the relationship between recruitment success and environmental variability changes through the study area, maps of correlations were built. Two different physical parameters were analysed which are likely to affect early life stages and thus recruitment success of hake: sea surface temperature anomaly and Ekman transport in both directions (north-south and east-west).

Pearson correlation coefficients were calculated for the northeastern Atlantic continental shelf area, delimited between 44ºN-60ºN and 0-16ºW. In the case of Ekman transports, the correlation grid has a resolution of 1ºx1º, whereas correlation coefficients between temperature anomaly and recruitment success build a spatial grid of 2ºx2º. Data grids presented in Figure 13a for temperature anomaly and in Figure 13b for Ekman transport (Chapter I) were used for this analysis.

Correlations were estimated for both, annual and spawning season means of environmental variables. Given the spatial and temporal variability in hake spawning, several spawning periods were selected according to literature. Table 7 summarises the considered spawning seasons for each spawning area and the corresponding references.

Table 7: Summarising information regarding main spawning areas and different spawning seasons for each area, according to literature.

Main spawning area	***Spawning season***	***References***
Bay of Biscay	January-May	Sarano, 1983; Martin, 1991
	January-March (peak)	Murua, 2006
	February-March (peak)	Lucio *et al.*, 2000; Álvarez *et al.*, 2004
Celtic Sea	January-August	Lannin, 2006
	April-June	Coombs and Mitchell, 1982; Fives *et al.*, 2001
	April-July	Hickling, 1930; O'Brien, 1986
	May-August	Hickling, 1930; O'Brien, 1986
Northeast Atlantic	February-July	ICES, 2009a

Given the 27 degrees of freedom (n=29) of data, the significance of the correlations was set at 0.37 and 0.47 for 95% ($p<0.05$) and 99% ($p<0.01$) of significance, respectively (Zar, 1999).

Contour plots were used to illustrate correlation maps, which were performed using interpolation by krigging with Surfer software (Golden software Inc.).

b. Spawning grounds. Regression analysis.

The present section of the chapter explores the abovementioned relationships but focusing only on hake main spawning areas. To do so, the first step was to define the limits of the spawning areas, in order to consider only the measurement points bounded by those limits. As explained in Chapter I (page 65), the spawning ground off the French coast has been limited to the continental shelf between 44-48ºN and 1-8ºW, whereas the spawning area of the Celtic Sea has been bounded by 48-52ºN and 5-12ºW (Figure 13c, d).

With the objective of estimating a representative index of temperature and Ekman transport for each of the spawning grounds, two were the methods used. On one hand, minimum, mean and maximum values of the environmental parameter averaged for the beforehand defined areas were calculated. On the other hand, and based upon the same measurement points within each spawning ground, a principal component analysis (PCA) was carried out and the component explaining the highest percentage of the variability was taken as the index representative for the given area (see pages 65-67 in Chapter I for more details). Finally, dispersion plots were built between hake recruitment success and such environmental indices in order to study the relationship between them (regression analysis).

For this regression analysis, January-May and April-June were the only spawning periods selected for the Bay of Biscay and the Celtic Sea, respectively. In the case of the Bay of Biscay, the month of March was also considered because it has been widely documented as a spawning peak (Lucio *et al*., 2000; Álvarez *et al*., 2001) (see General Introduction).

RESULTS

1. Temporal trend: Regime shift analysis.

a. Environmental data

The results of the method for determining the regime shift indices are plotted in Figure 55. The highest regime shift indices were obtained for three periods: 1988/1989, 1995 and the time period between 2001 and 2006, with 2003 showing the highest parameter values. However, this shift should be considered with caution since it may be too early to report that the changes in 2003 are due to a regime shift.

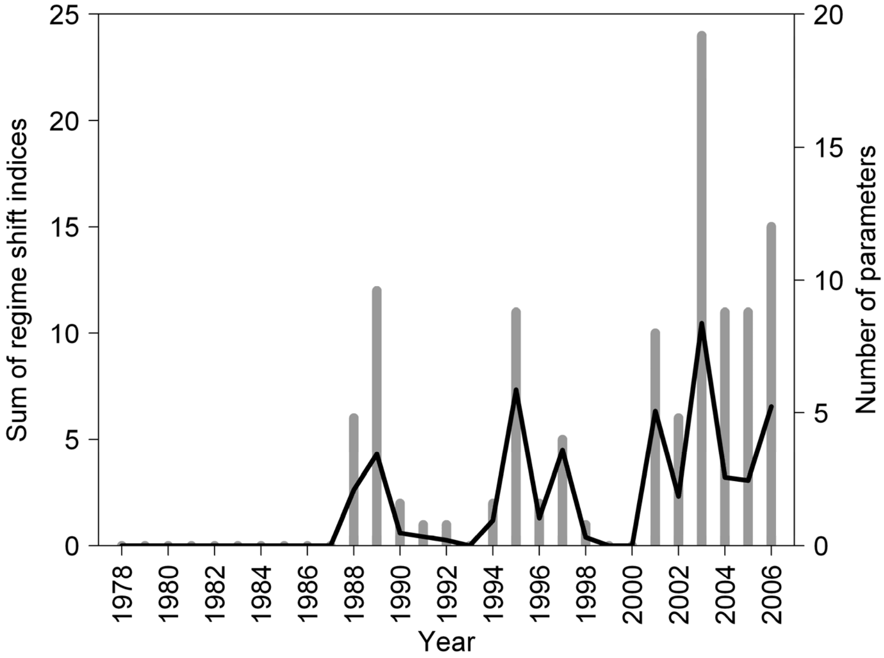


Figure 55: Plot showing the results of the regime shift detection method (target p=0.05, cut-off length=10, Huber parameter=1): sum of the regime shift indices (black solid line), and the number of parameters (grey bars) that showed a regime shift during the study. Note that there are no regime shifts detected for the first 10 years due to the 10-year cut-off length.

Figure 56 illustrates the time-series that showed a regime shift in 1988/1989. While the regime shift index had a negative value for copepod abundance, global indices such as the winter NAO and GSNW increased. Both eastward and southward transports increased in Porcupine, and temperature anomaly variables increased sharply. All the variables related to fluxes increased in magnitude (without taking into account the negative sign representing the direction of the flux) except for the sensible heat flux recorded in the Bay of Biscay.

In 1995, all the time-series except one showed a positive change, from lower values in the first regime to higher values in the second regime (Figure 57). The copepod abundance in Standard Area C4 was the only parameter that showed a negative shift.

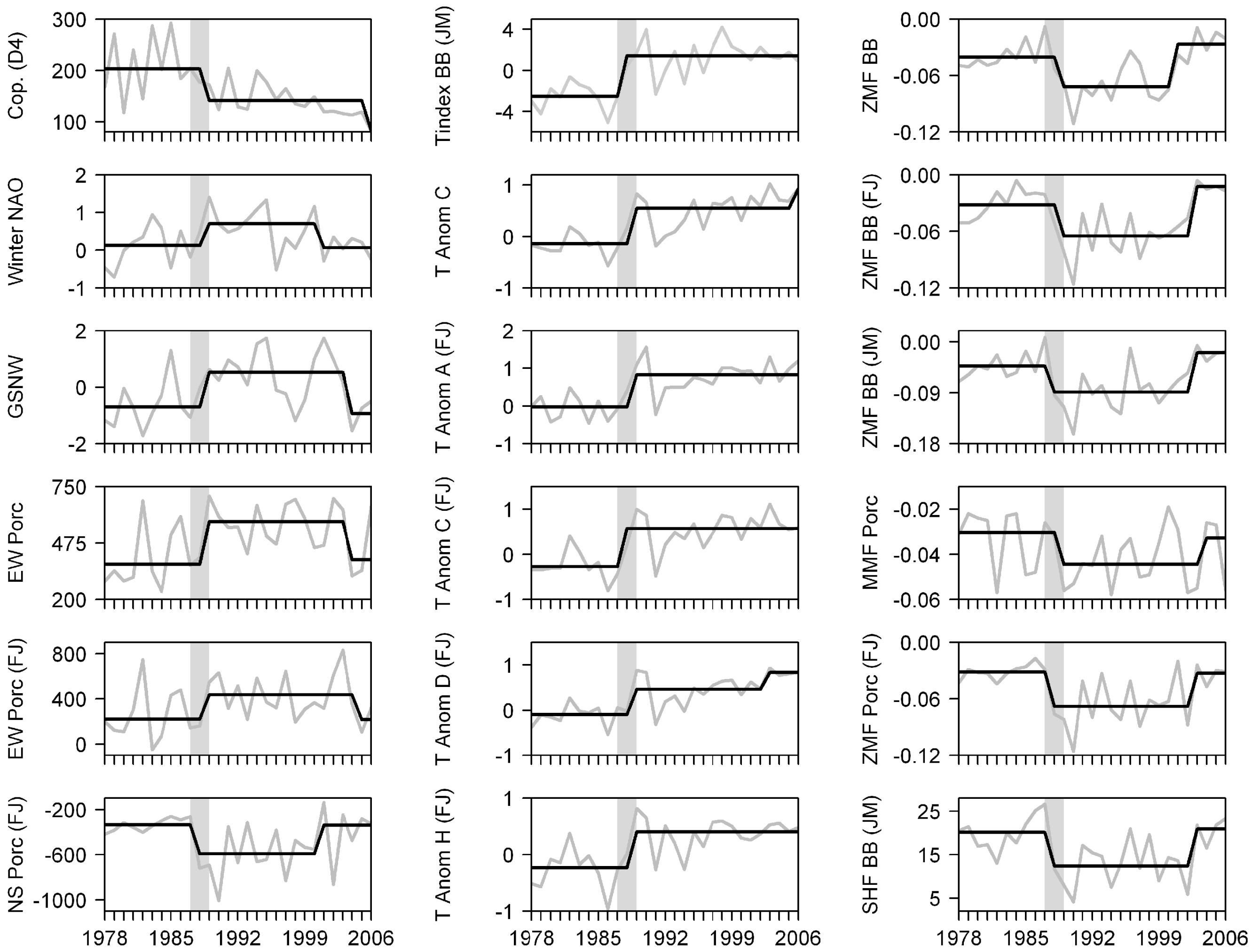


Figure 56: *Environmental and biological time-series showing regime shifts in 1988/1989 (shaded in grey). The grey line represents the interannual variability of the parameters, whereas the black line indicates the different regime states over the study period*

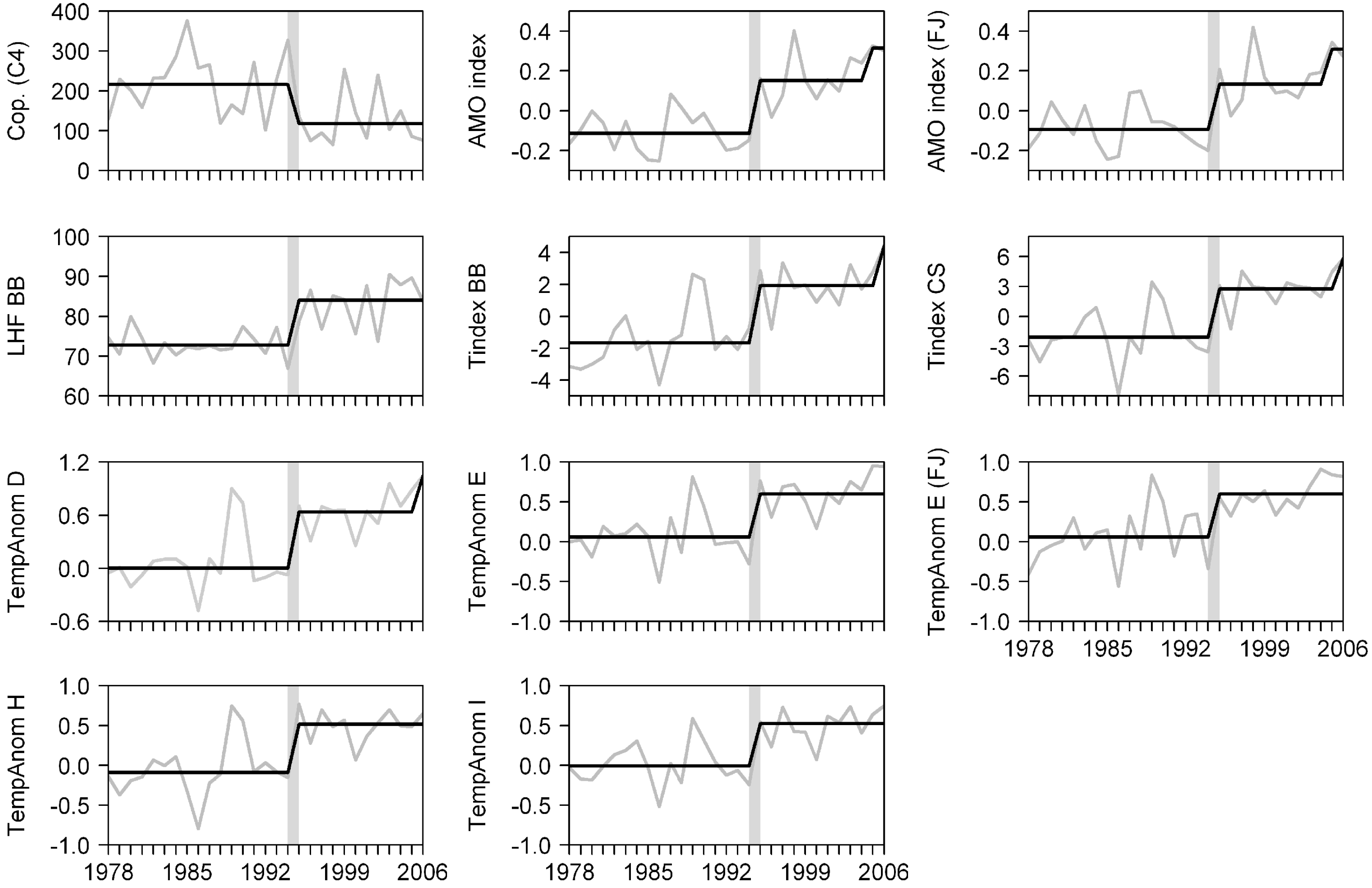


Figure 57: Environmental time-series showing regime shifts in 1995 (shaded in grey). The grey line represents the interannual variability of the parameters, and the black line indicates the different regime states over the study period

b. Recruitment success

The recruitment success time-series showed a pronounced change in the late 1980s from relatively low values until 1989 to relatively high values from 1990 onwards (Figure 58). The Welch t-test was applied due to the inequality of the variances of the two periods (F-test, $p>0.05$). According to the results of the t-test, the recruitment success was significantly higher in the second period (1990-2006) (mean=1.74) than in the first period (1978-1989) (mean=1.01; $t=6.73$, $p<0.001$, d.f.=21.26). Figure 58 represents the two regimes in recruitment success, with an increasing shift of about 0.73 points between 1989 and 1990. However, the potential change in 1995 is less evident and the difference in recruitment success before and after the possible shift was not significant for 1995 ($t= 1.90$, $p>0.05$, d.f.= 24.92). Note that using the Welch t-test the variance is estimated separately for the two periods and the Welch modification is applied to the degrees of freedom; this is why the degrees of freedom are not integer numbers.

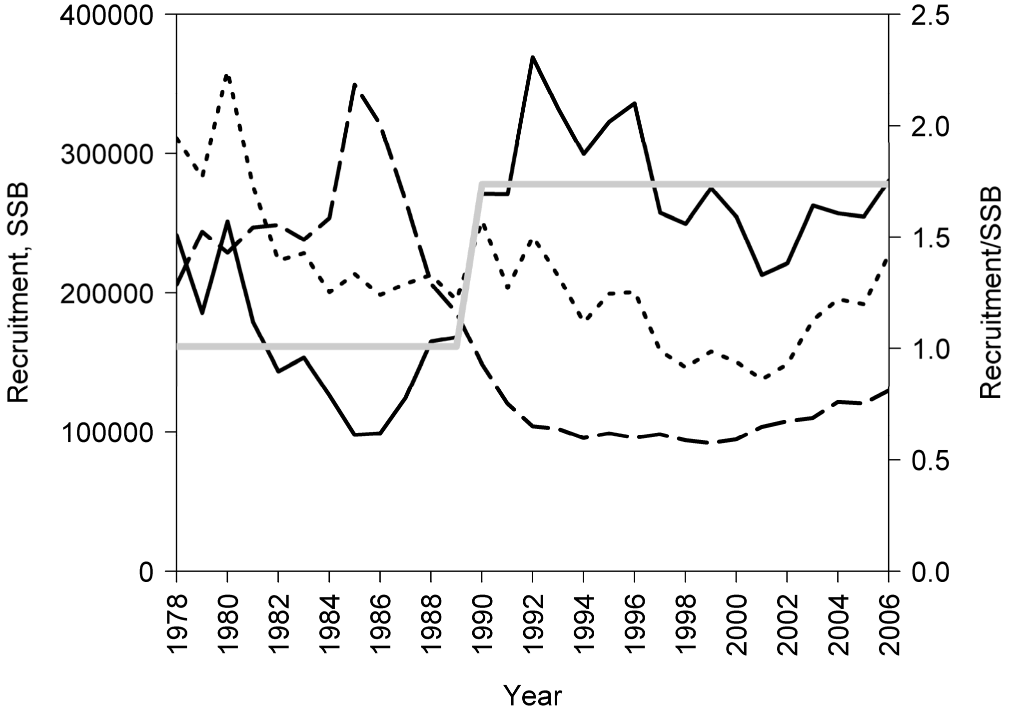


Figure 58: Time-series of northern European hake recruitment (in tonnes; dotted black line), SSB (in tonnes; dashed black line), and recruitment success (recruitment/SSB; solid black line) for the study period 1978-2006; The grey line represents the average state of recruitment success over time, and shows a regime shift in 1989/1990 (p<0.001).

2. Spatial pattern analysis.

a. North-East Atlantic. Correlation maps.

Annual mean temperature anomaly was positively correlated through the whole study area, although the relationship was stronger (significant at 95%) in waters around UK. The correlation coefficient decreases towards off the shelf (Figure 59). Regarding East-West Ekman transport, there was a clear spatial pattern, with positive although statistically non significant relationship above 50ºN and a significantly negative relationship at the shelf edge off the French coast (Figure 60). North-South Ekman transport showed no significant relationship with recruitment success for the whole Northeast Atlantic (Figure 61).

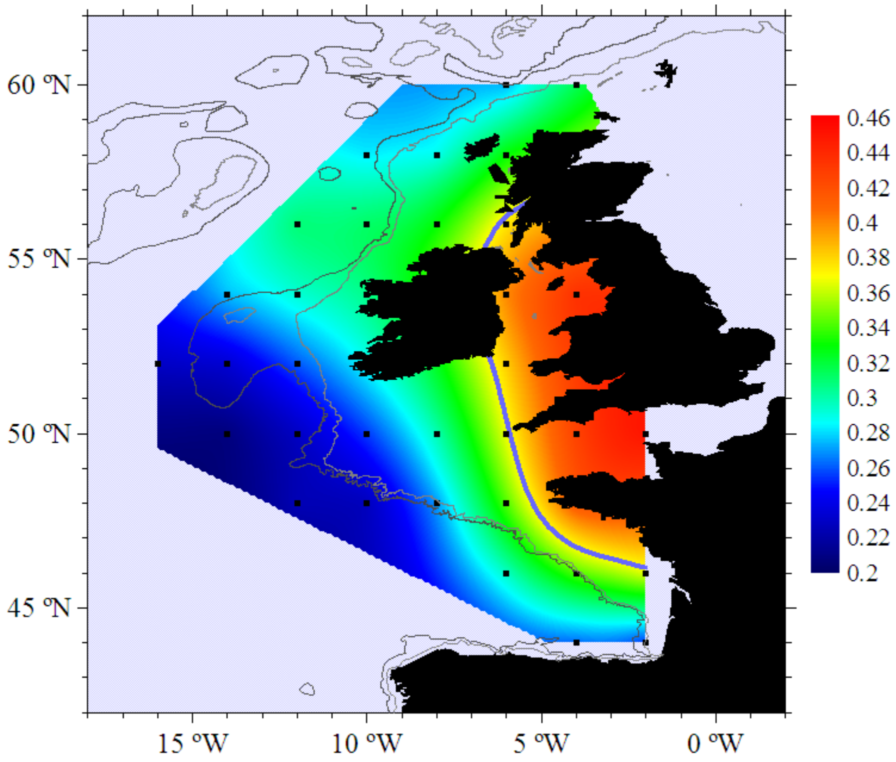


Figure 59: Distribution of correlation coefficients between recruitment success and annual temperature anomaly for the Northeast Atlantic continental shelf. The violet line limits the statistically ($p<0.05$) significant correlation coefficients ($R>0.37$).

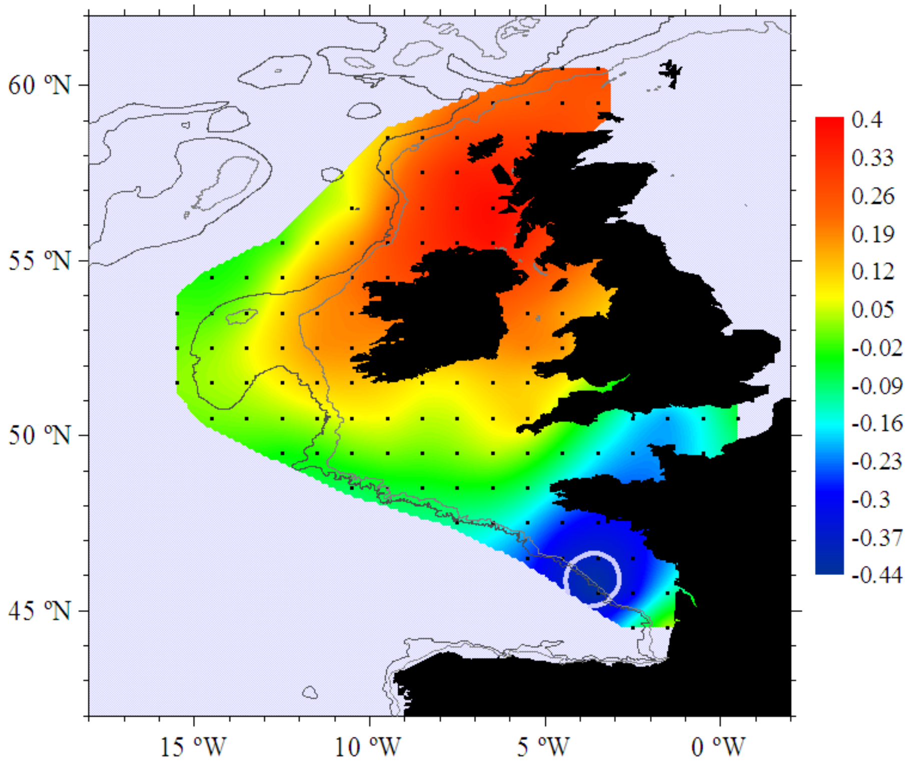


Figure 60: Distribution of correlation coefficients between recruitment success and annual E-W Ekman transport for the Northeast Atlantic continental shelf. The light violet line limits the statistically ($p<0.05$) significant correlation coefficients ($R<0.37$).

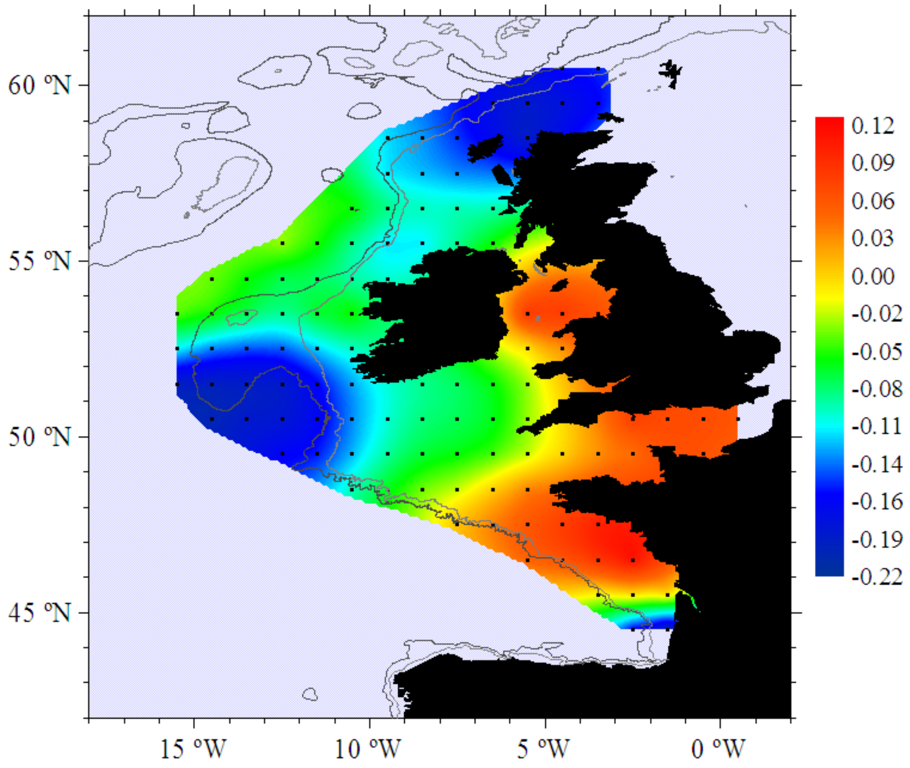


Figure 61: Distribution of correlation coefficients between recruitment success and annual N-S Ekman transport for the Northeast Atlantic continental shelf. No significant correlation coefficient was found.

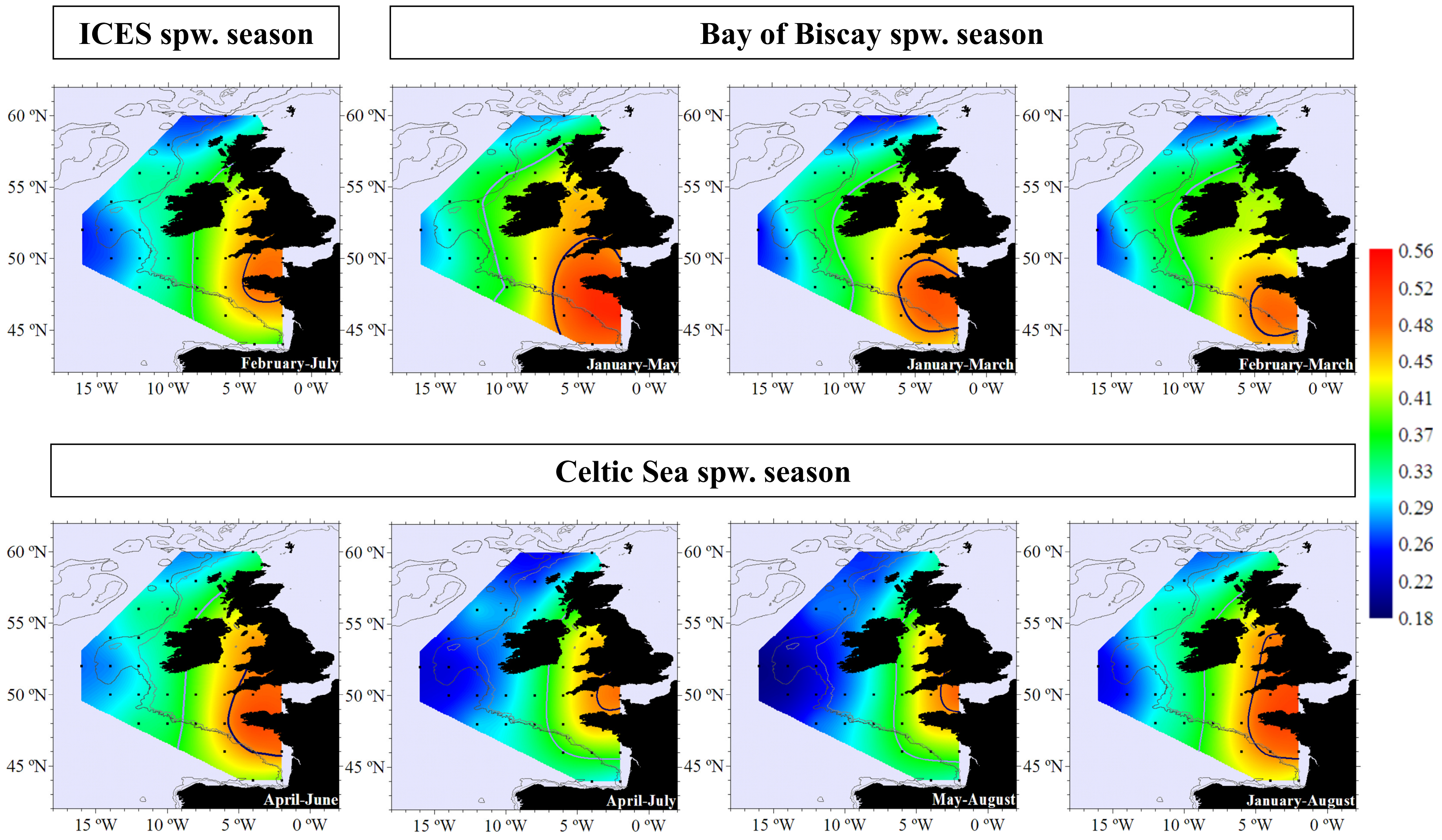


Figure 62: Distribution of correlation coefficients between recruitment success and mean temperature anomaly during different spawning periods. The violet line (light and dark) limits the statistically ($p<0.05$ and $p<0.01$) significant correlation coefficients ($|R|>0.37$ and $|R|>0.47$).

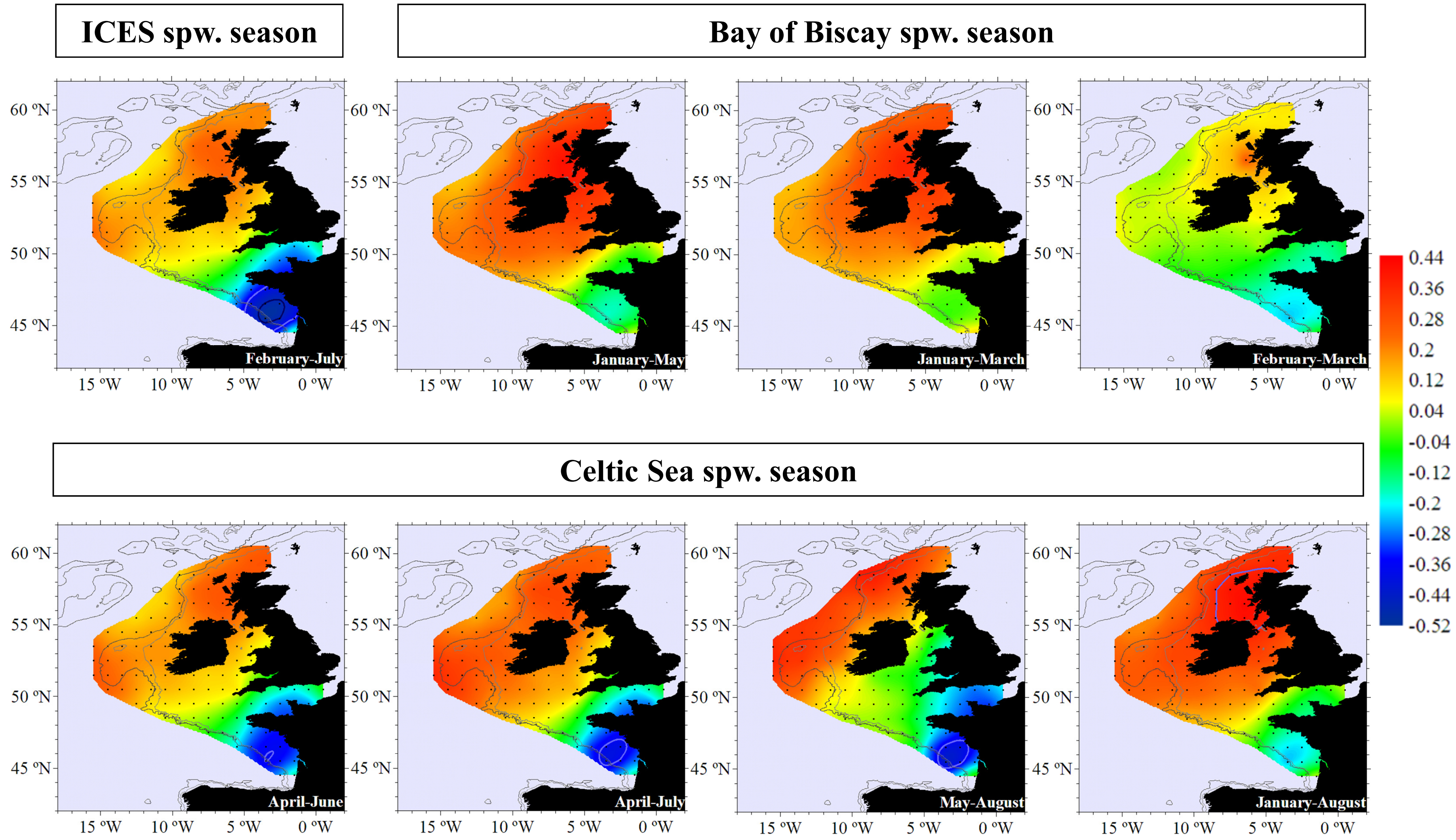


Figure 63: Distribution of correlation coefficients between recruitment success and mean E-W Ekman transport during different spawning periods. The violet line (light and dark) limits the statistically ($p<0.05$ and $p<0.01$) significant correlation coefficients ($|R|>0.37$ and $|R|>0.47$).

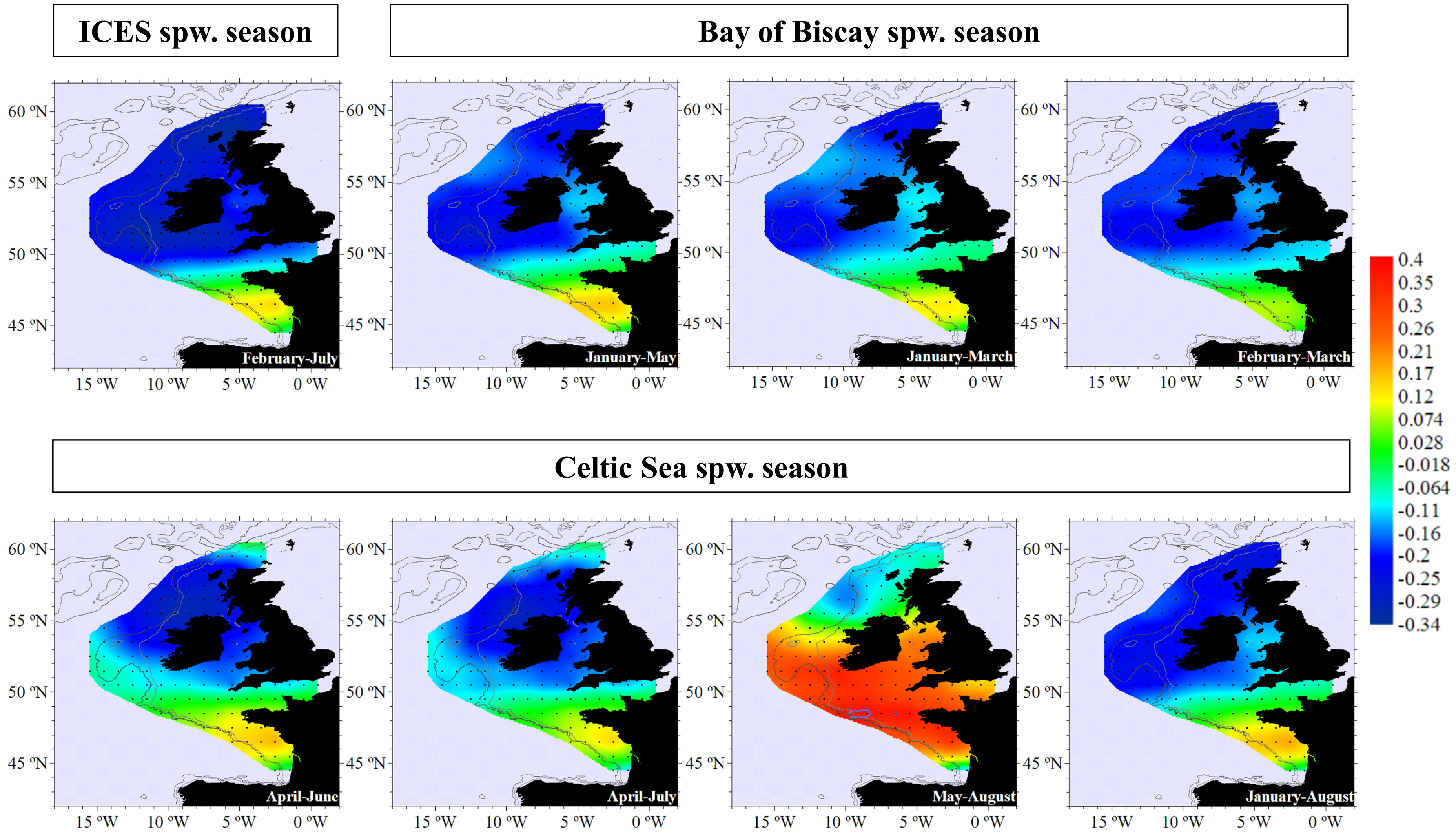


Figure 64: Distribution of correlation coefficients between recruitment success and mean N-S Ekman transport during different spawning periods. The blue line (light and dark) limits the statistically ($p<0.05$ and $p<0.01$) significant correlation coefficients ($|R|>0.37$ and $|R|>0.47$).

The distribution pattern changes slightly when spawning seasons are considered. A positive relationship has been found between recruitment success and sea surface temperature anomaly over the study area (Figure 62). Further, such correlation states statistically significant in the Bay of Biscay ($p<0.01$) and the Celtic Sea ($p<0.05$). However, the significance disappears when April-July and May-August spawning periods are considered. A clear pattern is observed for the Bay of Biscay spawning periods, with a significant correlation over the most of the continental shelf, and highly significant relationship over the Bay of Biscay.

Generally speaking, E-W Ekman transport and recruitment success are positively correlated. However, the pattern of the Bay of Biscay differs from the widely distributed positive correlation over the northern North-East Atlantic: the relationship disappears when Bay of Biscay spawning seasons are considered and it becomes negative for ICES ($p<0.01$) and Celtic Sea ($p<0.05$) spawning seasons (Figure 63).

In the case of N-S Ekman transport, the relationship is clearly negative above 48ºN and null in the Bay of Biscay, except for the spawning period May-August, where a positive relationship is seen over the most of the continental shelf of the northeastern Atlantic (Figure 64).

b. Spawning grounds. Regression analysis.

Figure 65 and 66 represent the influence of temperature anomaly upon recruitment success at the spawning grounds under study. In both cases, there is a clear significant positive dependence of recruitment success on temperature anomaly, being this relationship clearest in the Bay of Biscay when the period from January to May is considered. With regard to Ekman transport of the Bay of Biscay, the stronger the eastward and southward transport in March, the lower the recruitment success (Figure 67, 69). Considering the whole of the spawning period, such influence disappears. In the case of the Celtic Sea, no influence of Ekman transport has been observed (Figure 68, 70).

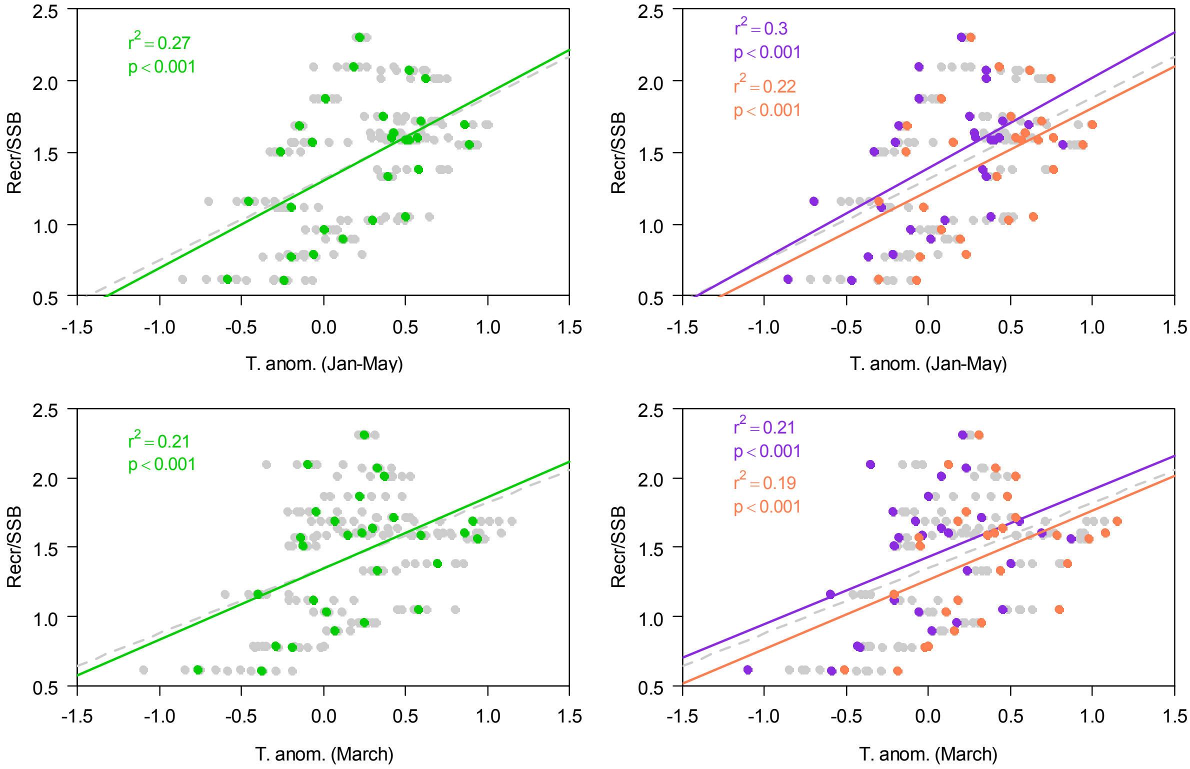


Figure 65: Dispersion plots between recruitment success and the mean (green), minimum (violet) and maximum (orange) values of temperature anomaly index for the Bay of Biscay. Note that grey points represent values for each measurement point of the corresponding spawning area. Trend lines are also plotted. When significant, determination coefficient and significance level are added on the plot.

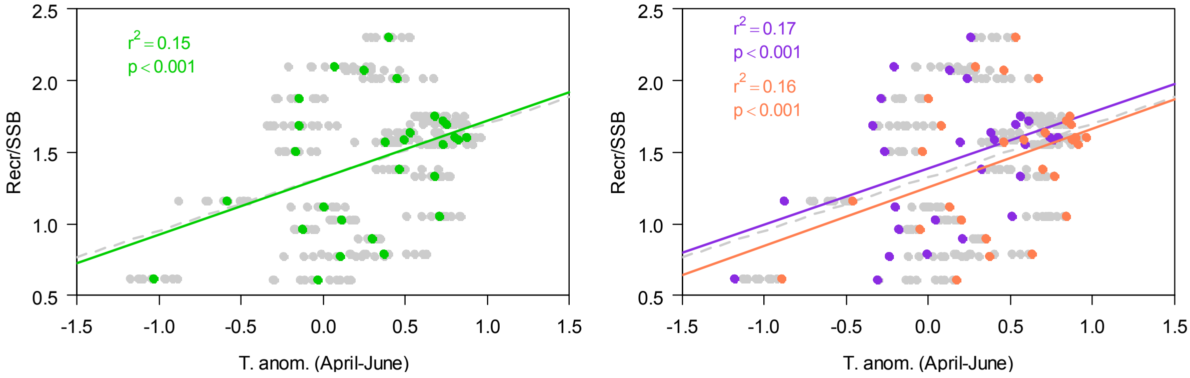


Figure 66: Dispersion plots between recruitment success and the mean (green), minimum (violet) and maximum (orange) values of temperature anomaly index for the Celtic Sea. Note that grey points represent values for each measurement point of the corresponding spawning area. Trend lines are also plotted. When significant, determination coefficient and significance level are added on the plot.

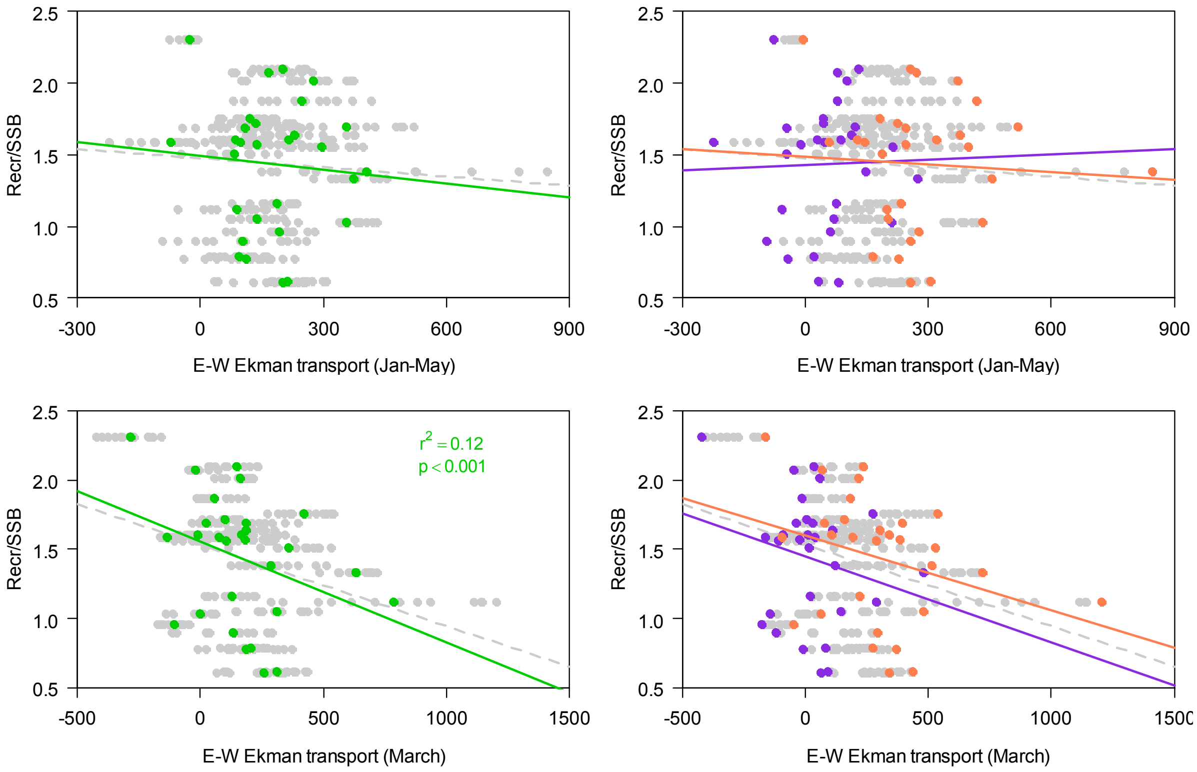


Figure 67: Dispersion plots between recruitment success and the mean (green), minimum (violet) and maximum (orange) values of E-W Ekman transport index for the Bay of Biscay. Note that grey points represent values for each measurement point of the corresponding spawning area. Trend lines are also plotted. When significant, determination coefficient and significance level are added on the plot.

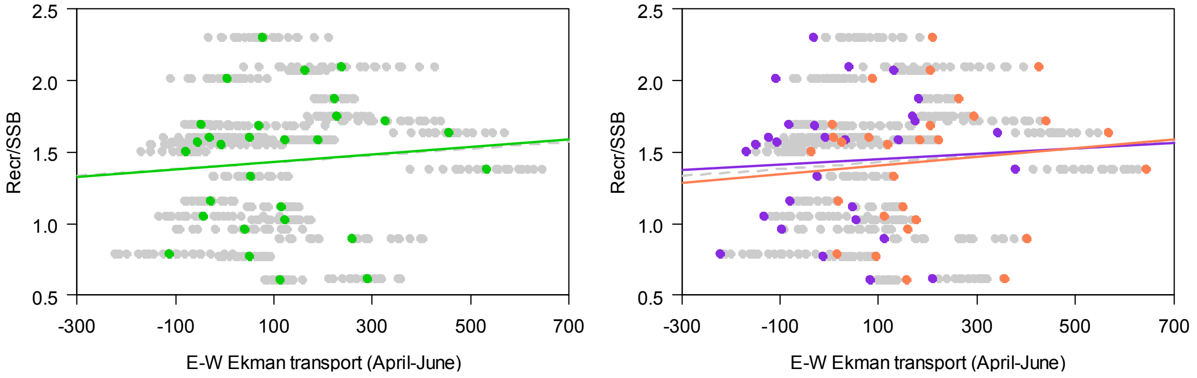


Figure 68: Dispersion plots between recruitment success and the mean (green), minimum (violet) and maximum (orange) values of E-W Ekman transport index for the Celtic Sea. Note that grey points represent values for each measurement point of the corresponding spawning area. Trend lines are also plotted. When significant, determination coefficient and significance level are added on the plot.

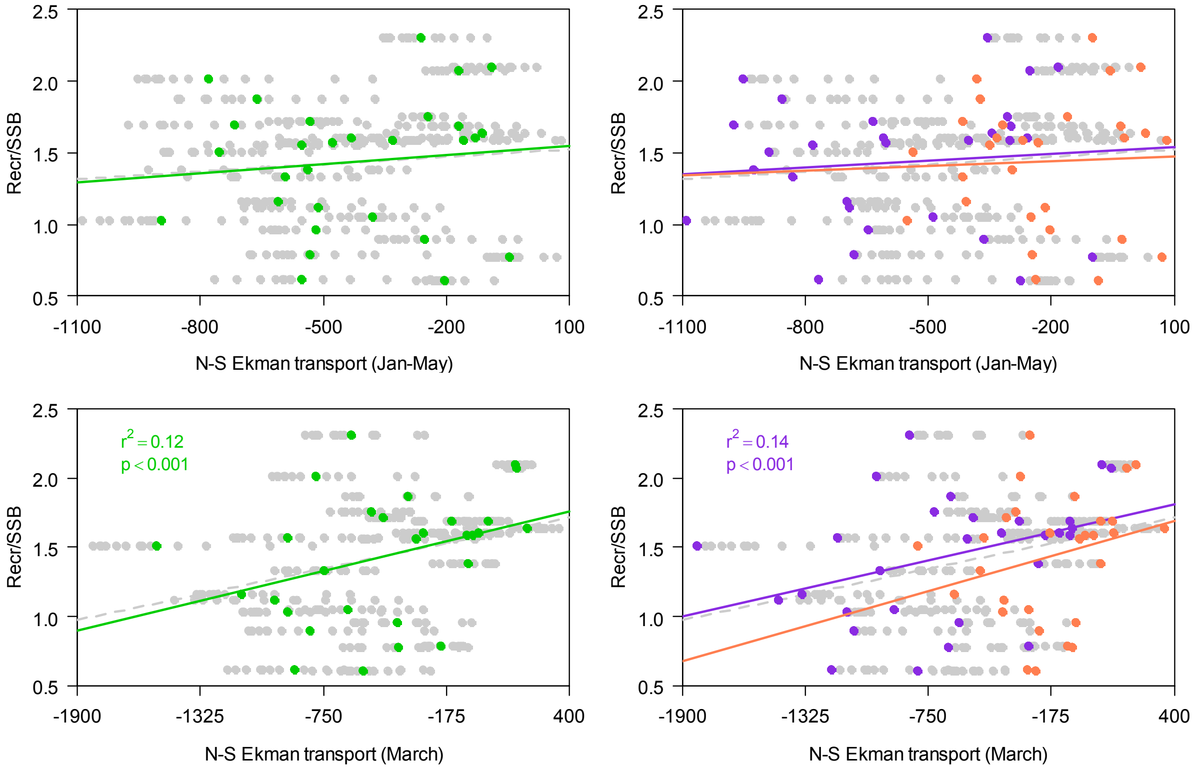


Figure 69: Dispersion plots between recruitment success and the mean (green), minimum (violet) and maximum (orange) values of N-S Ekman transport index for the Bay of Biscay. Note that grey points represent values for each measurement point of the corresponding spawning area. Trend lines are also plotted. When significant, determination coefficient and significance level are added on the plot.

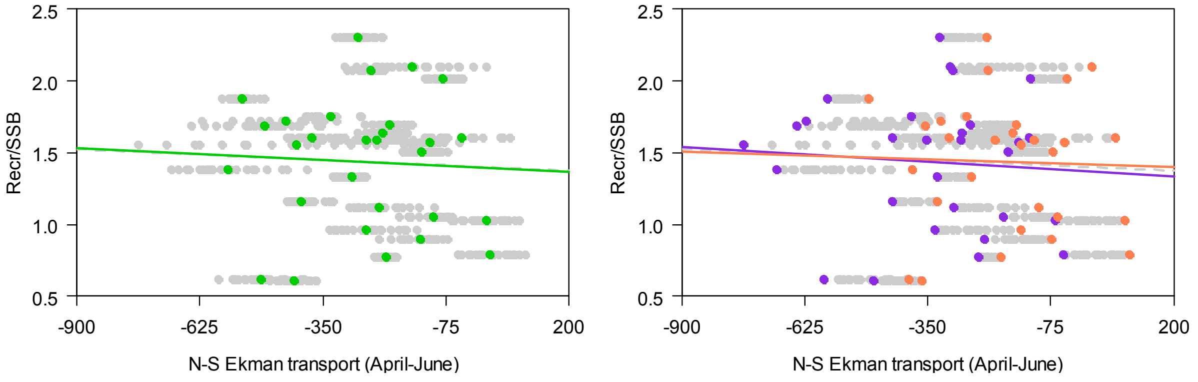


Figure 70: Dispersion plots between recruitment success and the mean (green), minimum (violet) and maximum (orange) values of N-S Ekman transport index for the Celtic Sea. Note that grey points represent values for each measurement point of the corresponding spawning area. Trend lines are also plotted. When significant, determination coefficient and significance level are added on the plot.

With regard to regression analysis between recruitment success and what have been defined as environmental indices (first principal components of the PCA), the same results as with area-averaged values have been obtained. The dispersion plots can be seen in Figure 71 for the Bay of Biscay and in Figure 72 for the Celtic Sea.

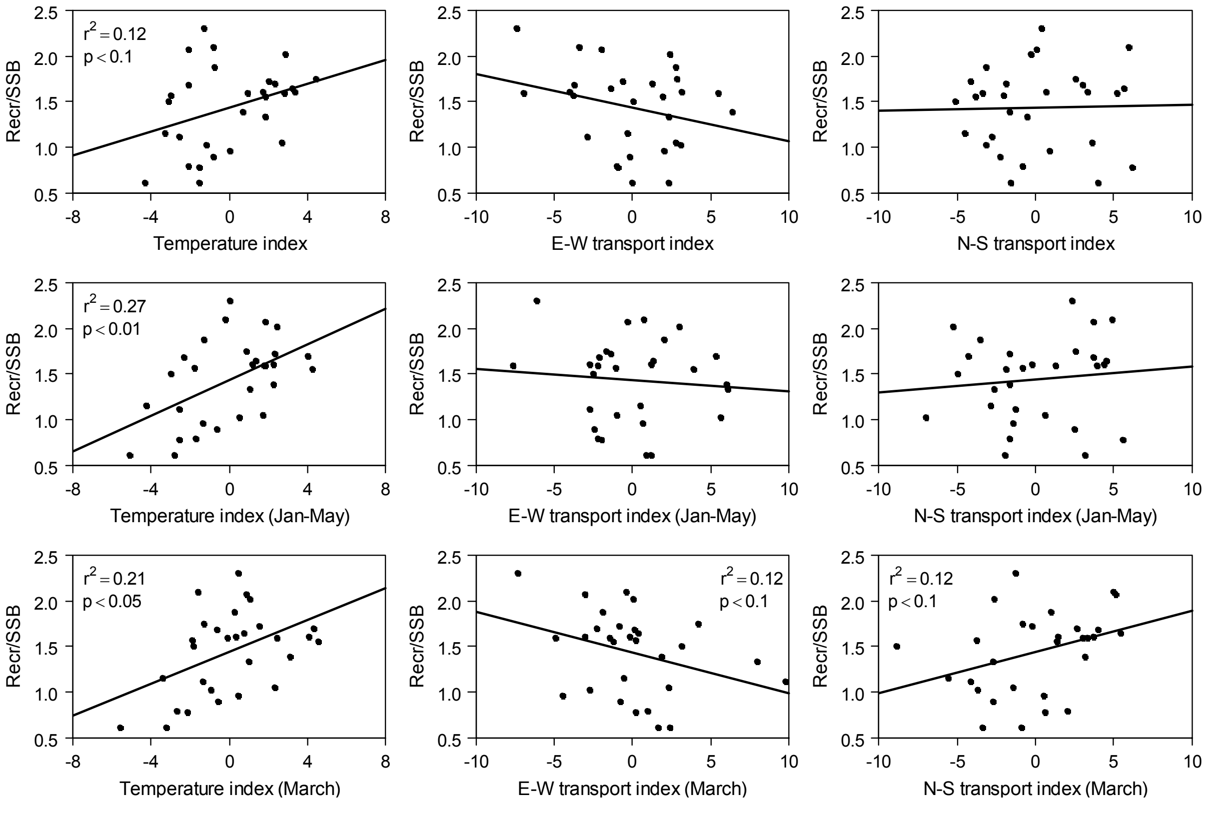


Figure 71: Dispersion plots between recruitment success and environmental indices (first components of PCAs) for the Bay of Biscay. Trend lines are also plotted. When significant, determination coefficient and significance level are added on the plot.

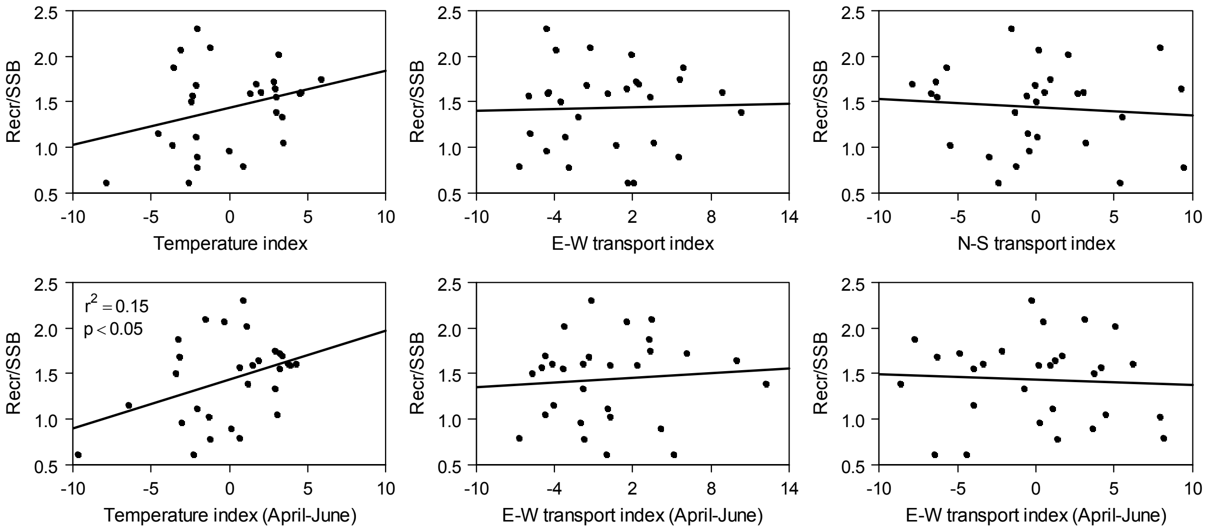


Figure 72: Dispersion plots between recruitment success and environmental indices (first components of PCAs) for the Celtic Sea. Trend lines are also plotted. When significant, determination coefficient and significance level are added on the plot.

DISCUSSION

Abrupt ecosystem shifts

Although the period after the regime shift (1988/1989) was apparently more favourable for hake recruitment, the SSB remained low. Furthermore, both hake and cod SSB had begun to decline before the regime shift. This fact strongly suggests that the decline and the low SSB levels recorded since the shift are due to overfishing: cod fishing mortality increased until the early 1980s (ICES, 2009c) and hake fishing mortality increased dramatically in the second half of the 1980s (Figure 46 in Chapter II). The recruitment success approach has been used previously for other groundfish species, such as cod. Brodziak and O'Brien (2005) and Möllmann *et al.* (2008) reported the importance of using the ratio between the annual number of recruits and spawner biomass instead of absolute recruitment strength in order to distinguish between the synergistic effects of maternal factors and those of environmental factors. They also cautioned against studying the effects of climate on exploited populations based only on biomass levels. Our study shows that after the regime shift, the conditions were more favourable for hake although the SSB remained low due to overfishing. In fact, it is likely that the favourable recruitment conditions contributed to sustaining the population under overfishing conditions and compensated the stock, thereby avoiding its depletion.

Within the eastern margin of the North Atlantic Ocean, the North Sea, the Baltic Sea and the Mediterranean Sea are three semi-enclosed marine ecosystems in which regime shifts have been described in both environmental variables and biological time-series. However, little has been found regarding regime shifts in the Northeast Atlantic continental shelf, despite it being a neighbouring marine system. In this context, the present study provides evidence that several global, regional and local parameters shifted in 1988/1989, which may have contributed to the stepwise increase in hake recruitment success.

Figure 73 shows a diagram of the potential relation between the different environmental and biological parameters that showed a shift in 1988/89 in the present study. The NAO is the most prominent mode of climatic variability in the North Atlantic Ocean. Decadal NAO variability influences regional temperatures, precipitation and wind speed and directions throughout Europe, as well as ocean heat content, ocean currents and their related heat transport (Hurrell, 1995; Hurrell and Deser, 2009). The positive phase of the NAO is linked to warmer-than-average SST and stronger-than-average surface westerlies across the middle latitudes of the Atlantic onto Europe (Hurrell and Deser, 2009). According to this, the shifts from negative to positive sea surface temperature anomalies over the northeastern continental shelf, and the change from relatively weaker to stronger westerly winds registered in Porcupine can be attributed to the increase in the winter NAO index observed in 1989/1990. However, recent studies demonstrated that the correlation between NHT anomalies and SST has strengthened in the North Atlantic Ocean (Beaugrand, 2009). Furthermore, Beaugrand (2003) also described stepwise changes in wind and temperature during the regime shift in the North Sea, which were attributed to variations in both the NAO and NHT anomalies. The regime shift described in the Mediterranean Sea has also been found to be mainly driven by the two major large scale climate indicators, i.e. the NAO and the Northern Hemisphere Temperature index (Conversi *et al.*, 2010).

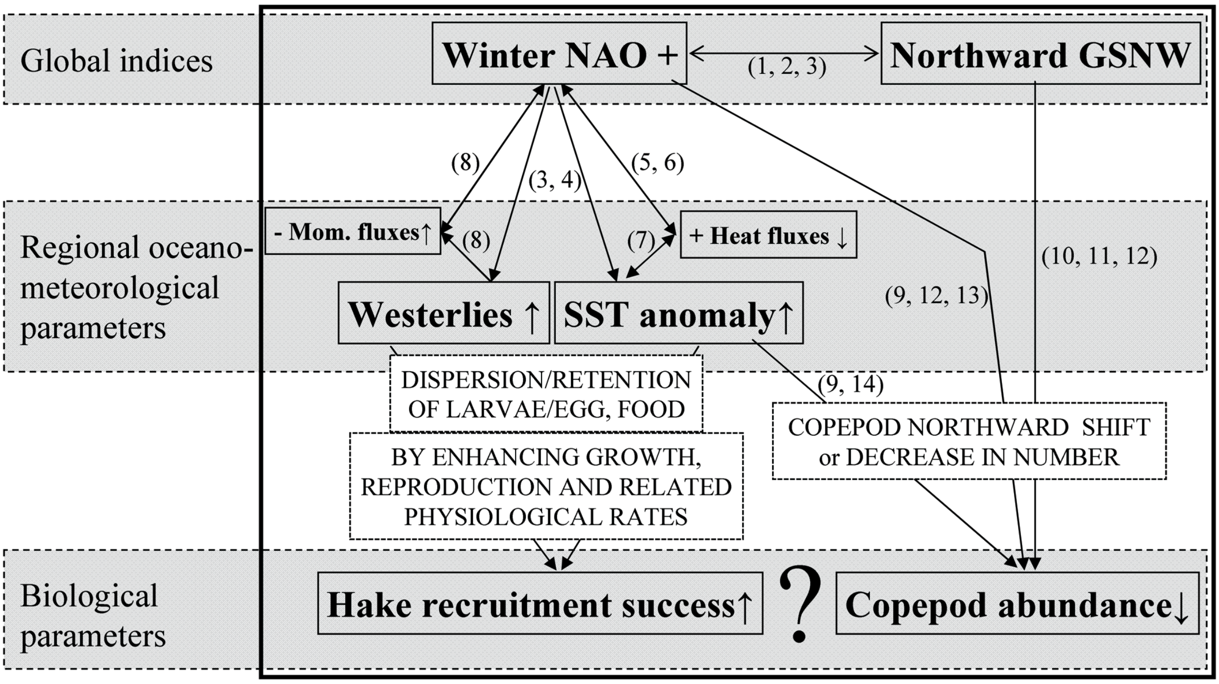


Figure 73: Conceptual diagram of a potential regime shift in 1988/89 in the Northeast Atlantic ecosystem. (1) Taylor and Stephens, 1998; (2) Taylor et al., 1998; (3) Hurrell and Deser, 2009; (4) Hurrell, 1995; (5) Cayan, 1992a; (6) Hurrell et al., 2003; (7) Cayan, 1992b; (8) Riviére and Orlanski, 2007; (9) Beaugrand et al., 2002; (10) Hays et al., 1993; (11) Taylor, 1995; (12) Reid et al., 1998; (13) Beaugrand et al., 2000; (14) Beaugrand and Reid, 2003.

In addition, during positive NAO phases, negative heat flux anomalies tend to occur in the Northeast Atlantic (Cayan, 1992a). Positive SST anomalies also influence heat fluxes from the oceans to the atmosphere. In our results, positive heat fluxes were found to compensate the positive temperature anomalies of the sea surface; however, there was a decline in heat fluxes due to the influence of the NAO. Indeed, heat fluxes depend on both atmospheric circulation anomalies and tendencies in SST anomalies (Cayan, 1992b). However, it has also been argued that variations in heat exchange between the atmosphere and the ocean could modulate NAO variability (Hurrell *et al.*, 2003) and sea surface temperature anomalies (Cayan, 1992b). Meridional (north-south) and zonal (east-west) momentum fluxes are considered to be associated with local wind patterns as well as low frequency global indices such as the NAO index (Riviére and Orlanski, 2007). Synchronous changes have been observed in hake recruitment success and heat and momentum fluxes, which suggest that they may be influential for hake. In addition, heat and momentum exchanges have been reported to determine growth, recruitment and migration patterns in marine populations (Stenseth *et al.*, 2002). However, from this work we cannot conclude that heat and momentum fluxes influence the hake population directly; rather they are believed to be part of a triangle formed by the NAO index, regional temperature anomalies and wind patterns (Figure 73).

The position of the GSNW, another index that changed in the 1988/89 period, also moves northward during positive NAO phases (Taylor and Stephens, 1998; Taylor *et al.*, 1998; Hurrell and Deser, 2009). Moreover, the position of the GSNW has been related to zooplankton abundance (Hays *et al.*, 1993; Taylor, 1995, 1996; Reid *et al.*, 1998) and the recruitment of different species (Nunn *et al.*, 2007).

Although Taylor (2002) did not find any evidence of a regime shift in the copepods of the European continental shelf, our study shows a change in total copepod abundance in the Celtic Sea, one of the main spawning areas for northern European hake. This stepwise change occurred at the same time as shifts in climate parameters, such as the NAO index, temperature anomalies and Ekman transport.

There is a wide range of studies on variations in zooplankton abundance and distribution (Fromentin and Planque, 1996; Beaugrand *et al.*, 2000; Beaugrand and Ibañez, 2002; Beaugrand, 2003, 2004, 2009; Reid *et al.*, 2003b). These changes have been mainly linked to modifications in the sign of the NAO index. A negative relationship has been found between plankton abundance and the winter NAO index in the English Channel (Beaugrand *et al.*, 2000). Elsewhere, plankton changes were found to be linked more to the peak of maximum variation for NHT anomalies detected around 1987 than to the NAO (Beaugrand and Reid, 2003). Moreover, Beaugrand *et al.* (2002) demonstrated a strong northward biogeographical shift in copepods related to both the increasing trend in the Northern Hemisphere temperature and the North Atlantic Oscillation. This relationship was confirmed in Beaugrand *et al.* (2009), with an updated and extended study over a longer study period.

Furthermore, in connection with the change in the NAO in 1988, Reid *et al.* (2001a) suggested that the advection of warmer water from off the Iberian coast northwards, following the shelf-edge current, up to the UK has accelerated. Indeed, an unusually strong northward shelf edge current was described in Rockall Trough (west of the British Isles) during 1988/1989. This eastern margin current had a peak of 7.9 Svedrups (Sv, 1 Sv = 10^6 m^3 s^{-1}) in 1989, and the mean transport section was 3.7 Sv (Reid *et al.*, 2001b). Holliday and Reid

(2001) linked the high water transport through the Rockall Trough and the 1989/90 regime shift in the North Sea. Fernandes *et al*. (2010) found a relation between warmer temperatures and hake recruitment. A rise in temperature is believed to increase the development rate (Ottersen and Sundby, 1995; Fiksen and Slotte, 2002) as well as fish behaviour and metabolism (Murua, 2006; Cury *et al*., 2008). In addition, Kirby and Beaugrand (2009) found that temperature has profound effects on marine ecosystem trophodynamics, with both direct and indirect effects on different levels of the food web. For instance, in the case of cod, sea surface temperature has been found to affect larval and juvenile growth directly; SST during early life stages has been described as an important factor for determining strong year classes (Ottersen and Sundby, 1995). European hake has been shown to have a preferential temperature range for spawning (10 ºC to 12.5 ºC) and larvae have been mainly found in water temperatures of between 10.5 ºC and 13 ºC (Álvarez *et al*., 2001; Ibaibarriaga *et al*., 2007). Consequently, it is logical that temperature changes would be influential for hake. Indeed, North Pacific hake (*Merluccius productus*) recruitment was found to be higher in years with positive temperature anomalies (Horne and Smith, 1997). This favourable influence is confirmed in this study, in which the northward advection of anomalously warmer water coincides with the stepwise increase in hake recruitment success.

Wind-induced Ekman transport is another critical factor during early life stages in terms of retention or dispersion of eggs, larvae or even juveniles. The Ekman transport in Porcupine showed higher February-July transports both eastward and southward after the shift in 1988/89: on one hand, this transport would favour keeping vulnerable individuals on the continental shelf, stopping them from being dispersed to oceanic areas; on the other hand, it may facilitate the transport of larvae and juveniles from spawning areas to nursery areas such as the Celtic Sea. Similarly, in the case of southern hake, the transport of larvae and pre-recruits from spawning areas to the open ocean has resulted in lower recruitment, whereas transport of larvae towards the recruitment areas has been found to aid recruitment (Sánchez and Gil, 2000).

The main food of hake larvae, copepods, decreased after the regime shift. Dickson *et al*. (1988) observed that northerly winds over the Northeast Atlantic are linked to a decline in zooplankton biomass in waters around the British Isles. This conclusion is in accordance with our results: stronger southward wind events in Porcupine coincided with the decline in copepod abundance in the Celtic Sea from 1989/1990 onwards. Nevertheless, we need to keep in mind that although we are discussing an increase in recruitment success, in absolute terms recruitment declined after the regime shift due to the low spawning biomass. Therefore, even if food was a limiting factor, copepod/recruitment ratio did not show a significant trend and thus the amount of food available per recruit did not change significantly (copepod abundance in the Celtic Sea declined by 33% and recruitment by 23%).

The change in hake recruitment success in 1988/89 coincides with a pronounced regime shift, which although it was first described for the North Sea, affected a much wider region, including the Baltic Sea and the oceanic area of the Northeast Atlantic (Beaugrand, 2004; Reid, 2005; Alheit, 2009). Changes in recruitment were particularly pronounced around 1987 for many fish populations of the NE Atlantic (Brunel and Boucher, 2007). In addition, a regime shift has also been described in the Mediterranean Sea in the late 1980s as part of a larger Northern Hemisphere climate shift (Conversi *et al*., 2010).

The regime shift in the 1988/89 period was not just restricted to the North Atlantic, since a regime shift in 1989 was also reported for the North Pacific. Alheit and Bakun (2010) described the regime shift in the late 1980s as a widespread Northern Hemisphere event. Indeed, North Pacific hake have also shown changes in distribution and spawning behaviour which are suggested to be linked to climate-ocean changes that occurred around 1989 (McFarlane *et al*., 2000).

Changes in temperature-linked parameters also occurred around 1995; higher AMO index values and positive regional temperature anomalies were recorded after a stepwise change in 1995, also described in Beaugrand *et al*. (2009). This regional water warming may have been caused by the retreat of the subpolar gyre to the west, which allowed warmer water from the subtropical gyre to penetrate up to the west of the British Isles in the mid-1990s (Hátún *et al*., 2005). Changes in the strength and extent of the subpolar gyre have been hypothesised to be the reason for the sharp increase in blue whiting (*Micromesistius poutassou*) recruitment in the west of the British Isles after 1995 (Hátún *et al*., 2009a, 2009b). However, these changes did not have a strong effect on hake. What is more, hake recruitment success declined in spite of the clear warming recorded after 1995. Therefore, favourable temperature conditions may not be enough for higher recruitment success in hake, transport during early life stages could also be critical as shown in the 1988/89 event. In addition, in 1995 a temperature anomaly shift was recorded in the Celtic Sea and the west of Ireland (areas D, E, H and I in Figure 12), which are areas that may be more affected by changes in the subtropical gyre due to their location. However, in 1988/89 positive temperature anomalies were recorded in the Bay of Biscay and Celtic Sea (areas A, C, D and H in Figure 12), the main spawning grounds of the northern stock of the European hake.

Based on the concept of *"regime shift"* proposed by deYoung *et al.* (2004) and defined as "changes in marine system function that are relatively abrupt (statistically significant different means), persistent (minimum time-scale of 10 years), occurring at large spatial scales (Northeast Atlantic), observed at different trophic levels (copepod abundance and hake recruitment success) and related to climate forcing (winter NAO index, temperature anomaly and wind strength)", this study provides additional evidence of the existence of a regime shift in 1988/1989 in the Northeast Atlantic continental shelf system. The regime shift in the Northeast Atlantic is presented as a part of a larger variation that resulted in synchronous analogous shifts in basins such as the North Sea, Baltic Sea, Mediterranean Sea and the Northeast Atlantic continental shelf.

Spatial variability of the environmental influence

Climate influences marine ecosystems particularly through sea surface temperature and wind conditions (Stenseth *et al.*, 2002). Ottersen and Sundby (1995) demonstrated that apart from density-dependent effects, sea temperature and the regional windfield are critical factors for the Arcto-Norwegian cod recruitment. Likewise, Pacific hake (*Merluccius productus*) distribution and spawning behaviour has been reported to be linked to changes in wind circulation and sea surface temperatures in winter (McFarlane *et al.*, 2000). In the case of the European hake, previous section has shown the importance of temperature and Ekman transport in terms of early life stages survival. However, such influence could spatially differ in distinct regions within the species distribution area.

In terms of annual means, temperature anomaly exerts a positive influence upon recruitment success, mainly in waters around UK, with weaker correlation towards off the shelf. In the case of East-West Ekman transport, there was a clear meridional pattern, with negative effect in the Bay of Biscay and positive influence above 50ºN. Such spatial difference is mainly related to the differences in Ekmant transport strength in both areas: 0-200 N/m^2 eastward transports are observed in the Bay of Biscay while, further north, Ekman transport reaches values between 400 and 600 N/m^2 (see Chapter I). Hake recruitment success showed no significant relationship with the annual southward Ekman transport over the study area.

However, the spatial variability in correlation coefficient distribution changes slightly when spawning seasons are considered. Although there is a positive correlation between sea surface temperature anomaly and recruitment success over the whole study area, such relationship becomes highly significant for the spawning periods of the Bay of Biscay. As it has been stated in Chapter I, temperature ranges between 10-12 ºC in the first months of the year in the Bay of Biscay, whereas the optimal temperature range for hake spawning goes from 10 ºC to 12.5 ºC (Ibaibarriaga *et al.*, 2007). Consequently, the positive temperature influence upon hake recruitment success remains highly significant for hake spawning optimal temperature range.

In contrast to annual eastward Ekman transport positive influence, the relationship becomes negative in the Bay of Biscay when different spawning seasons are considered. This comes explained by the modification in Ekman transport direction during these months (mainly, from April to August): in contrast to the general eastward pattern, Ekman transport takes westward direction. Consequently, there is an offshore transport of waters in the Bay of Biscay, with the resultant negative effect on hake recruitment success. It should be noted that spawning takes earlier in the Bay of Biscay (from January to May) and then eggs and larvae are transported coastward to the nursery areas. Therefore, offshore transport during April-August results in the dispersion of larvae, juveniles and food from the nursery areas with the subsequent negative influence on the survival of hake recruits.

In the case of N-S Ekman transport, the southward transport reported for the northeastern Atlantic exerts a negative influence upon hake above 48ºN and null in the Bay of Biscay. The exception comes for the spawning period May-August, where a positive relationship is seen over the most of the continental shelf of the northeastern Atlantic. During this period, Ekman transport turns northward. However, the correlations between N-S Ekman transport and recruitment success are not statistically significant.

In the Bay of Biscay, when temperature anomaly is considered, the average value over the whole of the spawning period is important, whereas for Ekman transport, it seems to be more influential the transport pattern registered in March, during the spawning peak month. This can be explained by the long-term/short-term influence of such environmental parameters. Temperature can directly (growth rate) or indirectly (copepods) influence the recruitment success of hake, but in both cases it needs a relatively long-time of optimal conditions. Ekman transport, instead, can affect positively (retention) or negatively (dispersion) but in a shorter period term. Indeed, Ottersen and Sundby (1995) concluded that when using data averaged over a large geographical area and for periods regarding more than one month, wind effect on recruitment may not be detectable, possibly due to its small-scale spatial and temporal variations.

Chapter IV

Hake recruitment dynamics: density-dependence and environmental influence

INTRODUCTION

Survival rates during early life stages can either increase or decrease due to environmental changes. For many populations recruitment is determined mainly during the first year, particularly during egg and larval stages (Pörtner and Peck, 2010). During this time mortality rate can vary either moderately or severely due to differences in environmental conditions from year to year, but may also bear some relation to the size of the existing stock (Ricker, 1975).

According to Gulland (1983), stock-recruitment relationships are curves fitted to mean recruitment as a function of the spawning stock biomass (SSB). He added that the observed recruitment is distributed around this curve, which is also dependant on environmental conditions. In Gulland's words, "the parent stock will determine a distribution of possible recruitment and the particular value within this distribution will be determined by the various environmental factors".

Although environmental parameters are important for understanding the fluctuations in fish populations they have not usually been incorporated into stock-recruitment models. The inclusion of environmental variables into stock-recruitment models could result in a better explained variance of recruitment. However, since environmental variables cannot themselves cause recruitment, a formulation that allows positive recruitment to be predicted by the environmental variable alone, is considered as inadmissible in stock-recruitment investigations (Iles, 1994). Thus, environmental variables can only moderate the number of recruits produced by the parental stock. The relationship between recruitment, SSB and the environment takes the following form:

$$R = f(SSB, E) \qquad (11)$$

where R is the recruitment, SSB is the stock spawning biomass and E refers to the environmental factor.

There are several articles that have analysed the inclusion of an additional environmental parameter, together with the spawning stock biomass, in a functional relationship in order to predict marine fish population recruitment (Iles and Beverton, 1998; Planque and Frédou, 1999; Chen, 2001; Chen and Irvine, 2001; Fiksen and Slotte, 2002; Uriarte *et al*., 2002; Levi *et al*., 2003; Planque *et al*., 2003; Brander and Mohn, 2004; Cook and Heath, 2005; Kell *et al*., 2005; Arregui *et al*., 2006). In such cases, the relationship between the number of recruits and their parental stock is given by a stock-recruitment model (e.g. Ricker, Beverton-Holt, Shepherd or Cushing amongst the most known models) which is slightly modified in order to introduce the environmental influence.

However, ecosystem responses are nonlinear and complex (Beaugrand, 2009). Generally, the response to environmental variability is unlikely to be monotonic, linear, or parametric and consequently, traditional linear models are often inappropriate for detecting and quantifying any environmental influence and their complex interaction with biological factors (Maravelias and Reid, 1997; Cardinale and Arrhenius, 2000). Chen and Irvine (2001) found that a nonlinear empirical approach described the relationship between environmental variables and recruitment better than a linear approach.

In such cases, generalized additive models (GAMs) have been demonstrated to be a powerful technique when analysing environmental influence on biological factors (Megrey *et al*., 2005). Their strength relies on the fact that they are not tied to any particular functional relationship. As such, GAMs have been widely used in order to explore the stock-recruitment-environment triangle, with no prior assumption regarding the form of the relationship that links the spawning stock biomass to its offspring (Jacobson and MacCall, 1995; O'Brien and Rago, 1996; Daskalov, 1999; Cardinale and Arrhenius, 2000; Chen *et al*., 2005; Schirripa and Colbert, 2006; Bartolino *et al*., 2008).

Both stock-recruitment relationships and environmental influence on northern European hake stock are subjects that have been hardly studied. Recruitment dependence on parental stock has been explored in Chapter II of this dissertation; in contrast, environmental improvement of the stock-recruitment relationship is still a pendant subject with regard to northern hake stock.

Given the need for a better understating of stock-recruitment-environment relationship, the main objective of this chapter was to determine if environmental factors could be used to develop a model of inter-annual hake recruitment variations both, assuming a Ricker stock-recruitment relationship and building a model with no density-dependent assumption.

For that purpose,

- An attempt to improve the stock-recruitment relationship described in Chapter II was made, by incorporating one or more additional environmental variables to the Ricker model.
- A non-linear approach was used with the aim of explaining recruitment variations over time by means of SSB or/and environmental parameters.

METHODOLOGY

The methodology section of this chapter can be divided into two subsections; firstly, a supervised classification methodology was applied with the aim of reducing the initial large number of explanatory parameters presented in Chapter I (summarised in Appendixes 1 to 4), candidates to explain hake recruitment success variability; lastly, the parameters selected by the algorithm were used in order to build an environmentally modified Ricker S-R model and a generalised additive model (GAM) with no Ricker SR relationship assumption.

1. Parameter selection

The methodology used in this study (a supervised classification based methodology) has been proposed by Fernandes *et al.* (2010). It mainly involves performing a set of steps to build a probabilistic model with recruitment success levels. These steps are: a) recruitment success discretization in three levels (low, medium, high); b) discretization of environmental parameters based on recruitment levels; c) selection of parameters based on recruitment levels; d) the use of Markov Blanket for reducing the number of selected parameters; and, e) learning a naïve Bayes probabilistic classifier. All the analyses are performed in a pipeline of sequential steps.

a. Recruitment success discretization

In order to be able to use probabilistic classification methods like Bayesian networks, the recruitment success variable needs to be discretized (Torgo and Gama, 1997; Frank *et al.*, 2000; Revoredo and Zaverucha, 2004). We decided to discretize the target parameter into 3 classes (low, medium and high recruitment success), due to their management implications on a further step. As such, a semi-automated discretization was undertaken.

The methodology presents a ranking of cut-off point sets with their corresponding estimated performance measures in order to be evaluated by the end-user. For the cut-off point selection, several criteria were taken into account: (i) to maximise the accuracy (the chance of forecasting the observed recruitment level); (ii) to search the lowest brier score (higher probability estimations for each recruitment level); (iii) to maximise the mean of true positive rate (the highest TP mean); (iv) to search an equilibrated true positive (TP) value between classes (TP1~TP2~TP3). “Accuracy” measures model performance without considering the estimated probability (win/loss measure), whereas the Brier score considers these estimated probabilities to each possible outcome (Brier, 1950; van der Gaag and Renooij, 2001; Yeung *et al.*, 2005). “True positive rate” measures the distribution of the error between different recruitment levels. “Accuracy” and “true positive rate” lies between 0% and 100%, with higher values indicating better results; while “Brier score” is measured between 0 and 2 (or normalised between 0 and 1, Fernandes *et al.*, 2010), where lower values indicate better results.

b. Explanatory variables supervised discretization

The parameters were discretized following the Fayyad and Irani’s MDL method (Fayyad and Irani, 1993), a supervised discretization that transforms continuous variables into categorical variables, taking into account recruitment success values. In other words, it looks for cut-off point sets, minimising the recruitment entropy (a measure of uncertainty), i.e. the lower the conditional entropy the better the discrimination power of a parameter (lower uncertainty) (Fernandes *et al.*, 2010).

c. Explanatory variables selection

The parameter selection was performed following the Hall's multivariate Correlation-based Feature Selection (CFS) method (Hall, 2000). This method assumes that a good subset of parameters correlates highly with the target class; and at the same time, the parameters have low correlation between them. Those correlations are measured by means of Symmetrical uncertainty score (SUS) between pairs of variables (see below). The most repeated subset of variables selected by CFS in a "leaving one out cross-validation scheme" (LOOCV) is considered as the most stable subset (Francis, 2006). Nevertheless, the fisheries expert has to select the set of variables to build the final model, from the raking provided by the cross-validated CFS.

As an additional step within this methodology, a univariate ranking was carried out based on uncertainty measures from information theory. The Symmetrical Uncertainty Score (SUS) is the normalised mutual information between two variables (Hall, 1998), i.e. it is the uncertainty reduction of a variable given a second variable. In this way, variables that are highly correlated with the recruitment, but have not been selected in the multivariate parameters selections (redundant) can be examined by the expert. Further, the order of the variables within the ranking will be taken into account on a later step, when introducing the explanatory parameters in the model.

d. Markov Blanket

In some cases, the CFS method returns subsets with large number of variables that are difficult to interpret or to use in practice. This could happen, for instance, when the number of instances in each variable is low or the correlation between the variables and recruitment success is very high. In such cases, it is possible to diminish the number of variables using the Markov blanket subset of variables based on the Markov property of a node in a Bayesian Network (Pearl, 1988; Peña *et al.*, 2007). The Markov blanket subset is made of those variables that once their value is known, the rest of variables do not influence on the recruitment success forecast with the available data, and thus it has minor effect on the classifier forecast estimates.

e. Classification model: Naïve Bayes classifier

The methodology proposed by Fernandes *et al*. (2010) uses Naïve Bayes (Duda and Hart, 1973; Langley *et al*., 1992) for the supervised classification step. Naïve Bayes is a Bayesian network, that is to say, a graphically presented mathematical model where nodes represent variables and arcs represent the links between variables (Uusitalo, 2007). Naïve Bayes assumes that given the target class, all of the parameters are independent. Due to their graphical representation, bayesian networks in general, extract knowledge and are easier to interpret than other supervised classification models (Correa *et al*., 2009). As such, the parameters subset selected with CFS and Markov Blanquet have been represented by means of Naïve Bayes with the main objective of graphically show the relationship between recruitment success and parameter variables; particularly, to examine the role of each parameter at each of the three recruitment success classes (low, medium and high).

All of the above steps were implemented using WEKA API machine-learning software (Witten and Frank, 2005). For ‘Markov blanket’ approach and ‘multinomial naive Bayes’ scenarios visualization, Bayesia software was used (www.bayesia.com).

2. Recruitment modelisation

Given the selected bio-physical parameters, two different recruitment models were built. Firstly, an attempt to improve the Ricker stock-recruitment relationship (previously described in Chapter II) was made, introducing the variables beforehand selected by the algorithm, in order of decreasing score in the univariate ranking. Secondly, generalized additive models were used in order to explain recruitment fluctuations, with no Ricker SR relationship assumption.

Data exploration

As a previous step, graphical data exploration was undertaken in order to decide if data transformation should be performed before applying the models. As such, data exploration was carried out focusing on the following steps:

- The existence of outliers in the response and explanatory variables was checked graphically by means of boxplots and Cleveland dotplots (Cleveland, 1985).
- Pairplots and correlation coefficients were used to see whether the explanatory variables showed collinearity or not.
- Relationships between the response and the explanatory variables were explored with scatterplots.

a. Environmentally modified Ricker S-R relationship

The following function describes the relationship between recruitment and spawning stock biomass proposed by Ricker (1975), with environment as an additional explanatory factor:

$$R = \alpha SSB e^{(-\beta SSB + \delta ENV) + \varepsilon} \qquad (12)$$

Where α is the maximum reproductive rate, β the recruitment optimality parameter and δ the environment coefficient. ε is a normally distributed error term with mean 0 and standard deviation σ.

Following the same procedure as in Chapter II, the model was reformulated to a generalized linear model (GLM) with a logarithmic link function:

```
glm(formula = Recruitment ~ offset(LogSSB) + SSB + ENV,
              family = quasi(link = log, variance = "mu"),
              data = data.SR, na.action = na.exclude ,
              control = list(epsilon = 1e-04,
              maxit = 50, trace = F))
```

Different models were built for different combinations of the three environmental parameters selected above: one environmental parameter per model, all parameters together and combination of pairs of environmental parameters. Model selection was based on hypothesis testing and the highest variance explained.

Residuals from the fitted model were tested by means of graphical representation. Residuals were plotted against predicted values to test their homogeneity. Besides, the normality was tested checking the Normal-QQ plot and further checked with Shapiro-Wilk normality test. Finally, Cook's distance was used to detect the presence of outliers.

b. GAM

The generalized additive modelling (GAM, Hastie and Tibshirani, 1990) was used to explore the dependence of hake recruitment on spawning stock biomass and environmental variables, with no assumption of any type of S-R relationship.

A generalized additive model is a nonparametric technique that can assist in the identification of appropriate nonlinear response functions. GAMs were first proposed by Hastie and Tibshirani (1990) and some of the first applications to fisheries survey data were by Swartzman *et al*. (1992, 1994, 1995). Further, their use in diverse fisheries applications has grown (Cury *et al*., 1995; O'Brien and Rago, 1996; Maravelias and Reid, 1997; Bigelow *et al*., 2006; Hazin and Erzini, 2008; Tserper *et al*., 2008; Voss *et al*., 2008; Murase *et al*., 2009; Sagarminaga and Arrizabalaga, 2010), and useful applications to spawner-recruit-environment models have been reported (Jacobson and MacCall, 1995; Daskalov, 1999, Planque and Frédou, 1999; Cardinale and Arrhenius, 2000; Chen *et al*., 2005; Bartolino *et al*., 2008).

GAMs model the data non-parametrically by using scatterplot data smoothers. Smoothers are tools for summarizing the trend of a response measure as a function of one or more parameter measurement. An important property of a smoother is its non-parametric nature since it does not assume a rigid form for the dependence of the response variable on the parameter variable (Megrey *et al*., 2005). Further, Cardinale and Arrhenius (2000) showed that the GAMs are a powerful technique for defining and quantifying the intricate multidimensional relationship between biotic and abiotic variables involved in recruitment processes.

i. Model selection

Since recruitment is a count variable (number of recruits), the error distribution used for the application of the GAM is a Poisson distribution (Zuur *et al.*, 2007) and the link function was the log of the response variable. Therefore, a GAM with Poisson distribution and log-link function was applied to the data, where the variance and the mean were assumed to be the same:

$$E(\mathrm{Y}) = \mu \qquad \text{and} \qquad \mathrm{var}(\mathrm{Y}) = \mu \tag{13}$$

Different models were built using all the possible combinations of response variables. Further, model selection was undertaken based on the lowest Akaike Information Criterion (AIC) test statistic (Chambers and Hastie, 1992). The AIC for an additive model is defined by (Zuur *et al.*, 2007):

$$AIC = -2\log(Likelihood) + 2df \tag{14}$$

AIC is a function of both the log likelihood function and the effective number of parameters being estimated; it accounts simultaneously for the degrees of freedom used and the goodness of the fit (Daskalov, 1999). The model with the lowest AIC is considered to have the best number of parameters to include in the final model.

Lastly, the residuals homogeneity (plotting residuals against the predicted values) and independence (plotting residuals against each explanatory variable) were checked. Further, residuals were tested to check whether they were normally distributed by means of plots such as residuals distribution histogram and QQplot and also using Shapiro-Wilk test. The autocorrelation of the residuals was checked by the autocorrelation function (ACF). Finally, the existence of any influential observation was analysed by the Cook distance function.

As the latest step, in order to compare the environmentally modified Ricker S-R model and the generalised additive model, fitting of both models was checked together.

Environmentally modified Ricker model was performed using the R statistical software available from the Comprehensive R Archive Network (http://cran.r-project.org), whereas GAMs were performed using the BRODGAR 2.5.9 program (www.brodgar.com).

RESULTS

1. Parameter selection

Table 8 presents a ranking of recruitment success cut-off point sets proposed by the methodology, together with their corresponding estimated performance measures. It also shows the selected parameters, and the stability score of each set of variables, for each of the cut-off point set (or recruitment levels definition).

The max_mean_tp discretization method suggested 1.08 and 1.81 as the cut-off points for hake recruitment success (TP_mean: 0.89). Besides, this set was found to present the highest accuracy value (90.91%) and the lowest brier score (0.048) compared to the rest of the sets proposed by the method. Additionally, the cut-off point sets of 1.14 and 1.81 accomplished a balanced true positive distribution between the different intervals, with also good scores for TP_mean and accuracy. Although the rest of the cut-off point sets showed better TP_mean and accuracy values than the last set (1.14 and 1.81), they were discarded due to the unbalanced distribution of the number of instances and the true positive values within each interval.

With reference to the multivariate parameters selection results, the transport index estimated from potential energy anomalies (TPEA) and Northern Hemisphere temperature anomaly for the February-July months (NH_temp_anom_FJ) were the two variables selected by the CFS for all the cut-off point sets presented in Table 8. Additionally, parameters related to copepod abundance and momentum and heat fluxes were also selected by the methodology. Despite all subset of parameters scored good stability values (between 30 and 35), the first and the last subsets were selected more times (15) comparing to the rest of the subsets.

Table 8: *List of recruitment success cut-off point sets proposed by the discretization algorithm. The sets selected by the expert are shaded in grey and the maxim performance scores are highlighted in bold. Note: only the sets showing the best performance values are presented in the table, from the whole list proposed by method. Ins1, Inst2 and Inst3 refers to as the number of instances at low, medium and high recruitment success, respectively; TP1, TP2 and TP3 stands for the positive score of each recruitment success interval*

Hake recruitment success discretization in 3 bin

Wrapper *max_mean_TP* **or** ***max_accuracy*** **(100 bootstrapps)**

CutPoint1	CutPoint2	#Inst1	#Inst2	#Inst3	TP1	TP2	TP3	TP mean	Accuracy	Brier Score	CFS St.	CFS
1.08	1.81	8.8	17	6.1	0.96	0.89	0.83	**0.89**	**90.91**	**0.048**	34	TPEA; NH_temp_anom_FJ; LHF_BB; Cop D3_FJ; Mean cop_FJ (15)
1.08	1.67	8.8	13.1	10.1	**0.97**	**0.96**	0.71	0.88	88.99	0.058	30	TPEA; NH_temp_anom_FJ; MMF_Porcup_Ajuly; LHF_BB; LHF_Porcup_Ajuly; Mean cop_FJ; Cop D4_May (10)
1.53	1.67	14	8	10.1	0.98	0.66	**0.91**	0.85	88.65	0.087	31	TPEA; NH_temp_anom_FJ; LHF_BB; LHF_Porcup_Ajuly (8)
1.25	1.81	11	14.9	6.1	0.88	0.88	0.8	0.85	87.53	0.064	35	TPEA; NH_temp_anom_FJ; LHF_BB; Mean cop (13)
1.14	1.81	9.9	15.9	6.1	0.84	0.86	0.82	0.84	85.54	0.078	34	TPEA; NH_temp_anom_FJ; Cop D4_FJ; Mean cop_FJ (15)

As a consequence of the above stated criteria, the shaded classifiers in table 8 were selected to continue with the following steps of the methodology. In addition to TPEA and NH_temp_anom_FJ, the subset of parameters for cut-off point set 1.08 and 1.81 was formed by latent heat flux in the Bay of Biscay (LHF_BB) and February-July copepod abundance for the whole area (Mean cop_FJ) and for the Standard area D3 (Cop D3_FJ); whereas, the subset selected for cut-off points 1.14 and 1.81 was formed by February-July copepod abundance for the whole area (Mean cop_FJ) and within the standard area D4 (Cop D4_FJ).

The univariate ranking performed for the recruitment success parameters scored better parameters concerning water temperature, heat fluxes and copepod abundances (Table 9). It should be also noted that TPEA index (the only parameter representing transport) was also selected in the two rankings. The parameters selected by the CFS (shaded in grey) are located on the upper positions of the univariate ranking, showing their importance as explanatory parameters of recruitment success.

Table 9: Univariate ranking of explanatory parameters for the selected two cut-off point sets: 1.08 and 1.81 (Max_mean TP and max_accuracy) and 1.14 and 1.81 (balanced prediction for all intervals). The parameters selected by the CFS are shaded in grey.

Max_mean_TP and max_accuracy		**Balanced prediction for all intervals**	
Score	**Parameters**	**Score**	**Parameters**
0.648	Mean cop_FJ	0.625	NH_temp_anom_FJ
0.586	NH_temp_anom_FJ	0.517	Cop D4_FJ
0.507	LHF_BB	0.509	Mean cop_FJ
0.426	Cop D4_FJ	0.381	TempAnom N
0.381	Cop D4_May	0.381	TempAnom M
0.375	TPEA	0.374	LHF_BB
0.362	LHF_Porcup_Ajuly	0.374	Mean cop
0.342	TempAnom N	0.374	NH_temp_anom
0.342	Cop D3_FJ	0.371	TPEA
0.342	TempAnom M	0.325	Mean cop_MJ
0.317	NH_temp_anom	0.32	TempAnom A_FJ
0.317	Mean cop	0.32	TindexAprilJune_CS

Table 10 compares the set of variables returned by the methodology before and after applying the "Markov Blanquet" property with the aim of reducing the number of selected parameters. In both cases, from two copepod-related variables one was discarded by the method: for 1.08 & 1.81 cut-off point set, February-July copepod abundance for D3 Standard area was the parameter rejected by the method; whereas, for 1.14 & 1.81 set mean February-July copepod abundance corresponding to the whole area was the parameter discarded. From the two sets of variables only one was selected in order to proceed with the Naïve Bayes classifier. As such, 1.08 and 1.81 were the cut-off points selected to define the three recruitment success classes (low, medium and high). Further, TPEA index, Northern Hemisphere temperature anomaly during February-July, latent heat fluxes for the Bay of Biscay and mean copepod abundance from February to July were selected as explanatory variables for hake recruitment success (shaded in grey in Table 10). Apart from showing maximum true positive and accuracy scores, the set of variables includes the latent heat flux parameter (not present in the other set of variables) which based in previous knowledge it was considered interesting as an additional explanatory variable for the model.

Table 10: Ranking of parameters subset selected before and after applying the Markov Blanquet property for the two cut-off point sets. Stability was defined as the number of times the subset of variables had been selected.

Cut-off points	Before "Markov Blanquet"	Stability	After "Markov Blanquet"
1.08 & 1.81	TPEA NH_temp_anom_FJ LHF_BB Cop D3_FJ Mean cop_FJ	15	TPEA NH_temp_anom_FJ LHF_BB Mean cop_FJ
1.14 & 1.81	TPEA NH_temp_anom_FJ Cop D4_FJ Mean cop_FJ	15	TPEA NH_temp_anom_FJ Cop D4_FJ

A graphical representation of the Naïve Bayes classifier can be observed in Figure 74. It represents the *a priori* distribution of hake recruitment success, where medium recruitment success was the most predominant (54%), followed by low (28%) and high (18%) recruitment success categories.

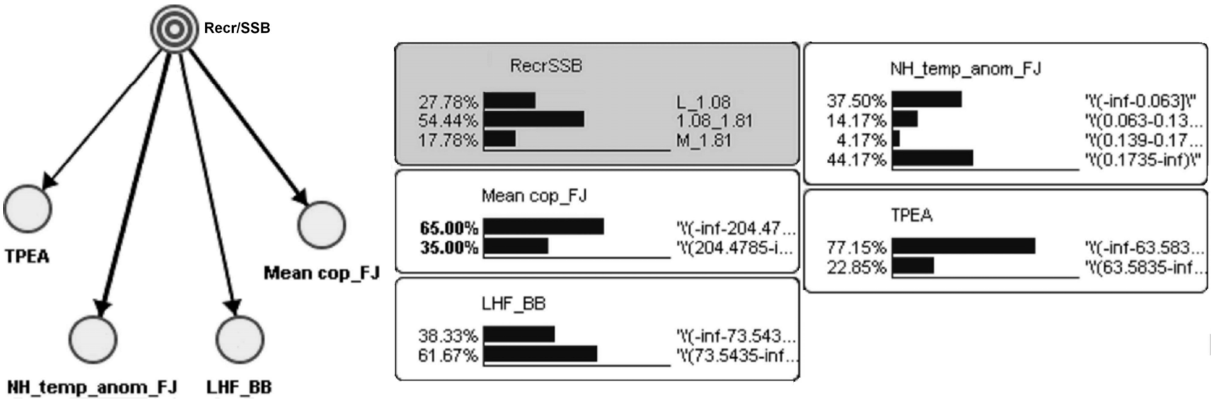


Figure 74: Naïve Bayes representation of the relationship between parameters selected and hake recruitment success.

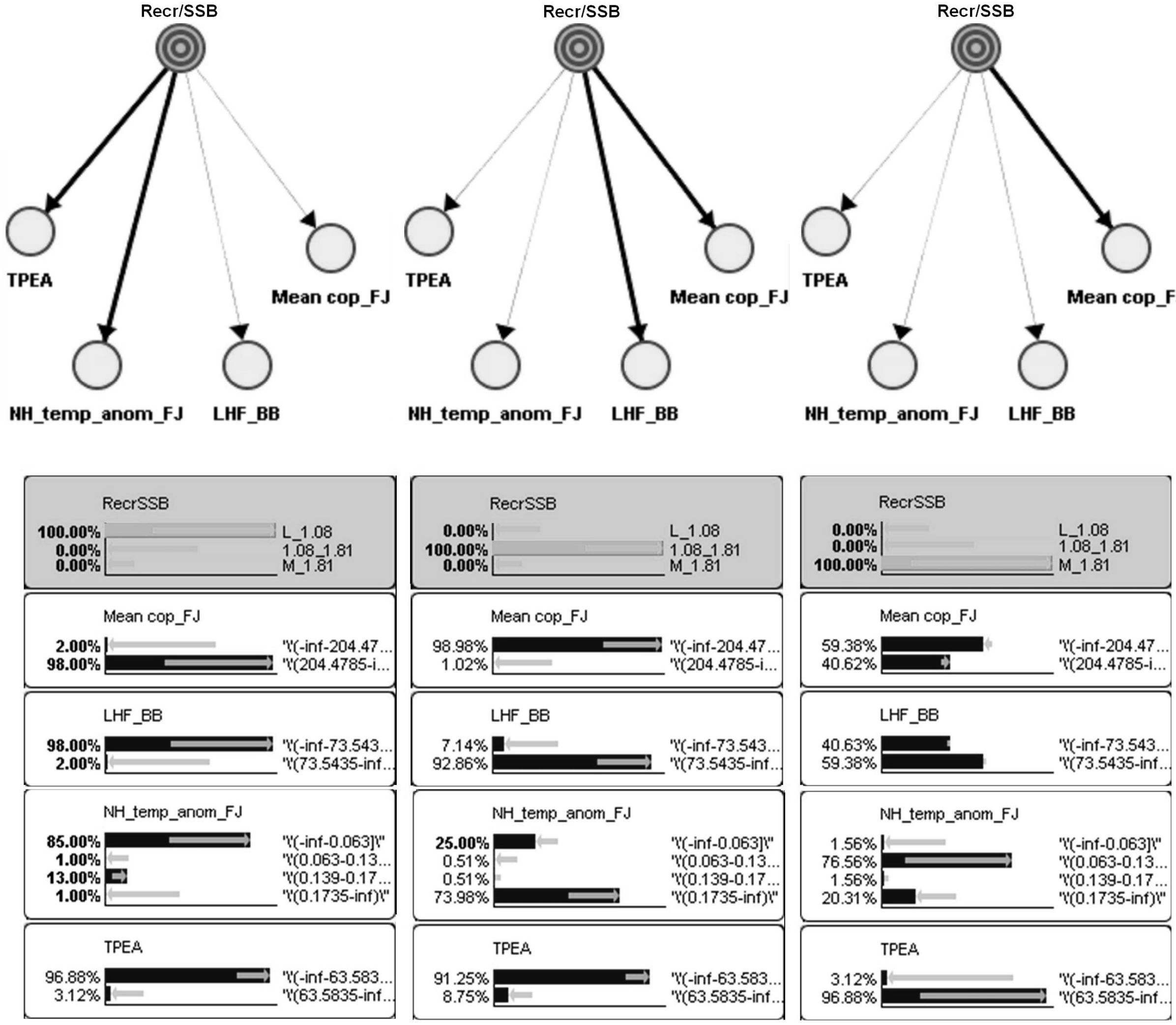


Figure 75: Selected parameters behaviour for low, medium and high recruitment success scenarios. The thickness of the arrow represents the strength of the probabilistic relationship.

In Figure 75 different scenarios for hake recruitment success are found: low recruitment success was characterised by low TPEA index values and low Northern Hemisphere temperature anomalies during hake spawning period (February-July); medium recruitment success was characterised by low copepod abundance values from February to July and high latent heat fluxes in the Bay of Biscay; and, high recruitment success episodes were characterised by probable low copepod abundance values. It should be noted that TPEA index classifies better high recruitment success instances, but the probabilistic relationship between both parameters is very weak (represented with a thin arrow).

2. Recruitment modelisation

In addition to the spawning stock biomass (SSB), the environmental parameters included in both models were as follows: mean copepod abundance (February-July), NH temperature anomaly (February-July) and LHF in the Bay of Biscay. It should be noted that TPEA index was not introduced in the models because the time-series was not complete.

Data exploration

In Figure 76, the response variable (recruitment) is plotted by means of boxplot and dotplot; in spite of the fact that two possible outliers appear in the boxplot (on the left), there were not so clear in the dotplot (on the right), and thus it was decided to keep those two points for the analysis. Regarding the explanatory variables, none parameter showed any outlier in the boxplots (Figure 77) or in the dotplots (Figure 78).

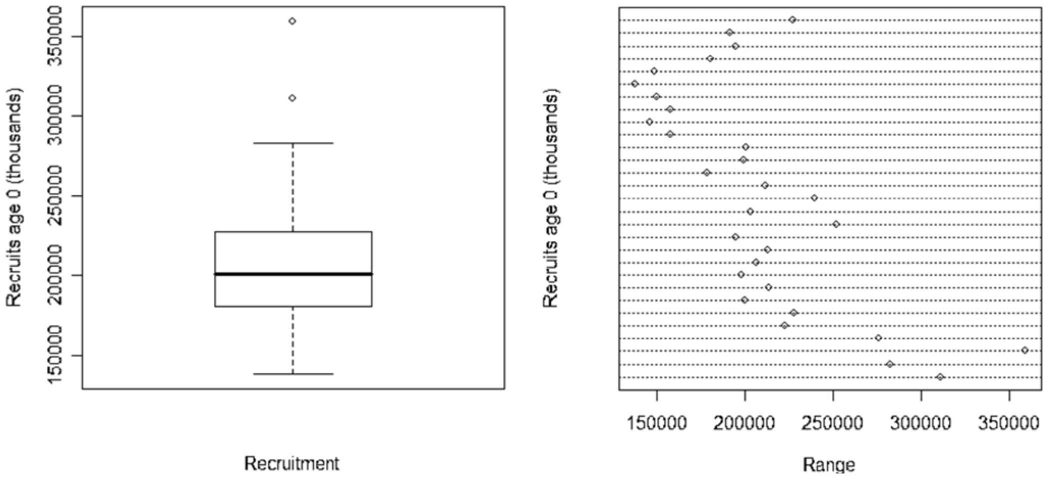


Figure 76: Boxplot (left) and dotplot (right) of northern hake recruitment.

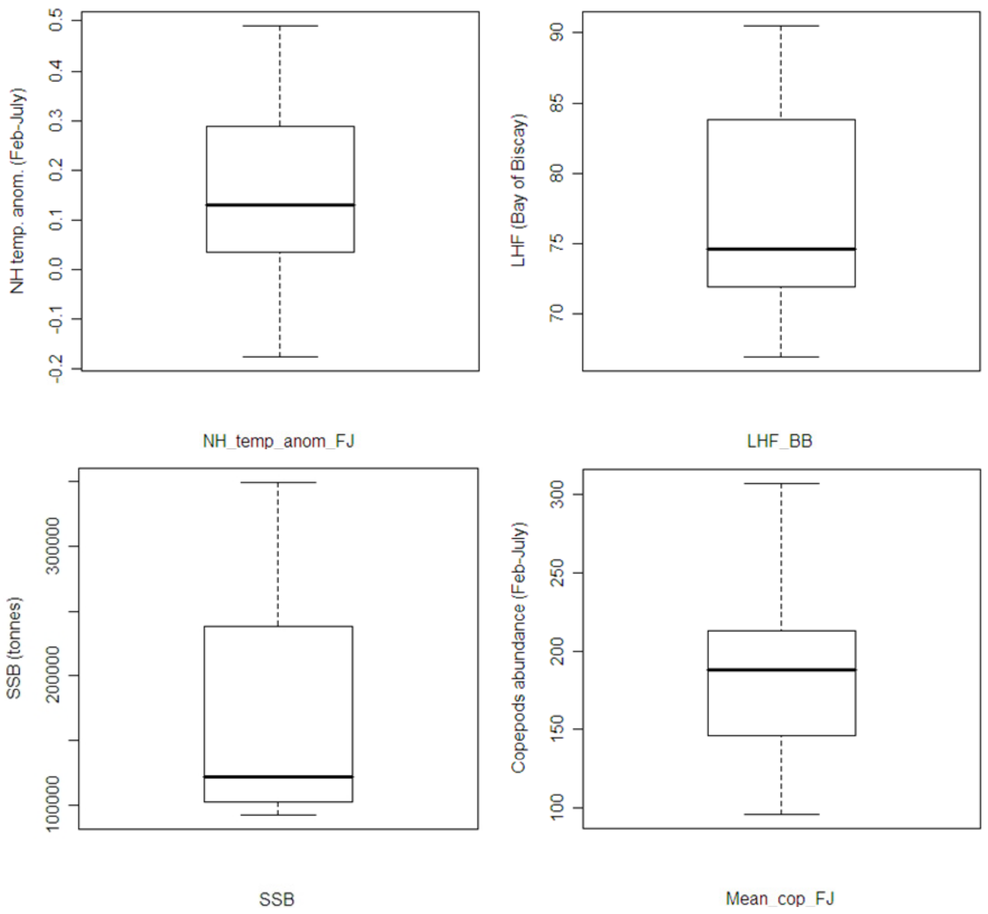


Figure 77: Boxplots of four explanatory variables selected for the model.

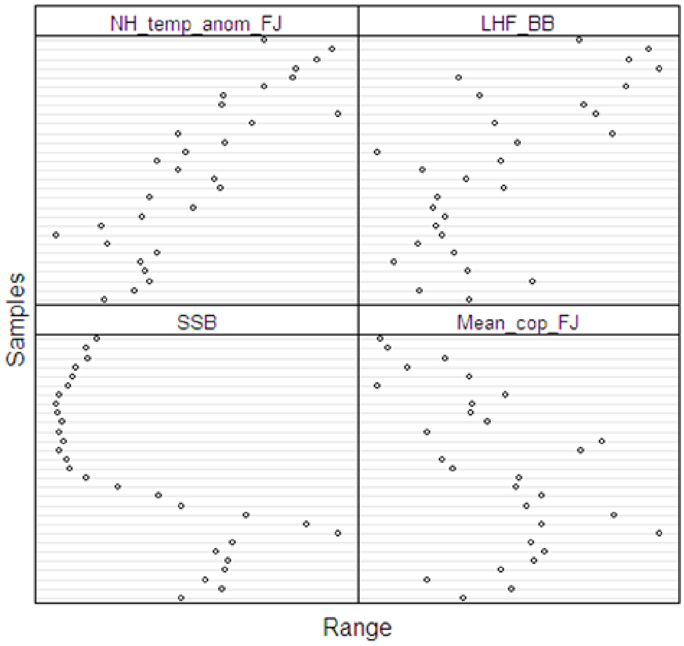


Figure 78: Multipanel Cleveland dotplots of explanatory variables selected for the model.

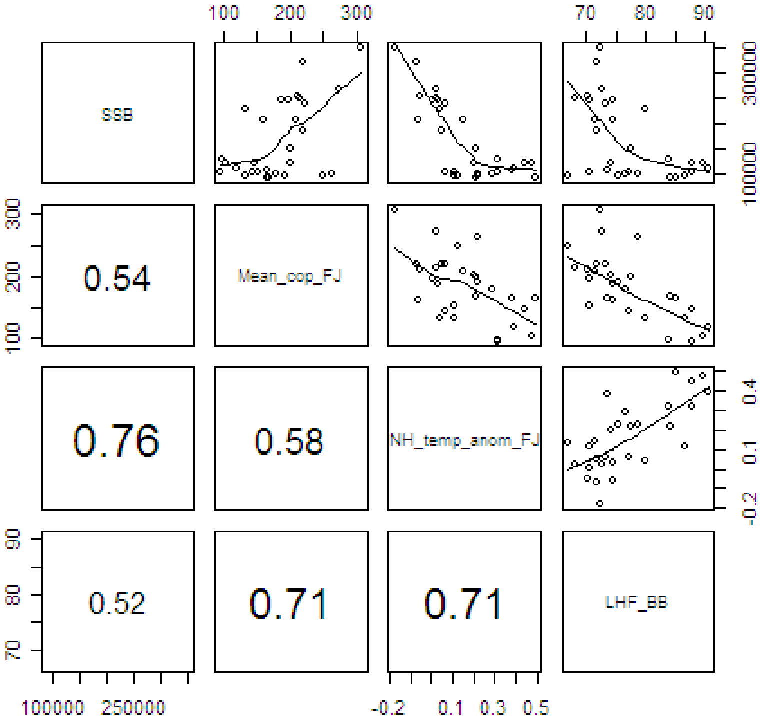


Figure 79: Pairplot of four explanatory variables. The lower diagonal panels contain the correlation coefficients, and their font size is proportional to the value.

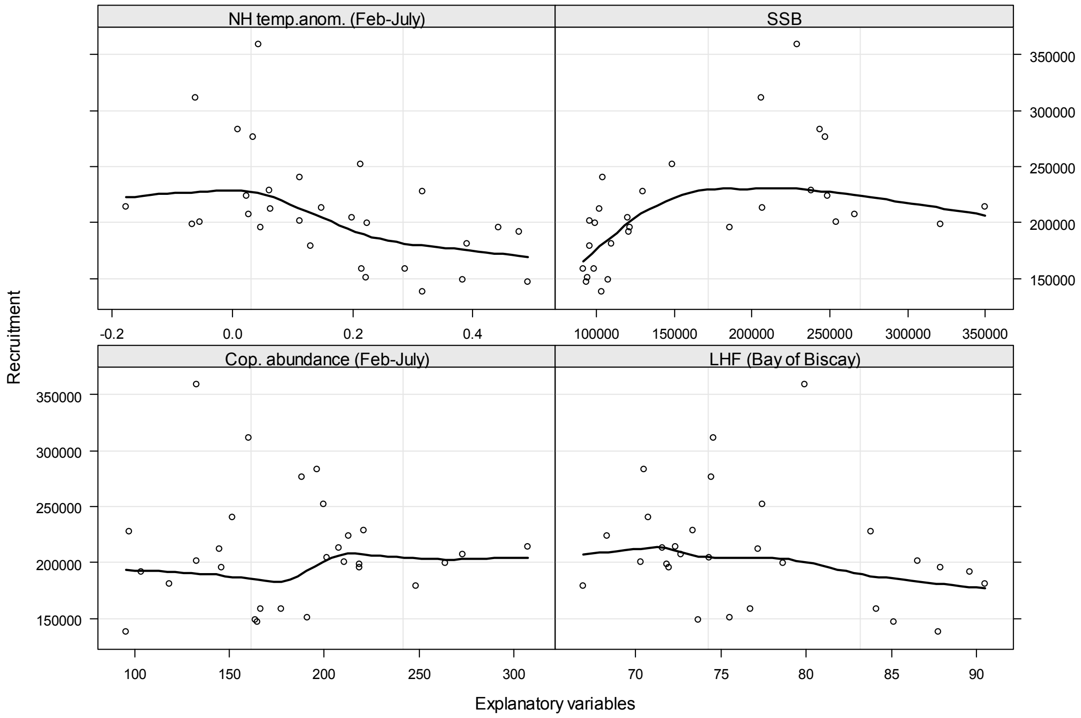


Figure 80: Multipanel scatterplot showing relationships between each of the explanatory parameters and hake recruitment.

The pairplots in Figure 79 represent the relationship between parameters. The correlation coefficients between the explanatory variables were less than 0.8 so we accepted that there was not colinearity between them (Zuur and Ieno, pers. comm).

The multipanel scatterplot in Figure 80 explores the relationships between recruitment and the four explanatory variables and it checks if they are linear or not in order to decide between a GAM and a GLM. Since no clear linear relationship can be appreciated in the figure, a priori it seems more appropriate the idea of building the model using a GAM.

From the graphical data exploration, it was concluded that there was no need for data transformation (no outliers) and no parameter was found to be redundant (no colinearity) when explaining hake recruitment variability. Further, GAM was found to be more appropriate in order to explain recruitment variability (no clear linear relationship). In spite of this fact, both a generalized linear model (environmentally modified Ricker) and a generalized additive model (non-linear approach) were applied with the aim of comparing the stock-recruitment-environment relationship of both models.

a. Environmentally modified Ricker S-R relationship

i. Model selection

Table 11 summarises all the different Ricker models that were built with environmental parameters selected at the “parameter selection” section. The environmentally modified Ricker with NH temperature anomaly FJ and copepod abundance FJ explained the highest percentage of variability of hake recruitment (85.70%; $p<0.01$). It should be noted that while both environmental parameters were not significant (NS, copepod abundance) or were less significant ($p<0.05$, temperature anomaly) when they were added separately to the model, they both were highly significant when combined in the same model. In contrast, LHF (Bay of Biscay) was not significant for any of the different models.

Table 11: *Different environmentally modified Ricker S-R relationships. The most significant model is shaded in grey.*

	MODEL	**Coefficients**		**p-value**	**% expl. var**
Environmentally modified Ricker (one parameter per model)	Recruitment ~ SSB + Copepod abundance FJ	Intercept	0.9359	p<0.001	80.60%
		SSB	-3.71E-06	p<0.001	
		Cop	-1.20E-03	NS	
	Recruitment ~ SSB + NH tempanom FJ	Intercept	1.191	p<0.001	81.96%
		SSB	-5.23E-06	p<0.001	
		NH tempanom	-6.24E-01	p<0.05	
	Recruitment ~ SSB + LHF_BB	Intercept	1.009	p<0.001	78.72%
		SSB	-4.13E-06	p<0.001	
		LHF_BB	6.69E-04	NS	
Environmentally modified Ricker (all parameters)	Recruitment ~ SSB + Cop FJ + NH tempanom FJ + LHF_BB	Intercept	1.14E+00	p<0.001	85.80%
		SSB	-4.93E-06	p<0.001	
		Cop	-1.56E-03	NS	
		NH tempanom	-8.67E-01	p<0.001	
		LHF_BB	2.97E-03	NS	
Environmentally modified Ricker (all parameters)	Recruitment ~ SSB + Cop FJ + NH tempanom FJ	Intercept	1.13E+00	p<0.001	85.70%
		SSB	-4.89E-06	p<0.001	
		Cop	-1.75E-03	p<0.05	
		NH tempanom	-8.03E-01	p<0.01	
Environmentally modified Ricker (Cop + LHF)	Recruitment ~ SSB + Cop FJ + LHF_BB	Intercept	9.57E-01	p<0.001	81.36%
		SSB	-3.84E-06	p<0.001	
		Cop	-1.76E-03	NS	
		LHF_BB	-7.14E-03	NS	
Environmentally modified Ricker (NH tempanom + LHF)	Recruitment ~ SSB + NH tempanom FJ + LHF_BB	Intercept	1.19E+00	p<0.001	83.67%
		SSB	-5.25E-06	p<0.001	
		NH tempanom	-9.16E-01	p<0.05	
		LHF_BB	1.04E-02	NS	

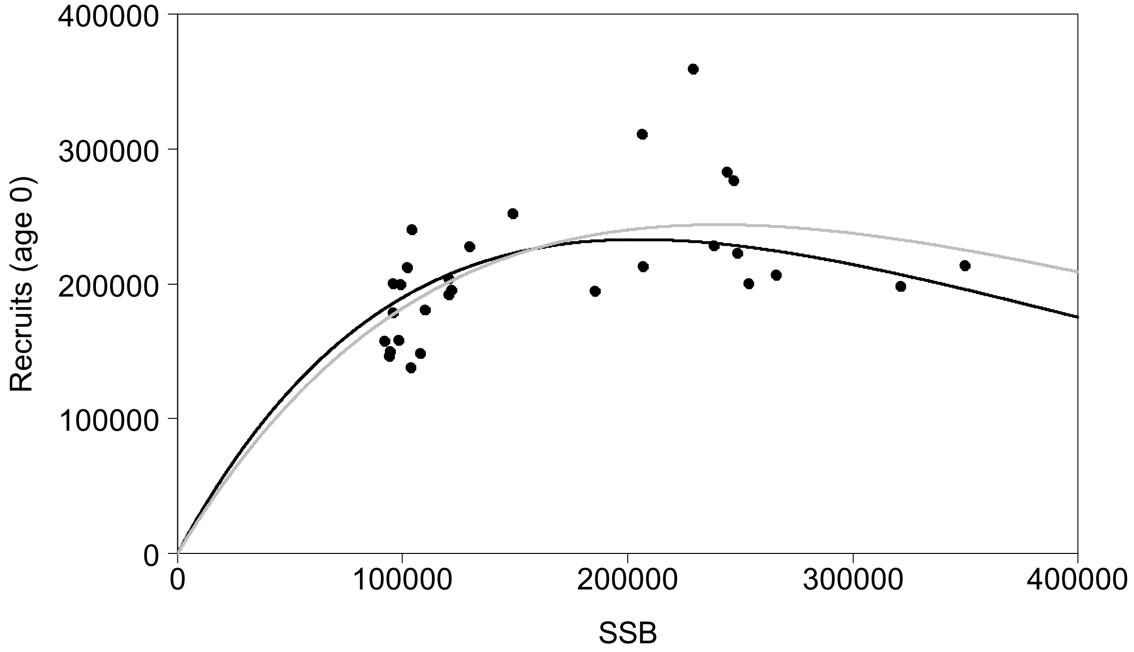


Figure 81: Ricker stock-recruitment relationship (in grey) and environmentally modified Ricker S-R relationship (in black) under February-July copepod abundance and Northern Hemisphere temperature anomaly influence.

The selected environmentally modified model is described by the following Ricker relationship:

$$R = 3.09 \cdot SSB \cdot e^{(-SSB \cdot 4.89 \cdot 10^{-6} + Cop \cdot 1.75 \cdot 10^{-3} + NHtempanom \cdot 8.03 \cdot 10^{-1})}$$

Figure 81 compares the Ricker model described in Chapter II (recruitment under SSB influence) to the environmentally modified Ricker model built under the influence of NH temperature anomaly FJ and copepod abundance FJ.

ii. Model validation

Residuals of the model showed quite homogeneous distribution at medium recruitment levels; there seems to be an underestimation at low and high recruitment levels. Normality was validated on the QQplot and demonstrated by the Shapiro-Wilk normality test (p>0.05). Further, no outliers were found checking the Cook’s distance (Figure 82).

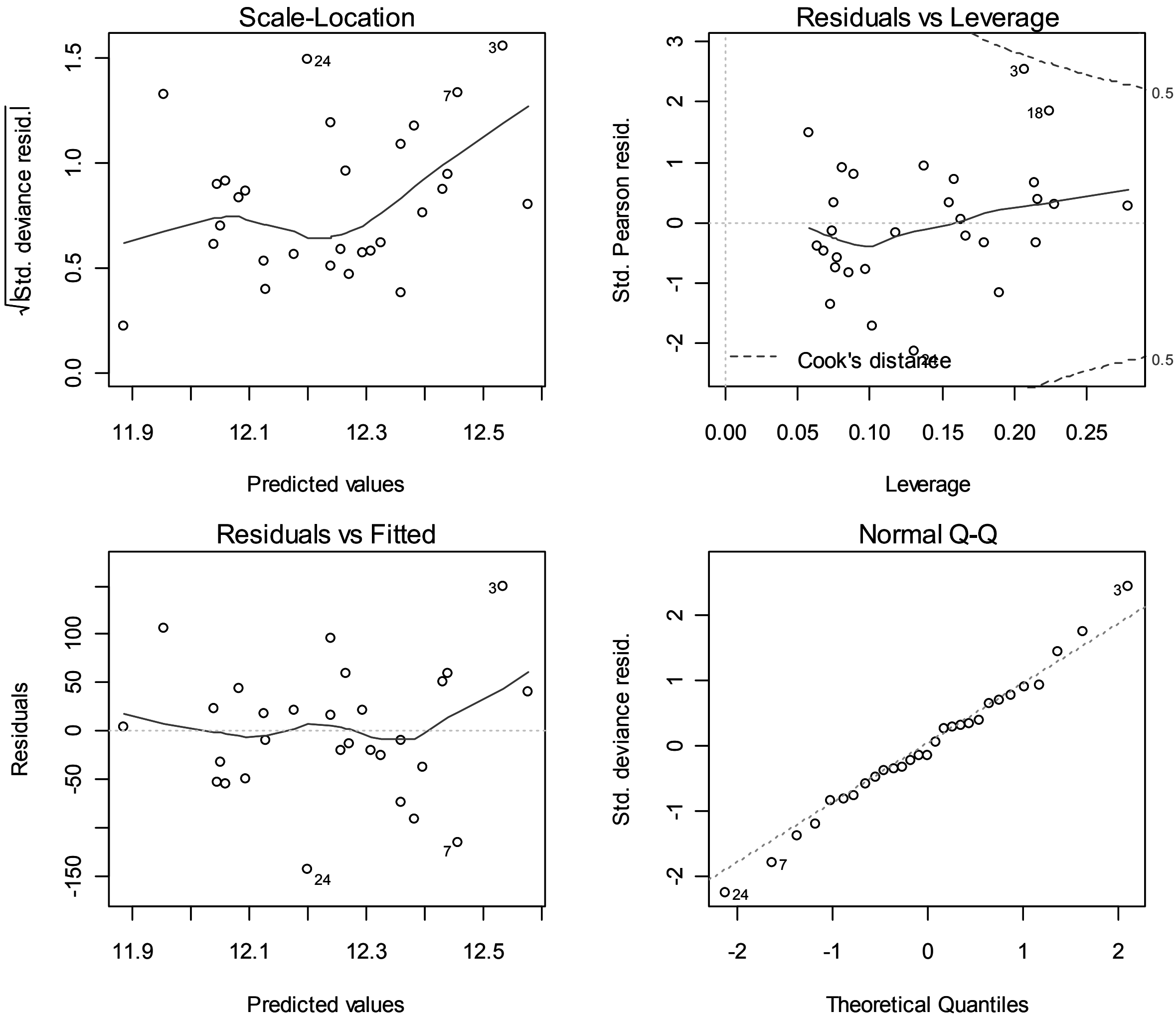


Figure 82: *Graphical representation of the residuals of the environmentally modified Ricker stock-recruitment relationship.*

b. GAM

i. Model selection

The GAM model with Poisson distribution and log-link showed the following results:

Deviance = 168045.59

Residual degrees of freedom = 24

Deviance/df.residual = 7001.9 >>>>> 1

In order to see if there was overdispersion, we divided deviance by the number of residual degrees of freedom. Since such division gave a number much higher than 1, the model was highly overdispersed and we could not accept the assumption of the mean being the same as the variance. Consequently, a quasi-Poisson GAM was applied, in which the mean of recruitment equals mu, and its variance rho * mu. Since the model was still overdispersed, a binomial negative distribution was selected, which showed the following deviance and residual degrees of freedom values.

Deviance = 24.05
Residual degrees of freedom = 24
Deviance/df.residual = 1

In this case, the division was equal to 1 which meant that the variance and the mean were the same and thus there was no overdispersion. In the binomial distribution (Hilbe, 2007) the mean and variance of Y are given by:

$$E(\mathrm{Y}) = \mu \qquad \text{and} \qquad \mathrm{var}(\mathrm{Y}) = \mu + \frac{\mu^2}{k} \tag{15}$$

where k is called the dispersion parameter. If k is large relative to μ^2, the term μ^2/k approximates 0, and the variance of Y is μ; in such cases the negative binomial converges to the Poisson distribution (Zuur *et al.*, 2007). The negative binomial distribution is for discrete and non-negative data and thus, it was an appropriate distribution to be used when modelling hake recruitment fluctuations over time.

Table 12 summarises the different models built and the corresponding AIC value for each combination of parameters, criteria used to select the optimal model. M11, the model with SSB, copepod abundance and NH temperature anomaly as covariates showed the lowest AIC value, and therefore those parameters were used to build the final recruitment model.

Table 12: Different models resulted from the combination of the SSB and the three environmental parameters selected. The model showing the lowest AIC value is shaded in grey.

Model	SSB	Cop	NH tempanom	LHF	AIC
M1	Yes	-	-	-	692.45
M2	-	Yes	-	-	709.90
M3	-	-	Yes	-	698.98
M4	-	-	-	Yes	707.68
M5	Yes	Yes	-	-	683.41
M6	Yes	-	Yes	-	678.55
M7	Yes	-	-	Yes	693.91
M8	-	Yes	Yes	-	695.39
M9	-	Yes	-	Yes	707.25
M10	-	-	Yes	Yes	699.62
M11	Yes	Yes	Yes	-	655.65
M12	Yes	Yes	-	Yes	676.25
M13	Yes	-	Yes	Yes	679.33
M14	-	Yes	Yes	Yes	700.59
M15	Yes	Yes	Yes	Yes	687

Since a relationship between copepods and SST has been widely reported in the bibliography (see Chapter III), the interaction between such parameters (smoothed and non-smoothed) was added to the model as an additional covariate. Therefore, the following three models were built and compared in order to select the optimal for the explanation of the recruitment variability:

Model 1: Recruitment ~ s(SSB) + s(cop) + s(NH temp anom)
Model 2: Recruitment ~ s(SSB) + (cop:NH temp anom)
Model 3: Recruitment ~ s(SSB) + s(cop:NH temp anom)

Table 13 summarises the results of the three GAM models performed. Model 1 showed the lowest AIC value and it explained the highest percentage of the deviance (96.4%), followed by Model 3 and Model 2. Therefore, the best model was with no interaction between copepod abundance and temperature anomaly. The shape of the smoothers of the explanatory variables for the selected model (Model 1) can be found in Figure 83.

Table 13: Different GAM modes with SSB, copepod abundance (Cop) and Northern Hemisphere temperature anomaly (NHTempAnom) as explanatory variables. The model showing the lowest AIC value is shaded in grey.

	Coef	test⍰	p-value	AIC	Deviance explained
Model 1	s(SSB) s(Cop) s(NHTempAnom)	13.373 5.300 5.506	p<0.001*** p<0.01 ** p<0.01 **	655.65	96.4%
Model 2	s(SSB) Cop*NHTempAnom	4.195 -2.786	p<0.01 ** p<0.05 *	685.69	74.2%
Model 3	s(SSB) s(Cop*NHTempAnom)	11.29 18.12	p<0.001 *** p<0.001 ***	660.97	91.7%

⍰F-test when smoothed variables (the value shown is the smoother)
t-test when non-smoothed variables (the value shown is the coefficient)

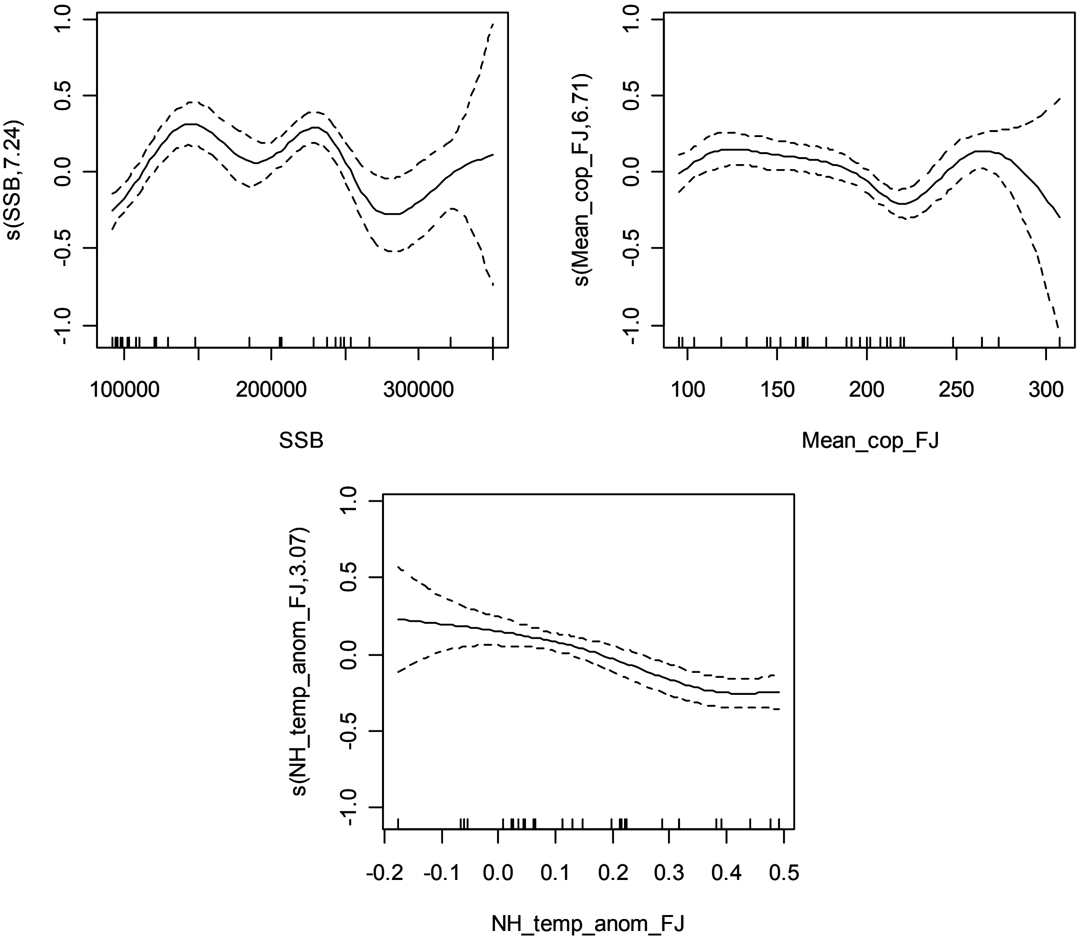


Figure 83: The shape of the estimated smoothing curves for the optimal GAM model.

ii. Model validation

Homogeneity of residuals was confirmed plotting standardised residuals against fitted values (Figure 84), whereas the independence of the residuals can be seen in Figure 85.

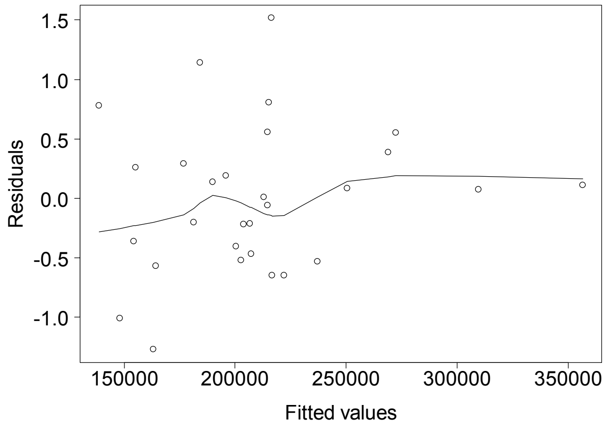


Figure 84: Standardised residuals plotted against fitted values.

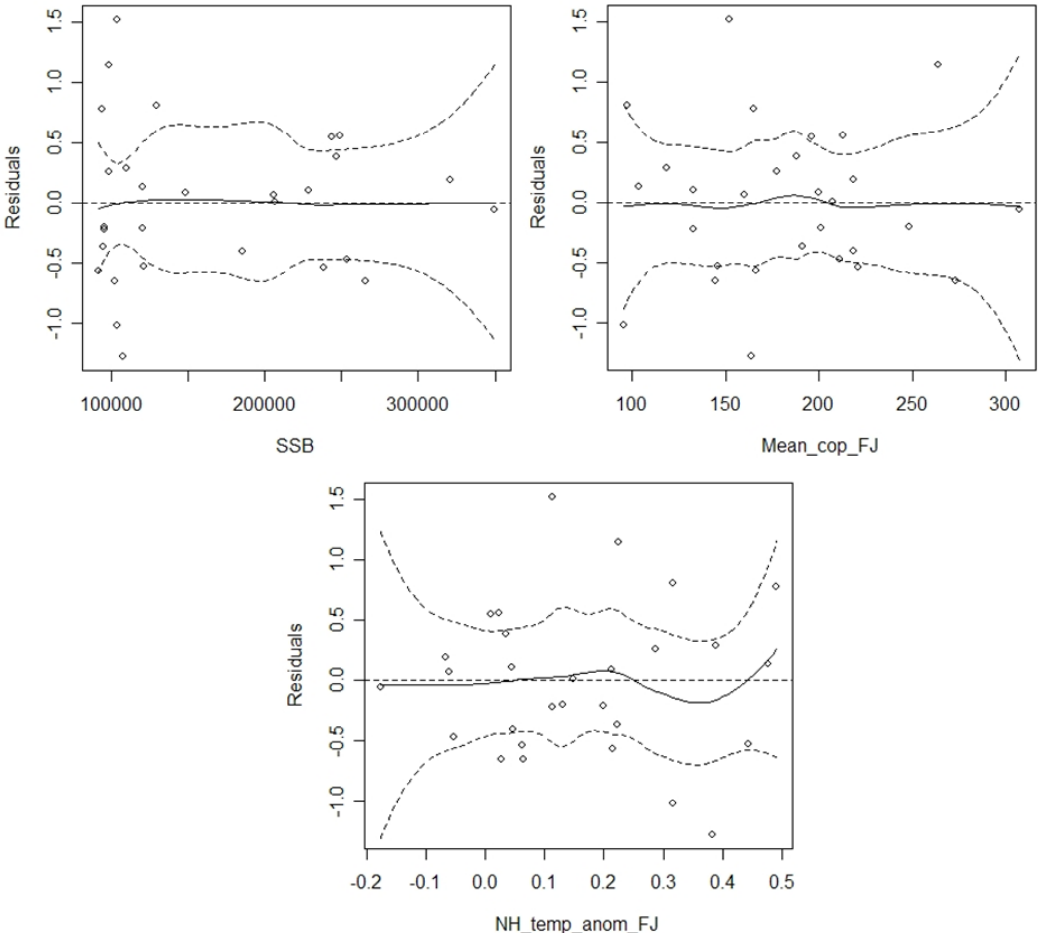


Figure 85: Scatterplots showing residuals against each explanatory variable of the selected model.

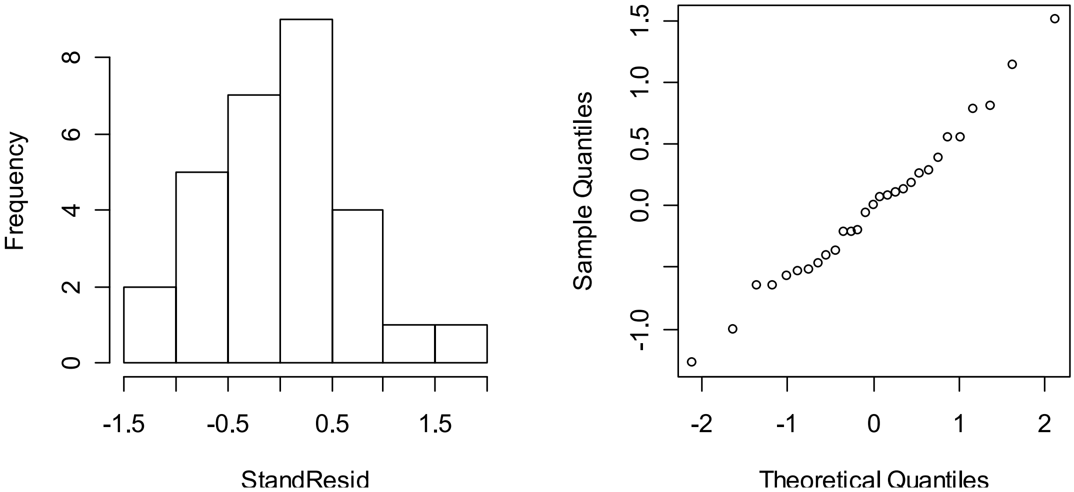


Figure 86: Histogram of standardised residuals (left) and QQ-plot (right).

Looking at the histogram and the QQ plot (Figure 86), residuals fill the assumption of normality. Shapiro-Wilk normality test confirmed the result ($p>0.05$). The ACF function of residuals (showing no autocorrelation for any lag time) and the Cook distance function (showing no influential observation) can be found in Figure 87. Summing up, residual plots did not show any signal of violations of the model assumptions.

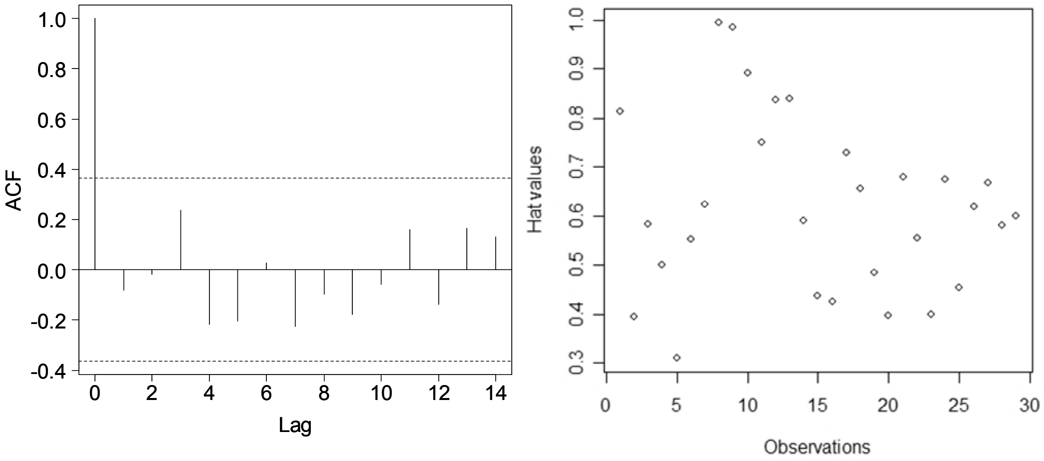


Figure 87: Autocorrelation function of residuals (left) and scatterplot for the identification of any influential observation (right).

c. Model fitting comparison

It should be noted that the best models selected for both cases included temperature anomaly and copepod abundance as explanatory variables, in addition to the spawning stock biomass. However, comparing the fitting of both models (Figure 88), environmentally modified Ricker model result did not fit very well with the observed recruitment values (R^2=0.61, 0<0.001). Instead, in the second case, the fitting between the GAM model result and the observed values improved significantly (R^2=0.97, 0<0.001).

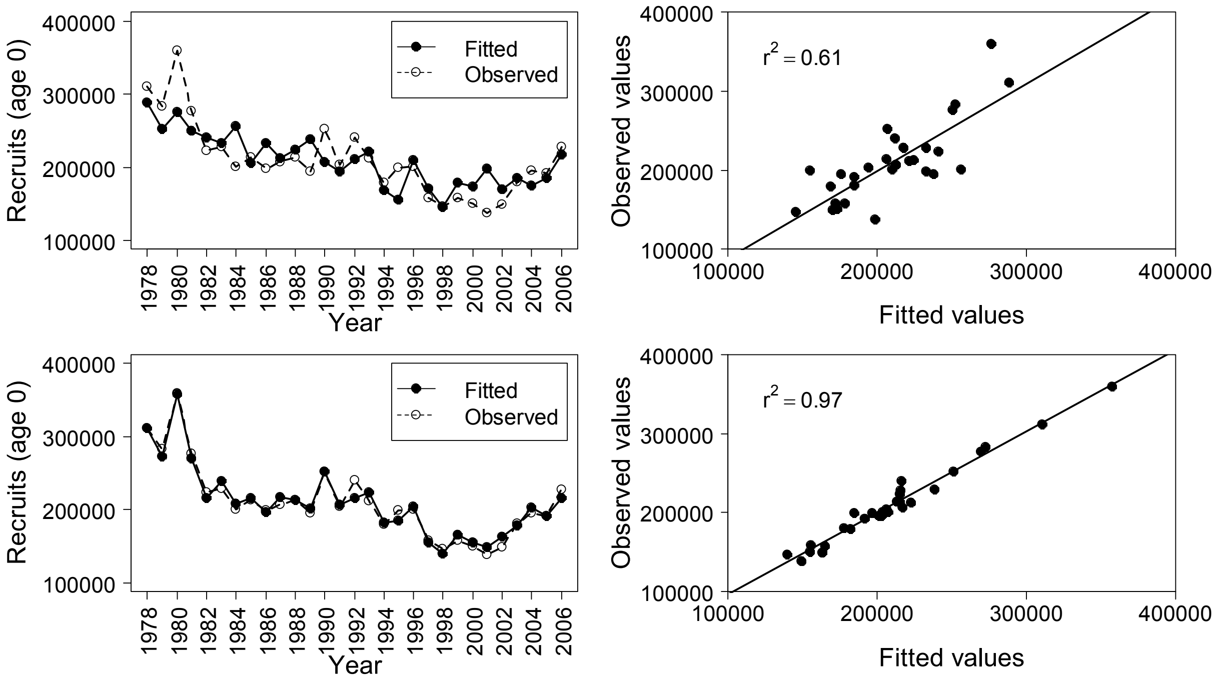


Figure 88: Fitting comparison between the environmentally modified Ricker model (above) and the GAM model (below). On the left, fitted and observed recruitment values over time; on the right, model adjustment with the corresponding R-squared value.

DISCUSSION

The introduction of environmental influence when studying annual recruitment to fish stocks reduces the uncertainty in stock assessment. However, when a large number of environmental parameters are considered, there is the risk of exaggerating the ability to predict recruitment (Francis, 2006). In such cases, it is critical to perform a selection of potential parameters to be introduced in the model.

Machine learning techniques (supervised classification methods) were used in order to reduce the large number of potentially affecting environmental parameters, and to select only those with a major effect on recruitment success forecast. It should be noted that good forecasts may be limited when available data are sparse and “noisy” (Francis, 2006), as it is the case for environmental data. However, machine-learning techniques have been proposed as an appropriate approach with some desirable properties to address small and incomplete data sets (Uusitalo, 2007; Fernandes *et al*., 2010).

From the large dataset presented to the methodology, it only selected four parameters which are believed to be enough for classifying hake recruitment success into low (lower than 1.08), medium (from 1.08 to 1.81) and high (higher than 1.81) levels. The factors that are influential during hake early life stages, that is, the trajectory from eggs until they recruit to the population, are as follows: the annual transport index (TPEA), annual latent heat fluxes in the Bay of Biscay (LHF_BB), sea surface temperature anomaly over the Northern Hemisphere from February to July (NH_temp_anom_FJ) and mean copepod abundance in waters around the UK and Ireland from February to July (Mean cop_FJ). It should be noted that while transport and heat fluxes are influential as annual average values, temperature anomaly and copepod abundance parameters are influential during the hake spawning season defined by ICES (February-July).

According to the discretization performed by the methodology, along the study period 1978-2006, more than half of the years showed medium recruitment success, whereas less than 30% of the years produced low recruitment success and only around 18% of the years recorded high recruitment success values. Further, low recruitment success years were characterised by low transport values and colder than average temperature values at the Northern Hemisphere. Medium recruitment success was found with high latent heat fluxes in the Bay of Biscay and low copepod abundances from February to July. Lastly, high recruitment success years were recorded coinciding with probable low copepod abundances. Plankton integrates temperature effect throughout its whole life cycle, so it is not surprising that the link between plankton and fish for example can be higher that the link between temperature and fish (Beaugrand *et al*., 2003), as it may be the case for medium and high recruitment levels.

Previous chapters focused on recruitment success (recruitment/SSB) as the dependent variable, with the main objective of exploring environmental influence on the survival of early life stages, independently from the parental stock influence on recruitment. This chapter attempts to model recruitment variations taking into account both, density-dependent and density-independent features. For that purpose, hake spawning stock biomass was introduced in the models, as additional explanatory variable. Despite selected by the methododology, TPEA was not introduced in the models since the time-series was not complete and it had missing values that were not allowed when building the models. However, its importance as an explanatory variable must be highlighted since it can control the drift of larvae to either nursery areas or offshore (Álvarez *et al*., 2001; Agostini and Bakun, 2002); additionally, it may drive the dispersion and retention of plankton, hake juvenile main trophic resource.

Summing up, recruitment variability was modelled under the influence of SSB representing the density-dependent part, and Northern Hemisphere temperature anomaly, copepod abundance and latent heat fluxes as density-independent features. To do so, two different models were selected: an environmentally modified Ricker S-R model and a GAM with no prior assumption regarding the relationship between stock and recruitment.

Both optimal models selected same environmental covariates as explanatory variables; latent heat flux was left out of the models, whereas Northern Hemisphere temperature anomaly and copepod abundance, both representing February-July period, remained in the last models.

Elsewhere, temperature has been reported as an influential factor for several species. As such, Cury *et al*. (2008) concluded that temperature can modulate species distribution, interactions and trophodynamics, though its effect on physiology. It has also been found that temperature influences marine fish metabolism (Neill *et al*., 1994; Pörtner and Peck, 2010); higher temperatures contribute to increased development rates and thus enhanced growth during early life stages (Ottersen and Sundby, 1995; Fiksen and Slotte, 2000). This implies a reduction in the time spent in vulnerable life stages and thus a greater survival of larvae and juvenile individuals, with the subsequent increase in recruitment success. For cod, temperature affects juvenile growth and survival (Planque and Frédou, 1999; Clark *et al*., 2003; Vikebo *et al*., 2005). Regarding hake species, water temperature plays an important role in egg development and larval growth (Steves and Cowen, 2000). Morales-Nin and Moranta (2004) reported that Mediterranean hake survival during early life stages was related to growth, because periods with faster growth rates produced greater abundances. In contrast, Bartolino *et al*. (2008) found that positive thermal anomalies in summer resulted in a decrease in the number of recruits in autumn.

Climate impact on populations can affect either directly through metabolic and reproductive processes, or indirectly through the ecosystem (prey, predators and competitors) (Stenseth *et al*., 2002; Vikebo *et al*., 2005). In the case of the northern hake, temperature impacts directly on physiology, whereas the indirect influence comes by affecting copepods, larvae and juvenile main prey. Beaugrand *et al*. (2002) demonstrated a strong northward biogeographical shift in copepods related to both the increasing trend in Northern Hemisphere temperature and the North Atlantic Oscillation. Hake larvae feed upon copepods (Reiss *et al*., 2005), which highlights copepod abundance importance as an explanatory variable.

In addition, SSB was also found to be a significant factor for hake recruitment. Although, in the Ricker model SSB was part of the function from the beginning, in the second model (non-parametric approach) it was freely selected by the model due to its significant contribution to the explained variance (data do not include 0,0 point). This is in accordance with other studies that found density-dependence as an aspect that must be considered (Rothschild *et al*., 2005). Ottersen and Sundby (1995) concluded that both environmental and spawning stock biomass issues should be considered; spawning stock biomass is nearly as important as high sea temperature values during early life stages. According to Cook (2000), the dynamics of an exploited stock will depend on the recruits, i.e. the number of offspring produced by the spawning biomass, but also on the subsequent survival of these fish into the future spawning biomass, which is in turn dependant on the environment.

The environmentally modified Ricker stock-recruitment model, explained 85.70% of the hake recruitment variability, with Northern Hemisphere temperature anomaly and copepod abundance during the spawning period as covariates of the spawning stock biomass. Similarly, the best GAM model selected temperature anomaly, copepod abundance and SSB as explanatory variables, but this model explained 96.4% of the variability. Consequently, even if the same covariates were selected in both models, the non-parametric approach accounted for more of the variation and showed a better fitting than the Ricker S-R mode. This highlights that although SSB is an important factor to define recruitment variability we cannot assume that this density-dependence takes a Ricker form.

Fish population dynamics are complex ecological processes affected by a multitude of inter-connected factors, whose effects are often non-linear (Bjornstad and Grenfell, 2001). Generalized additive modelling is a highly flexible statistical approach that offers the main advantage to be able to model non-linearities that often relate biological data to environmental factors (Hastie and Tibshirani, 1990). GAMs extend the power of any conventional regression technique (e.g. GLMs) by fitting nonparametric functions to estimate relationships between the response and the predictors (Cardinale and Arrhenius, 2000). In contrast to GLMs, GAMs are not tied to any particular functional relationship (i.e., linearity) or to any statistical distribution of the data (i.e., normality). In the case of northern hake, the inclusion of environmental information in the GAM approach explained an additional 10% of the deviance compared to the GLMs.

Factors affecting recruitment in marine populations are poorly understood and often the relationship between environment and ecosystem is unknown. In such cases, applying a non-parametric approach such as GAMs is a very useful tool, above all in the case of a hardly studied species such as the northern hake as it has been demonstrated by this study. Other studies also found appropriate the use of GAMS as a suitable tool for fisheries and environmental data analysis, as a way to explore and model non-linear relationships (Daskalov, 1999; Bartolino *et al*., 2008).

General discussion

GENERAL DISCUSSION

A number of studies have focused on European hake of the Northeast Atlantic. Genetic structure of the population (Roldán *et al*., 1998; Castillo *et al*., 2005), feeding ecology (Velasco and Olaso, 1998; Mahe *et al*., 2007), growth rate studies (Álvarez and Cotano, 2005; Kacher and Amara, 2005; dePontual *et al*., 2003, 2006; Piñeiro *et al*., 2007; Domínguez-Petit *et al*., 2008), reproduction (Murua and Motos, 2006; Murua *et al*., 2006; Korta *et al*., 2010a, 2010b), egg and larvae distribution (Álvarez *et al*., 2001, 2004) are issues that have been subject of several scientific papers. Likewise, the International Council for the Exploration of the Sea (ICES) produces annual reports with the review of the stock and up-to-date biomass and recruitment estimations. These evaluations mainly aim to the assessment and correct management of the stock. However, little has been done concerning the study of the long-time variability and the likely causes of interannual fluctuations. Some references can be found regarding the southern European hake (Sánchez and Gil, 2000; Sánchez *et al*., 2003). Nevertheless, the studies on the northern European hake are scarce and they are based on particular surveys, with short temporal and small spatial coverage.

Further, a recent ICES Cooperative Research Report called “Resolving climate impacts on fish stocks” (Rijnsdorp *et al*., 2010) has investigated climate variability influence on different species. Several works have been reviewed with reference to the Mediterranean hake (Abella *et al*., 2008; Massuti *et al*., 2008); however, despite studying several species that inhabit the northeastern Atlantic, this report does not mention the northern European hake.

The lack in this area makes evident the need for further research, above all with the northern European hake as the target species. In this regard, the present thesis is an exploratory study of the influence on the environmental factors on the northern hake recruitment variability.

Northern European hake: temporal evolution

At the beginning of the study period (1978-1987), the northern hake stock was in a sustainable situation with low fishing mortality and relatively high SSB values. However, at the end of the decade, the rapid increase in fishing pressure resulted in the sharp decrease in SSB, reaching values below the limit reference point (100,000 tonnes) in the 1990s (Figure 89). At this point, the stock was being overfished and the risk of recruitment failure was high. Consequently, given the critical state of the stock, an emergency plan was implemented in 2001 and 2002 (EC 1162/2001, EC 2602/2001 and EC 494/2002). Afterwards, fishing mortality decreased considerably and SSB slightly recovered bringing the stock to a safer situation. Once above the limit SSB level, the next objective was to reach the precautionary level of 140,000 tonnes, and with that purpose a recovery plan was implemented in 2004 (Chapter II). In the recent years, the stock has continued to increase probably reaching the precautionary level in 2008 (Figure 89). According to the article 3 of the recovery plan, a management plan should be implemented when the northern hake stock meets the precautionary reference point in two consecutive years. ICES reckons that SSB has been approximately 140,000 tonnes in 2008 and 2009 (years not considered in this study) and thus, such a plan is under development by the EC (ICES, 2010).

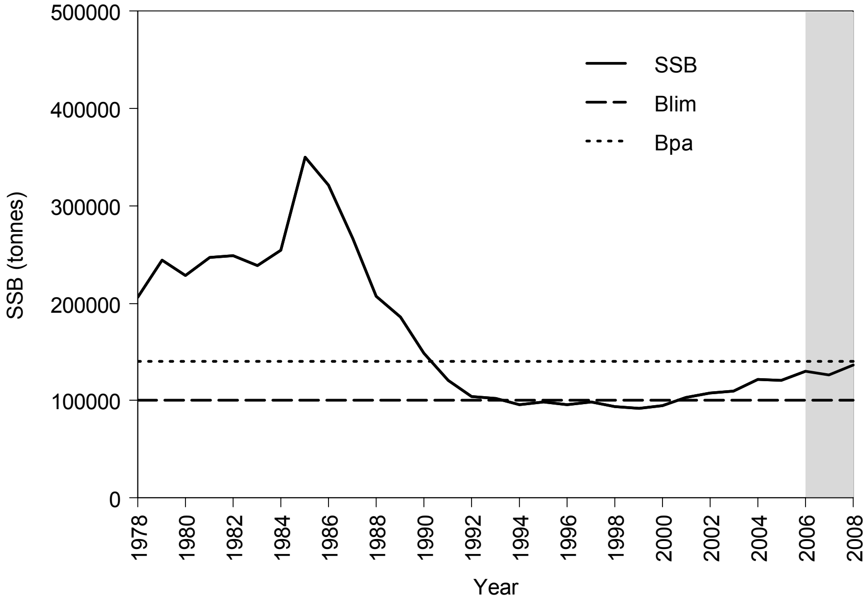


Figure 89: Time-series of northern European hake SSB (in tonnes) for the period 1978-2008. Precautionary biomass level (140000 t) and biomass limit level (100000 t) are also plotted. The grey rectangle shows the last two years not considered in the present study.

Overfishing is a critical factor in the decrease, and sometimes collapse, of a stock (Myers *et al*., 1996, 1997; Pauly *et al*., 2002; Hutchings and Reynolds, 2004). It goes without saying that overfishing exerted great pressure on northern hake population, leading to the unsafe situation of the SSB. Control measurements in fishing mortality resulted in a slight and slow recovery of the stock, letting us believe that the implementation of the different plans helped in the improvement of the stock situation. However, in extreme cases, fishing makes the population dynamics almost exclusively driven by recruitment fluctuations, which is likely to increase stock sensitivity to climate variability (Hsieh *et al*., 2006, 2008). In the 1990s, at such low SSB values, unfavourable environmental conditions could have worsened the stock situation. By contrast, the recruitment success per parental biomass did increase which made possible to compensate the stock for the depletion (Chapter II) and it helped to the recent recovery of the stock.

According to Beverton (2002), hake stock-recruitment relationship suggests a fishing generated event, where both recruitment and stock size decreases whereas the reproductive rate increases. This is the case for the second half of the 80s and the beginning of the 90s when the fishing pressure increased. By contrast, from the decade of the 90s onwards, both the stock and recruitment declined and the recruitment success rate either stayed constant or declined slightly. This is likely to be an environmentally mediated event (Beverton, 2002) (Chapter II). This decade was characterised by a pronounced warming that affected not only the Northern Hemisphere but in particular the Northeast Atlantic continental shelf (Chapter I). Our results suggest that the resulting environmental conditions became favourable for successful hake recruitment (Chapter III) (Figure 90). In fact, it is likely that the favourable recruitment conditions contributed to sustain the population under overfishing conditions and compensated the stock, contributing thereby to avoid collapse. Therefore, it is hypothesised that at low stock levels, the resilience of northern hake population is environmentally-dependant; similar statements could be found in literature for exploited stocks (Worm and Myers, 2004; Planque *et al*., 2010). In the case of European Shelf cod stocks for instance, environment affects recruitment more strongly when their spawning biomass is low (Brander, 2005). In the following sections, the environmental influence on early life stages of northern European hake is discussed.

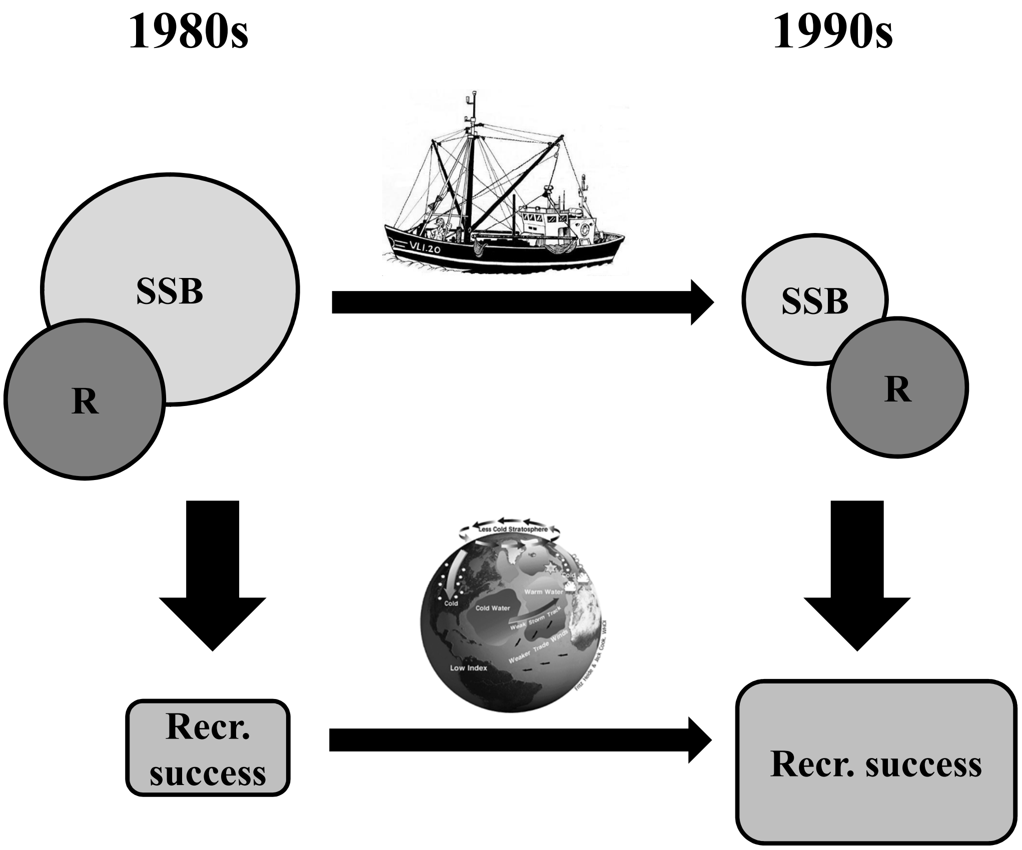


Figure 90: Schematic representation of the changes in northern European hake stock between 1980s and 1990s. SSB: spawning stock biomass; R: recruitment; Recr. successs: recruitment success. The fishing vessel represents the fishing activity and the Earth represents the optimal environmental conditions.

“Recruitment success” approach

Many of the works that investigated the environmental influence on recruitment analysed the relation between the observed number of recruits and the various climate variables without taking into account the variability that could have been caused by changes in the reproductive biomass (Planque and Frédou, 1999; Brander, 2005; Drinkwater, 2005; Megrey *et al*., 2005). With the aim of distinguishing the effects of synergistic maternal factors and those of environmental factors, it is important to use the ratio between the annual number of recruits and spawning biomass, instead of absolute recruitment strength (Brodziak and O’Brien, 2005; Möllmann *et al*., 2008). As such, the “recruitment success approach” accounts for the effect of the SSB on recruitment by relating recruitment success (the number of recruits produced per biomass of adult individuals) to various climate variables (Cardinale and Hjelm, 2006). Therefore, in this thesis, recruitment success was used as the recruitment proxy when studying environmental effect on hake population dynamics; in this way, the effect of SSB on recruitment was reduced.

Northeast Atlantic regime shift

Despite the low SSB and recruitment values, hake recruitment success increased from mid-1980s to mid-1990s. This increase occurred as a stepwise abrupt shift from low to high reproductive rate period. Within the eastern margin of the North Atlantic Ocean, the North Sea, the Baltic Sea and the Mediterranean Sea are three semi-enclosed marine ecosystems in which regime shifts have been described in both environmental and biological time-series. However, little has been reported regarding regime shifts in the Northeast Atlantic continental shelf, despite it being a neighbouring marine system. In this context, the present thesis provides evidence that several global, regional and local parameters shifted in 1988/89, which may have contributed to the stepwise increase in hake recruitment success (Chapter III).

The regime shift described in the Northeast Atlantic continental shelf has been found to be mainly driven by two major large-scale climate indicators such as the NAO index and the Northern Hemisphere temperature anomalies. Similarly, regime shifts in the North Sea (Beaugrand, 2003), Baltic Sea (Alheit *et al*., 2005) and the Mediterranean Sea (Conversi *et al*., 2010) were also attributed to variations in these global parameters (Alheit and Bakun, 2010).

In 1988/89, the NAO index suffered a stepwise increase that resulted in positive sea surface temperature anomalies over the northeastern Atlantic continental shelf and relatively stronger wind-induced Ekman transports in Porcupine after the regime shift. Despite it is also located within the NAO affected region, the northern Bay of Biscay is a more protected area characterised by weaker transports in comparison to the more dynamic Porcupine (Chapter I), and thus no such shift was detected. Another global index that changed in the 1988/89 period was the position of the GSNW. During positive NAO phases, the GSNW locates northward (Taylor and Stephens, 1998; Taylor *et al*., 1998; Hurrell and Deser, 2009) and both the Gulf Stream and the North Atlantic Current strengthen (Curry and McCartney, 2001). Further, Grey *et al*. (2000) identified an intense warm anomaly in the subtropical gyre in 1988-94 with greater northward heat transport linked to the intensification in the Gulf Stream.

The environmental shift was also detectable in local heat fluxes (linked to SST anomalies) and momentum fluxes (associated with local wind patterns). Additionally both parameters have been found to be linked to low frequency global indices such as the NAO index (Cayan, 1992a; Hurrell *et al*., 2003; Riviére and Orlanski, 2007). Heat and momentum fluxes have been reported to determine growth, recruitment and migration patterns in marine populations (Stenseth *et al*., 2002); in fact, latent heat flux in the Bay of Biscay was initially selected as an explanatory variable for recruitment variability (Chapter IV). However, from this work we cannot conclude what was their relative influence on the hake population; rather they are believed to be part of a triangle formed by the NAO index, regional temperature anomalies and wind patterns (Chapter III).

A shift in total copepod abundance in the Celtic Sea was also observed in 1988/89. The Celtic Sea is one of the main nursery areas of the European hake, where recruits concentrate to feed on copepods (General introduction). Elsewhere, variations on zooplankton abundance and distribution were related to changes in the position of the GSNW (Hays *et al*., 1993; Taylor, 1995, 1996; Reid *et al*., 1998), modifications in the sign of the NAO index (Fromentin and Planque, 1996; Beaugrand *et al*., 2000; Beaugrand and Ibañez, 2002; Beaugrand, 2003, 2004, 2009; Reid *et al*., 2003b) or to the increasing trend in the Northern Hemisphere temperature (Beaugrand *et al*., 2002, 2009).

In addition, the form of the stock-recruitment relationship changed considerably after the regime shift. Before 1989, the S-R model follows a typical S-R Ricker curve; by contrast, for observations after 1989, the curve only illustrates the positive relationship between the stock and recruitment (the beginning of the curve), given the higher recruitment success observed in this period (Chapter II).

To sum up, the shift in hake recruitment success in 1988/89 coincides with a pronounced regime shift, which although it was first described for the North Sea, affected a much wider region, including the Baltic Sea, the Mediterranean and the oceanic area of the

Northeast Atlantic (Beaugrand, 2004; Reid, 2005; Alheit, 2009; Conversi *et al*., 2010) as part of a larger Northern Hemisphere climate shift.

A shift was also detected around 1995 (Chapter III). Temperature-linked parameters such as AMO index and regional temperature anomalies suffered a stepwise increase (Chapter I) which was also described in Beaugrand *et al*. (2009). This regional water warming may have been caused by the retreat of the subpolar gyre to the west, which allowed warmer water from the subtropical gyre to penetrate up to the west of the British Isles in the mid-1990s (Hátún *et al*., 2005). Actually, the sharp increase in blue whiting recruitment was linked to changes in the strength and extent of the subpolar gyre (Hátún *et al*., 2009a, 2009b). By contrast, hake recruitment success declined in spite of the clear warming recorded after 1995. Therefore, favourable temperature conditions may not be enough for higher recruitment success in hake; transport during early life stages could also be critical as shown in the 1988/89 event. In addition, the temperature shift of 1995 was detected in the Celtic Sea and west of Ireland, and not in the other main spawning ground of the northern European hake (Bay of Biscay).

Stock-recruitment relationship

The stock-recruitment relationship involves the hypothesis that recruitment is dependant on spawner abundance (Myers, 1997). Nevertheless, not all the stock data fits well to the relationship described by stock-recruitment models (Walters and Ludwig, 1981; Walters, 1985; Amstrong and Sheltoon, 1988; Koslow, 1992; Hilborn and Walters, 1992; Gilbert, 1997); for some stocks SSB and recruitment are independent (Gilbert, 1997) whereas in the case of other stocks they are not related following the worldwide well-known stock-recruitment relationships (Koslow, 1992).

Concerning northern European hake, spawning stock biomass explained more than 75% of hake recruitment variability under the Ricker SR form. The stock-recruitment relationship forms such a curve where the maximum recruitment occurs at an optimum stock size (Figure 91). At lower stock levels, the relationship between the spawning biomass and recruitment is positive up to reaching the maximum recruitment for an optimum stock size. At higher stock size, recruitment begins to decrease because of the cannibalism of adult individuals on its progeny. Actually, cannibalism has been observed in the northern Bay of Biscay and the Celtic Sea (Mahe *et al.*, 2007). However, despite the high percentage of variability explained by the model, the lack of data over the whole range of SSB values could be an error source that should be taken into account. No data has been registered between 0 and 90,000 tonnes of SSB. Thus, for this range of SSB the model has carried out an interpolation based only in two points, one of them being a fictitious point (recruitment is bound to be zero at zero stock size) (Chapter II).

The lack of observations at low biomass levels makes impossible to distinguish whether the stock shows a compensatory or depensatory behaviour. An additional debate is whether the stock-recruitment relationship should pass through the origin, or the intercept should be defined for a determined value of SSB below which no recruitment takes place (Allee effect); also positive recruitment might take place at SSB=0, when due to migration new recruits (for example from the southern stock) enter the local stock (Figure 91). In our case, if the model is not forced through the origin (e.g. considering potential Allee effects), and no Ricker form is assumed, the variability explained decreases to 46.7%, which makes quite clear the strong implications of using the assumption that the stock goes through (0,0).

The density-dependence of northern hake recruitment suggested in Chapter II was confirmed in Chapter IV; in the non-parametric approach, the model freely selected SSB as an explanatory variable due to its significant contribution to the explained variance. Indeed, density-dependence is an aspect that must be considered in recruitment dynamic studies (Rothschild *et al.*, 2005). However, the dynamics of an exploited stock not only depends on spawning biomass; it is a balance between the number of offspring produced by the parental stock and the subsequent survival of these fish into the future spawning biomass (Cook, 2000).

Chapter III and Chapter IV demonstrated that environmental variability could be critical for understanding recruitment variability. However, the environmental aspect has not usually been incorporated into stock-recruitment models although the inclusion of environmental variables into stock-recruitment models could result in a better explained variance of recruitment. For northern hake, both models (environmentally modified Ricker and the non-parametric approach) explained a greater percentage of variability when, in addition to the parental stock, environmental parameters were considered. Further, both models selected temperature anomaly, copepod abundance and SSB as explanatory variables of recruitment dynamics. However, the GAM model accounted for more than 95% of the variability whereas the environmentally modified Ricker explained about 85% of hake recruitment fluctuations. Consequently, although the parental biomass is an important factor to understand northern hake recruitment variability, it cannot be assumed that this density-dependence takes a Ricker form.

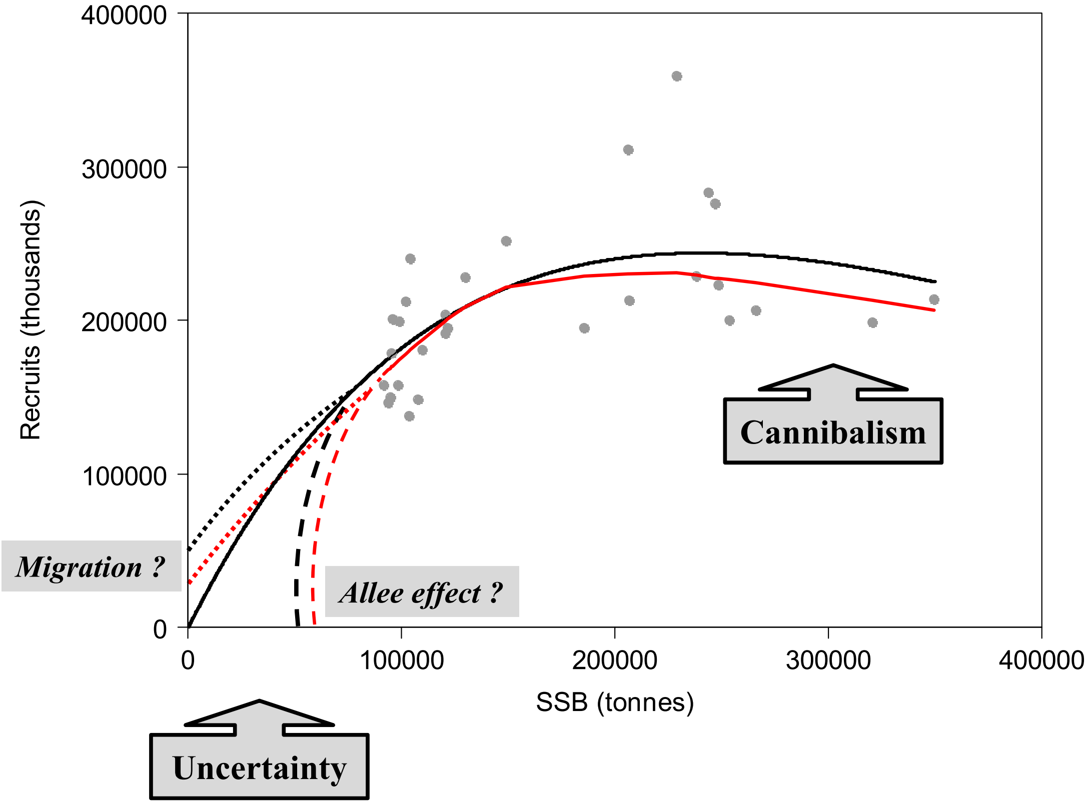


Figure 91: Schematic representation of the stock-recruitment relationship on northern European hake both, following a Ricker model (in black) and with no assumption of any SR relationship (in red). The hypothetical SR behaviour at low SSB values is also plotted: Allee effect (dashed) and migration (dotted).

Potential environmental influence on early life stages

Mortality rates of early-life-history stages are very high and variable (Pörtner and Peck, 2010) and because applying to large numbers, the strength of an incoming year class is determined at the early stages of a marine fish population. According to Cushing (1971), the larval period is the major cause of marine fish production variability. Therefore, it is important to know which environmental conditions affect hake survival during this critical period of early life development.

A wide range of global, regional and local environmental parameters was considered in this thesis. They were selected because of their direct and/or indirect likely influence on either northern hake population dynamic itself or its habitat (Chapter I). However, from the whole of the oceano-meteorological dataset used few are the parameters that have been found to be significantly influential for northern European hake recruitment success (Chapter IV).

Sea water temperature is a determinant factor constraining the onset and duration of the spawning season of many marine fish populations. Indeed, European hake eggs are found in water temperatures from 10 ºC to 12.5 ºC (Ibaibarriaga *et al.*, 2007) and larvae are found mainly in temperatures between 10.5 ºC and 13 ºC (Álvarez *et al.*, 2001; Ibaibarriaga *et al.*, 2007). During months with spawning activity in the Bay of Biscay (January to May), sea surface temperature showed values between 10 ºC and 14 ºC; in particular, during the peak spawning season (January to March) the temperatures recorded ranged from 10 ºC to 12 ºC (Chapter I), i.e. the optimal temperature range for European hake spawning. As the season progressed, with the warming of the sea, the optimal temperature conditions for spawning were found northwards. Actually, latitudinal differences in temporal spawning patterns given to differences in temperature have already been documented (Álvarez *et al.*, 2001). In the Celtic Sea it takes place from April to July, whereas west of Ireland spawning can last until August. Indeed, European hake eggs can be found in warmer temperatures of up to 15 ºC (Álvarez *et al.*, 2004; Ibaibarriaga *et al.*, 2007). Further, despite the positive correlation between SST anomaly and recruitment success over the whole of the study area, such relationship becomes highly significant for the spawning season (including the peak spawning period) of the Bay of Biscay (Chapter III). One of the effects of increased temperature may have been therefore to increase the temporal and spatial window for hake spawning (Figure 92). As a result larvae may have found additional opportunities for survival.

Likewise, temperature influences marine fish metabolism (Neill *et al.*, 1994; Pörtner and Peck, 2010); higher temperatures contribute to increased development rates (O'Connor *et al.*, 2007) and thus enhanced growth during early life stages. (Ottersen and Sundby, 1995; Fiksen and Slotte, 2000). For marine animals whose offspring develop in the water column (as it is the case for northern hake), the duration of the larval period determines the length of time when larvae are more vulnerable (O'Connor *et al.*, 2007). Therefore, the shorter the larval period the higher the survival rate of early life stages. In the case of Pacific hake, slower growing larvae were observed to suffer higher mortality than larvae with faster growth rates (Butler and Nishimoto, 1997). In this regard, warmer temperatures, through greater growth rates, imply a reduction in the time spent in vulnerable life stages and thus a greater survival of larvae and juvenile individuals, with the subsequent increase in recruitment success. Steves and Cowen (2000) has already demonstrated the important role of temperature in hake egg development and larval growth. Further, Morales-Nin and Moranta (2004) highlighted the link between faster growth rates and hake survival during early life stages. The results of this thesis seem to agree with the optimal effect of temperature. The reproductive rate of the northern European hake increased sharply when the environment shifted from a relatively cooler to a warmer regime (Chapter III). Besides, Northern Hemisphere temperature anomalies during hake spawning period (February-July) has been selected in order to explain hake recruitment dynamics over the study period (Chapter IV). Therefore, a second effect of increased temperatures may have been to increase the reproductive rate and to decrease larval mortality because faster growth (Figure 92).

After hatching, hake larvae remain in the plankton until they metamorphose to the juvenile stage. During the planktonic stage, the drift of larvae from spawning areas to nursery grounds depends on the physical characteristics of the area, particularly on the current regime (Sánchez and Gil, 2000). In the case of northern hake, transport has been found to be an explanatory variable for recruitment success (Chapter IV); it may drive the dispersion or retention of planktonic egg and larvae, or even control the transport of copepods, hake juveniles' main trophic resource (Agostini and Bakun, 2002).

Focusing on spawning and nursery grounds, the influence of transport on early life stages becomes clearer (Figure 92). After the shift in 1988/89, wind-induced Ekman transport in Porcupine showed higher eastwards and southwards transports during hake spawning season, coinciding with the stepwise increase in hake recruitment success; on one hand, this transport would favour keeping vulnerable individuals on the continental shelf, stopping them from being dispersed to oceanic areas; on the other hand, it may facilitate the transport of larvae and juveniles from spawning areas to nursery areas such as the Celtic Sea (Chapter III). By contrast, correlation between E-W Ekman transport and recruitment success in the Bay of Biscay was significantly negative for the period February-July. Analysing the spatial distribution of E-W Ekman transport for these months (Chapter I), it is observed that the eastward component of the transport weakens, even showing westward direction from April to August. Westward Ekman transport leads to the offshore dispersion of egg and larvae, moving them away from the nursery areas; it is therefore detrimental for hake recruitment (Chapter III). This negative relationship was not observed in the case of the Celtic Sea or west of Ireland since both areas showed eastward transport for all months; what is more, the correlation, though not statistically significant, is positive for these two areas. The spatial distribution of correlation coefficients between N-S Ekman transport and hake recruitment success was not statistically significant.

Copepod abundance in the Celtic Sea declined after the shift in 1988/89 (Chapter III). The decrease in copepod abundance could be explained by environmental changes occurred synchronously. Dickson *et al* (1988) linked northerly winds over the Northeast Atlantic to the decline in zooplankton biomass around the British Isles. Accordingly, stronger southward wind events in Porcupine coincided with the decline in copepod abundance in the Celtic Sea. Copepods are hake larvae and juvenile main prey (Reiss *et al*., 2005; ICES, 2008). Higher copepod abundance at larval period would guarantee enough food for early life stages and thus could be critical for early life stages survival (Figure 92). Indeed, copepod abundance during the overall hake spawning season (February-July) was selected as an explanatory variable for recruitment dynamics (Chapter IV). However, despite the increase in recruitment success, in absolute terms recruitment declined due to the low spawning biomass. Therefore, the amount of food available per recruit did not change significantly and was not likely to be a limiting factor for hake growth. Thus, even if hake larvae feed upon copepods (Reiss *et al*., 2005), we cannot conclude from this study the direct relationship between them; it is more likely that the same parameter (e.g. temperature) could be affecting both, leading to the decrease in both time-series.

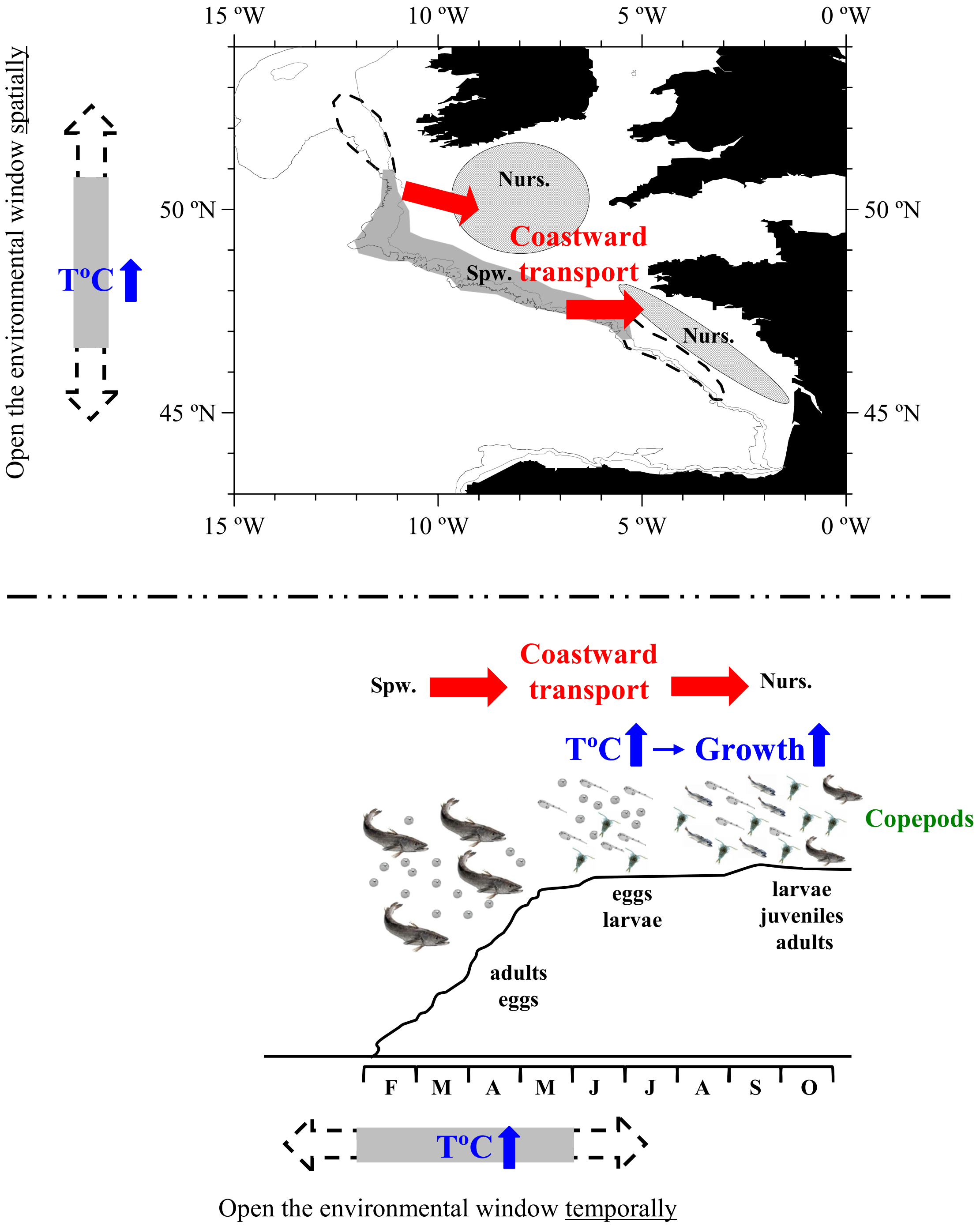


Figure 92: Schematic representation of the potential environmental influence on early life stages of northern European hake: above, the influence of temperature and transport in spatial terms; below, a more detailed cross section from the spawning area on the shelf edge to the nursery ground on the shelf.

Recruitment dynamics of northern European hake

The number of young individuals that each year recruits to the adult stock depends on the parental stock size (density-dependence), which in turn is strongly determined by the fishing pressure. The larger the spawning stock size the higher the recruit abundance; however, from the optimal stock size (at which maximum recruitment occurs) upwards, recruitment seems to decrease as the stock rises, due to cannibalism on the young fraction of the population. Thus, a Ricker-like stock-recruitment relationship is suggested for northern European hake stock. However, it is not possible to confirm it because of the lack of data at the whole range of SSB.

When the optimal temperature range is reached, parental stock spawns at the shelf edge of the northeastern Atlantic continental shelf. Afterwards, post-hatch larvae need to be transported from spawning areas to nursery grounds in the Celtic Sea and in the French shelf of the Bay of Biscay (Figure 92), where they would find optimal conditions for growing and developing. The survival rate from eggs to juveniles is influenced by environmental conditions (density-independence), such as coastward transport and warmer temperatures. Similar results were found for cod (Vikebo *et al*., 2005).

The warming of the oceans might result in an advancement of spring phenology (Durant *et al*., 2007); in particular the timing of reproduction (Stenseth and Mysterud, 2002). In addition, the optimal temperatures for spawning could be found in a more extended area over the shelf. The increase in temporal and spatial window for hake spawning may lead to more opportunities for early life stages' survival; for instance, through the overlapping of the peak of prey production and the peak of predator requirement ("match-mismatch" hypothesis, Cushing, 1990; Durant *et al*., 2007). Further, individuals with highest growth rates have a better chance to survive due to the reduction of time in the most vulnerable stage ("growth-mortality" hypothesis, Anderson, 1988). In the case of the northern hake, the shortening of the vulnerable period has been proven to depend mainly on two factors. On one hand, transport of early life stages from spawning areas to nursery grounds will lead to the retention of hake within suitable areas during early life history ("Member-vagrant" hypothesis, Sinclair, 1988).

On the other hand, higher water temperatures, through greater growth rates, will result in larger larvae which are less susceptible to predation ("Bigger is better" hypothesis) and metamorphosis at earlier ages giving place to lower cumulative mortality ("Stage duration" hypothesis) (Leggett and Deblois, 1994).

Conclusions

CONCLUSIONS

Oceano-climatic characterisation of the Northeast Atlantic Ocean

1. The study period of the present thesis (1978-2006) was characterised by a positive NAO phase from late 1980s to mid-1990s. Synchronously, the Gulf Stream and the North Atlantic Current strengthened, with the subsequent increase in warm water transport northeastward. From 1995 onwards, the study area was under the influence of a positive EA pattern; as a result, a second intense warming in Northern Hemisphere temperature was observed.

2. The general warming reported for the Northern Hemisphere also affected regional waters over the continental shelf of Northeast Atlantic. However, the warming rate showed latitudinal differences: SST warming was more pronounced in the Bay of Biscay, whereas northwards the increase in SST was lower.

3. Generally speaking, wind-driven Ekman transport showed mean eastward and southward direction over the study period. However, transport strength differed latitudinally, with weak values in the Bay of Biscay and strongest transports at the Rockall Trough.

4. In the spawning grounds of the Bay of Biscay and the Celtic Sea, the warming was more pronounced in early summer (May and June). Bay of Biscay also showed seasonality with regard to Ekman transport: weak westward and northward transport in spring and summer and stronger eastward and southward transport in winter.

Northern European hake: temporal evolution

5. During the period 1985-1990, the SSB of northern hake declined dramatically, event that has been related to a strong fishing pressure. However, both recruitment and SSB have recently registered a recovery after a relatively long period at low levels.

6. The recruitment success (the number of recruits per parental stock) of the northern stock of European hake significantly increased since 1989/90 despite the continuous decrease in both spawning stock biomass and absolute recruitment values during much of the study period.

7. Northern hake stock seems to be affected by both, fishing pressure and environmental variability; while the former may have been more critical until the decade of the 90s, environment seems to have been the driving force at the last part of the study period, helping to the recovery of the stock through an increase in recruitment success.

Northeast Atlantic regime shift

8. An ecological regime shift occurred in the Northeast Atlantic shelf system in 1988/89. This regime shift was detected in global indices, such as the North Atlantic Oscillation and Gulf Stream index, as well as the Northern Hemisphere temperature anomalies to a small spatial scale: climatology of the Northeast Atlantic (temperature, wind patterns and fluxes) and copepod variability in the Celtic Sea.

9. The NAO winter index changed from a negative to a positive phase, and thus the region went from a period of cool temperatures and relatively weak winds (1978-1989) to a period of warmer temperatures and stronger westerly winds (1990-2006). Given the synchronous stepwise increase in hake recruitment success, we can deduce that the environment shifted to a regime that was favourable for northern hake.

10. The regime shift described in the Northeast Atlantic shelf system is part of wider-scale change that also affected other neighbouring basins, such as the North Sea, the Baltic Sea and the Mediterranean Sea.

Stock-recruitment relationship

11. The parental biomass is an important factor to understand northern hake recruitment variability. However, the lack of observations at the whole range of SSB makes impossible to study the recruitment behaviour at low SSB values.

12. The fitting of the models considerably increases when environmental information is taken into account, and thus environmental variability is an important factor explaining recruitment dynamics. Consequently, environmental information should be considered in the stock assessment and fisheries management.

13. Northern European hake dynamics are synergistically driven by fishing pressure through its effect on parental stock, and environmental variability. Therefore, both density-dependent (spawning stock biomass) and density-independent factors (oceano-meteorological parameters) are crucial to understand hake recruitment variability over time.

14. The relationship between environmental parameters (SSB, temperature anomaly and copepod abundance) was better explained by the nonlinear empirical approach (GAM) than the linear approach (environmentally modified Ricker). Even if parental biomass importance is demonstrated, it is not possible to understand the recruitment variability under Ricker S-R relationship, since recruitment variability model is improved when no Ricker S-R relationship is assumed.

Potential environmental influence on early life stages

15. When studying the environmental influence on early life stages' survival and thus, the subsequent recruitment production, the use of the recruitment success (recruitment/SSB) is suggested as a proxy for recruitment, given the density-dependence of hake recruitment.

16. Hake recruitment depends on parental biomass, but this density-dependent factor is modulated by environmental parameters such as wind-induced Ekman transport, Northern Hemisphere temperature anomaly and copepod abundance during hake spawning season.

17. Warmer temperatures may increase the temporal and spatial window for hake spawning, with the subsequent additional opportunities for larvae survival. In addition, increased temperatures may decrease larval mortality because faster growth and development, and thus increase the reproductive rate due to the reduction of time in the most vulnerable stage.

18. Transport of early life stages from spawning areas to nursery grounds, will avoid the dispersion of eggs and larvae and will lead to the retention of hake within suitable areas.

19. The decrease in copepod abundance was not likely to be a limiting factor for hake growth since, despite the increase in recruitment success, in absolute terms recruitment declined and thus the amount of food available per recruit should not have changed significantly.

Northern Euopean hake recruitment dynamics are concluded to be driven by parental stock fluctuations as well as environmental variability. Therefore, the need for further research is highilighted in order to consider both density-dependent and density-independent factors in the assessment and management procedures of northern hake stock.

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Appendix

Appendix 1: Global indices

Parameter	Description	Influence area	Study Period	Observations
NAO	North Atlantic Oscillation index	North Atlantic	Annual mean	
Winter NAO	Winter North Atlantic Oscillation	North Atlantic	Winter mean (Dec.-March)	
EA	East Atlantic pattern	North Atlantic	Annual mean	
EA (F-J)	EA pattern during ICES hake spawning period	North Atlantic	February-July mean	
AMO	Atlantic Multidecadal Oscillation	North Atlantic	Annual mean	
AMO (F-J)	AMO index during ICES hake spawning period	North Atlantic	February-July mean	
NOI	Northern Oscillation Index	North Pacific	Annual mean	
NOI (F-J)	NOI index during ICES hake spawning period	North Pacific	February-July mean	
TPEA	Transport index from potential energy anomalies	North Atlantic	Annual mean	Incomplete time-series (Missing years: 1979, 1980, 1982-1984). Not considered in the regime shift detection method.
GSNW	Gulf Stream index	North Atlantic	Annual mean	
GSNW (F-J)	GSNW index during ICES hake spawning period	North Atlantic	February-July mean	
Sunspot number	Sunspot number	Global	Annual mean	
Sunspot number (F-J)	Sunspot number for ICES hake spawning period	Global	February-July mean	

Appendix 1 (cont.): Global indices

Parameter	**Description**	**Influence area**	**Study Period**	**Observation**
AA index	Disturbance level of Earth’s magnetic field	Global	Annual mean	
AA index (F-J)	AA index for ICES hake spawning period	Global	February-July mean	
NHT	Northern Hemisphere temperature anomaly	Northern Hemisphere	Annual mean	
NHT (F-J)	NHT for ICES hake spawning period	Northern Hemisphere	February-July mean	
CLI1	Climatic index 1	Global	Annual mean	Composite index of six global variables
CLI2	Climatic index 2	Global	Annual mean	Composite index of six global variables
CLI3	Climatic index 3	Global	Annual mean	Composite index of six global variables

Appendix 2: Regional parameters

Parameter	**Description**	**Influence area**	**Study Period**	**Observations**
Temp. anom. A	Mean temperature anomaly in the A area	40-45N; 5-0W	Annual mean	Base period: 1961-1990
Temp. anom. C	Mean temperature anomaly in the C area	45-50N; 5-0W	Annual mean	Base period: 1961-1990
Temp. anom. D	Mean temperature anomaly in the D area	45-50N; 10-5W	Annual mean	Base period: 1961-1990
Temp. anom. E	Mean temperature anomaly in the E area	45-50N; 15-10W	Annual mean	Base period: 1961-1990
Temp. anom. H	Mean temperature anomaly in the H area	50-55N; 10-5W	Annual mean	Base period: 1961-1990
Temp. anom. I	Mean temperature anomaly in the I area	50-55N; 15-10W	Annual mean	Base period: 1961-1990
Temp. anom. M	Mean temperature anomaly in the M area	55-60N; 10-5W	Annual mean	Base period: 1961-1990
Temp. anom. N	Mean temperature anomaly in the N area	55-60N; 15-10W	Annual mean	Base period: 1961-1990
Temp. anom. A (F-J)	Mean temperature anomaly in the A area for ICES hake spawning period	40-45N; 5-0W	February-July mean	Base period: 1961-1990
Temp. anom. C (F-J)	Mean temperature anomaly in the C area for ICES hake spawning period	45-50N; 5-0W	February-July mean	Base period: 1961-1990
Temp. anom. D (F-J)	Mean temperature anomaly in the D area for ICES hake spawning period	45-50N; 10-5W	February-July mean	Base period: 1961-1990
Temp. anom. E (F-J)	Mean temperature anomaly in the E area for ICES hake spawning period	45-50N; 15-10W	February-July mean	Base period: 1961-1990
Temp. anom. H (F-J)	Mean temperature anomaly in the H area for ICES hake spawning period	50-55N; 10-5W	February-July mean	Base period: 1961-1990

Appendix 2 (cont.): Regional parameters

Parameter	**Description**	**Influence area**	**Study Period**	**Observations**
Temp. anom. I (F-J)	Mean temperature anomaly in the I area for ICES hake spawning period	50-55N; 15-10W	February-July mean	Base period: 1961-1990
Temp. anom. M (F-J)	Mean temperature anomaly in the M area for ICES hake spawning period	55-60N; 10-5W	February-July mean	Base period: 1961-1990
Temp. anom. N (F-J)	Mean temperature anomaly in the N area for ICES hake spawning period	55-60N; 15-10W	February-July mean	Base period: 1961-1990
T. anom. index BB	Temperature anomaly index in the Bay of Biscay	Bay of Biscay spawning area	Annual mean	PCA result first component Base period: 1971-2000
T. anom. index BB (J-M)	Temperature anomaly index for hake spawning period in the Bay of Biscay	Bay of Biscay spawning area	January-May mean	PCA result first component Base period: 1971-2000
T. anom. index CS	Temperature anomaly index in the Celtic Sea	Celtic Sea spawning area	Annual mean	PCA result first component Base period: 1971-2000
T. anom. index CS (A-J)	Temperature anomaly index for hake spawning period in the Celtic Sea	Celtic Sea spawning area	April-June mean	PCA result first component Base period: 1971-2000
E-W transp. BB	East-West Ekman transport index in the Bay of Biscay	Bay of Biscay spawning area	Annual mean	PCA result first component
E-W transp. BB (J-M)	East-West Ekman transport index for hake spawning period in the Bay of Biscay	Bay of Biscay spawning area	January-May mean	PCA result first component
E-W transp. CS	East-West Ekman transport index in the Celtic Sea	Celtic Sea spawning area	Annual mean	PCA result first component

Appendix 2 (cont.): Regional parameters

Parameter	**Description**	**Influence area**	**Study Period**	**Observations**
E-W transp. CS (A-J)	East-West Ekman transport index for hake spawning period in the Celtic Sea	Celtic Sea spawning area	April-June mean	PCA result first component
N-S transp. BB	North-South Ekman transport index in the Bay of Biscay	Bay of Biscay spawning area	Annual mean	PCA result first component
N-S transp. BB (J-M)	North-South Ekman transport index for hake spawning peak in the Bay of Biscay	Bay of Biscay spawning area	March	PCA result first component
N-S transp. CS	North-South Ekman transport index in the Celtic Sea	Celtic Sea spawning area	Annual mean	PCA result first component
N-S transp. CS (A-J)	North-South Ekman transport index for hake spawning period in the Celtic Sea	Celtic Sea spawning area	April-June mean	PCA result first component

Appendix 3: Local parameters

Parameter	**Description**	**Influence area**	**Study Period**	**Observations**
Slope temp.	Sea water temperature at 100m depth	47.5N; 6.5W	Annual mean	Incomplete time-series (No data from 2001 onwards). Not considered in the regime shift detection method
Slope temp. (F-J)	Sea water temperature at 100m depth for ICES hake spawning period	47.5N; 6.5W	February-July mean	Incomplete time-series (No data from 2001 onwards). Not considered in the regime shift detection method
Slope temp. (J-M)	Sea water temperature at 100m depth for the hake spawning period in the Bay of Biscay	47.5N; 6.5W	January-May mean	Incomplete time-series (No data from 2001 onwards). Not considered in the regime shift detection method
Upwelling index	Upw. Index off the French coast	46.5N; 4.5W	Annual mean	Considered coast angle: 120º
Upwelling index (F-J)	Upw. Index off the French coast for ICES hake spawning period	46.5N; 4.5W	February-July mean	Considered coast angle: 120º
Upwelling index (J-M)	Upw. Index off the French coast for hake spawning period in the Bay of Biscay	46.5N; 4.5W	January-May mean	Considered coast angle: 120º
Upwelling index (D-M)	Upw. Index off the French coast in winter (period showing the highest values)	46.5N; 4.5W	December-March mean	Considered coast angle: 120º

Appendix 3 (cont.): Local parameters

Parameter	**Description**	**Influence area**	**Study Period**	**Observations**
Turb. BB	Turbulence index in the Bay of Biscay	46.5N; 4.5W	Annual mean	
Turb. BB (F-J)	Turbulence index in the Bay of Biscay for ICES hake spawning period	46.5N; 4.5W	February-July mean	
Turb. BB (J-M)	Turbulence index for hake spawning period in the Bay of Biscay	46.5N; 4.5W	January-May mean	
Turb. GSB	Turbulence index at Great Sole Bank	48.5N; 9.5W	Annual mean	
Turb. GSB (F-J)	Turbulence index at Great Sole Bank for ICES hake spawning period	48.5N; 9.5W	February-July	
Turb. GSB (A-J)	Turbulence index at Great Sole Bank for hake spawning period in the Celtic Sea	48.5N; 9.5W	April-June	
Turb. Porcup.	Turbulence index in Porcupine	52.5N; 11.5W	Annual mean	
Turb. Porcup. (F-J)	Turbulence index in Porcupine for ICES hake spawning period	52.5N; 11.5W	February-July	
Turb. Porcup. (A-J)	Turbulence index in Porcupine for hake spawning period in western Ireland	52.5N; 11.5W	April-July	
E-W transp. BB	East-West Ekman transport in the Bay of Biscay	46.5N; 4.5W	Annual mean	
E-W transp. BB (F-J)	East-West Ekman transport in the Bay of Biscay for ICES hake spawning period	46.5N; 4.5W	February-July	
E-W transp. BB (J-M)	East-West Ekman transport for hake spawning period in the Bay of Biscay	46.5N; 4.5W	January-May	

Appendix 3 (cont.): Local parameters

Parameter	**Description**	**Influence area**	**Study Period**	**Observations**
E-W transp. GSB	East-West Ekman transport at Great Sole Bank	48.5N; 9.5W	Annual mean	
E-W transp. GSB (F-J)	East-West Ekman transport at Great Sole Bank for hake spawning period in the Celtic Sea	48.5N; 9.5W	February-July	
E-W transp. GSB (A-J)	East-West Ekman transport at Great Sole Bank in the Celtic Sea	48.5N; 9.5W	April-June	
E-W transp. Porcup.	East-West Ekman transport in Porcupine	52.5N; 11.5W	Annual mean	
E-W transp. Porcup. (F-J)	East-West Ekman transport in Porcupine for ICES hake spawning period	52.5N; 11.5W	February-July	
E-W transp. Porcup. (A-J)	East-West Ekman transport for hake spawning period in western Ireland	52.5N; 11.5W	April-July	
N-S transp. BB	North-South Ekman transport in the Bay of Biscay	46.5N; 4.5W	Annual mean	
N-S transp. BB (F-J)	North-South Ekman transport in the Bay of Biscay for ICES hake spawning period	46.5N; 4.5W	February-July	
N-S transp. BB (J-M)	North-South Ekman transport for hake spawning period in the Bay of Biscay	46.5N; 4.5W	January-May	
N-S transp. GSB	North-South Ekman transport at Great Sole Bank	48.5N; 9.5W	Annual mean	
N-S transp. GSB (F-J)	North-South Ekman transport at Great Sole Bank for ICES hake spawning period	48.5N; 9.5W	February-July	
N-S transp. GSB (A-J)	North-South Ekman transport at Great Sole Bank for hake spawning period in the Celtic Sea	48.5N; 9.5W	April-June	

Appendix 3 (cont.): Local parameters

Parameter	**Description**	**Influence area**	**Study Period**	**Observations**
N-S transp. Porcup	North-South Ekman transport in Porcupine	52.5N; 11.5W	Annual mean	
N-S transp. Porcup. (F-J	North-South Ekman transport in Porcupine for ICES hake spawning period	52.5N; 11.5W	February-July	
N-S transp. Porcup. (A-J)	North-South Ekman transport for hake spawning period in western Ireland	52.5N; 11.5W	April-July	
MMF BB	Meridional Momentum Flux in the Bay of Biscay	46.5N; 4.5W	Annual mean	
MMF BB (F-J)	Meridional Momentum Flux in the Bay of Biscay for ICES hake spawning period	46.5N; 4.5W	February-July mean	
MMF BB (J-M)	Meridional Momentum Flux for hake spawning period in the Bay of Biscay	46.5N; 4.5W	January-May mean	
MMF GSB	Meridional Momentum Flux at Great Sole Bank	48.5N; 9.5W	Annual mean	
MMF GSB (F-J)	Meridional Momentum Flux at Great Sole Bank for ICES hake spawning period	48.5N; 9.5W	February-July mean	
MMF GSB (A-J)	Meridional Momentum Flux at Great Sole Bank for hake spawning period in the Celtic Sea	48.5N; 9.5W	April-June mean	
MMF Porcup.	Meridional Momentum Flux in Porcupine	52.5N; 11.5W	Annual mean	
MMF Porcup. (F-J)	Meridional Momentum Flux in Porcupine for ICES hake spawning period	52.5N; 11.5W	February-July mean	
MMF Porcup. (A-J)	Meridional Momentum Flux in Porcupine for hake spawning period in the western Ireland	52.5N; 11.5W	April-July mean	

Appendix 3 (cont.): Local parameters

Parameter	Description	Influence area	Study Period	Observations
ZMF BB	Zonal Momentum Flux in the Bay of Biscay	46.5N; 4.5W	Annual mean	
ZMF BB (F-J)	Zonal Momentum Flux in the Bay of Biscay for ICES hake spawning period	46.5N; 4.5W	February-July mean	
ZMF BB (J-M)	Zonal Momentum Flux for hake spawning period in the Bay of Biscay	46.5N; 4.5W	January-May mean	
ZMF GSB	Zonal Momentum Flux at Great Sole Bank	48.5N; 9.5W	Annual mean	
ZMF GSB (F-J)	Zonal Momentum Flux at Great Sole Bank for ICES hake spawning period	48.5N; 9.5W	February-July mean	
ZMF GSB (A-J)	Zonal Momentum Flux at Great Sole Bank for hake spawning period in the Celtic Sea	48.5N; 9.5W	April-June mean	
ZMF Porcup	Zonal Momentum Flux in Porcupine	52.5N; 11.5W	Annual mean	
ZMF Porcup. (F-J)	Zonal Momentum Flux in Porcupine for ICES hake spawning period	52.5N; 11.5W	February-July mean	
ZMF Porcup. (A-J)	Zonal Momentum Flux in Porcupine for hake spawning period in the western Ireland	52.5N; 11.5W	April-July mean	
SHF BB	Sensible Heat Flux in the Bay of Biscay	46.5N; 4.5W	Annual mean	
SHF BB (F-J)	Sensible Heat Flux in the Bay of Biscay for ICES hake spawning period	46.5N; 4.5W	February-July mean	
SHF BB (J-M)	Sensible Heat Flux for hake spawning period in the Bay of Biscay	46.5N; 4.5W	January-May mean	

Appendix 3 (cont.): Local parameters

Parameter	**Description**	**Influence area**	**Study Period**	**Observations**
SHF GSB	Sensible Heat Flux at Great Sole Bank	48.5N; 9.5W	Annual mean	
SHF GSB (F-J)	Sensible Heat Flux at Great Sole Bank for ICES hake spawning period	48.5N; 9.5W	February-July mean	
SHF GSB (A-J)	Sensible Heat Flux at Great Sole Bank for hake spawning period in the Celtic Sea	48.5N; 9.5W	April-June mean	
SHF Porcup.	Sensible Heat Flux in Porcupine	52.5N; 11.5W	Annual mean	
SHF Porcup. (F-J)	Sensible Heat Flux in Porcupine for ICES hake spawning period	52.5N; 11.5W	February-July mean	
SHF Porcup. (A-J)	Sensible Heat Flux in Porcupine for hake spawning period in the western Ireland	52.5N; 11.5W	April-July mean	
LHF BB	Latent Heat Flux in the Bay of Biscay	46.5N; 4.5W	Annual mean	
LHF BB (F-J)	Latent Heat Flux in the Bay of Biscay for ICES hake spawning period	46.5N; 4.5W	February-July mean	
LHF BB (J-M)	Latent Heat Flux for hake spawning period in the Bay of Biscay	46.5N; 4.5W	January-May mean	
LHF GSB	Latent Heat Flux at Great Sole Bank	48.5N; 9.5W	Annual mean	
LHF GSB (F-J)	Latent Heat Flux at Great Sole Bank for ICES hake spawning period	48.5N; 9.5W	February-July mean	
LHF GSB (A-J)	Latent Heat Flux at Great Sole Bank for hake spawning period in the Celtic Sea	48.5N; 9.5W	April-June mean	

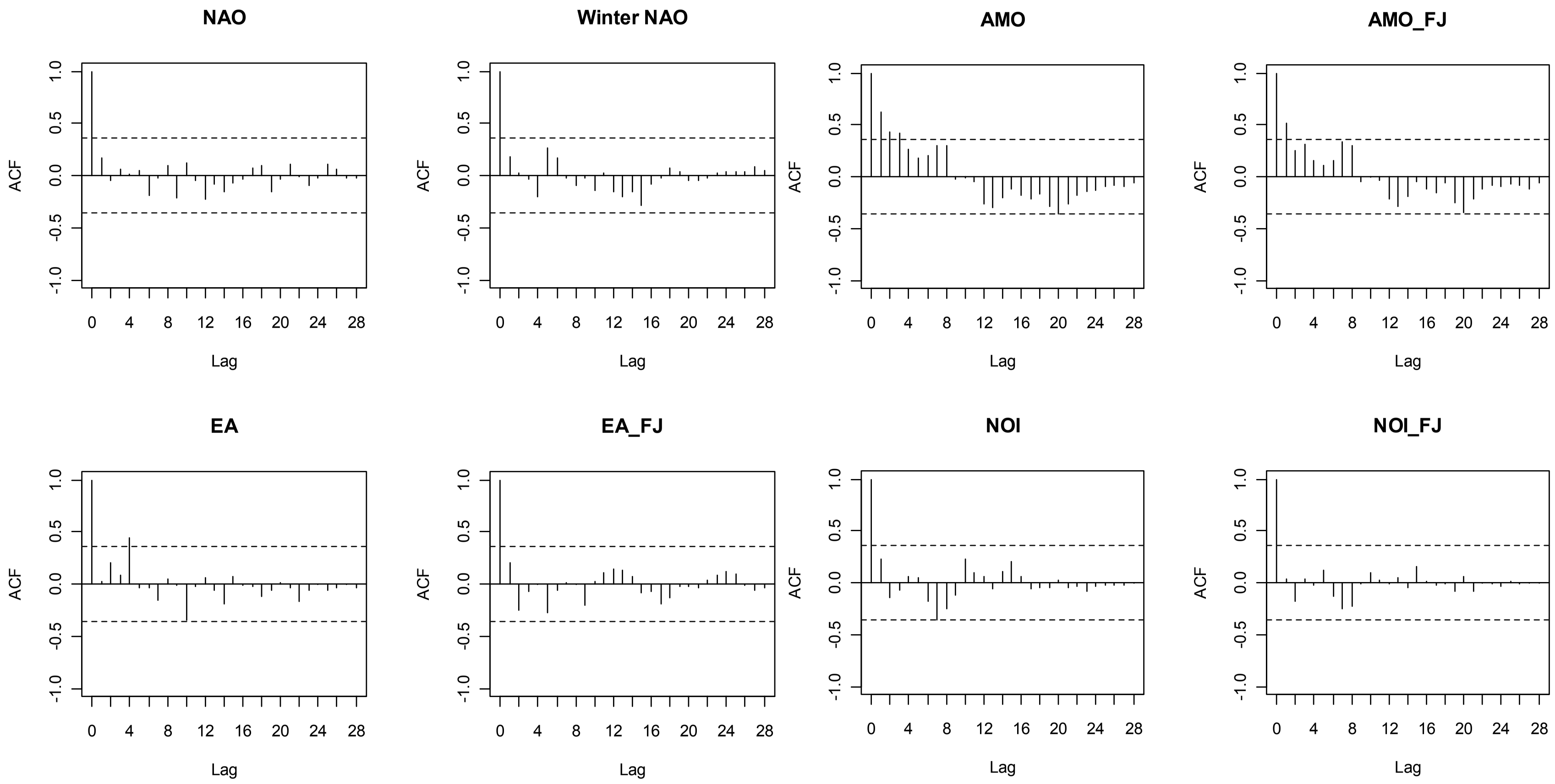
Appendix 3 (cont.): Local parameters

Parameter	**Description**	**Influence area**	**Study Period**	**Observations**
LHF Porcup.	Latent Heat Flux in Porcupine	52.5N; 11.5W	Annual mean	
LHF Porcup. (F-J)	Latent Heat Flux in Porcupine for ICES hake spawning period	52.5N; 11.5W	February-July mean	
LHF Porcup. (A-J)	Latent Heat Flux in Porcupine for hake spawning period in the western Ireland	52.5N; 11.5W	April-July mean	

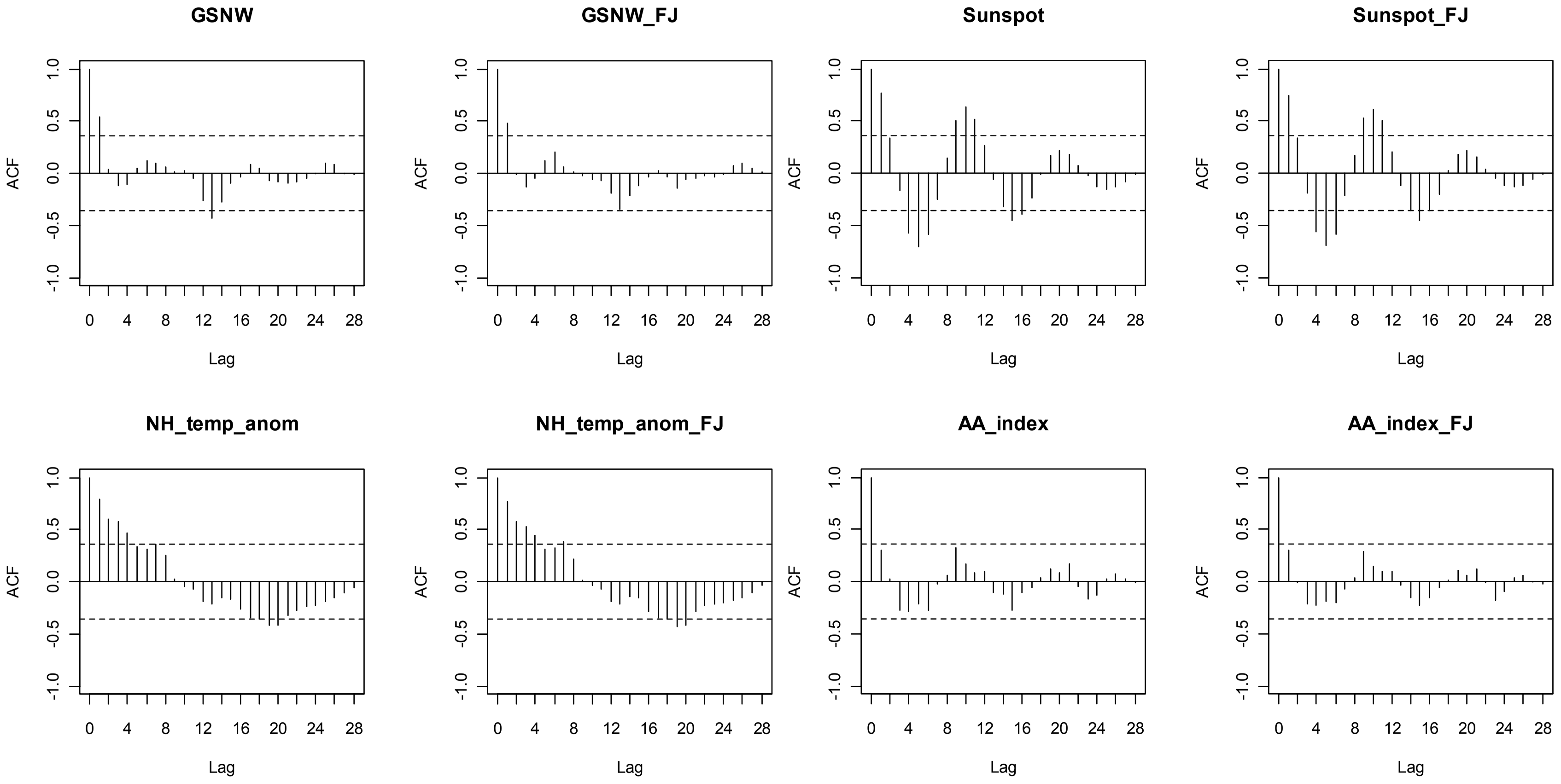
Appendix 4: Biological regional parameters

Parameter	Description	Influence area	Study Period	Observations
Cop. C3	Copepod abundance in CPR box C3	East of Ireland	Annual mean	
Cop. C4	Copepod abundance in CPR box C4	North of Ireland	Annual mean	
Cop. D3	Copepod abundance in CPR box D3	South of England	Annual mean	
Cop. D4	Copepod abundance in CPR box D4	Celtic Sea	Annual mean	
Mean cop.	Mean copepod abundance of CPR boxes C3, C4, D3 and D4	Waters around UK and Ireland	Annual mean	
Cop. C3 (F-J)	Copepod abundance in CPR box C3 for ICES hake spawning period	East of Ireland	February-July mean	
Cop. C4 (F-J)	Copepod abundance in CPR box C4 for ICES hake spawning period	North of Ireland	February-July mean	
Cop. D3 (F-J)	Copepod abundance in CPR box D3 for ICES hake spawning period	South of England	February-July mean	
Cop. D4 (F-J)	Copepod abundance in CPR box D4 for ICES hake spawning period	Celtic Sea	February-July mean	
Mean cop. (F-J)	Mean copepod abundance of CPR boxes C3, C4, D3 and D4 for ICES hake spawning period	Waters around UK and Ireland	February-July mean	
Cop. D4 (May)	Copepod abundance in May in CPR box D4	Celtic Sea	May mean	Copepod peak abundance within the spawning area of the Celtic Sea
Mean cop. (M-J)	Mean copepod abundance of CPR boxes C3, C4, D3 and D4 for the period May-June	Waters around UK and Ireland	May-June mean	Copepod peak abundance for the whole area

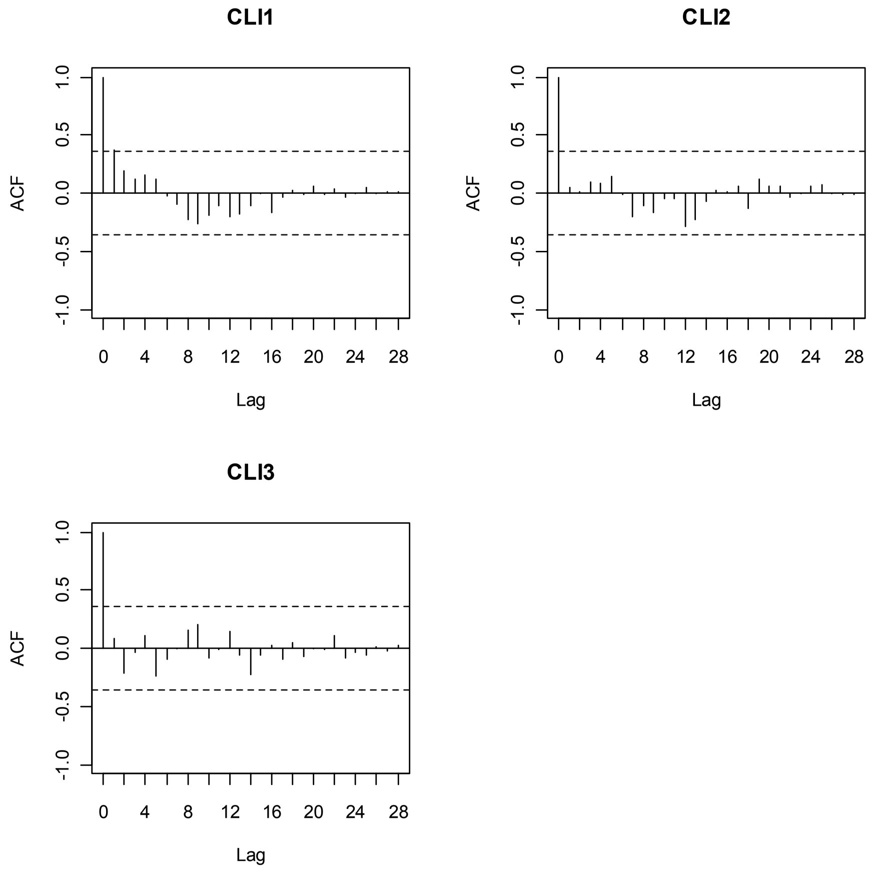
Appendix 5: Graphical representation of the ACF results of global indices



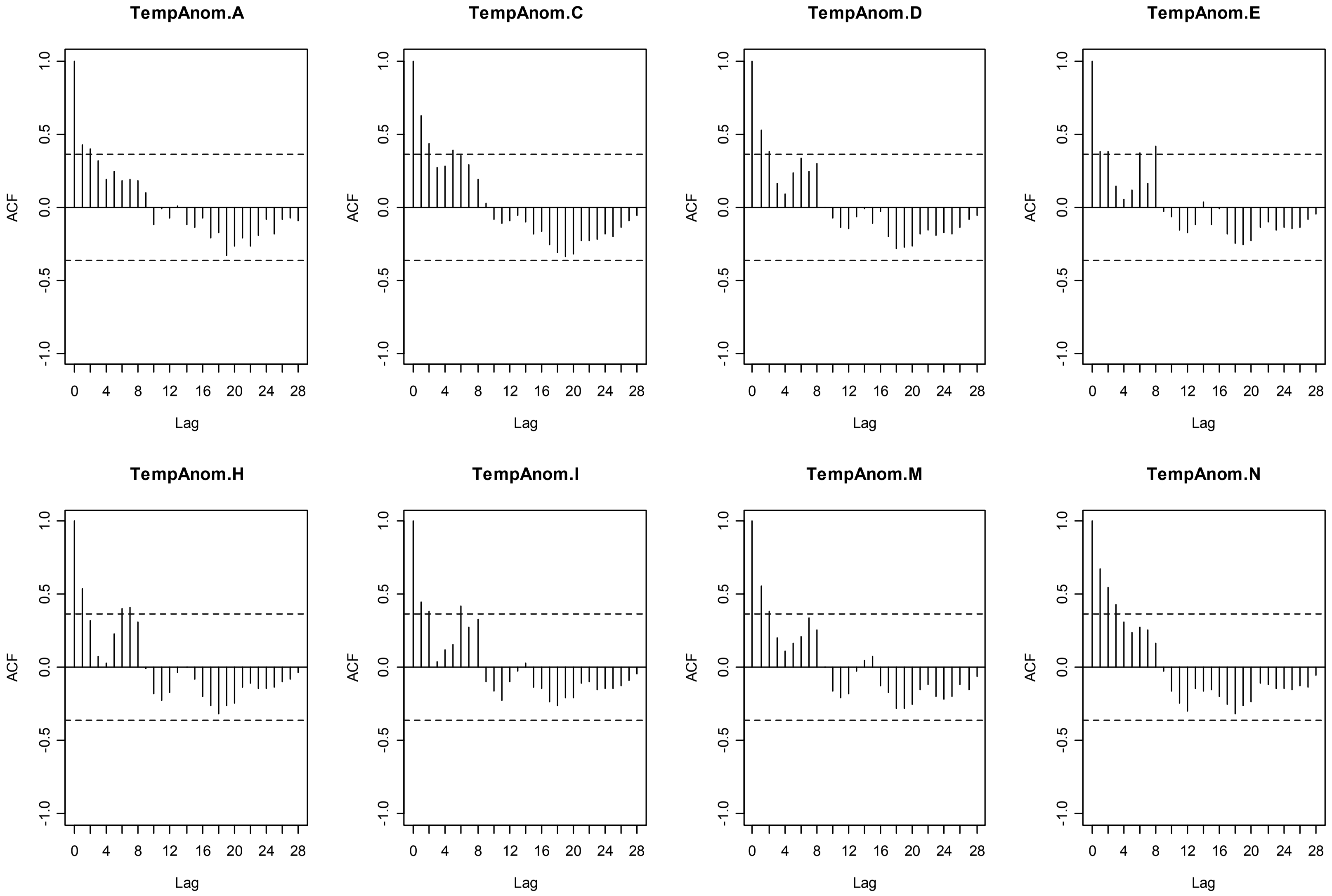
Appendix 5 (cont.): Graphical representation of the ACF results of global indices



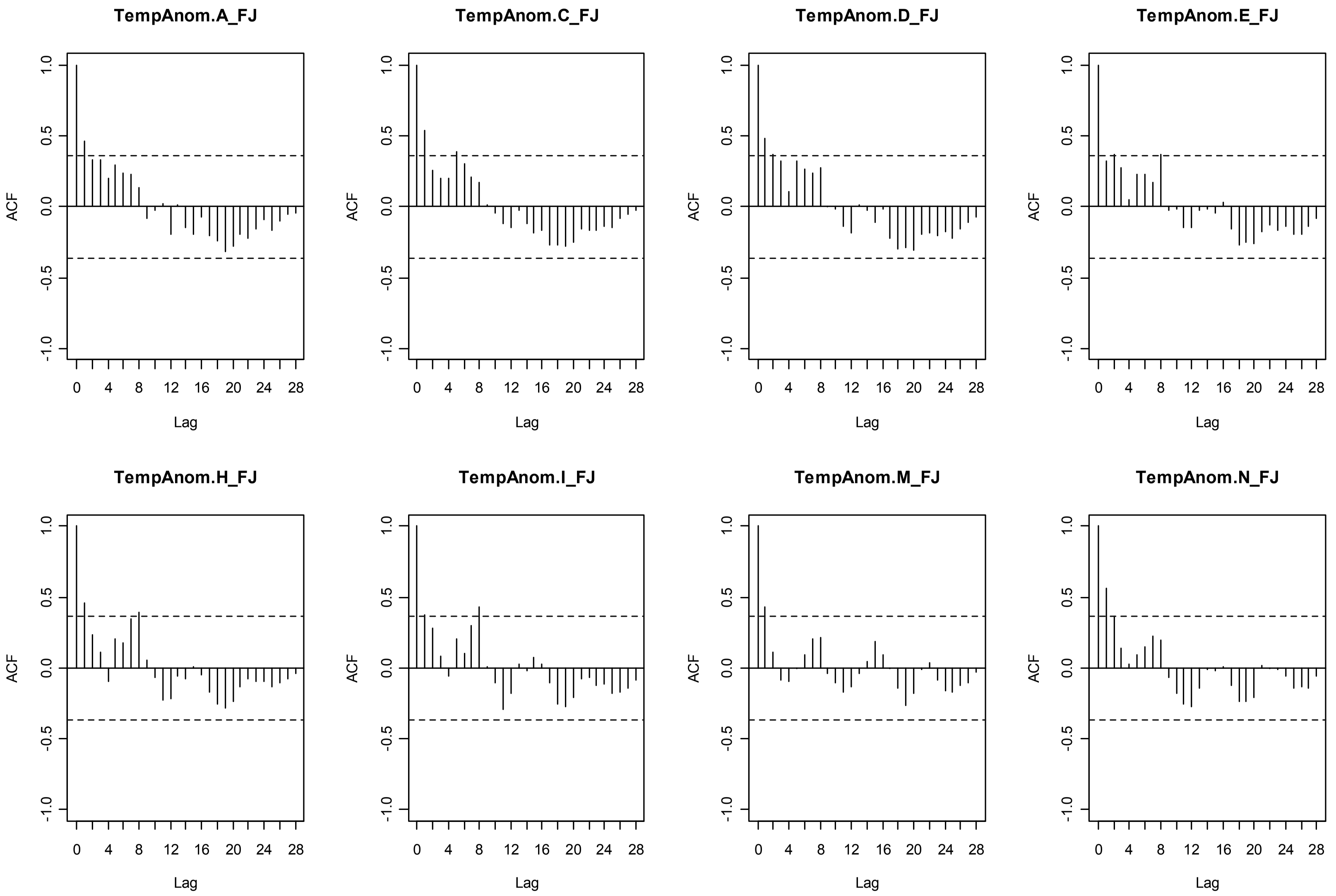
Appendix 5 (cont.): Graphical representation of the ACF results of global indices



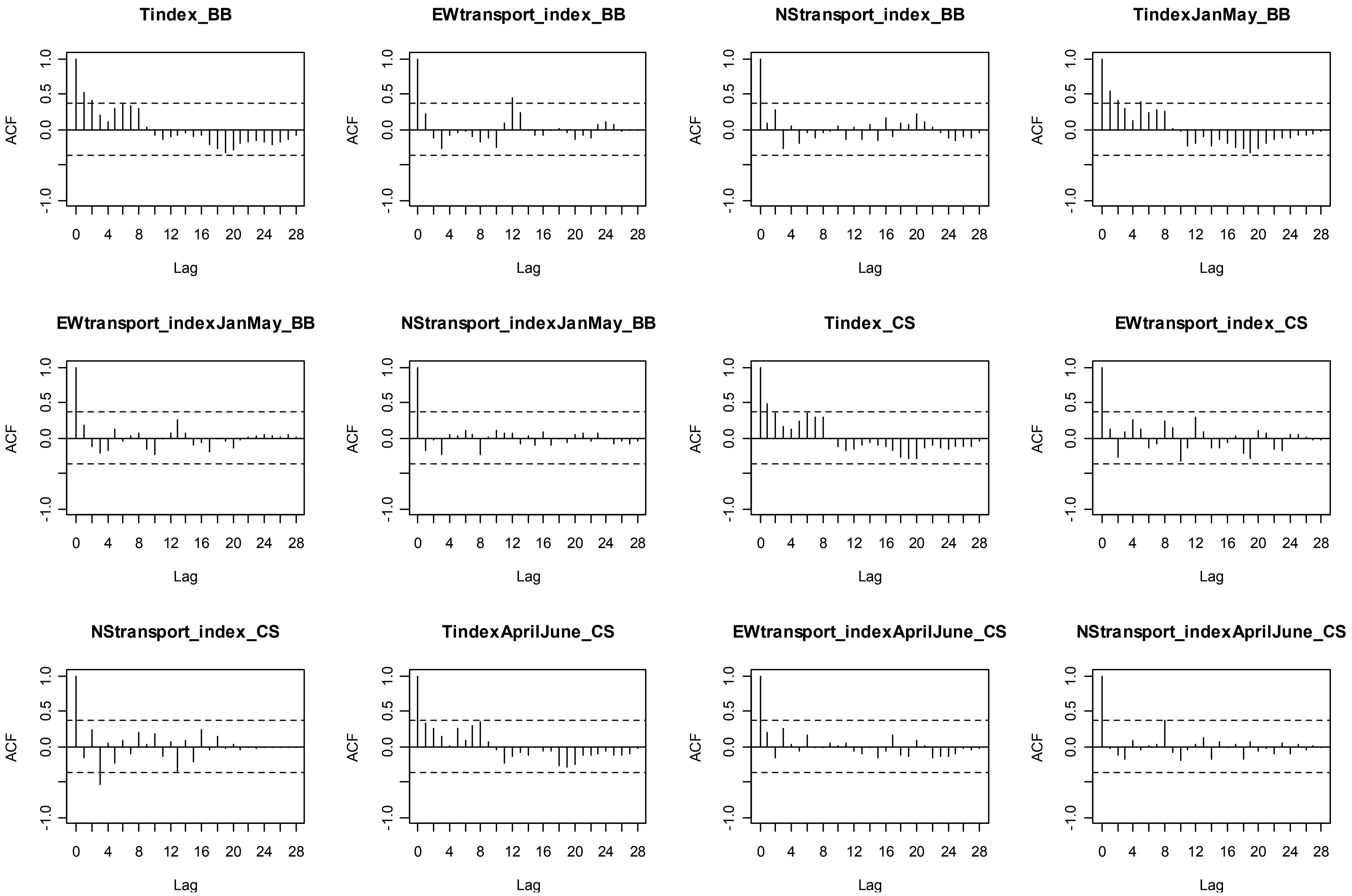
Appendix 6: Graphical representation of the ACF results of regional parameters



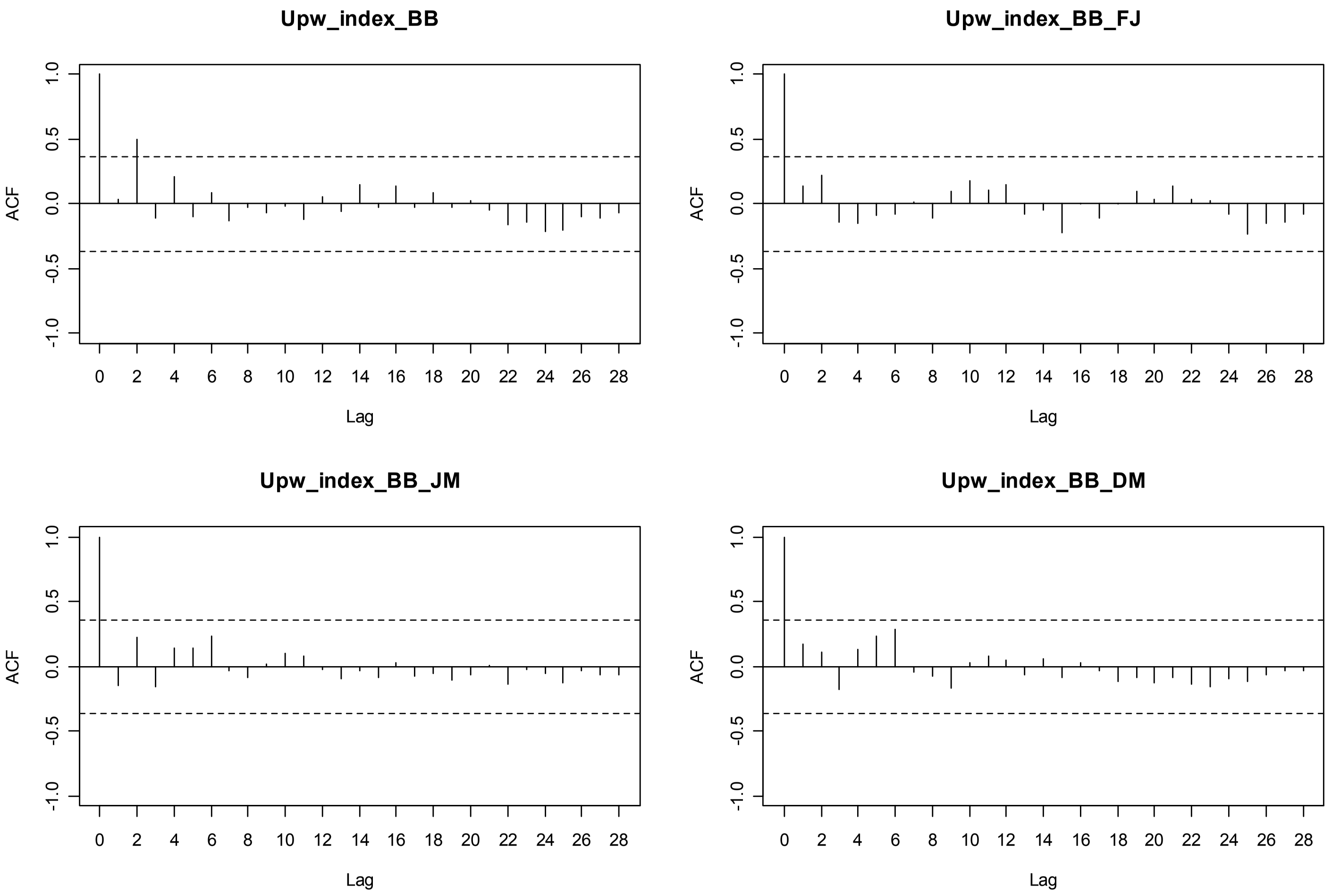
Appendix 6 (cont.): Graphical representation of the ACF results of regional parameters



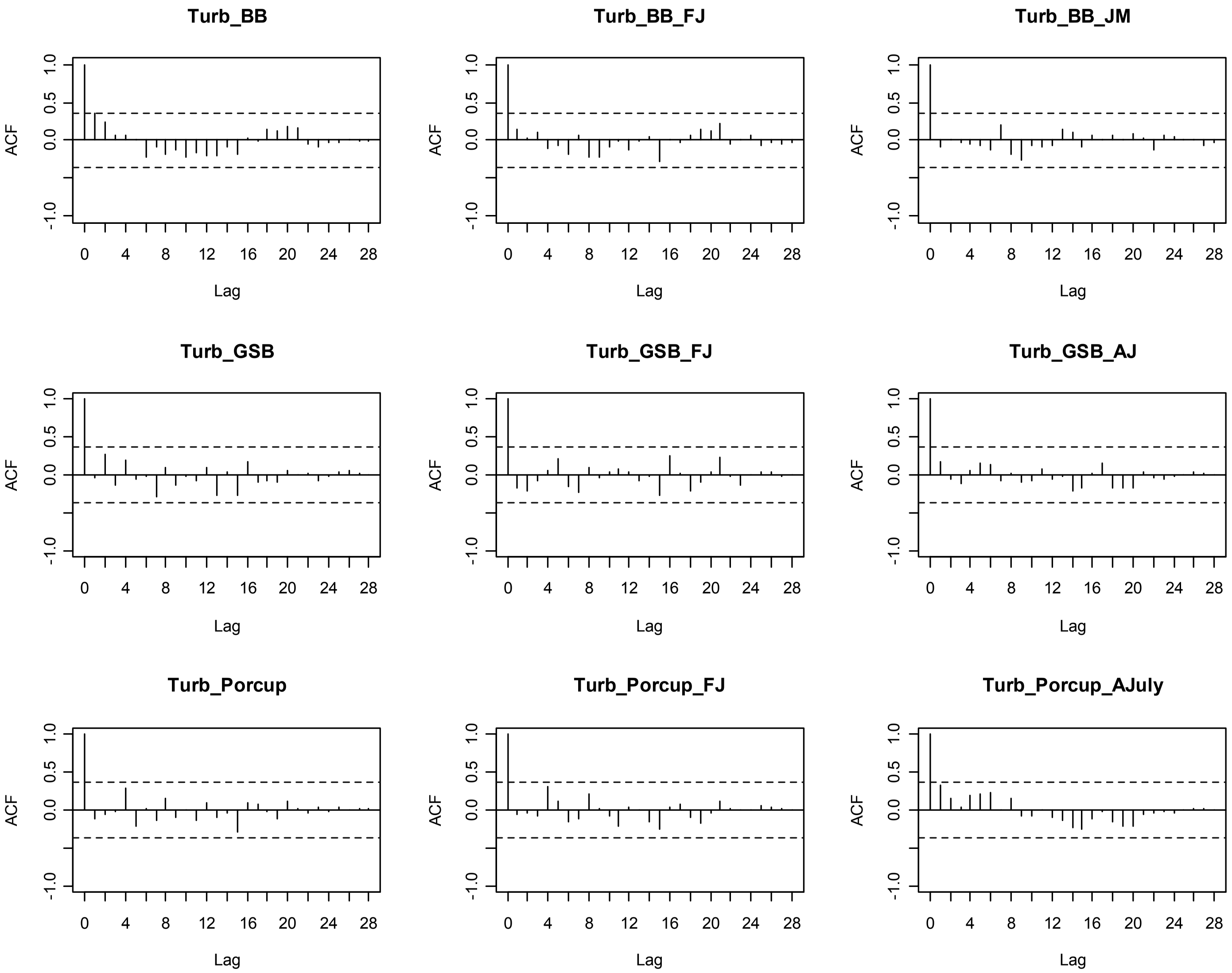
Appendix 6 (cont.): Graphical representation of the ACF results of regional parameters



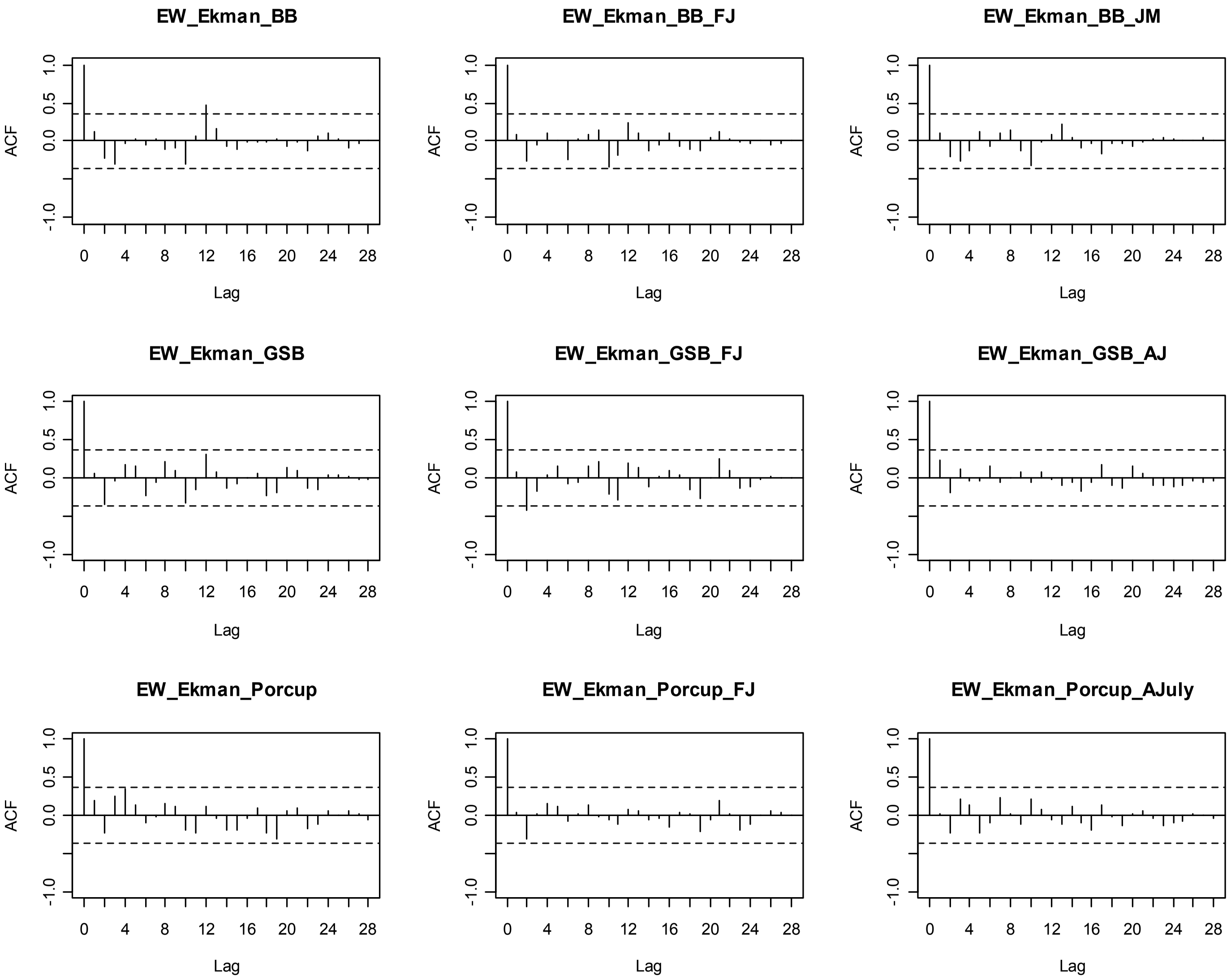
Appendix 7: Graphical representation of the ACF results of local parameters



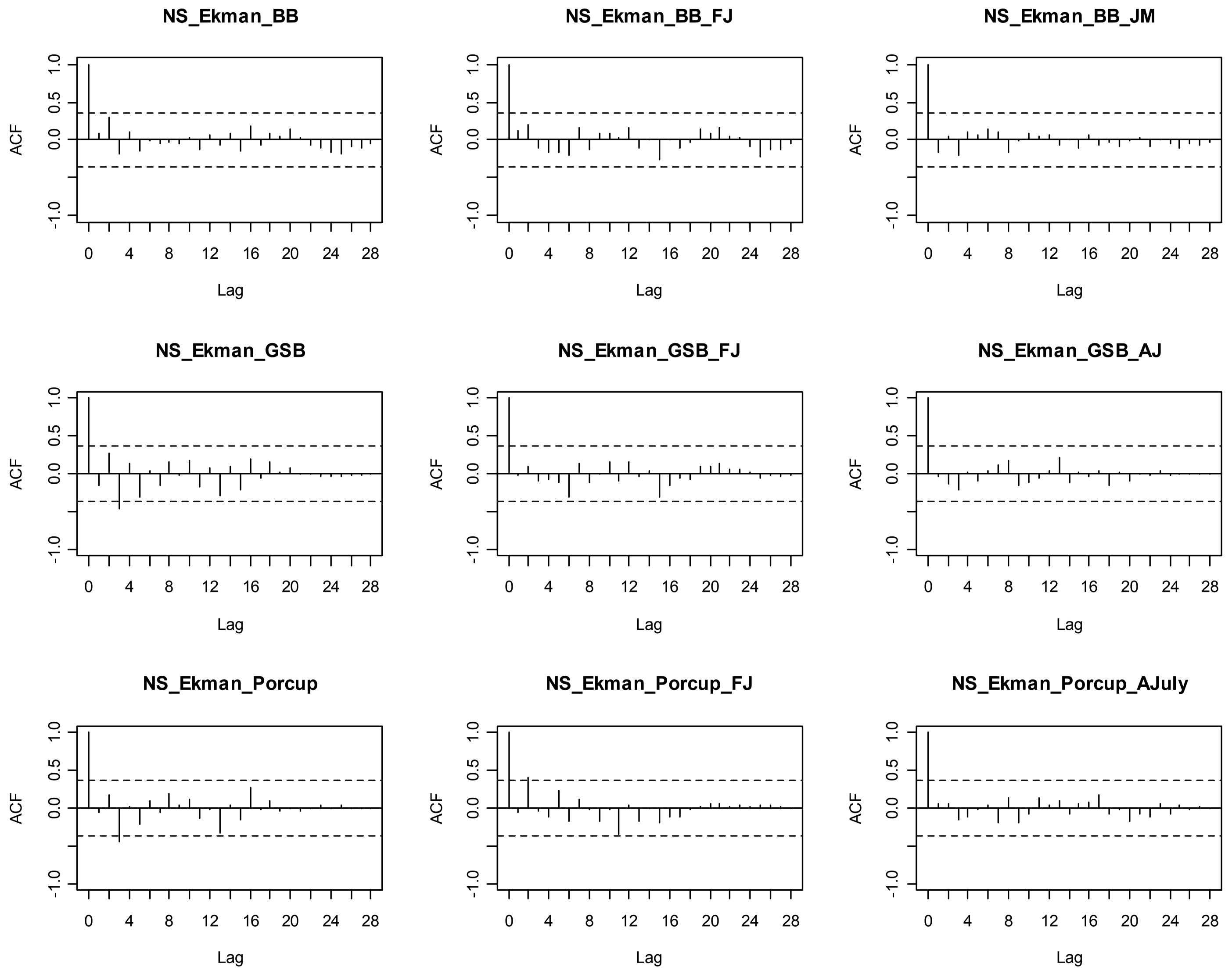
Appendix 7 (cont.): Graphical representation of the ACF results of local parameters



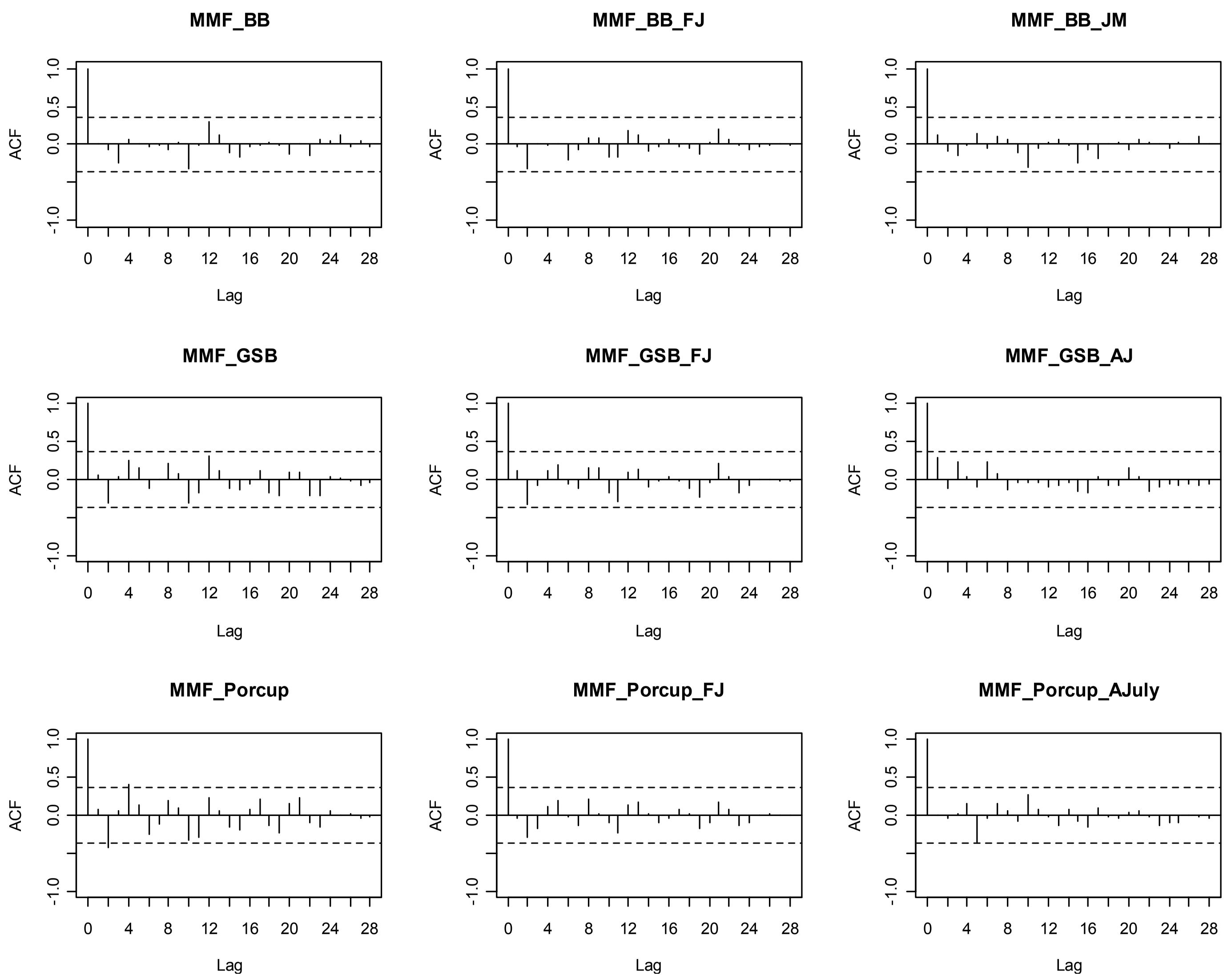
Appendix 7 (cont.): Graphical representation of the ACF results of local parameters



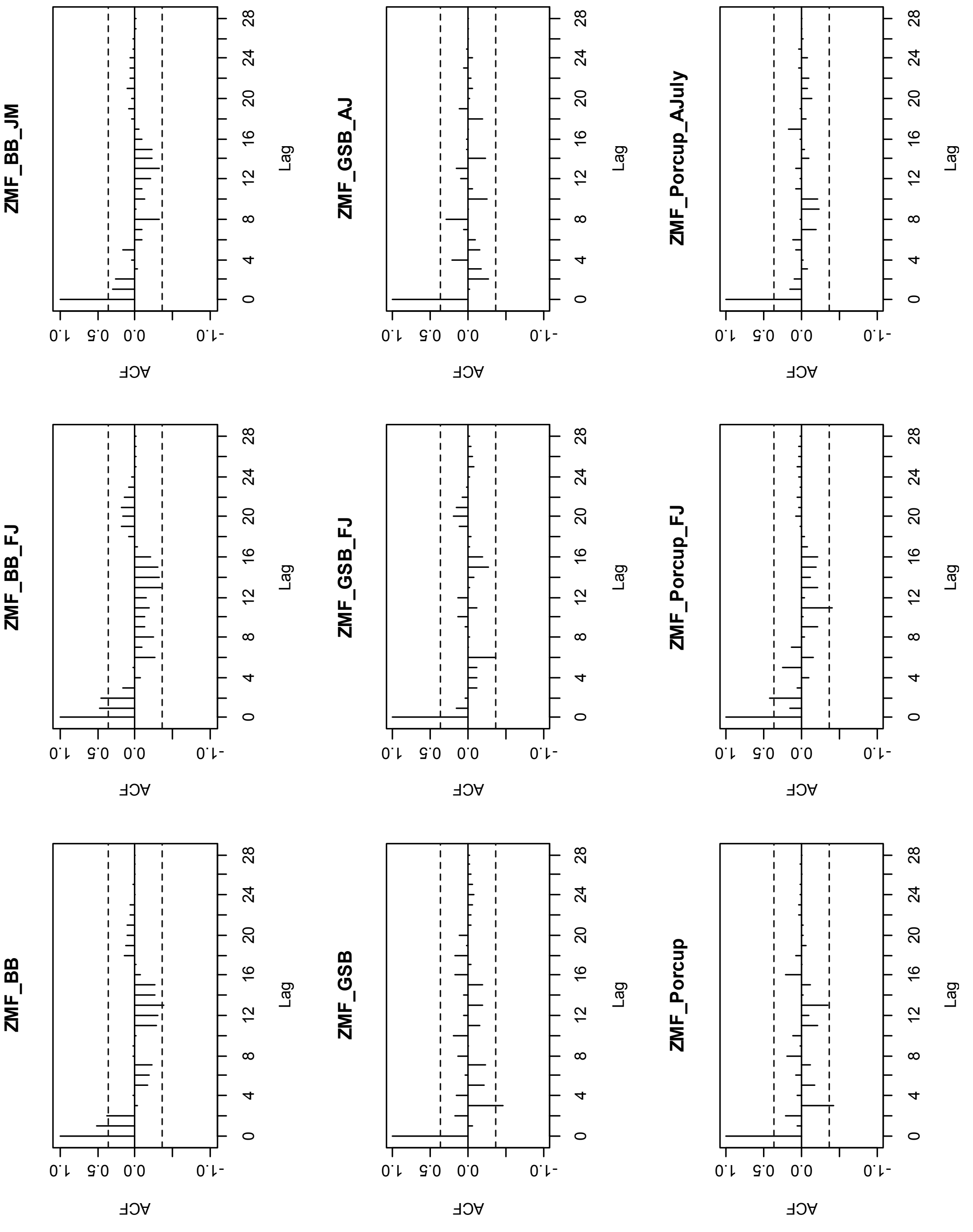
Appendix 7 (cont.): Graphical representation of the ACF results of local parameters



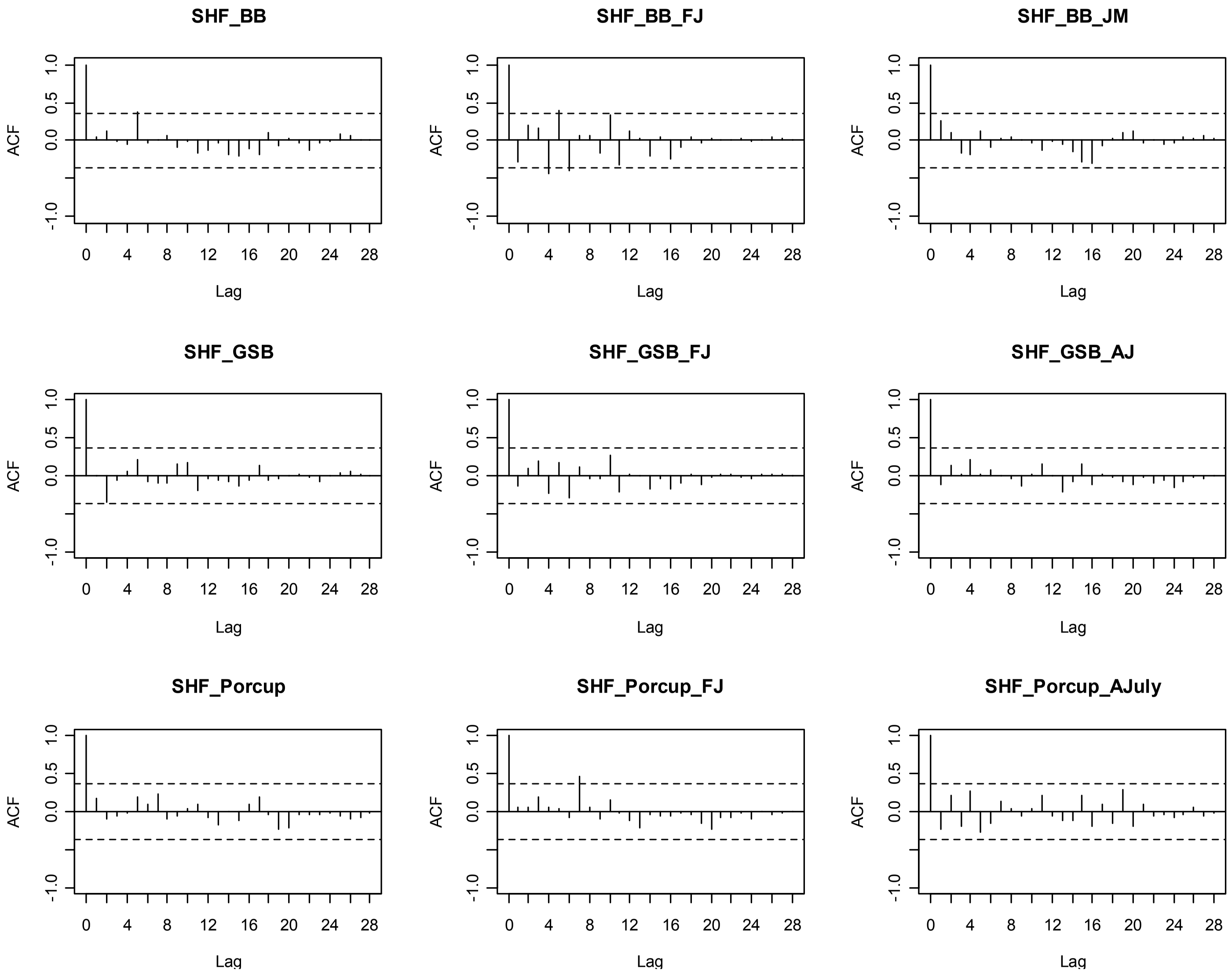
Appendix 7 (cont.): Graphical representation of the ACF results of local parameters



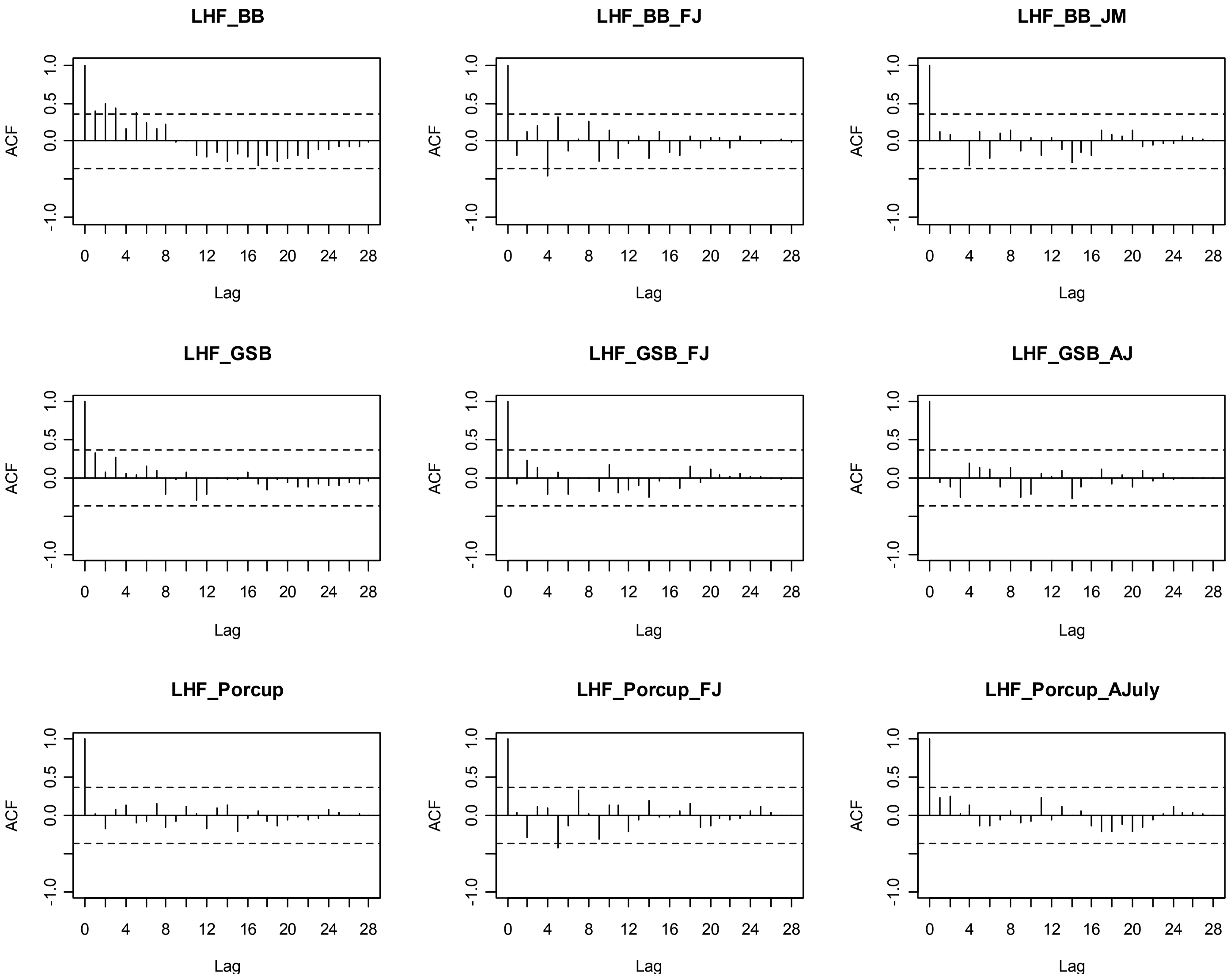
Appendix 7 (cont.): Graphical representation of the ACF results of local parameters



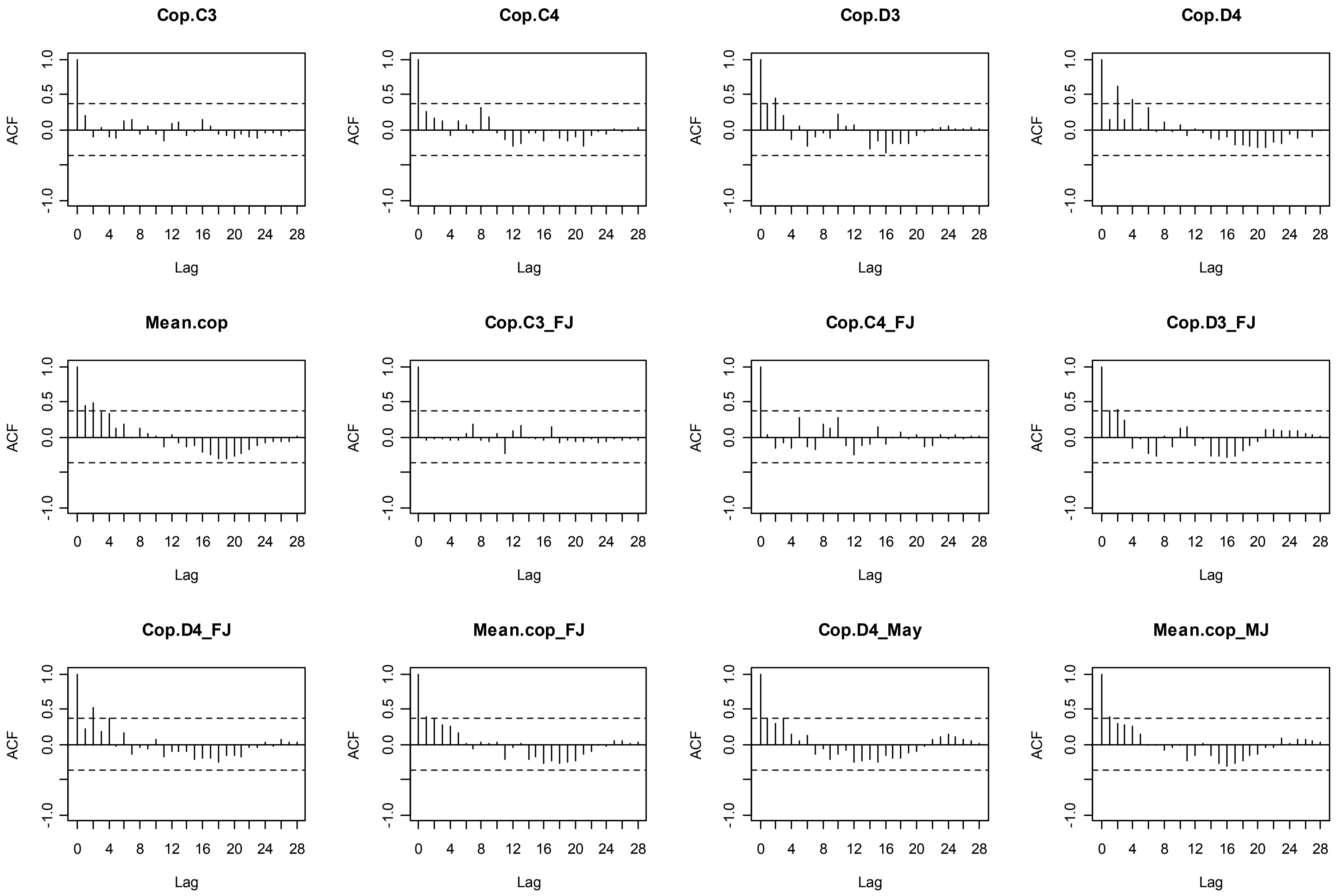
Appendix 7 (cont.): Graphical representation of the ACF results of local parameters



Appendix 7 (cont.): Graphical representation of the ACF results of local parameters



Appendix 8: Graphical representation of the ACF results of biological parameters



Appendix 9: List of parameter that showed AUTOCORRELATION

AMO, AMO_FJ

Cop.D3, Cop.D4, Mean.cop, Cop.D3_FJ, Cop.D4_FJ, Mean.cop_FJ, Cop.D4_May, Mean.cop_MJ

GSNW, GSNW_FJ

NH_temp_anom, NH_temp_anom_FJ

LHF_BB, LHF_BB_FJ

Tindex_BB, TindexJanMay_BB, Tindex_CS

Sunspot, Sunspot_FJ

Temp. anom. A, Temp. anom. C, Temp. anom. D, Temp. anom. E, Temp. anom. H, Temp. anom. I, Temp. anom. M, Temp. anom. N

Temp. anom. A_FJ, Temp. anom. C_FJ, Temp. anom. D_FJ, Temp. anom. E_FJ, Temp. anom. H_FJ, Temp. anom. I_FJ, Temp. anom. M_FJ, Temp. anom. N_FJ

ZMF_BB, ZMF_BB_FJ

Appendix 10: List of parameter that showed NO AUTOCORRELATION

NAO, Winter NAO, EA, EA_FJ

NOI, NOI_FJ

CLI1, CLI2, CLI3

Cop.C3, Cop.C4, Cop.C3_FJ, Cop.C4_FJ

EW_Ekman_BB, EW_Ekman_BB_FJ, EW_Ekman_BB_JM, EW_Ekman_GSB, EW_Ekman_GSB_FJ, EW_Ekman_GSB_AJ, EW_Ekman_Porcup, EW_Ekman_Porcup_FJ, EW_Ekman_Porcup_Ajuly

NS_Ekman_BB, NS_Ekman_BB_FJ, NS_Ekman_BB_JM, NS_Ekman_GSB, NS_Ekman_GSB_FJ, NS_Ekman_GSB_AJ, NS_Ekman_Porcup, NS_Ekman_Porcup_FJ, NS_Ekman_Porcup_Ajuly

LHF_BB_JM, LHF_GSB, LHF_GSB_FJ, LHF_GSB_AJ, LHF_Porcup, LHF_Porcup_FJ. LHF_Porcup_AJuly

MMF_BB, MMF_BB_FJ, MMF_BB_JM, MMF_GSB, MMF_GSB_FJ, MMF_GSB_AJ, MMF_Porcup, MMF_Porcup_FJ, MMF_Porcup_AJuly

SHF_BB, SHF_BB_FJ, SHF_BB_JM, SHF_GSB, SHF_GSB_FJ, SHF_GSB_AJ, SHF_Porcup, SHF_Porcup_FJ, SHF _Porcup_AJuly

EWtransport_index_BB, NStransport_index_BB, EWtransport_indexJanMay_BB, NStransport_indexJanMay_BB

EWtransport_index_CS, NStransport_index_CS, EWtransport_indexAprilJune_CS, NStransport_indexAprilJune_CS

TindexAprilJune_CS

AA_index, AA_index_FJ

Turb_BB, Turb_BB_FJ, Turb_BB_JM, Turb_GSB, Turb_GSB_FJ, Turb_GSB_AJ, Turb_Porcup, Turb_Porcup_FJ, Turb_Porcup_AJuly

Upw_index_BB, Upw_index_BB_FJ, Upw_index_BB_JM, Upw_index_BB_DM

ZMF_BB_JM, ZMF_GSB, ZMF_GSB_FJ, ZMF_GSB_AJ, ZMF_Porcup_ZMF_Porcup_FJ, ZMF_Porcup_AJuly

…ailega gara Gorbea puntara…

…eta bai, bistak ederrak dira hemetik goitik!