Deciphering the past and the future response of marine pelagic fishes to global warming

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eman ta zabal zazu

Universidad
del País Vasco

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Deciphering the past and the future response of marine pelagic fishes to global warming

Presented by

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“Itsasoa defendatzeko modurik onena hau maitatzea da eta ezin da maitatu ezagutzen ez dena”

Jacques Cousteau

"La mejor forma de defender el mar es amándolo, y no se ama lo que no se conoce”

Jacques Cousteau

“El aprendizaje es experiencia,

todo lo demás es información”

Albert Einstein

A mi familia

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I appreciate all the economic, time and knowledge resources made available to me; the Basque Government Department of Economic Development and Competitiveness scholarship for training young researchers; CLIPES (funded by the Basque Government), CLIREMAR (funded by Fundación Biodiversidad) and CLIOTOP (Climate Impacts on Oceanic Top Predators) projects, and all scholarships granted to attend international conferences and summer schools given by the Integrated Marine Biosphere Research Project (IMBeR), the National Oceanic and Atmospheric Administration (NOAA), the Ocean Carbon and Biochemistry (OCB) and Monterrey Bay Aquarium. Thank you all.

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Dedicado a tod@s aquell@s que han transitado parte de este camino conmigo

SCIENTIFIC PRODUCTION

As a result of the research conducted in this Ph.D. thesis, the following publications in SCI journal and oral communications in international conferences and symposiums have been published and presented. In addition, some of the publications have been spread in the media (radio, television, and newspapers) to the public out of the scientific community.

Publications

Erauskin-Extramiana M., Herzka SZ, Hinojosa-Arango G, Aburto-Oropeza O (2017) An interdisciplinary approach to evaluate the status of large-bodied Serranid fisheries: The case of Magdalena-Almejas Bay lagoon complex, Baja California Sur, Mexico. Ocean & Coastal Management, **145**, 21-34. https://doi.org/10.1016/j.ocecoaman.2017.05.005

Erauskin-Extramiana, M., Alvarez, P., Arrizabalaga, H., Ibaibarriaga, L., Uriarte, A., Cotano, U., Santos, M., Ferrer, L., Cabré, A. and Irigoien, X. (2019). "Historical trends and future distribution of anchovy spawning in the Bay of Biscay." Deep-Sea Research Part II: Topical Studies in Oceanography **159**: 169-182. https://doi.org/10.1016/j.dsr2.2018.07.007

Erauskin-Extramiana, M., Arrizabalaga, H., Hobday, AJ., Cabré, A., Ibaibarriaga, L., Arregui, I., Murua, H. and Chust, G. (2019). "Large-scale distribution of tuna species in a warming ocean." Global Change Biology 25(6): 2043-2060. https://doi.org/10.1111/gcb.14630

Erauskin-Extramiana, M., Arrizabalaga, H., Cabré, A., Coelho, R., Rosa, D., Ibaibarriaga, L., Chust, G. (2019). "Are shifts in species distribution triggered by climate change? Application to the swordfish global case." Deep-Sea Research (Part II, Topical Studies in Oceanography). https://doi.org/10.1016/j.dsr2.2019.104666

Oral communications

Erauskin-Extramiana, M., Alvarez, P., Arrizabalaga, H., Ibaibarriaga, L., Uriarte, A., Cotano, U., Santos, M., Ferrer, L., Cabré, A. and Irigoien, X.: *"Evaluación de los impactos del cambio climático en las pesquerías vascas"*. 11th International Postgraduate Course Research in Marine Environment & Resources in San Sebastian, January 30th-3rd February 2017.

Erauskin-Extramiana, M., Alvarez, P., Arrizabalaga, H., Ibaibarriaga, L., Uriarte, A., Cotano, U., Santos, M., Ferrer, L., Cabré, A. and Irigoien, X.: "*Will Climate change impact the anchovy spawning habitat in the Bay of Biscay*". Drivers of Dynamics of Small Pelagic Fish Resources, Victoria, CANADA, March 6-11, 2017.

Erauskin-Extramiana, M., Arrizabalaga, H., Hobday, AJ., Cabré, A., Ibaibarriaga, L., Arregui, I., Murua, H. and Chust, G.: "*Climate change impact in past and future distribution of six tuna species*". The 69th Tuna Conference, Lake Arrowhead, California, USA. May 21-2, 2018.

Erauskin-Extramiana, M., Alvarez, P., Arrizabalaga, H., Ibaibarriaga, L., Uriarte, A., Cotano, U., Santos, M., Ferrer, L., Cabré, A. and Irigoien, X.: "*Assessment of Climate Change Impacts in the Bay of Biscay anchovy*". Isobay 16 (5-7th June 2018) Anglet (France). *Prize for the best oral communication.*

Erauskin-Extramiana, M., Arrizabalaga, H., Hobday, AJ., Cabré, A., Ibaibarriaga, L., Arregui, I., Murua, H. and Chust, G.: "*Large-scale distribution of tuna species in a warming ocean*".
IMBeR ClimEco6 Summer School. Interdisciplinary approaches for sustainable oceans. Gadjah Mada University, Yogyakarta, Indonesia, August 1-8, 2018.

Erauskin-Extramiana, M., Arrizabalaga, H., Hobday, AJ., Cabré, A., Ibaibarriaga, L., Arregui, I., Murua, H. and Chust, G.: "*Large-scale distribution of tuna species in a warming ocean*". 4th CLIOTOP Symposium, National Taiwan Ocean University, Keelung, Taiwan 15-19 October 2018.

Erauskin-Extramiana, M., Arrizabalaga, H., Hobday, AJ., Cabré, A., Ibaibarriaga, L., Arregui, I., Murua, H. and Chust, G.: "*Large-scale distribution of tuna species in a warming ocean*". 13th International Postgraduate Course Research in Marine Environment & Resources in San Sebastian, January 28th-1st February 2019.

Erauskin-Extramiana, M., Arrizabalaga, H., Hobday, AJ., Cabré, A., Ibaibarriaga, L., Arregui, I., Murua, H. and Chust, G.: "*Large-scale distribution of tuna species in a warming ocean*". IMBeR *Future Oceans$_2$* Open Science Conference and workshops from 15-21 June 2019 in Brest, France.

Projects

CLIPES project for predicting and anticipating the effects of variability in oceanographic conditions and global climate change on Basque fleet fisheries founded by the Basque Government.

CLIREMAR (Climate scenarios of vulnerable marine resources in Spain) project funded by Fundación Biodiversidad with the aim to predict the effect of climate change over Spanish marine resources and fisheries.

CLIOTOP (Climate Impacts on Oceanic Top Predators) project which wants to answer big and important questions related to climate change, ecosystems, fishing, and marine top predators.

Surveys

BIOMAN (BIOMass of ANchovy) surveys sponsored since 1987 to 2016 by the Department of fisheries of the autonomous Basque Government within Spain and since 2003 by the European Union within the Community framework for the Data Collection Regulation (Council Regulations (EC) No 1543/2000 and No199/2008). The survey has also been supported by the Spanish General Secretariat of Sea providing the R/V Emma Bardán since 2003. I participated in the 2016 and 2017 BIOMAN surveys as part of the process of data collection for the first chapter of the thesis.

Other

Chust G., **Erauskin-Extramiana M.**, Arrizabalaga H., Hobday A., Cabré A., Ibaibarriaga L., Arregui I., Murua H. CLIREMAR (Climate scenarios over vulnerable marine resources in Spain) project results' presentation conference, Derio, June 5th, 2018.

Arrizabalaga H., **Erauskin-Extramiana M.**, Hobday A., Cabré A., Ibaibarriaga L., Arregui I., Murua H., Chust G. Klima aldaketaren eragina atunengan. Arrain Azoka. Bermeo tuna world capital. Bermeoko Arrantzaren Museoa, Maiatza 2019.

Arrizabalaga H., **Erauskin-Extramiana M.**, Coelho R. Relative habitat size for swordfish stocks based on a global habitat model. SCRS/2018/043. Report presented in the ICCAT Methods' Working Group, 2018.

Many news in **local newspapers** and an interview on **television** were conducted to show to the general public the findings of the effect of climate change within main commercial tuna species in the past and in the future.

This **Ph.D. thesis** presented under the **international mention** from the **University of the Basque Country**, have been reviewed and approved for its defense by three scientific experts from non-Spanish research institutions:

- **Dr. Stephanie Brodie**, from the Southwest Fisheries Science Center Department of the National Oceanic and Atmospheric Administration (NOAA).
- **Dr. Gabriel Reygondeau**, from the Changing Oceans Research Unit (CORU) of the University of British Columbia (UBC).
- **Professor Ph.D. Myron Peck**, from the Biology Department of the University of Hamburg.

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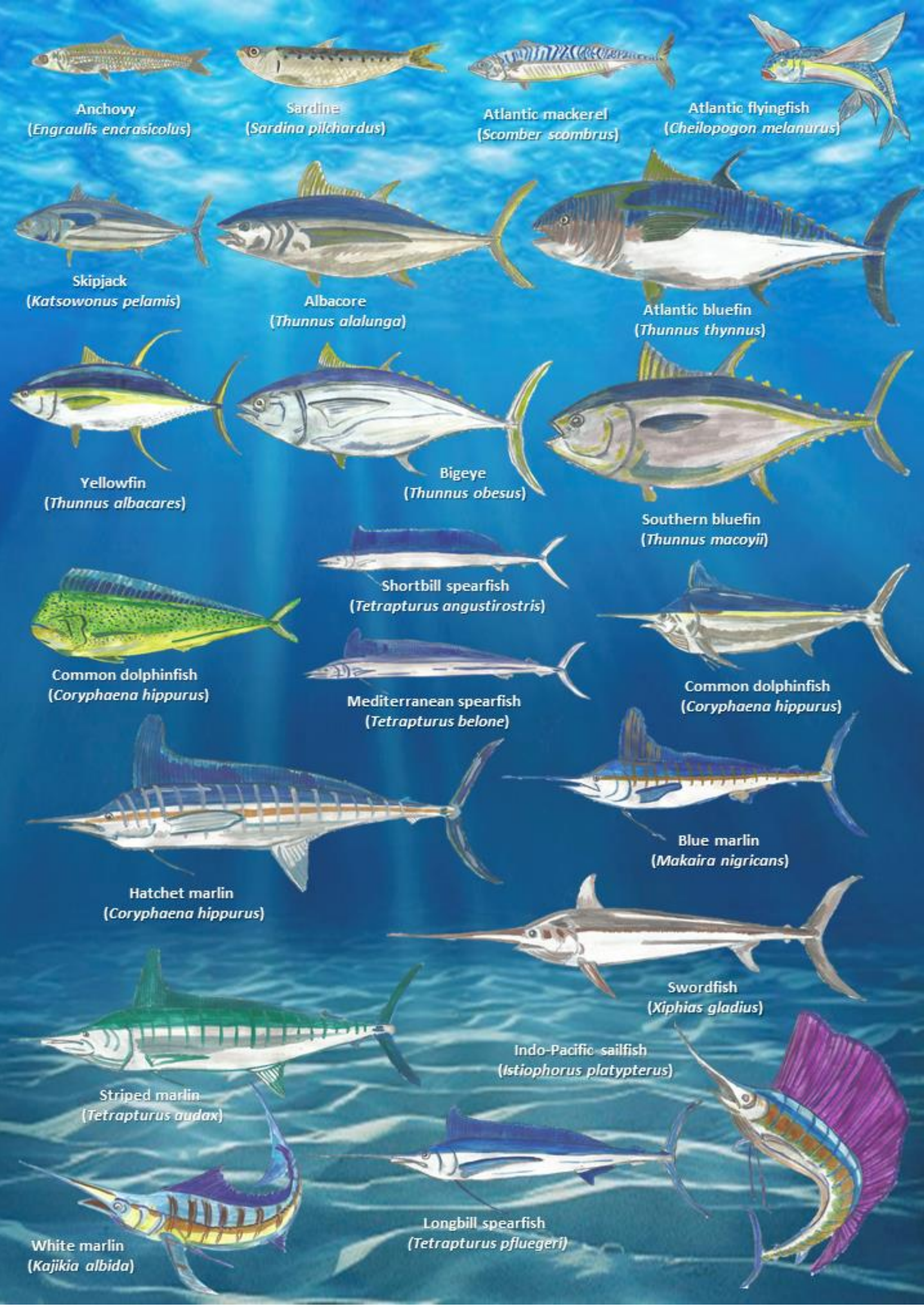
Anchovy
(*Engraulis encrasicolus*)
Sardine
(*Sardina pilchardus*)
Atlantic mackerel
(*Scomber scombrus*)
Atlantic flyingfish
(*Cheilopogon melanurus*)
Skipjack
(*Katsowonus pelamis*)
Albacore
(*Thunnus alalunga*)
Atlantic bluefin
(*Thunnus thynnus*)
Yellowfin
(*Thunnus albacares*)
Bigeye
(*Thunnus obesus*)
Southern bluefin
(*Thunnus macoyii*)
Shortbill spearfish
(*Tetrapturus angustirostris*)
Common dolphinfish
(*Coryphaena hippurus*)
Mediterranean spearfish
(*Tetrapturus belone*)
Common dolphinfish
(*Coryphaena hippurus*)
Hatchet marlin
(*Coryphaena hippurus*)
Blue marlin
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Swordfish
(*Xiphias gladius*)
Indo-Pacific sailfish
(*Istiophorus platypterus*)
Striped marlin
(*Tetrapturus audax*)
Longbill spearfish
(*Tetrapturus pfluegeri*)
White marlin
(*Kajikia albida*)

LABURPENA

Klima sistemaren beroketa ukaezina da. Azken hamarkadetan, honek ekosistemen alderdi ugarietan eragin du, hala nola, tenperatura, estratifikazioa, zirkulazioa, oxigenoaren erabilgarritasuna, kimika (pH) eta lehen eta bigarren mailako produkzioan. Ondorioz, ingurumen baldintzen aldaketa horiek lurreko eta itsasoko ekosistemetan, eskualdeetan, espezieetan eta bizitzako etapetan eragina dute, bai modu zuzenean baita zeharkakoan ere. Espezieen banaketan, ugaritasunean eta fenologian (baldintza klimatikoekin lotutako urtaroko fenomeno biologikoak) ere aldaketak izan dira. Alde batetik, klima beroketa Lurreko bizitza birbanatzen ari da, sarritan ingurune-baldintzarik onenei jarraituz, kaltetutako espezieen lehen erantzuna migrazioa baita. Oro har, itsasoko espezieak poloetara eta sakonera handiagotara mugitzen dira, haien optimo termikoa mantentzeko. Bestalde, itsaso gainazaleko tenperaturaren hazkuntzak ugaltze eta migrazio garaiei, lehen heldutasunari, gorputzaren neurriari eta hazkundeari eragiten die.

Itsas ekosistemetan, itsasoko baldintzen aldaketak asko eragin dezake itsasoko espezieetan eta, ondorioz, arrantzan, zeinek, herrialdeetako elikagai segurtasunean eta ekonomian ere, zerikusi handian duen, alegia. Munduko harrapaketen proportziorik handiena espezie pelagikoek osatzen dute (%21, 19.6 milioi tona). Klima aldaketak arrain populazioen produktibitatean eragina izan dezake, habitaten egokitasuna, ekosistema mailako produktibitatea eta dinamika ez ezik, harrapari-harrapakinen arteko elkarrekintza ere eraldatuz. Eskualde askotan, arrain pelagiko handiek paper ekologiko garrantzitsua betetzen dute ekosistemaren egituran duten eraginagatik. Arrantza neurrigabearen bidez harrapari nagusien ustiaketak itsasoko ekosistemen egitura eralda dezake, kate trofiko mailetan zehar.

Arrain pelagikoek klima aldaketari emandako erantzunak ulertzeko hainbat ahalegin egin dira. Espezieen banaketa geografikoan eta ugaritasunean izandako aldaketa historikoak aztertu dira eta hainbat arrazoiri egotzi zaizkio. Hala ere, ikusitako aldaketak hainbat ingurumen-faktorek eragin ditzakete, baita antropogenikoak eta biztanleriaren dinamikatik eratorritako beste batzuek ere; beraz, espezieen distribuzioan eta ugaritasunean izandako bariazioen arrazoi zehatzak jakitea erronka garrantzitsu bat da. Datuek estaldura espazio-tenporal homogeneoa ez duten kasuetan, laginketa esfortzuaren distribuzio aldaketak espezierenekin nahastu daitezke eta ingurumenak bultzatutako aldaketei oker egotzi. Hori dela eta, aldaketen faktoreak ondo ezberdindu behar dira; klima beroagoak edo beste faktore batzuek bariazio horiek eragiten dituzten edo berriz, laginketa heterogeneoek edo alborapenenek.

Iragana ulertzea bezain garrantzitsua da ekosistemen, populazioen eta espezieen egoera klima aldaketaren baldintzetan aurreikusten saiatzea. Etorkizunean, itsasoko baldintzen

aldaketek lehen mailako produktibitatea eta biodibertsitatea eraldatuko dituela espero da. Etorkizuneko proiekzioekin lotutako ziurgabetasunagatik, itsaso zabalean lehen mailako produkzioa birbanatu egingo da eta mundu mailan %2 eta %20 artean murriztuko da 2100. urterako. Bertako populazioen desagerpen nabarmenak aurreikusten dira 2050. urterako, bereziki eskualde subpolarretan, baita zonalde tropikal eta itsaso erdi-itxietan ere. Klima-aldaketak ondorio anitzak ditu arrain pelagikoen espezie eta biztanleriengan, habitat elkarte eta jokabide ezberdinak dituzte eta. Horren ondorioz, klima-aldaketak eragin garrantzitsua du alderdi ekologiko eta ekonomikoetan, hala nola arrantzan. Bizitza estrategia ezberdinak eta habitaten aukera zabala direla eta, efektu klimatikoak espezieen artean, baita bizitzako etapa desberdinetan ere, asko aldatzea espero liteke, etorkizuneko distribuzio iragarpena eta kudeaketa planen diseinua prozesu konplexua bilakatuz. Etorkizuneko baldintzen aurreikuspena azken behaketa historikoen tartetik kanpo egon liteke eta erantzun biologikoak eta espezieen egoera berrira egokitzeko gaitasuna askotan ezezagunak izanik, alderdi hau kudeaketaren erronka osagarria bilakatzen da.

Ikerketa honen helburua, eredu biogeografiko globalak eta arrain espezie pelagikoen klima-aldaketaren aurrean dituzten erantzunak ulertzea da, batez ere antxoarena eta harrapari nagusienenak (atuna, ezpata-arraina).

Lan-hipotesia honela definitu da: "*Klima aldaketak eta mundu mailako tenperatura igoerak itsas-espeziengan eragina dute eta etorkizunean eragiten jarraitzea espero da. Espezie pelagikoen habitataren aldaketek poloetara migrazioak, ugaritasun bariazioak, tamainen murrizketak eta prozesu biologikoen fenologiaren alterazioak eragin dituzte. Aldaketa horiek kostaldeko herrialdeetako arrantzan, ekonomian eta animalien proteinen hornikuntzan eragina dute.* "

Aztertutako espezieen gailentasuna dela eta (ekologikoa zein ekonomikoa), iraganeko joerak eta etorkizuneko proiekzioak ezagutzea ezinbestekoa da. Joera historikoak (distribuzioa eta ugaritasuna) aztertu eta etorkizuneko egoera ezberdinak proiektatu dira. Oro har, doktorego tesiak honako **galdera** hauei erantzuna eman nahi izan die:

1- Nola eragin du klima aldaketak espezie pelagikoen distribuzioan eta uragitasunean azkeneko hamarkadetan zehar?

2- Zeintzuk dira antxoa, atuna eta ezpata-arrainaren habitat egokienak?

3- Nola eragingo die klima aldaketak espezie pelagikoen distribuzioari eta ugaritasunari etorkizunean, klima aldaketaren egoera ezberdinetan?

4- Atunetako espezie komertzial nagusien ugaritasun eta distribuzio aldaketek nola eragingo lukete herrialde desberdinetako arrantzan?

5- Klima aldaketak eragina izan al du harrapari nagusien gorputzaren tamainan eta nola eragingo du etorkizunean?

Lan-hipotesia baieztatzeko eta aurreko galderei erantzuna emateko, doktoregotza tesi honen **helburu** nagusiak hauek izan dira:

1- Espezie bakoitzeko distribuzio modeloak garatzea.
2- Espezie bakoitzaren distribuzio eta ugaritasun aldaketen joera historikoak aztertzea azken mende erdian zehar.
3- Espezieen distribuzio eta ugaritasunean izandako aldaketen eragile nagusiak aztertzea.
4- Joera historikoen atzean dauden eragileak bereizteko esparru metodologikoa garatzea.
5- Ingurumen-baldintzak proiektatzea eta espezieen distribuzioan eta ugaritasunean aurreikusitako aldaketak aztertzea.
6- Kostaldeko herrialdeetako eremu ekonomiko esklusiboetako atun espezie nagusien harrapaketa komertzialetan eragina aztertzea etorkizunean.
7- Ekosistema modelo bat erabiliz, goi mailako harrapari espezieen tamainaren aldaketak balioestea.

Helburu horiek betetzeko eta klima-aldaketak espezie pelagikoetan izan ditzakeen eraginak aztertzeko, eredu eta tresna estatistiko ezberdinak aplikatu dira tokiko eta mundu mailako datu baseetan. Espezieen distribuzio modeloek, habitat edo nitxo ekologikoan oinarrituriko modeloak deiturikoak, espezieen presentzia datuak ingurumenaren ezaugarriekin erlazionatzen dituzte. Habitat modeloak askotan aldagai anitz izaten dituzte eta Hutchinsonen nitxo ekologiko (1957) kontzeptuan oinarritzen dira, organismoa hobeto egokitzen den eta lehia gutxitzen duen ingurumen-baldintzen multzo gisa definitzen dena, hain zuzen ere.

1. kapituluak klima aldaketaren ondorioz, Bizkaiko Golkoan antxoaren errunaldi joera historikoak baita etorkizuneko aldaketak ere aztertzen ditu. 1987-2015 urteen artean egindako azterketa historikoek erakutsi zuten, antxoaren errunaldi gailurrak hamarkadako 5.5 eguneko aurrerapena izan duela eta orokorrean indize gonadosomatikoa (errunaldiaren proxy gisa) hazi egin zela, fitopkankton ugaritasun aldaketekin lotuta egon zitekeena. Gainera, arrautzen ekoizpen osoaren arabera, errunaldi eremua zabaldu eta uzkurtu zen; beraz, antxoaren mugimenduak, itsasoaren beroketarekin baino gehiago, biztanleriaren dinamikarekin lotuta dirudite. Etorkizunean, Kantauri itsasoan antxoa arrautzen ugaritasuna 1.05 eta 2.66 bider haziko dela aurreikusten da (XXI. Mendearen erdialdearen eta amaieran, hurrenez hurren), RCP8.5 klima-aldaketaren egoeran. Ingurumen aldaketek errunaldi eremuaren hedapena (%7.8 eta %16.4 mendearen erdialde eta amaieran) eta arrautzen dentsitate handiagotzea eragitea espero da. Lortutako emaitzek Kantauri itsasoko antxoaren biztanleriaren habitat-lehentasunei eta itsasoko gainazalaren berotzeak errunaldiarengan duten eraginari buruzko ezagutza baliotsuak eskaintzen dituzte.

2. kapituluak gero eta klima epelagoko ozeanoan atun espezieen distribuzioa ikertzen du. Ekonomia globalean zein etorkizuneko elikagaien hornikuntzan atunaren garrantzia handia izan arren, habitataren aldaketa historikoak jorratu eta etorkizuneko distribuzioak eskaintzen dituen interes komertzialeko atun espeziei buruzko ikerketa global bat falta da. Kapitulu honetan, ingurumen-baldintzek interes komertzialeko sei atun espezieen distribuzio eta ugaritasun erlatiboan 1958 eta 2004 artean izan duten eragina aztertu dugu, baita mende bukaerarako aldaketak estimatu ere, berotegi efektuko gasen kontzentrazio handiko egoeretan oinarrituz (RCP8.5). Garai historikoan zehar, 22tik 20 biztanlerien grabitate zentroak edo/eta habitat optimoen distribuzio mugak poloetara mugitu ziren. Batez beste, hamarkadako 6.5 km ipar hemisferioan eta 5.5 km hego hemisferioan. Horrez gain, etorkizunean distribuzio eta ugaritasun erlatibo aldaketa handiagoak aurreikusten dira, batez ere mende bukaerarako (2080-2099). Atun epel (hegaluzea, hegalaburra eta hegoaldeko hegalaburra) eta patudoaren ugaritasunean beherakada eta poloetara migrazioa aurreikusten da. Aitzitik, listaua eta hegats horia ugariagoak izatea espero da zonalde tropikaletan, baita kostaldeko herrialdeen zonalde esklusibo gehienetan ere. Atunaren biztanleria ezberdinak kudeatzeko kapitulu honetako aurkikuntzak garrantzitsuak izan daitezke baita arrantza eta herrialde arrantzaleengan klima-aldaketak izan ditzakeen eraginak ulertzeko ekarpen nabarmena ere.

3. kapituluak espezieen aldaketa historikoen oinarrian egon daitezkeen eragileak aztertzen ditu. Erronka handia da espezieen aldaketak eragile ezberdinei egoztea adierazle espazialak erabiliz, hala nola grabitate zentroa. Hau bereziki zaila da komertzialki ustiatutako itsasoko espezieentzat, informazioa ikerketa inkestetatik, arrantza komertzialetatik edo denbora eta espazioan modu homogeneoan erregistratzen ez diren bestelako datuak biltzeko metodoetatik baitator. Espezieen distribuzioan gertatzen diren aldaketen zergatiak bereizteko esparru kontzeptual berria garatu da, edozein espezieri egokitu daitekeelarik. Kasu konkretu honetan, esparru kontzeptuala mundu osoan sakabanatutako itsas espezie batekin berretsi zen, ezpata-arrainarekin, alegia. Emaitzek, 1958tik 2004ra bitartean mundu mailan sei ezpata-arrainen biztanlerietatik bi latitudean mugitu zirela erakutsi zuten, baina Mediterraneo itsasoan soilik izan zen habitataren aldaketek bultzatuta. Etorkizunean, berotegi-efektuko gasen emisio altuen egoeran (RCP8.5), ezpata-arrain CPUE-a (ahalegin-unitate bakoitzeko harrapaketa) %22ko gutxitzea aurreikusten da, batez ere eremu tropikaletan, hazkuntza arin batzuk erakutsiz ipar eta hego hemisferioetako distribuzio mugetan.

4. kapituluan klima eta arrantza presioaren eraginak aztertzen dira goi mailako harraparien komunitatean. Ikerketa hau jorratzeko tresna, biztanleriaren dinamika, sakabanaketa (larbak eta helduak) eta ekofisiologia barne hartzen dituen SS-DBEM ekosistema modeloa da; espezieen tamaina, ugaritasuna eta arrantzatua izatearen aukeraren iragarpen espazialak eta tenporalak ematen dituena, beraz, toki bakoitzean bakarkako espezieak jasan dezakeen biomasa. Espezieen tamaina eta ugaritasun aldaketak aztertu dira, bai aldi historikoetan baita etorkizunean ere, eta atun, ezpata-arrain eta zuzeneko lehiakideen kasuetan, tamainen beherakada orokorra aurkitu da. Norbanako tamainen jaitsierarik handienak arrantza presio altuago eta berotze handiagoa duten eszenatoki klimatikoei egotzi zaizkie.

Oro har, doktorego-tesi honetan egin diren ikerketek arrain espezie pelagikoetan klimak eragindako aldaketen inguruko informazio berria, esanguratsua eta baliotsua eman dute, bai historikoki bai etorkizunerako ere, gaur egungo negutegi efektuko gas emisio joerari eutsiz. Informazio hau, espezieen aldaketen zergatiak bereizteko proposatutako esparru kontzeptual berriarekin batera, kudeaketa egokian laguntzeko tresna boteretsua bihur daiteke. Arrantza eta klimaren arteko elkarreragin sendoen ondorioz, populazio iraunkorrak bermatzeko, harrapaketak eta irabaziak egonkortzeko eta itsas ekosistemetan zehar-inpaktuak murrizteko kudeaketa egokia beharrezkoa da.

RESUMEN

La evidencia del calentamiento del sistema climático es inequívoca; es por ello por lo que en las últimas décadas se han visto afectados múltiples aspectos de los ecosistemas, tales como la temperatura, la estratificación, la circulación, la disponibilidad de oxígeno, la química (pH) y la producción primaria y secundaria. Como consecuencia, esos cambios en las condiciones ambientales impactan en los ecosistemas terrestres y marinos, regiones, especies y etapas de la vida a través de una variedad de vías directas e indirectas. Se han registrado cambios en la distribución y abundancia de especies, así como en la fenología (fenómenos biológicos estacionales en relación con las condiciones climáticas). Por un lado, el calentamiento global está redistribuyendo la vida en la Tierra porque la primera respuesta de las especies afectadas es a menudo, una migración, siguiendo sus condiciones ambientales óptimas. En general, las especies marinas se mueven hacia los polos y hacia mayores profundidades para mantener su óptimo termal. Por otro lado, el aumento en la temperatura superficial del mar afecta a los tiempos de desove y migración, a la talla de primera madurez, al tamaño corporal y al crecimiento.

En los ecosistemas marinos, los cambios en las condiciones del océano pueden afectar en gran medida a las especies marinas y, en consecuencia, a la pesca, que juegan un papel muy importante en la seguridad alimentaria y en la economía de muchos países. La mayor proporción de capturas mundiales está compuesta por especies pelágicas (21%, 19.6 millones de toneladas). El cambio climático puede afectar a la productividad de las poblaciones de peces alterando la idoneidad del hábitat, la productividad a nivel del ecosistema y la dinámica poblacional, así como las interacciones depredador-presa. Los grandes peces pelágicos juegan un papel ecológico importante en muchas regiones debido a su influencia en la estructura del ecosistema. La captura desproporcionada de los principales depredadores a través de la pesca puede alterar la estructura de los ecosistemas marinos a través de las cascadas tróficas.

Se han llevado a cabo diversos esfuerzos para comprender las respuestas de los peces pelágicos al cambio climático. Las variaciones históricas en la distribución y abundancia de las especies han sido analizadas y atribuidas a diferentes causas. Sin embargo, los cambios observados pueden ser impulsados por una variedad de factores ambientales y antropogénicos, así como los derivados de la dinámica de las poblaciones; por lo tanto, la atribución correcta de las causas de los cambios en la distribución y abundancia de las especies es un verdadero desafío. En los casos en que los datos no tienen una cobertura espacio-temporal homogénea, los cambios en la distribución de las especies pueden atribuirse erróneamente a los cambios ambientales cuando en realidad vienen generados por los cambios en el esfuerzo de muestreo. Por lo tanto, es clave distinguir los cambios en las especies debidos a un muestreo heterogéneo o sesgo de muestreo de los causados por un clima más cálido u otros factores.

Tan importante como comprender el pasado es tratar de predecir el futuro de los ecosistemas, las poblaciones y el estado de las especies en condiciones de cambio climático. Se espera que los cambios en las condiciones del océano alteren los patrones de la productividad primaria marina global y la biodiversidad. A pesar de la incertidumbre asociada con las proyecciones futuras, se prevé que la producción primaria neta en mar abierto se redistribuya y disminuya entre el 2% y el 20% a nivel mundial para el año 2100. Se proyectan sustanciales extinciones de poblaciones locales para el año 2050, particularmente en regiones subpolares y tropicales y mares semicerrados. La amplia gama de asociaciones de hábitat y comportamientos de las diferentes especies de peces pelágicos tiene implicaciones a la hora de predecir los impactos del cambio climático en las poblaciones y, como consecuencia, en aspectos ecológicos y económicos, tales como la pesca. Debido a las diversas estrategias de vida y la amplia gama de hábitats, es probable que los efectos climáticos varíen fuertemente entre las especies e incluso durante las distintas etapas de vida, convirtiendo la predicción de distribuciones futuras y el diseño de planes de gestión en un proceso complejo. El desafío adicional para el manejo de los recursos pesqueros es que las condiciones futuras proyectadas probablemente estén fuera de los rangos de observación histórica reciente, y las respuestas biológicas y la capacidad de las especies para adaptarse o aclimatarse a ellas siguen siendo en gran medida desconocidas.

El objetivo de este estudio es comprender los patrones biogeográficos globales y la respuesta al cambio climático de las especies de peces pelágicos, en particular la anchoa y los principales depredadores (atún, pez espada).

La **hipótesis de trabajo** se ha definido como: *"El cambio climático y el calentamiento global afectan a las especies marinas y se espera que continúen impactando en el futuro. Alteraciones en el hábitat de las especies pelágicas provocan migraciones hacia los polos, cambios en la abundancia, en la fenología de sus procesos biológicos o en el tamaño de sus tallas. Estos cambios afectan a las pesquerías, economía y suministro de proteínas animales de los países costeros".*

Debido a la relevancia de las especies objetivo estudiadas (tanto ecológica como económica), la información sobre tendencias pasadas y proyecciones futuras es importante. Se han analizado las tendencias históricas (en la distribución espacial y la abundancia), y se han proyectado los escenarios futuros. En general, la tesis de doctorado ha tenido como objetivo responder las siguientes **preguntas**:

1- ¿Cómo ha afectado el cambio climático a la distribución y abundancia de las especies pelágicas marinas en las últimas décadas?
2- ¿Cuáles son los hábitats óptimos para la anchoa, los atunes y el pez espada?
3- ¿Cómo se espera que el cambio climático afecte a la distribución y abundancia de las especies pelágicas marinas en el futuro bajo escenarios de cambio climático?
4- ¿Cómo podrían afectar los cambios en la abundancia y distribución de las principales especies comerciales de atún en las capturas de los diferentes países?
5- ¿Ha afectado el cambio climático al tamaño corporal de los principales depredadores y cómo lo hará en el futuro?

Para probar la hipótesis de trabajo y responder las preguntas anteriores, los **objetivos** principales de esta tesis de doctorado han sido:

1- Desarrollar modelos de distribución para cada una de las especies.
2- Analizar las tendencias históricas en la distribución y abundancia de las especies durante el último medio siglo.
3- Analizar las principales causas potenciales de los cambios en la distribución y abundancia de las especies.
4- Desarrollar un marco metodológico para distinguir las diferentes causas que subyacen en dichas tendencias históricas.
5- Proyectar las condiciones ambientales futuras y analizar los cambios predichos en la distribución y abundancia de especies.
6- Estimar el impacto en las capturas comerciales de las principales especies de atún dentro de las Zonas Económicas Exclusivas de los países costeros.
7- Estimar los cambios de tamaño de las especies de depredadores-tope mediante un modelo ecosistémico.

Para abordar estos objetivos y analizar los impactos del cambio climático sobre las especies pelágicas, se han aplicado diferentes modelos y herramientas estadísticas en conjuntos de datos locales y globales. Se han desarrollado modelos de distribución de especies también llamados modelos de hábitat o basados en el nicho ecológico, que asocian datos de presencia de las especies objetivo con las características de su entorno para predecir su distribución geográfica potencial. Los modelos de hábitat suelen ser multivariados y se basan en el concepto de nicho ecológico de Hutchinson (1957) que definió el nicho como la variedad de condiciones ambientales a las cuales el organismo se adapta mejor y se minimiza la competencia.

El **Capítulo 1** examina los cambios en las tendencias históricas y la distribución futura del desove de la anchoa en el Golfo de Vizcaya debido al cambio climático. El análisis histórico mostró que el pico de puesta de la anchoa avanzó a una velocidad de 5.5 días por década entre

1987 y 2015, y el índice gonadosomático (como proxy de la actividad de puesta) aumentó en general, lo que podría estar asociado a cambios en la abundancia de fitoplancton. Además, el área de desove se expandió y contrajo dependiendo de la producción total de huevos, por lo que los posibles desplazamientos de la anchoa se relacionan más con la dinámica de la población que con el calentamiento superficial del mar. En el futuro, se estima un aumento de la abundancia de huevos de anchoa en el Golfo de Vizcaya entre 1.05 y 2.66 veces (para mediados y finales del siglo XXI, respectivamente) bajo el escenario de cambio climático RCP8.5. Además, los cambios ambientales también pueden inducir a una expansión del área de desove (7.8% y 16.4% para mediados y finales de siglo) y una mayor densidad de huevos. Los resultados obtenidos proveen de un valioso conocimiento sobre las preferencias de hábitat de la población de anchoa del Golfo de Vizcaya y los impactos del calentamiento superficial del mar en el desove.

El **Capítulo 2** evalúa la distribución a gran escala de las especies de atún en un océano cada vez más templado. A pesar de la relevancia del atún en la economía global y en el suministro futuro de alimentos, falta un estudio a escala global que aborde los cambios históricos de su hábitat y proporcione distribuciones futuras basadas en las proyecciones del cambio climático para todas las principales especies comerciales de atún. Aquí investigamos el efecto de las condiciones ambientales en la distribución global y la abundancia relativa de seis especies de atún entre 1958 y 2004 y estimamos los cambios para el final de siglo basados en un escenario de alta concentración de gases de efecto invernadero (RCP8.5). Durante el período histórico, los centros de gravedad y/o los límites de distribución de los hábitats óptimos se desplazaron hacia los polos en 20 de las 22 poblaciones de atún. En promedio, los límites de distribución del hábitat del atún se han desplazado hacia los polos 6.5 km por década en el hemisferio norte y 5.5 km por década en el hemisferio sur. Además, se esperan mayores cambios en la distribución y abundancia relativa en el futuro, especialmente para fines de siglo (2080-2099). Se predice una disminución de los atunes templados (atún blanco, atún rojo del Atlántico y atún rojo del sur) y del patudo en los trópicos y un desplazamiento hacia los polos. Por el contrario, se prevé que el listado y el rabil se vuelvan más abundantes en las zonas tropicales, así como en la mayoría de las zonas económicas exclusivas de los países costeros. Los hallazgos pueden ser relevantes para la gestión de los distintos stocks de atún y una contribución importante para comprender los posibles impactos del cambio climático en la pesca y las naciones pesqueras.

El **Capítulo 3** explora las posibles causas de los cambios históricos de las especies. La estimación precisa y la atribución de los cambios de las especies a las distintas causas utilizando indicadores de distribución espacial, como el centro de gravedad, es un desafío. Esto es particularmente problemático para las especies marinas explotadas comercialmente cuya información proviene de encuestas de investigación, pesquerías comerciales u otros métodos de recopilación de datos que no se registran de manera homogénea en el tiempo y el espacio. Se desarrolla un nuevo marco conceptual para distinguir las causas tras de los cambios en la distribución de especies, que puede ser aplicado a cualquier especie. En este caso particular, el marco conceptual se corroboró con el pez espada, la principal especie de picudo distribuida mundialmente. Los resultados mostraron que, a escala global, 2 de las 6 poblaciones de pez espada se habían desplazado latitudinalmente entre 1958 y 2004, pero solo en el Mar Mediterráneo fueron debidas a variaciones en el hábitat. Las proyecciones futuras bajo el escenario de mayor emisión de gases de efecto invernadero (RCP8.5) estiman una disminución general del pez espada del 22% en CPUE (captura por unidad de esfuerzo), principalmente en las áreas tropicales, y un ligero aumento en los límites de su rango de distribución, tanto en el hemisferio norte como sur.

El **Capítulo 4** describe los cambios en la comunidad de depredadores-tope bajo distintos escenarios climáticos y de esfuerzo pesquero. La herramienta para abordar este estudio es el modelo ecosistémico SS-DBEM que incluye la dinámica poblacional, la dispersión (de larvas y adultos) y la ecofisiología para proporcionar predicciones espaciales y temporales de los cambios en el tamaño, la abundancia y el potencial de captura de las especies, es decir, la biomasa soportada para cada especie en esa área. Los cambios en el tamaño y la abundancia de las especies se analizaron tanto en períodos históricos como futuros y se encontró un decremento generalizado en las tallas de los túnidos, picudos y sus competidores directos. Los decrementos en las tallas de los individuos de mayor tamaño se atribuyen a mayores presiones de pesca, así como a escenarios climáticos con un mayor calentamiento.

En general, los estudios desarrollados en el marco de esta tesis doctoral han proporcionado información nueva, relevante y valiosa sobre los cambios provocados por el clima en las especies de peces pelágicos, tanto históricamente como en el futuro bajo el escenario de la tendencia actual de emisión de gases de efecto invernadero. Esta información, junto con el nuevo marco conceptual propuesto para distinguir las causas de los cambios en las especies, puede convertirse en una herramienta poderosa para apoyar una correcta gestión. Las fuertes interacciones entre la pesca y el clima requieren de una buena gestión para garantizar poblaciones sostenibles, estabilizar las capturas y ganancias y reducir los impactos colaterales en los ecosistemas marinos.

SUMMARY

The evidence of warming of the climate system is unequivocal and in the last decades, multiple aspects of the ecosystems such as temperature, stratification, circulation, oxygen availability, chemistry (pH) and primary and secondary productions have been affected. Consequently, those changes in the environmental conditions impact through a variety of direct and indirect pathways across terrestrial and marine ecosystems, regions, species and life stages. Changes in species distribution and abundance as well as on phenology (seasonal biological phenomena in relation to climatic conditions) have been recorded. On one hand, global warming is redistributing all life on Earth because the first response of the species affected is often a shift of location, following their preferred environmental conditions. Marine species are in general moving poleward and greater depths in order to maintain their thermal optimum. On the other hand, sea surface temperature increases affect spawning and migration timing, length at maturity, body size and individual growth.

In marine ecosystems, ocean conditions changes can greatly affect marine species and consequently to fisheries, which play a very important role in food security and the economy in many countries. The largest proportion of global catches (21%, 19.6 million tons) is comprised of pelagic species. Fish stock productivity can be impacted by climate change by altering habitat suitability, ecosystem-level productivity, and dynamics such as predator-prey interactions. Large pelagic fishes play ecologically important roles in many regions due to their top-down influence on the ecosystem structure. The disproportionate removal of top predators through fishing mortality can alter the structure of marine ecosystems through top-down processes and trophic cascades.

Many efforts have been made to understand pelagic fish responses to climate change. Historical changes in distribution and abundance of species have been analyzed and attributed to different drivers. However, observed changes can be driven by a variety of environmental, anthropogenic factors, as well as derived from population dynamics; thus, the causal attribution of species distribution and abundance changes is challenging. In cases where data have non-homogeneous spatio-temporal coverage, changes in the distribution of sampling effort may be confounded with species distribution shifts and wrongly attributed to environmentally driven changes. Therefore, disentangling species changes due to a heterogeneous sampling or sampling bias and the correct attribution of those changes associated with a warming climate from other drivers is key.

As important as understanding the past is trying to predict the future of ecosystems, populations and species status under changing climate conditions. Changes in ocean conditions are expected to alter patterns of global marine primary productivity and biodiversity. In spite of the uncertainty associated with future projections, open-ocean net primary production is projected to redistribute and to decrease between 2% and 20% globally by 2100. Substantial local population extinctions are projected by 2050, particularly in subpolar and tropical regions and semi-enclosed seas. The wide range of habitat associations and behaviors across different pelagic fish species have implications in predicting climate change impacts on populations and as a consequence, in ecological and economic aspects, such as fisheries. Due to diverse life-history strategies and a broad range of habitats, climate effects are likely to vary strongly across species and by life stages, becoming the prediction of future distributions and best management plans a complex process. The additional challenge to marine resources management is that projected future conditions are likely to be outside the ranges of recent historical observation, and biological responses and the ability of species to adapt or acclimatize to them remain largely unknown.

This study aims to gain an understanding of the global biogeographical patterns of pelagic fish species, in particular, anchovy, and top predators (tuna, swordfish), and its response to a changing climate.

The **working hypothesis** is defined as *“Climate change and ocean warming affect marine species and it is expected to continue impacting in the future. Disturbances in the habitat of pelagic species provoke poleward shifts, changes in abundance, phenological changes of their biological processes and decreasing body size. These changes affect the fisheries of coastal countries, the economy, and animal protein supply”.*

Due to the relevance of studied target species (both ecologically and economically), information about past trends and future projections are important. Historical trends (in spatial distribution and abundance) have been analyzed, as well as future changes have been projected. Overall, the Ph.D. thesis aimed to answer the following **questions**:

1- How climate change has affected the marine pelagic fish species distribution and abundance in the last decades?

2- Which are the suitable habitats of anchovy, tuna, and swordfish?

3- How climate change is expected to affect the marine pelagic fish species distribution and abundance in the future under climate change scenarios?

4- How the tuna abundance and distribution changes could affect the catches of different countries?

5- Has climate change affected the body size of top predators and how is it going to affect in the future?

In order to test the working hypothesis and answer previous questions, the main **objectives** of this Ph.D. thesis were to:

1- Develop marine pelagic fish species' distribution models.
2- Analyze historical trends in marine pelagic fish species distribution and abundance through the last decades using long time-series.
3- Analyze the main potential drivers triggering marine species shifts.
4- Develop a methodological framework to disentangle the reasons behind those historical trends.
5- Project future environmental conditions and analyze expected changes in marine pelagic fish species' distribution and abundance.
6- Estimate impacts in main commercial tuna species catches inside coastal countries Exclusive Economic Zones.
7- Use the ecosystem-based model to predict future distribution and abundance of top predators and their changes in size due to fishing effort and climate change.

To address these objectives, and analyze climate change impacts over pelagic species, different models and statistical tools have been applied in both, local and global datasets.

Species distribution models, also called habitat or niche-based models, have been developed associating known presence locations of the target species with the characteristics of their environment to predict their potential geographical distribution. Habitat models are usually multivariate and are based on the ecological niche concept of Hutchinson (1957) which defined the niche as the variety of environmental conditions for which the organism is best suited and the competition is minimized.

Chapter 1 examines changes in historical trends and future distribution of anchovy spawning in the Bay of Biscay due to climate change. The historical analysis of anchovy spawning showed that spawning peak advanced at a rate of 5.5 days/decade from 1987 to 2015, and the gonadosomatic index (as a proxy of spawning activity) increased in general, which might be associated to changes in phytoplankton abundance. In addition, the spawning area expanded and contracted depending on the total egg production, therefore, possible anchovy shifts depend on the population dynamics instead of sea surface warming. In the future, the overall anchovy egg abundance in the Bay of Biscay is expected to increase between 1.05 and 2.66-fold under the RCP8.5 climate change scenario by the mid and end-of-the-21st-century, respectively, as projected environmental changes might induce an expansion of the spawning area (7.8% and 16.4% for mid- and end-of-the-century) and higher egg density. The results obtained added valuable knowledge about habitat preferences of Bay of Biscay anchovy's population and expected sea surface warming impacts mainly in spawning.

Chapter 2 assesses the large-scale distribution of tuna species in a warming ocean. Despite the relevance of tuna in the global economy and the future supply of food, a global-scale study addressing the historical changes of the tuna habitat and providing future distributions based on climate change projections for all major commercial species is lacking. Here we investigated the effect of environmental conditions on the worldwide distribution and relative abundance of six tuna species between 1958 and 2004 and estimated the expected end-of-the-century changes based on a high greenhouse gas concentration scenario (RCP8.5). Over the historical period, suitable habitats shifted poleward for 20 out of 22 tuna stocks, based on their gravity center and/or one of their distribution limits. On average, tuna habitat distribution limits have shifted poleward 6.5 km per decade in the northern hemisphere and 5.5 km per decade in the southern hemisphere. Larger tuna distribution shifts and changes in abundance are expected in the future, especially by the end-of-the-century (2080-2099). Temperate tunas (albacore, Atlantic bluefin, and southern bluefin) and the tropical bigeye tuna are expected to decline in the tropics and shift poleward. In contrast, skipjack and yellowfin tunas are projected to become more abundant in tropical areas as well as in most coastal countries' Exclusive Economic Zones. The findings may be relevant for tuna stock management and an important contribution to understanding the potential impacts of climate change on fisheries and fishing nations.

Chapter 3 explores the possible drivers behind species historical shifts. The accurate estimation and causal attribution of species shifts using spatial distribution indicators, such as the center of gravity, is challenging. This is particularly problematic for commercially exploited marine species with data from research surveys, commercial fisheries or other data collection methods that are not recorded homogeneously over time and space. A new framework to disentangle the reasons behind species distribution changes is described, which may be applied to any species. In this particular case, the framework was tested with the worldwide distributed main billfish species, the swordfish. On a global scale, 2 out of 6 stocks of swordfish shifted latitudinally from 1958 – 2004 but only in the Mediterranean Sea was habitat-driven. Future projections under the RCP8.5 greenhouse gas emission scenarios estimate an overall swordfish decrease of 22% in CPUE (catch per unit of effort), with substantial decreases in most tropical areas, and a slight increase in its distribution range limits, both in the north and southern hemispheres.

Chapter 4 described changes in the top predator community under different climate and fishing effort scenarios. The tool to address this study is the ecosystem-based model SS-DBEM which includes population dynamics, dispersal (larval and adults) and ecophysiology to provide spatially and temporally resolved predictions of changes in species' size, abundance and catch potential, therefore, the biomass of that species that can be supported in this area. Changes in species sizes and abundance were analyzed in both, historical and future periods and a generalized decrease in body size was found for tuna, billfish, and direct competitors. Body size of the largest fishes decreases with to highest fishing pressure and worse climatic scenarios.

Overall, the studies developed within the framework of this Ph.D. thesis have provided new and valuable insights about the climate-driven changes over pelagic fish species both historically and in the future under the business as usual greenhouse gas emission scenarios. This information together with the proposed new framework to disentangle species shifts drivers can become a powerful tool to support management. The strong interactions between fishing and climate require management to guarantee sustainable populations, stabilize catches and profits and reduce collateral impacts on marine ecosystems.

GENERAL INTRODUCTION

0. GENERAL INTRODUCTION

0.1. Ocean characteristics under climate change

> *"By absorbing a disproportionate amount of heat from global warming and by taking up the rapidly increasing emissions of carbon dioxide, the ocean has shielded the world from even more rapid changes in climate. However, the extent to which it can continue to do so in the near and distant future is far from clear."*
>
> *Chapter 1 author Reid (2016)*

The evidence of warming of the climate system is unequivocal and in the last decades, atmospheric and oceanic temperatures rose, snow and ice coverage had decreased and as a consequence, the sea level has risen (Bahri *et al.*, 2018; IPCC, 2013; Reid & Hill, 2016; Rhein *et al.*, 2013). The principal contribution to this warming is believed to be the exponential increase in the emission of greenhouse gases (GHG) to the atmosphere, such as carbon dioxide (CO_2), methane (CH_4) and nitrogen dioxide (NO_2) (IPCC, 2013; Peck & Pinnegar, 2018). As a result, the atmospheric concentration of these gases has increased by 40 percent since pre-industrial times and are unprecedented in the last 800.000 years (Ciais *et al.*, 2013; IPCC, 2013, 2014b; Le Quéré *et al.*, 2017; Peck & Pinnegar, 2018).

The ocean, as the major water, heat and carbon reservoirs of the world, plays an especially crucial role in climate regulation (Reid et al., 2009; Rhein et al., 2013), becoming the main heat buffer (Peck & Pinnegar, 2018). Only 1% of the additional heat caused by anthropogenic climate change is retained in the atmosphere, 2% in land, 3-4% by the melting of ice and snow, whilst 93 percent has been absorbed by the global ocean (**Figure 0.1**) (Reid & Hill, 2016). Any small change in the atmosphere-ocean balance of heat would have huge impacts on global air temperature (Reid & Hill, 2016). In addition to its thermal capacity, the ocean has also sequestered about 25% of the CO_2 released (Le Quéré *et al.*, 2017) primarily caused by the carbon emissions to the atmosphere from deforestation and other land-use change activities (Ciais *et al.*, 2013).

Climate change affects multiple aspects of the ecosystems, such as temperature, stratification, circulation, oxygen availability, chemistry (pH) and primary and secondary productions (Bahri *et al.*, 2018; Doney *et al.*, 2012; IPCC, 2014b; Pörtner & Knust, 2007). Aquatic systems that sustain fisheries and aquaculture are undergoing significant changes through a variety of direct and indirect pathways; across life stages, species and regions (Bell *et al.*, 2013a; Doney *et al.*, 2012).

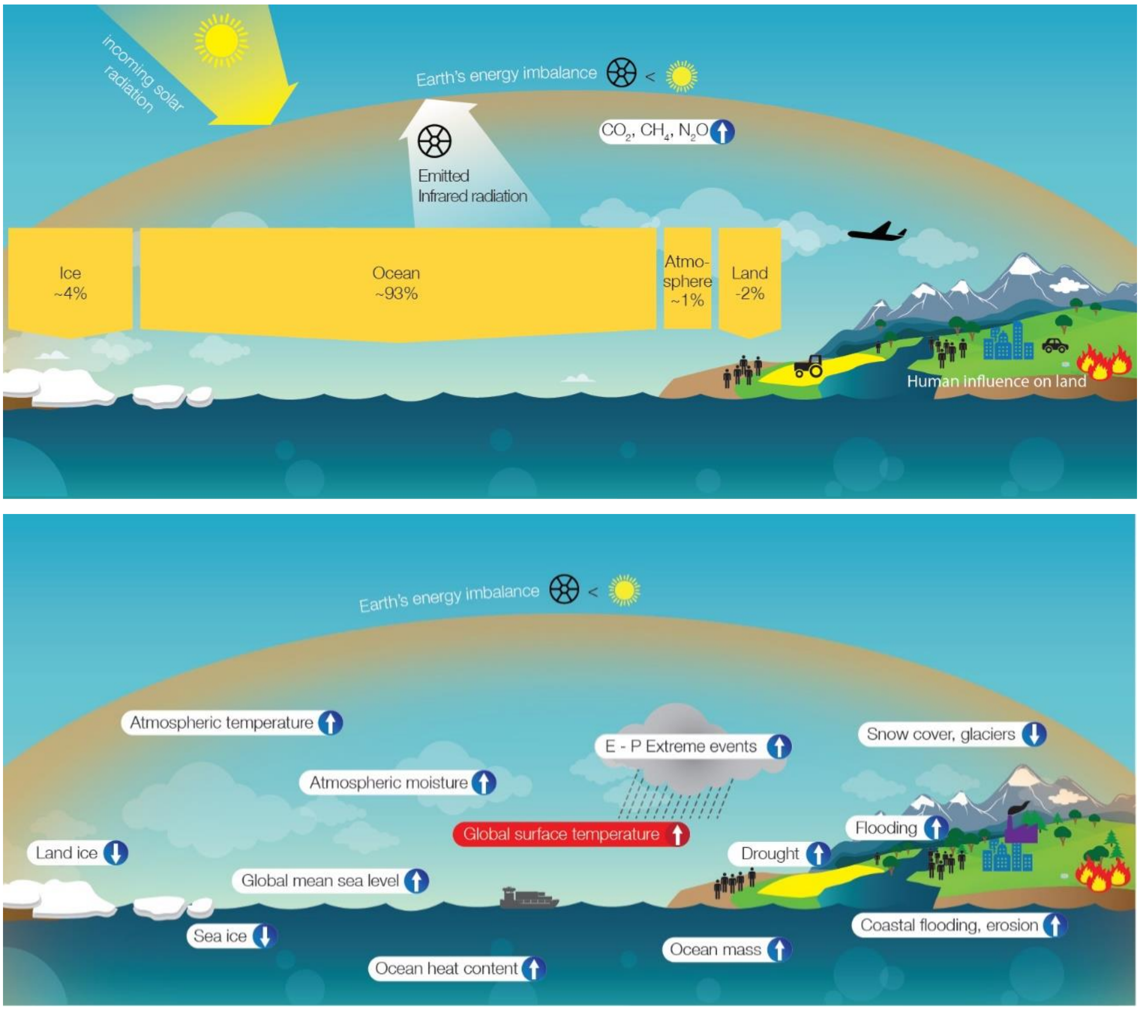


Figure 0.1: Flow and storage of energy in the Earth's climate system and consequences of Earth's energy imbalance (sourced from Reid and Hill (2016) which was modified from Von Schuckmann et al. (2016)).

0.1.1. Temperature and stratification

Globally, the Earth's average surface temperature has increased by more than 0.8°C since 1950 (IPCC, 2013), and is now warming at a rate of more than 0.1°C per decade (Hansen *et al.*, 2010). The atmospheric temperatures of the last three decades had been the highest since 1850 (IPCC, 2013), whilst temperatures in the upper layers of the ocean (0-75 m) have shown an increase of 0.11 ± 0.02 ºC per decade over the period 1971-2010, causing an increase of 4% in stratification (IPCC, 2013; Rhein *et al.*, 2013). Ocean warming is not homogeneous but is positive over most of the globe, warming much faster in some of the regions (Gupta *et al.*, 2015) such as the Northern Hemisphere (especially in the North Atlantic) (Bahri *et al.*, 2018). Sea surface warming, combined with changes in salinity, is likely to cause a higher stratification in some areas (Bopp *et al.*, 2013; Sarmiento *et al.*, 2004). Among other effects of ocean warming, there are a decrease of the mixed layer depth and the nutrients supplied to the surface (Polovina *et* *al.*, 1995) and an increase of the mean sea level due to the thermal expansion of the oceans (IPCC, 2013). Sea level is also affected by the melting of ice and snow coverage and the reduction of mountain glaciers (Bahri *et al.*, 2018).

0.1.2. Oxygen concentration

Dissolved oxygen is an important component of aquatic systems and marine life (Bahri *et al.*, 2018; Pörtner & Knust, 2007). Changes in its concentrations may affect the global carbon and nitrogen cycles (IPCC, 2014b), marine organisms' distribution, abundance, performance, and survival, as well as the biogeochemical cycles dependent on organisms' function (Seibel, 2011; Seibel & Dierssen, 2009). A large variety of systems exist, with a dissolved oxygen concentration range from super-saturated Antarctic waters to zero in coastal sediments due to the fast oxygen consumption which exceeds the supply (Bahri *et al.*, 2018). There are some areas where the oxygen concentration is very low, called oxygen minimum zones (OMZs) that are located in the open ocean, coastal upwelling zones, deep basins of semi-enclosed seas, deep fjords, and other areas with restricted circulation (Bahri *et al.*, 2018). In recent decades, OMZs have expanded by several million square kilometers in the tropical Pacific, Atlantic and Indian Oceans (Breitburg *et al.*, 2018; Keeling *et al.*, 2010). This oxygen loss, or deoxygenation, is occurring as a consequence of reduced ventilation and O_2 solubility in warmer, more stratified oceans (Breitburg *et al.*, 2018; IPCC, 2014b; Keeling *et al.*, 2010). Oxygen plays a very important role in the ecophysiological response of many organisms to climate change (e.g. Pörtner and Knust (2007)), mainly in regions where dissolved oxygen at depth already limits species distributions. Further decreases in oxygen may constrain the vertical habitat for species intolerant of hypoxia, such as for some tunas and billfishes in the tropical Pacific and Atlantic (Lehodey *et al.*, 2011; Stramma *et al.*, 2012).

0.1.3. Ocean circulation

Climate change impacts oceanographic structure through all spatial and temporal scales, from basin-scale circulation down to coastal upwelling events (Muhling *et al.*, 2017a). Redistribution of heat and freshwater across the globe is mainly driven by the meridional overturning circulation (MOC) (Bahri *et al.*, 2018; Buckley & Marshall, 2016). MOC is responsible for the redistribution of the big part of the heat excess from the tropics to middle and high latitudes and for the ocean's sequestration of carbon (Buckley & Marshall, 2016). Atlantic meridional overturning circulation (AMOC) is progressively weakening due to the climate change (Rahmstorf *et al.*, 2015), affecting spatial patterns of warming, mixing and transport potential and having as a result, a cooling of sea surface temperature in the subpolar Atlantic Ocean and a warming and northward shift of the Gulf Stream (Rhein *et al.*, 2013). Western boundary currents (Gulf Stream, Kuroshio Current and Somali Current in the Northern Hemisphere; Agulhas Current, Brazil Current and East Australia Current in the Southern Hemisphere) have undergone rapid warming at a rate three times faster than the global mean surface ocean warming, causing strong changes in their intensity and position (Wu *et al.*, 2012). Apart from the Gulf Stream, which is expected to weaken together with the AMOC, all the western boundary currents are likely to intensify (Wu *et al.*, 2012).

The consequences of the AMOC weakening would include disruption of climate patterns in the subtropical Atlantic that would translate into increased storminess and frequency of heatwaves, as well as a warming of tropical Atlantic waters (Bahri *et al.*, 2018). However, wind-driven upwelling may increase in the future as a result of differential heating between land and sea (Sydeman et al., 2014), affecting particularly to small pelagic fishes and fisheries, which are frequently associated with upwelling regions (Muhling *et al.*, 2017a). In addition, changes in ocean circulation may also affect marine ecosystems through the dispersal of reproductive or juvenile life stages (van Gennip *et al.*, 2016).

0.1.4. Ocean acidification

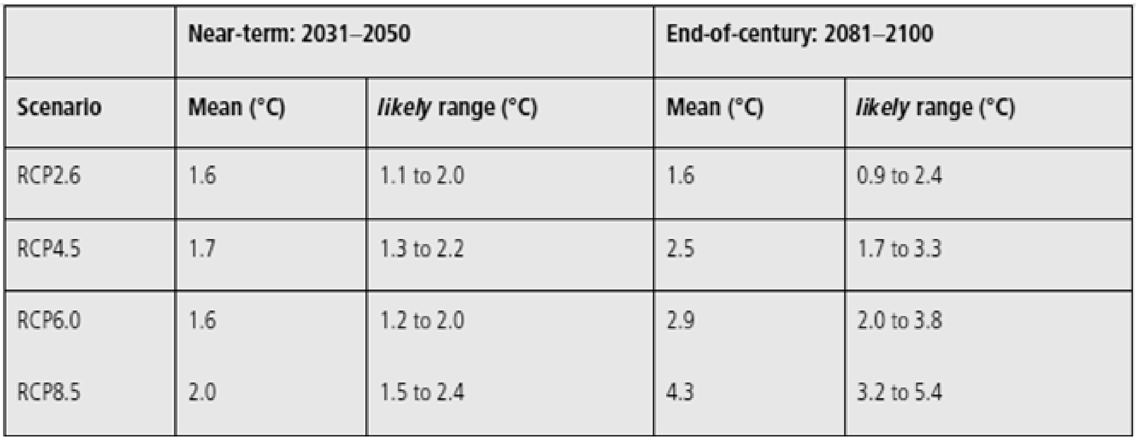
Ocean acidification refers to a long-term reduction in the pH of the ocean mainly caused by the uptake of atmospheric CO_2 (Bahri *et al.*, 2018; IPCC, 2014b). Due to the increase in GHG since the beginning of the industrial era, oceanic uptake of CO_2 has resulted in increasing acidification of the ocean; the pH of ocean surface water has decreased by an average of 0.1, corresponding to a 26% increase in acidity (IPCC, 2014b). The acidification of the water affects the saturation state of mineral forms of calcium carbonate ($CaCO_3$), which is important for all shell-forming aquatic life (IPCC, 2014c). Acidification rate is not homogeneous across the surface waters: it is already 50% higher in the Northern than in the subtropical Atlantic, and due to the higher solubility of CO_2 in cold waters, Arctic waters are acidifying faster than the global average (Bahri *et al.*, 2018; IPCC, 2014b).

0.1.5. Future projections

Anthropogenic greenhouse gas emissions are mainly driven by population size, economic activity, lifestyle, energy use, land use patterns, technology and climate policy (IPCC, 2013, 2014b). Based on the previous factors (IPCC, 2013, 2014b), four different scenarios of GHG emissions and atmospheric concentrations, air pollutant emissions and land use were defined as The Representative Concentration Pathways (RCPs, **Figure 0.2**) (IPCC, 2013, 2014b). The RCPs include (**Table 0.1**): (i) a stringent mitigation scenario (RCP2.6), which is representative of a scenario that aims to keep global warming likely below 1.5°C above pre-industrial temperatures, (ii) two intermediate scenarios (RCP4.5 and RCP6.0), in which total radiative forcing are stabilized shortly after 2100 with differential speeds and (iii) one scenario with very high GHG emissions (RCP8.5) characterized by increasing GHG emissions over time (IPCC, 2014b; Van Vuuren *et al.*, 2011). This last scenario is commonly called “the business as usual RCP”.

All RCP scenarios except RCP2.6 predict a warming higher than 1.5 °C relative to the average of the 1850 to 1900 period for the end of the 21st century (IPCC, 2014b) and under current climate change conditions, the warming is expected to continue in the future (Bopp *et al.*, 2013; IPCC, 2014c; Rhein *et al.*, 2013). Under the highest CO_2 concentration scenario (RCP8.5), surface ocean temperatures may increase by 2°–4°C by the end of the 21st century (Gupta *et al.*, 2015; IPCC, 2014b). The trend in sea surface temperature already exceeds the range in natural seasonal variability in the subtropical areas and in the Arctic (Henson *et al.*, 2017; IPCC, 2014b) and climate change is considered to be irreversible for centuries or even millennia, even after a complete cessation of anthropogenic CO_2 emissions (Bahri *et al.*, 2018; IPCC, 2014b).

Table 0.1: Projected mean Surface temperature change relative to 1850-1900 for two time periods under four RCPs. Source from IPCC (2019b).



	Near-term: 2031–2050		End-of-century: 2081–2100	
Scenario	Mean (°C)	*likely* range (°C)	Mean (°C)	*likely* range (°C)
RCP2.6	1.6	1.1 to 2.0	1.6	0.9 to 2.4
RCP4.5	1.7	1.3 to 2.2	2.5	1.7 to 3.3
RCP6.0	1.6	1.2 to 2.0	2.9	2.0 to 3.8
RCP8.5	2.0	1.5 to 2.4	4.3	3.2 to 5.4

In overall and with high uncertainty and some regional exceptions, an increase in sea surface temperature, stratification, ocean acidification (Bahri *et al.*, 2018; Gattuso *et al.*, 2015), a sea-level rise (Kopp *et al.*, 2014), a decrease in the primary production (IPCC, 2014b; Kwiatkowski *et al.*, 2018) and a decrease in oxygen availability (Keeling *et al.*, 2010) are expected in the future. Ocean models predict declines of 1 to 7% in the global ocean O_2 inventory over the next century (Keeling *et al.*, 2010) whilst the global volume of OMZs is expected to increase by 10-30% by 2100, depending on the oxygen concentration threshold considered in the models (Bahri *et al.*, 2018). The expansion of those areas might affect macrofauna (Keeling *et al.*, 2010). However, the impacts are very dependent on widely varying oxygen tolerances of different species and taxonomic groups (Bahri *et al.*, 2018). In particular, the presence and expansion of low oxygen in the water column reduce vertical migration depths for some species (e.g. tunas and billfishes), compressing vertical habitat and changing their prey distribution (Stramma *et al.*, 2012). Regarding the sea ice melting, the estimations for the end of the century projected global mean sea level rise between 0.5 m and 1.2 m under RCP8.5 (Kopp *et al.*, 2014). In addition, observed trends in global ocean pH have already exceed the range in natural seasonal variability and ocean acidification is expected to overpass it further in coming years (Gattuso *et al.*, 2015).

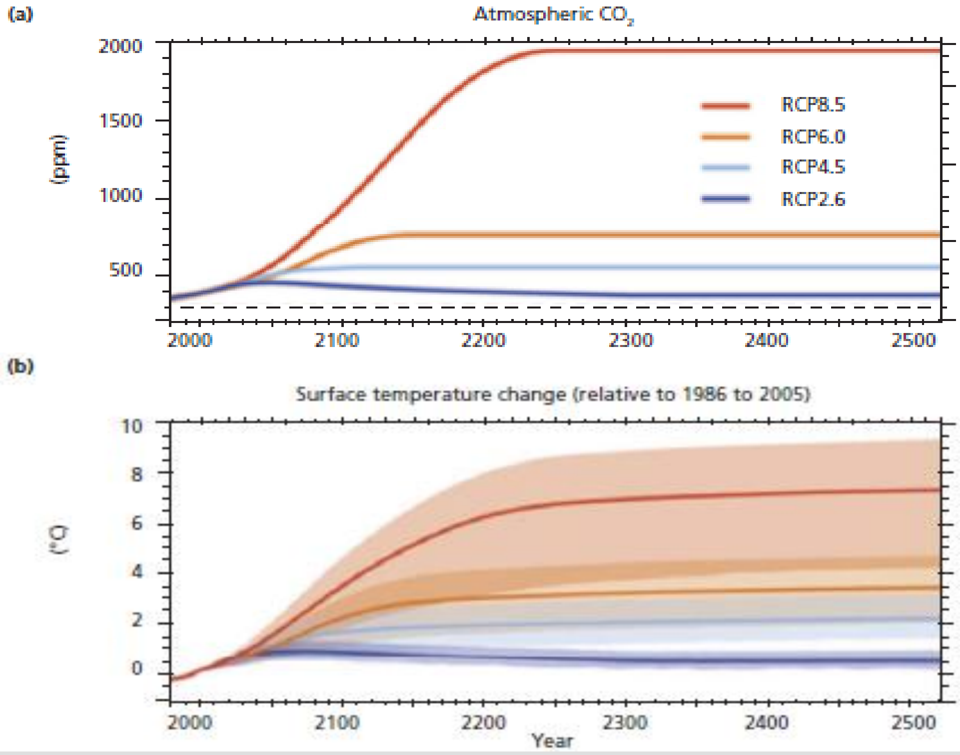


Figure 0.2: (a) Atmospheric CO_2 and projected global mean surface temperature changes for the four RCPs up to 2500 (relative to 1986 to 2005). The dashed line on (a) indicates the pre-industrial CO_2 concentration and four different GHG concentrations: low, below 500 ppm as in RCP2.6; medium, 500 ppm to 700 ppm as in RCP4.5; high, above 700 ppm and below 1500 ppm as in RCP6.0 and RCP8.5. Source from IPCC (2014b).

0.2. Climate change effects on ecosystems

Climate change is expected to trigger a significant impact across all marine ecosystems, latitudes and trophic levels (Ottersen *et al.*, 2010; Scheffers *et al.*, 2016). Many studies have showed global warming effects on species distribution and abundance (Burrows *et al.*, 2011; Cheung *et al.*, 2013b; IPCC, 2014c; Pecl *et al.*, 2017; Poloczanska *et al.*, 2016; Portner & Peck, 2010; Richardson *et al.*, 2012), as well as on phenology (seasonal biological phenomena in relation to climatic conditions) (Asch, 2015; Poloczanska *et al.*, 2013; Poloczanska *et al.*, 2016). Global change is redistributing all life on Earth because the first response of the species affected is often a shift location, following their preferred environmental conditions (Burrows *et al.*, 2011; Monahan & Tingley, 2012; Pecl *et al.*, 2017; Randin *et al.*, 2009; Richardson *et al.*, 2012). All organisms live within a limited range of temperatures; increasing complexity causes narrower thermal windows for whole-organism functions. Extreme temperatures could have, as a result, a functional constraint (Pörtner & Farrell, 2008). On land, species are in general moving to colder, higher elevations (Chen *et al.*, 2011; Kelly & Goulden, 2008; Wilson *et al.*, 2005) whilst in the ocean, they are moving to colder waters and greater depths (Dueri *et al.*, 2014; Dulvy *et al.*, 2008; Perry *et al.*, 2005) in order to maintain their thermal optimum.

Climate change is causing potentially significant alteration in primary production, variation in species interactions, shifts in species distribution and abundance, changes in growth and mortality rates as well as in ocean characteristics and it is expected to follow causing those changes in the future (Bahri *et al.*, 2018; Doney *et al.*, 2012). Ocean warming can impact primary and secondary production, modify the ecophysiology and distribution of marine organisms, change relationships between species, food webs and alter the ecosystem function (Beaugrand *et al.*, 2003; Chust *et al.*, 2014a; Doney *et al.*, 2012). Phytoplankton production is the process at the base of the marine food web, controlling the energy and food available to higher trophic levels (Bahri *et al.*, 2018) and is defined by the availability of light and nutrients (nitrogen, phosphate, iron) (Behrenfeld *et al.*, 2006). In general terms, the increases in upper-ocean temperature, and hence vertical stratification, result in decreases in phytoplankton biomass and primary production, especially in mid- to low latitudes (Behrenfeld *et al.*, 2006). Declines in historical phytoplankton abundance have already been detected over the past century (Boyce *et al.*, 2010). In some particular areas, the upwelling intensification could have a positive impact on nutrient inputs and primary production. However, this process could also increase the presence of low oxygen waters in shelf habitats (Bakun *et al.*, 2015). Due to the generalized reduction of primary production, the energy flow to higher trophic levels decrease, as a consequence of the increasing fraction of small phytoplankton (picophytoplankton) (Morán *et* *al.*, 2010). Nevertheless, the propagation of a hydroclimatic signal up the food web can magnify (or depress) the biomass values along one or more trophic pathways through the trophic amplification (or attenuation) (Chust *et al.*, 2014a). In spite of the uncertainty associated with future projections (Bopp *et al.*, 2013; Hoegh-Guldberg *et al.*, 2014), open-ocean net primary production is projected to redistribute and to decrease from 2% to 20% globally by 2100 (IPCC, 2014b). Highest declines are predicted in mid- to low latitudes due to reduced nutrient input into the euphotic zone, and gains in the Southern Ocean and the Arctic due to warmer temperatures and less sea ice (Doney *et al.*, 2012; Steinacher *et al.*, 2010). These latitudinal changes in primary production together with the sea warming may lead to a large-scale redistribution of global catch potential with a 30–70% increase in high-latitude regions and a 40% decrease in the tropics (Cheung *et al.*, 2009b). Moreover, climate change may increase the average temperature preference of exploited species of the fisheries catches (Cheung *et al.*, 2013b; Cheung *et al.*, 2009b). Besides, key interactions among species are often disrupted and new interactions might emerge due to different response rates and varying degrees across species (Pecl *et al.*, 2017).

While these signals are comparatively robust at the global level, future changes show a much more heterogeneous picture at the regional level (Bahri *et al.*, 2018). Changes in ocean conditions are expected to continue to alter patterns of global marine primary productivity (Bopp *et al.*, 2013) and biodiversity (Jones & Cheung, 2014). Living marine resources (LMR) models project future changes in biomass of upper trophic level consumers or exploited fish stocks under scenarios of changing ocean conditions (Cheung *et al.*, 2018). Substantial local population extinctions are projected by 2050 under climate change scenarios, particularly in subpolar and tropical regions and semi-enclosed seas such as the Mediterranean Sea (Cheung *et al.*, 2009b). The resilience of species to environmental change is influenced by life-history strategies of species involved (Muhling *et al.*, 2017a). Those expected changes may likely impact importantly in species distribution and abundance (Burrows *et al.*, 2011; Cheung *et al.*, 2013b; IPCC, 2014c; Pecl *et al.*, 2017; Poloczanska *et al.*, 2016; Portner & Peck, 2010; Richardson *et al.*, 2012), potential fisheries catches (Cheung *et al.*, 2009b) and therefore, in food security (Bell *et al.*, 2013b; FAO, 2016; IPCC, 2014d; Lam *et al.*, 2016). Many human components that depend on marine resources for food, income, recreation, and cultural purposes are and will be also affected (Weng *et al.*, 2015).

0.2.1. Physiological effects, larval survival, recruitment and populations

Temperature impacts directly in physiology, through oxygen utilization, food conversion efficiency, growth, reproduction, foraging, and immune competence, with subsequent effects on health, fitness, behaviors, and competitiveness (Barange & Perry, 2009; Deutsch *et al.*, 2015; Pörtner *et al.*, 2001; Pörtner & Farrell, 2008). However, the importance and limiting influence of temperature is highly variable across species (**Figure 0.3,** *e*.g. Portner and Peck (2010), Peck *et al.* (2013)) and the response of a population or community to climate may be linear or non-linear, direct or indirect (Ottersen *et al.*, 2010).

Knowledge of the eco-physiology of different life stages will provide a strong basis to infer the response of a species to a change in temperature (and other climate-driven changes in abiotic factors) (Rijnsdorp *et al.*, 2009).

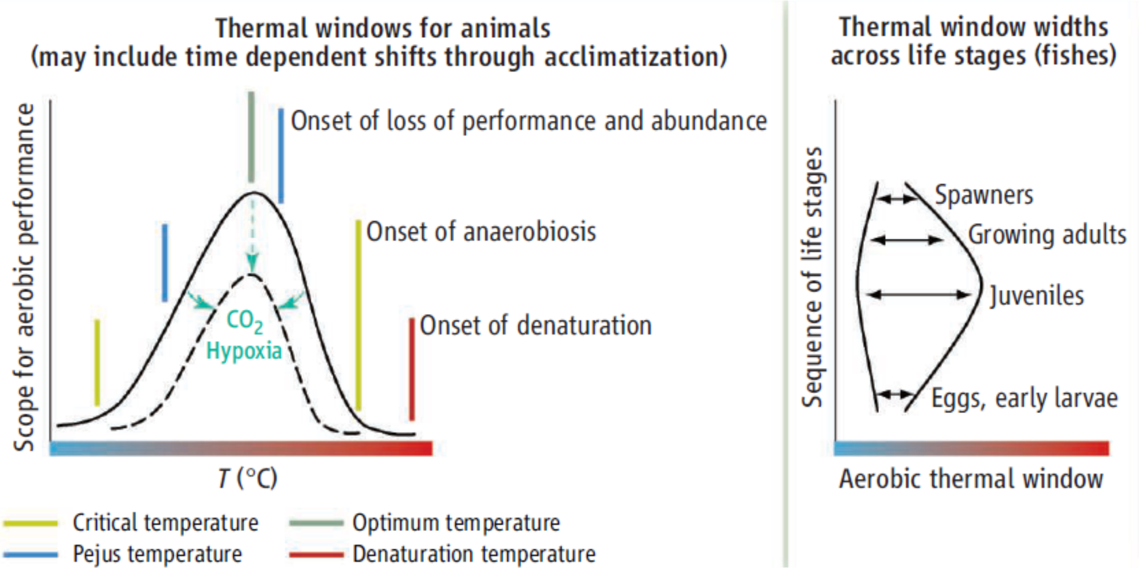


Figure 0.3: Temperature effects on aquatic animals. The thermal windows of aerobic performance (left) display optima and limitations by turning worse, critical, and denaturation temperatures, when tolerance becomes increasingly passive and time-limited. Positions and widths of windows on the temperature scale shift with life stage (right). Source from Pörtner and Farrell (2008).

Higher temperatures generally increase respiratory and energy demands, implying a need for higher prey concentrations and feeding rates to compensate (Doney *et al.*, 2012; Lefort *et al.*, 2015). There is high uncertainty related to the ability of species to acclimatize to changes in environmental conditions (Munday *et al.*, 2013). For example; in cases where additional food is not available, animals may grow to smaller sizes or shift to a new habitat if conditions are intolerable (Doney *et al.*, 2012; Muhling *et al.*, 2017a).

As higher temperatures decrease the aerobic capacity, individuals with smaller body sizes have a reduced risk of oxygen deprivation. Different mechanisms (physiological and evolutionary) could produce this theoretically predicted and empirically observed life-history pattern but both of them have similar consequences such as a decrease in body size, increase in proportion of small-sized species, young age classes and earlier maturation (Audzijonyte *et al.*, 2016; Daufresne *et al.*, 2009). Changes in size distribution has been recorded (Audzijonyte *et al.*, 2016; Baudron *et al.*, 2014; Cheung *et al.*, 2013a; Daufresne *et al.*, 2009; Genner *et al.*, 2010) and decreasing body size has been proposed as the third universal ecological response to increasing temperatures (Cheung *et al.*, 2013a; Daufresne *et al.*, 2009) together with the shift of species ranges and the seasonal variations in life cycle events. Lefort *et al.* (2015) modeled the effects of ocean warming on biological communities and suggested that small body-size organisms might be more resilient to climate change than large ones. The capacity to fulfill their metabolic needs under reduced energy supply increases the resilience of small body-size organisms and is further favored by the release of predation pressure due to the decline of large organisms (Lefort *et al.*, 2015).

Apart from acclimation, significant adaptation to changing physiological conditions may be possible if populations have sufficient genetic variation, evolutionary processes becoming important over decadal to centennial timescales (Munday *et al.*, 2013). Theoretically, local population extinction can occur if the rate of change in the timing in suitable habitat exceeds the population’s inherent capacity for variability, or it's capacity to change its phenology (Anderson *et al.*, 2013). The adaptative capacity of the populations can be difficult to determine, although those with high phenotypic plasticity (phenomenon of a single genotype producing different phenotypes in response to different environmental conditions) may be more successful (Anderson *et al.*, 2013). The early life stages of organisms, particularly fishes, are also very sensitive to changes in their environment and as a result, projecting the future state of recruitment potential or stock sizes under a changing climate is very difficult (Muhling *et al.*, 2017a).

0.2.2. Range shifts

Probably the best direct evidence of the effects of climate change on marine ecosystems comes from distributional shifts of marine organisms (Ottersen *et al.*, 2010). However, range shifts can be driven by a variety of environmentally-sensitive processes, such as changes in local survival, immigration/emigration into newly favorable/unfavorable habitats and relocation of spawning and/or feeding grounds (Rijnsdorp *et al.*, 2009). Strongest responses to ocean warming occur in populations that currently exist near thermal limits (Barange & Perry, 2009; Drinkwater *et al.*, 2010; Myers, 1998). It has been suggested that populations at the limit of the species range are more susceptible to density-independent factors than those at the center (review in Myers (1998)), then, the relative variability in population density should be greater at the boundaries (Gaston, 1990). Species with more opportunistic life-history strategies, such as short generation times, early reproduction and small body sizes, may quickly take advantage of new habitats (Bates *et al.*, 2014). Phenotypic plasticity, broad physiological tolerances, and generalist species are also advantageous (Muhling *et al.*, 2017a). However, the complexity of interactions between population characteristics and environment complicates efforts to assign distribution changes to temperature or other environmental effects (Muhling *et al.*, 2017a). Many efforts have been made to disentangle the causes of species shift (Currie *et al.*, 2019; Thorson *et al.*, 2017; Thorson *et al.*, 2016). Other variables, such as oxygen, dispersal processes or the presence of prey species, are also important to define species distribution (Bates *et al.*, 2014; Deutsch *et al.*, 2015; Pörtner *et al.*, 2001). However, most of the species shifts have been attributed to water warming; such as fish species that have been reported to be expanding their northern distribution limits and accelerating the general latitudinal movement detected for past decades, e.g. Atlantic mackerel (*Scomber scombrus*), Atlantic cod (*Gadus morhua*), bib (*Trisopterus luscus*), blue whiting (*Micromesistius poutassou*), Norway pout (*Trisopterus esmarkii*) and scaldfish (*Arnoglossus laterna*) (Beare *et al.*, 2004; Bruge *et al.*, 2016; Lenoir *et al.*, 2011; Montero-Serra *et al.*, 2015; Perry *et al.*, 2005).

The temperature tolerances of important prey species can affect the observed temperature preference of target species, more than the physiological restrictions on the predator (Muhling *et al.*, 2017a). Consequently, future conditions may be physiologically tolerable for the predator, but unable to sustain their energy requirements; then, new habitats may be characterized mainly by prey distribution (e.g. Polovina (1996)). The ecosystem complexity and interactions between biotic and abiotic factors can cause difficulties in projecting future habitat use, as the primary mechanisms and drivers are difficult to define (Muhling *et al.*, 2017a; Thorson *et al.*, 2016). This suggests that caution is needed when defining thermal limits and related to the realized niches or distribution, because they may not represent physiological limits (Peck *et al.*, 2013).

0.2.3. Migration, spawning and feeding conditions

Modifications in the phenology of annual migrations to feeding and spawning grounds can be driven by changes in temperature (Huse & Ellingsen, 2008). Changes in spawning timing, length at maturity, egg sizes, larval development and growth and time to hatch have been recorded due to water warming (Asch, 2015; Barange & Perry, 2009; Peck *et al.*, 2013; Petitgas *et al.*, 2013). Decreases in overall productivity, due to changes in oceanographic characteristics and ocean warming can reduce (and in some cases increase, e.g., with more intense coastal upwelling, or less ice coverage in high latitudes) the carrying capacity of regional food webs (Behrenfeld *et al.*, 2006). Spatial and temporal mismatches can occur between predator and prey (Cushing, 1990; Cushing, 1975) due to varying sensitivities of different organisms, and regional-specific changes in biophysical characteristics (Drinkwater *et al.*, 2010; Rijnsdorp *et al.*, 2009). In addition, interactions between environmental conditions, fishing mortality and population sizes are likely to occur in the future, presenting challenges for understanding and management (Muhling *et al.*, 2017a).

0.3. Marine fisheries

Fisheries and aquaculture play a very important role on food security, contributing in a significant way to the livelihoods of millions of people, as a creator of employment, supplier of nutritious food, generator of income and economic growth through harvesting, processing and marketing fish (FAO, 2016; Gillett, 2000; IPCC, 2014d; Vannuccini *et al.*, 2018). Food security was defined as: "all people, at all times, have physical, social and economic access to sufficient, safe and nutritious food which meets their dietary needs and food preferences for an active and healthy life" (FAO, 1996). Several countries, including underdeveloped countries, depend on these sectors for their social, economic and nutritional benefits (Bell *et al.*, 2018a; FAO, 2016; Weng *et al.*, 2015).

Total fisheries and aquaculture production reached its maximum in 2016 with about 171 million tons; 53% corresponding to fisheries catches and 47% from aquaculture production (FAO, 2018). Catches across FAO major fishing areas have undergone changes since the middle of the 20th century. While in the 1950s more than half of the production was caught in the Atlantic Ocean, the higher marine capture fisheries production has moved to the Pacific Ocean (FAO, 2018). In recent years, most of the temperate areas have experienced a decreasing in the captures. However, catches in the Northwest Pacific and Northeast Pacific have maintained and also shown an increasing trend as well as in tropical areas due to an increase in the production of large and small pelagics (FAO, 2018).

The stock production in different areas can be affected by the level of development of the countries surrounding those areas, the fisheries management measures being adopted, the composition of the species being caught, the amount of the illegal, unreported and unregulated (IUU) fishing, as well as the status of stocks (Vannuccini *et al.*, 2018). In addition, climate, ocean, and ecosystem conditions can greatly affect fish stock productivity (referred as the total biomass or number of fish that a stock can produce and relates to how much it can theoretically support for removal) by altering habitat suitability, ecosystem-level productivity, dynamics (e.g. predator-prey interactions), and a stock's life history parameters (Farley Jr *et al.*, 2016; Hare *et al.*, 2010; Karp *et al.*, 2019).

0.3.1. Importance of pelagic fishes in fisheries

Fisheries for pelagic species have existed for thousands of years (evidence exists for systematic pelagic fishing from 42 ka) (O'Connor *et al.*, 2011) and some artisanal fisheries are still active today (e.g. Adams and Dalzell (1994)). However, technological developments in vessels, gear, navigation equipment, and fishing procedures resulted in a significant increase in fishing efficiency, economic gain, even if fishing efficiency is held constant, and the capacity of fishing has become easier, safer and less labor-intense (FAO, 2010; Miyake, 2005; Muhling *et al.*, 2017a). Besides, the development of industrialized fisheries in different regions of the world has almost always been followed by a period of massive stock decline (Pinnegar & Engelhard, 2008) with management regulations often applied too late or in an inefficient way to prevent stock depletion below levels that produce maximum sustainable yield (MSY) (Muhling *et al.*, 2017a). Climate change is an additional stressor that fisheries managers will need to continuously evaluate; how fish populations respond to changing environmental conditions, test adaptation options and their outcomes, and share information regarding successful adaptation strategies with other fisheries managers (Gregg *et al.*, 2016). Traditional fisheries management tools, such as allowable catch, size restrictions, seasonal closures, gear restrictions, marine protected areas, essential fish habitat protection, and protection of spawning aggregations, may not be sufficient to sustain fisheries in the face of the combined effects of climatic and non-climatic stressors, which will affect both fish stock populations and the economies of fisheries-dependent communities (Gregg *et al.*, 2016).

Pelagic species, including both small pelagic fishes and large top predators (tunas and billfishes), comprise the largest proportion (21%, 19.6 million tons) of global catches (including crustacean, mollusks, and freshwater fishes) (FAO, 2016). Pelagic fisheries target species are separated here into those targeting small pelagics (such as sardines, anchovies, herring, chub mackerels) and large pelagics (tunas, billfishes, sharks, Spanish mackerels). Small pelagics, which are targeted using purse-seines, mid-water or pelagic-trawls, and other methods, are mainly fished for human consumption (especially in African markets) and the production of fishmeal and fish oil, used primarily as feed ingredients in the aquaculture and livestock industries (FAO, 2018). Engraulidae family has more than 140 species, however, *Engraulis* species are the most important industrial fishery targets followed by the family Cupleidae (with more than 190 species, including sardines, herring, spat, and menhaden) (Muhling *et al.*, 2017a). Other species with lengths <50 cm, such as small scombrids of genus *Scomber*, as well as capelin and several carangid species are also considered small pelagic species with commercial interest (Muhling *et al.*, 2017a).

Tunas are the main large pelagic target species and pelagic longlines, purse-seines, pole-and-line/greenstick methods, and other gears are used to catch them (Muhling *et al.*, 2017a). The annual catch of tuna and tuna-like species leveled off at around 7.5 million tonnes after an all-time maximum of 7.7 million tons in 2014 (FAO, 2016, 2018) and represents an economically important contribution to many nations (Brill & Hobday, 2017). The most economically important tuna species are referred to as principal market tunas and are caught by industrial pelagic fisheries around the globe (FAO, 2011). These principal market tunas include albacore (*Thunnus alalunga*), Atlantic bluefin tuna (*T. thynnus*), bigeye tuna (*T. obesus*), Pacific bluefin tuna (*T. orientalis*), southern bluefin tuna (*T. maccoyii*), yellowfin tuna (*T. albacares*), and skipjack tuna (*Katsuwonus pelamis*). Catches of principal market tunas reached 4.9 million tons in 2016 (ISSF, 2018); being the highest landings for skipjack tuna (2.8 million t) followed by yellowfin tuna (1.5 million t) (FAO, 2018). However, the total adult biomass of tuna has been estimated to decline by 49% between 1954 and 2006 (Juan-Jordá *et al.*, 2011), and this decline has been attributed to intensive exploitation (Worm & Tittensor, 2011). Bonitos (*Sarda spp.*), Spanish mackerels (*Scomberomorus spp.*), sharks as well as billfishes also support large pelagic commercial fisheries (Muhling *et al.*, 2017a). The main shark species by landings is the blue shark (*Prionace glauca*) and swordfish (*Xiphias gladius*), which is the only member of the Xiphiidae family, for the billfish fishery. Other species in the family Istiophoridae (marlins, sailfish, spearfish) are also important to both, commercial fleets and recreational fishermen (Muhling *et al.*, 2017a).

0.3.2. Pelagic fishes: biology, ecology, and climate change impacts

While evidence for changes in physical signals is often distinct, impacts on fishes inhabiting oceanic systems are not easily identified, and therefore, quantification of responses is difficult (Hobday & Evans, 2013). The ability to move away from temporarily unsuitable habitats due to the high mobility and migratory behavior and the plasticity in spatial habitat use of many pelagic fish species, makes the determination of climate change impacts a complex problem (Hobday & Evans, 2013).

Increases in the proportion of tropical tuna in sub-tropical regions between 1965 and 2011 were related to ocean warming (Monllor-Hurtado *et al.*, 2017). Due to the socio-economic value of tuna species, understanding and predicting responses to global climate change are a priority for the scientific community to design effective fishery management to ensure the sustainability of tuna populations and, hence, the development of the human societies depending on them (Barange *et al.*, 2018; Hobday *et al.*, 2017). Recently, Arrizabalaga *et al.* (2015) described the global habitat preferences of commercially valuable tuna but did not explore historical or future changes in these distributions. Other regional, single ocean or single species projections have predicted tuna distribution and tuna population responses to climate change (Bell *et al.*, 2013b; Christian & Holmes, 2016; Druon *et al.*, 2017; Dueri *et al.*, 2014; Lehodey *et al.*, 2013; Michael *et al.*, 2017). Those efforts are particularly important in the case of tunas because they are widely distributed and highly migratory species (Arrizabalaga *et al.*, 2015; FAO, 1994, 2011), playing ecologically important roles in many regions due to their top-down influence on the ecosystem structure (Cox *et al.*, 2002; Sibert *et al.*, 2006). The disproportionate removal of top predators through fishing mortality can alter the structure of marine ecosystems through top-down processes and trophic cascades (Pauly *et al.*, 1998; Pinnegar & Engelhard, 2008; Pitcher, 2001), and may generate additive and synergistic effects with environmental and climate variability.

As tuna or tuna-like species, small pelagic fish dynamics are often related to environmental fluctuations (Borja *et al.*, 2008; Checkley *et al.*, 2009) and respond rapidly to climate variability (Montero-Serra *et al.*, 2015) due to bottom-up effect which might amplify or depress the impacts occurring in higher trophic levels (Chust *et al.*, 2014a; Field *et al.*, 2006). Therefore, they can be good biological indicators of climate-driven changes in marine ecosystems (Peck *et al.*, 2013). However, other important drivers of fish population, such as exploitation, can also complicate efforts to determine the relative importance of environment and fishing mortality on stock variability (Muhling *et al.*, 2017a). In addition, climate and fisheries' effects may also interact strongly, then, attributing observed behaviors of stocks to natural versus anthropogenic stressors can be difficult (Brander, 2010; Hollowed *et al.*, 2013).

The resilience to environmental changes is lower in heavily exploited populations and their fluctuations are higher through time (Anderson *et al.*, 2008; Bates *et al.*, 2014; Hsieh *et al.*, 2006). This increased in variability is probably due to the truncation of the age structure and often results in localized depletions (Berkeley *et al.*, 2004; Hsieh *et al.*, 2006). Berkeley *et al.* (2004) suggested that an old-growth age structure, combined with a broad spatial distribution of spawning and recruitment, is at least as important as spawning biomass in maintaining long-term sustainable population levels. In addition, both, climate-related warming and fishing can select for smaller body sizes in some species and increase the sensitivity to climate change (Ottersen *et al.*, 2006; Pauly *et al.*, 1998). Compensatory responses at the level of individuals and populations are expected under fishing pressure because fishing leads to substantial modifications in the size structure of exploited communities (**Figure 0.4**) (Shin *et al.*, 2005).

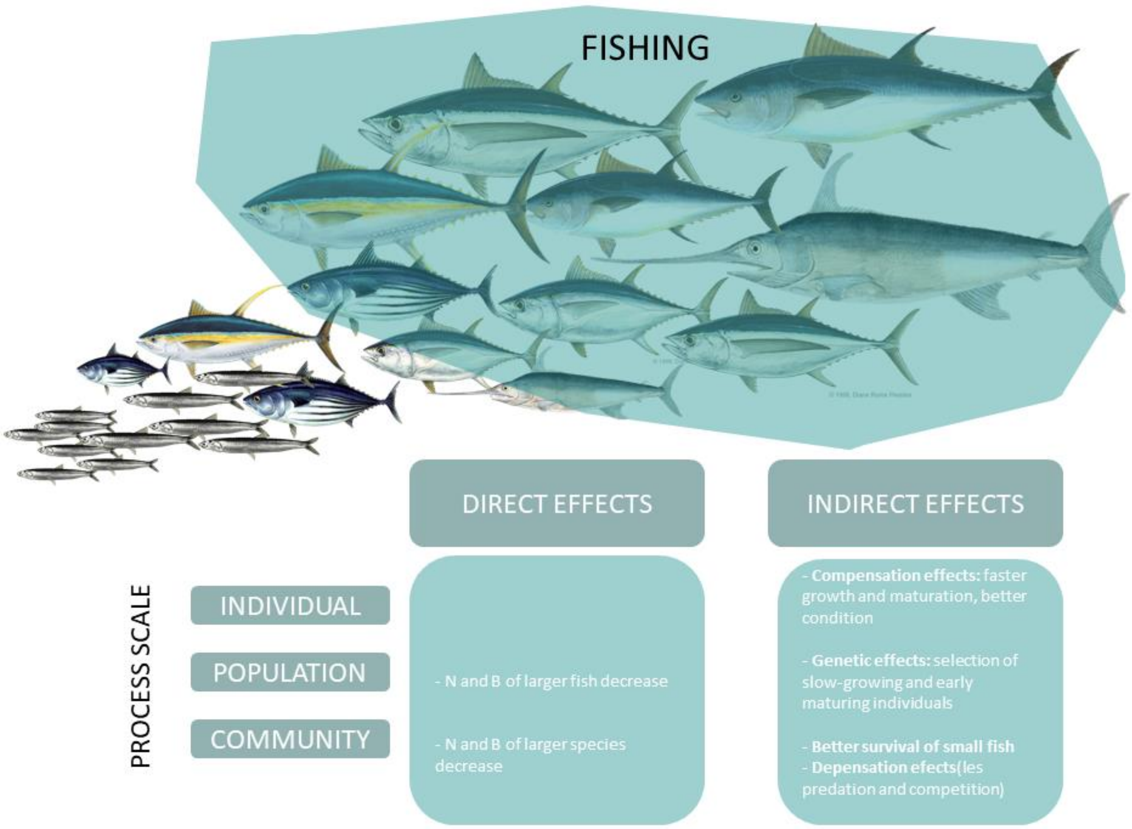


Figure 0.4*: Theoretical direct and indirect effects of fishing on fish population and communities (N: abundance, B: biomass). Redrawn from Shin et al. (2005).*

The wide range of habitat associations and behaviors across different pelagic fish species have implications in predicting climate change impacts on populations and therefore, in ecological and economic aspects, such as fisheries management (**Figure 0.5**) (Muhling *et al.*, 2017a). Due to diverse life-history strategies and a broad range of habitats, climate effects are likely to vary strongly across species and also by life stages in the same species, becoming a complex process the prediction of future distributions and abundances and best management plans (Muhling *et al.*, 2017a). The additional challenge to management is that projected future conditions, are likely to be outside the ranges of recent historical observation, and biological responses and the ability of species to adapt or acclimatize to them remain largely unknown (Muhling *et al.*, 2017a).

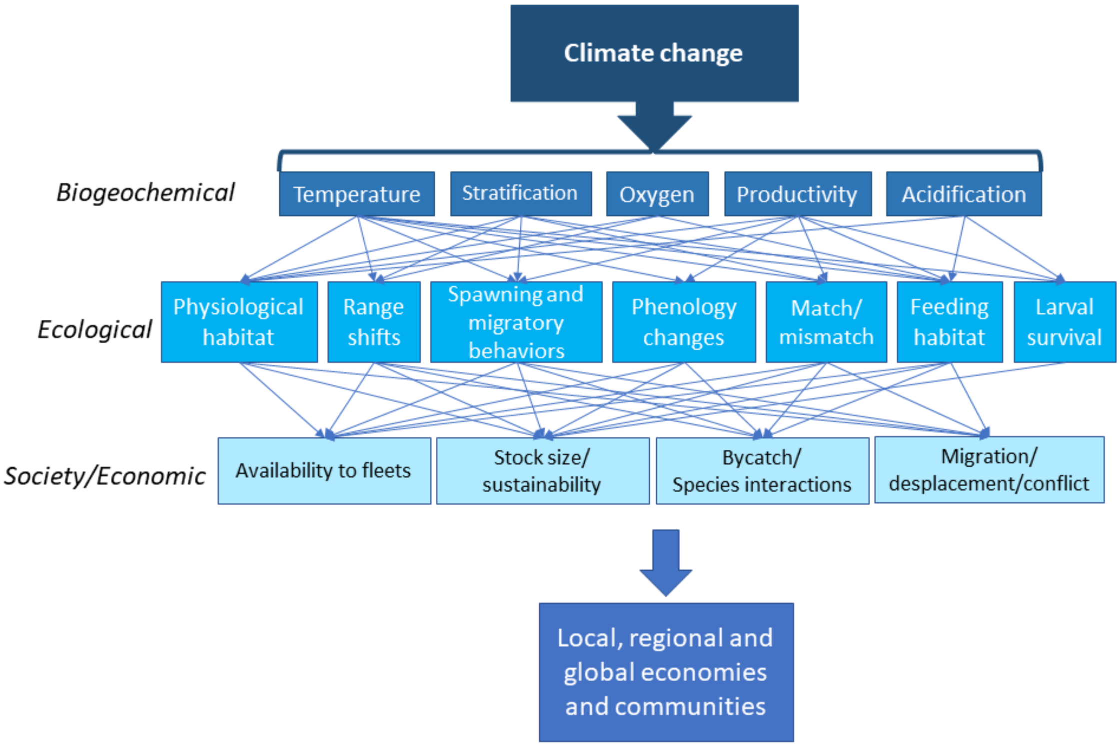


Figure 0.5: A simplified conceptual model of some of the major impacts of climate change on pelagic fish and fisheries. Modified from Muhling et al. (2017a).

0.3.2.1. Small pelagics: the European anchovy

Small pelagics are distributed widely across different habitats and areas. However, many species are associated with regions of high primary productivity, such as upwelling boundary currents, continental shelves, and areas of freshwater inflow to the marine environment (Checkley *et al.*, 2009). Anchovies are typically associated with productive upwelling environments, herring and sprat with temperate to cold latitudes while clupeids are usually found in warmer, subtropical environments (Checkley *et al.*, 2009). The small pelagic species which was selected as a case of study was the European anchovy, then, a further description of this species and the particular population distributed in the Bay of Biscay (BB) was developed.

The European anchovy (*Engraulis encrasicolus,* Linnaeus 1758) is a small pelagic fish (**Figure 0.6**) which presents a wide distribution across the eastern North and Central Atlantic including Mediterranean Sea, Black Sea and Azov Sea (Reid, 1966) but with differentiated populations often related to local features such as upwellings, bays, estuaries (Zarraonaindia *et al.*, 2012), shelf edge fronts and oceanic eddies due to their higher primary production (Motos *et al.*, 1996). It is a species with fast growth, high mortality and fecundity (Motos, 1996) and a short life cycle (Motos, 1996; Petitgas *et al.*, 2012; Uriarte *et al.*, 2016). The anchovy spawning peak generally occurs during a period of rapid environmental changes. This peak can be initiated by changes in daylight, changes in the wind, decreases in freshwater runoff, or warming of atmospheric and seawater temperatures (which vary between 12ºC at the end of winter and 20ºC at the beginning of summer in the BB) (Koutsikopoulos & Le Cann, 1996; Sanz & Uriarte, 1989). The peak of the spawning activity (when most fish present are actively spawning) in the Bay of Biscay occurs in May (Sanz & Uriarte, 1989), and it is associated with temperature between 14 and 18ºC (Montero-Serra *et al.*, 2015; Motos *et al.*, 1996; Portner & Peck, 2010; Sagarminaga *et al.*, 2004).

Figure 0.6: The European anchovy (Engraulis encrasicolus, Linnaeus 1758)

0.3.2.2. Large pelagics; tuna and billfishes

Large pelagic fishes are highly migratory (FAO, 1994) and play a very important role in the ecosystems, due to their top-down influence on the ecosystem structure (Cox *et al.*, 2002; Sibert *et al.*, 2006). Both tunas and billfishes are broadly, distributed, inhabiting a wide range of environments from low nutrient tropical waters to productive sub-polar seas (Muhling *et al.*, 2017a).

Tunas have high energetic costs, but they can vary between species (Korsmeyer & Dewar, 2001); e.g. the larger tunas such as bluefin, bigeye, and albacore have greater endothermic capabilities, with greater temperature elevation and are therefore, the most cold-tolerant (Korsmeyer & Dewar, 2001). It can become an advantage because they can inhabit highly productive seasonal feeding grounds, dealing with high changes in temperature (dropping below 10ºC) as a result of both vertical and horizontal movements in the ocean (Block & Stevens, 2001; Brill *et al.*, 1999; Holland, 1990). Yellowfin tuna prefers warmer tropical and subtropical regions, and smaller species like skipjack are the most warm-water associated, distributed mainly in tropical areas (FAO, 1994; Muhling *et al.*, 2017a). Tunas show three types of spawning patterns; 1) confluent throughout tropical and subtropical regions (e.g. skipjack, yellowfin, and bigeye), 2) migratory and spatiotemporally confined (e.g. albacore, southern bluefin tuna, Atlantic bluefin tuna) and 3) regionally confined and protracted (other small tuna species). All species spawn in sea surface temperatures greater than 24ºC and in most tuna species, males show greater size than females, which is the opposite of what is observed for most marine fish (Schaefer, 2001). Tunas also have a vertical migration (Block & Stevens, 2001; Brill *et al.*, 1999); bigeye tuna inhabit depths of several hundred meters during the day, and return to near-surface waters at night, while bluefin and yellowfin are associated with shallower depths, diving deeply for some hours (Block & Stevens, 2001; Brill *et al.*, 1999). The overall external design similarity between tunas and billfishes has led to the assumption that both groups locomote in a similar manner and billfishes are often assumed to be tunniform swimmers with a propulsive wave of low amplitude and high frequency (Walters, 1962). Recent studies showed that the swimming pattern differed from that of the tuna by the distribution of the aerobic red muscle mass (Block, 1991) and determined that billfishes are highly specialized for life in the pelagic ocean and use different strategies than tunas to optimize performance (review in Block (1991)). While tunas have long fascinated marine scientist and their importance has promoted further researches, the billfishes have received far less study.

- **Albacore (*Thunnus alalunga*)**:

Albacore (Bonnaterre, 1788, **Figure 0.7a**) is a highly migratory species (Collette & Nauen, 1983) found in all of the oceans of the world, mainly in temperate latitudes (Christian & Holmes, 2016) and prefers cooler sea temperatures ranging from 10 to 20ºC (Graham & Dickson, 1981) although temperatures outside that range can be tolerated for short periods (Collette & Nauen, 1983). They are known to concentrate along thermal discontinuities such as the Transition Zone in the North Pacific and the Kuroshio Front east of Japan because of richer forage organisms but poorer in oxygen content (Collette & Nauen, 1983). Thermal preference seems to be the goal of the periodical vertical migrations that albacore undertake moving from warm surface waters to deep cooler waters because they feed during the day and at night (are both, diurnal and nocturnal) of fishes, crustaceans and squids (Collette & Nauen, 1983). Albacore is one of the smallest tuna species, with a maximum length of 140 cm (Torres Jr & Pauly, 1991), 60 kg (IGFA, 2001) and 9 years of maximum age reported (Altman & Dittmer, 1962). Albacore from mixed schools with skipjack, yellowfin, and bluefin tunas, which may be associated with floating objects (Collette & Nauen, 1983). Mature adults move to the tropics to spawn but go back to temperate waters after it (Kailola *et al.*, 1993).

- **Atlantic bluefin tuna (*Thunnus thynnus*)**

Bluefin tuna (Linnaeus, 1758, **Figure 0.7b**) are highly migratory, fast swimmers (Porch, 2005), oceanic but seasonally coming close to shore, moving between cooler feeding grounds and warmer spawning areas (Fromentin & Powers, 2005). Among tuna species, bluefin tuna has the widest geographical latitudinal distribution (Fromentin & Fonteneau, 2001). Trans-Atlantic movements related to feeding have been reported; juveniles from the Mediterranean Sea foraging grounds in the eastern coast of the USA (Rooker *et al.*, 2008) and, conversely, western

Atlantic juveniles foraging in the central North Atlantic (Rooker *et al.*, 2007). Variations in the food spectrum are attributed primarily to behavioral differences in feeding: preying on small schooling fishes (anchovies, sauries, hakes) or on squids and red crabs (Collette & Nauen, 1983). They school by size, sometimes together with albacore, yellowfin, bigeye, skipjack, etc. Atlantic bluefin tuna may weight up to 900 kg (Fromentin & Powers, 2005), 458cm total length (Claro, 1994) and live up to 40 years in the western Atlantic (ICCAT, 2009). This species is becoming rare in the ecosystems due to its massive overfishing (Muus *et al.*, 1999).

- **Southern bluefin tuna (*Thunnus macoyii*)**

Southern bluefin tuna (Castelnau, 1872, **Figure 0.7c**), is an oceanic highly migratory species distributed in Atlantic, Indian and Pacific oceans (Collette & Nauen, 1983; FAO, 1994). It is distributed in temperate and cold seas, mainly between 30°S and 50°S, to nearly 60°S. Southern bluefin tuna may reach 245 cm, 260 kg and 20 years (Collette & Nauen, 1983; Nakamura, 1990). Young fish are generally closely associated with coastal and continental shelf waters while by maturity, more individuals are oceanic and with a pelagic existence (Kailola *et al.*, 1993). Adults migrate seasonally between warm water spawning- and cold water feeding-grounds and are considered opportunistic feeders, preying on a wide variety of fishes, crustaceans, cephalopods, salps, and other marine animals (Collette & Nauen, 1983).

- Yellowfin tuna (*Thunnus albacares*)

Yellowfin tuna (Castelnau, 1872, **Figure 0.7d**) is highly migratory and it is distributed worldwide in tropical and subtropical seas, but it is absent from the Mediterranean Sea (FAO, 1994; ICCAT, 2006b). It is an oceanic species occurring above and below the thermoclines but due to its sensitivity to low concentrations of oxygen, it tends to exclude their presence in waters below the discontinuity layer, mainly in the tropics (Brill *et al.*, 1999; Brill & Holland, 1990; Kailola *et al.*, 1993; Sharp, 1978). In those areas where the decrease in oxygen with depth is not limiting, the vertical movements of yellowfin tuna appear to be restricted by the effects of water temperature on cardiac muscle function (Brill *et al.*, 1999). They school primarily by size, either in monospecific or multi-species groups like porpoises or other tuna species (skipjack) and also associated with floating debris and other objects (Kailola *et al.*, 1993). They are diurnal and nocturnal feeders, foraging fishes, crustaceans and squids (Kailola *et al.*, 1993).

- Bigeye (*Thunnus obesus*)

Bigeye (Lowe, 1839, **Figure 0.7e**), is a species distributed in tropical and subtropical waters of the Atlantic, Indian and Pacific oceans but it is absent in the Mediterranean Sea (FAO, 1994). It is a highly migratory species which generally inhabits open waters (FAO, 1994; ICCAT, 2006a) and can reach 250 cm total length (Reiner, 1996) and 210 kg in weight (Frimodt, 1995) with a maximum age of 11 years (Stéquert & Marsac, 1989). Bigeye prefers water temperatures between 17ºC and 22ºC; it is not found in waters where the temperature exceeds approximately 29ºC (Collette & Nauen, 1983) but it dives at night to great depths where it is exposed to temperatures close to 5ºC (Brill *et al.*, 2005). During the day, it remains within the surface layer, around 50 m (Brill *et al.*, 2005). Bigeye is the tuna species that are able to withstand lower concentrations of dissolved oxygen and therefore is capable of inhabiting deeper waters (Brill *et al.*, 2005; Stéquert & Marsac, 1989). It feeds on a wide variety of fishes, cephalopods, and crustaceans during the day and at night (Collette, 1955). Juveniles and small adult schools at the surface in mono-species groups (which is less common) (Calkins, 1980) or mixed with other tunas such as yellowfin and skipjack tuna. Although adults tend to be solitary (Kailola *et al.*, 1993), they are also found associated with floating objects (Stéquert & Marsac, 1989).

- Skipjack tuna (*Katsuwonus pelamis*)

Skipjack (Linnaeus, 1758, **Figure 0.7f**) is a cosmopolitan species in tropical and warm-temperate waters but it is absent from the Black Sea (FAO, 1994). It is found in offshore waters and tend to school in surface waters (with other species such as birds, drifting objects, sharks, whales) with characteristic behavior like jumping, feeding, foaming, etc. (Collette & Nauen, 1983). Skipjack aggregations tend to be associated with convergence, boundaries between cold and warm water masses upwelling and other hydrographic discontinuities (Collette & Nauen, 1983). Skipjack needs high levels of oxygen to maintain a minimum swimming speed and this level increase when active, then, these requirements generally restrict skipjack tuna to water above the thermocline (Sharp, 1978). It is one of the smallest main commercial tuna species with 110 cm of maximum length (McMillan *et al.*, 2011), weight of 34.5 kg and 12 years, but it usually does not exceed the meter-long (Collette & Nauen, 1983). Its principal predators are other tuna species and billfishes (Collette & Nauen, 1983) and it feeds on fishes, crustaceans, cephalopods, and mollusks. It is an opportunistic feeder preying on any forage available mainly in the morning and late in the afternoon; cannibalism is also common (Collette & Nauen, 1983).

In billfishes, habitat preferences also vary across species (Muhling *et al.*, 2017a); swordfish migrate seasonally into cold-water areas to feed (Neilson *et al.*, 2014) while other species prefer warmer environments. There are also differences in the vertical migration and distribution of billfish species; swordfish and marlin have a daily migration, foraging in deep water during the day and staying in the mixed layer at night (Abascal *et al.*, 2009; Young *et al.*, 2006). In contrast, sailfish are more associated with shallower waters (Holland, 1990).

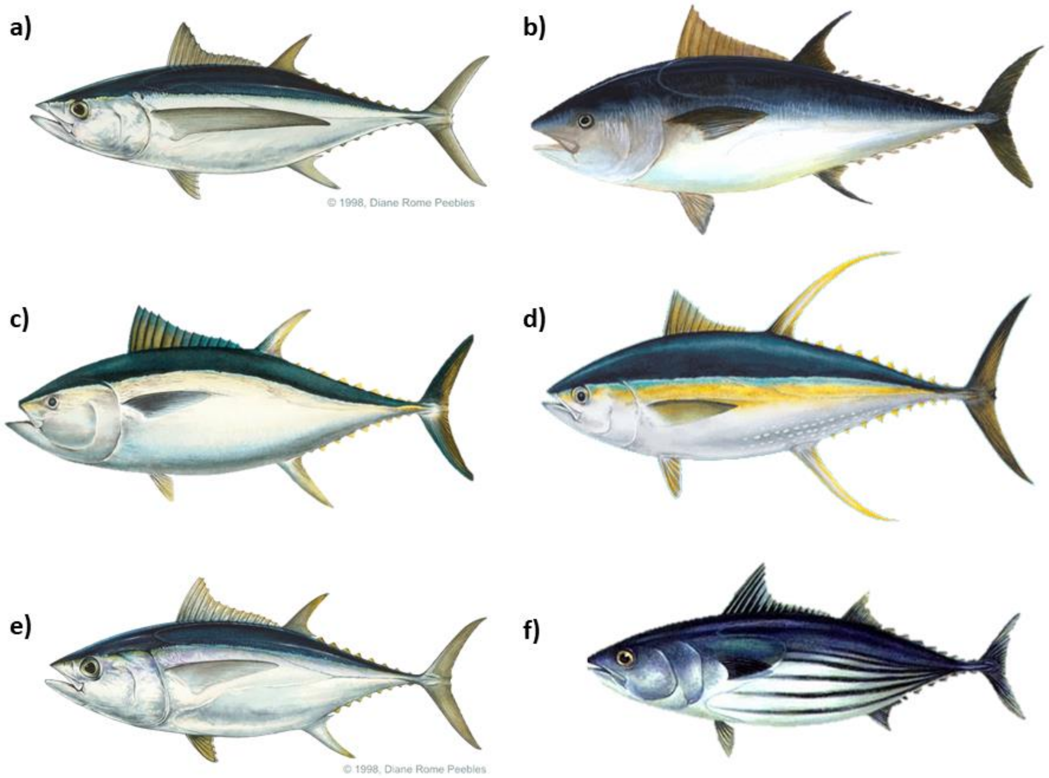


Figure 0.7: Main commercial tuna species. a) Albacore (Thunnus alalunga, Bonnaterre 1788), source from Diane Rome Peebles, b) Atlantic bluefin tuna (Thunnus thynnus, Linnaeus, 1758), c) Southern bluefin tuna (Thunnus macoyii, Castelnau, 1872), d) yellowfin tuna (Thunnus albacares, Bonnaterre, 1788), e) bigeye tuna (Thunnus obesus, Lowe, 1839), source from Diane Rome Peebles and f) skipjack tuna (Katsuwonus pelamis, Linnaeus, 1758).

- **Swordfish (*Xiphias gladius*)**

Swordfish (Linnaeus 1758, **Figure 0.8**) is the most widely distributed species of billfish, occurring in tropical, subtropical and temperate waters from 45ºN to 45ºS (Palko *et al.*, 1981; Sakamoto *et al.*, 1986). Swordfish are large, reaching 3 m (Collette, 1995) and 650 kg (Nakamura, 1986), highly migratory (FAO, 1994) and predatory fishes. It is an important target and by-catch species (Ward & Elscot, 2000) considered as Least Concern (LC) by the IUCN Red List, although the population abundance is decreasing (Collette *et al.*, 2011). This species has shown a 28% decline over a three-generation (20 years) period (Collette *et al.*, 2011). Some assessments carried out in recent years seem to indicate that total and spawning biomass are above levels that would maintain maximum sustainable yield (MSY), including in the Pacific Ocean (Hinton *et al.*, 2005; Kolody *et al.*, 2006), North Atlantic (ICCAT, 2017) and Indian Ocean (IOTC, 2017). Other indicators, such as average size or catch rates in certain areas and fisheries, have raised concerns about fishery sustainability (Abascal *et al.*, 2009). Most of the uncertainty associated with the assessments of swordfish is attributable to the scarce information on the biology of the species, such as on stock-recruitment relationships, mortality, age-at-first-maturity and stock structure (Abascal *et al.*, 2009).

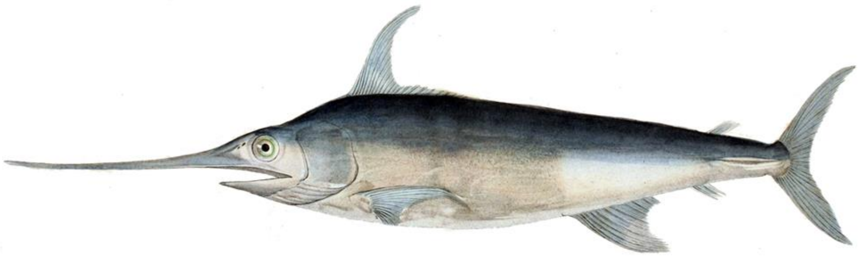


Figure 0.8*: Swordfish (Xiphias gladius, Linnaeus, 1758).*

0.4. Habitat and ecological models

In recent years, predictive modeling of species distribution has become an increasingly important tool to address various issues in ecology, biogeography, evolution and more recently, in conservation biology and climate change research (reviewed in Guisan and Thuiller (2005)). However, a wide range of modeling methods are used, each with different data requirements, assumptions and inherent error and bias (Evans *et al.*, 2015; Fernandes *et al.*, 2013; Hollowed *et al.*, 2013; Stock *et al.*, 2011).

Specifically, habitat predictions present opportunities for quantifying spatio-temporal distribution changes while accounting for sources of natural climate variation (Champion *et al.*, 2018). The simplest class of impact models can broadly be described as correlative habitat models. Commonly, species distribution models (SDM), also called habitat or niche-based models (Anderson *et al.*, 2002), associate known presence locations of the target species with the characteristics of their environment to predict their potential geographical distribution (**Figure 0.9**) (Elith *et al.*, 2006; Guisan & Zimmermann, 2000). Those models are based on the ecological niche concept of Hutchinson (1957) which defined the niche as the variety of environmental conditions for which the organism is best suited. Niche theory further suggests that each organism might occupy a space in order to minimize competition with other organisms (Hardin, 1960; Levins, 1968; Vandermeer, 1972).

Habitat models are usually multivariate, and can be linear (e.g., generalized linear models), or more usually non-linear (e.g., generalized additive models, classification and regression trees, artificial neural networks, Bayesian approach, Maximum entropy) (Guisan & Thuiller, 2005). When species and environmental data are sampled during a limited period of time and/or space, the models fitted with those data can only reflect a snapshot view of the expected relationship (Guisan & Thuiller, 2005).

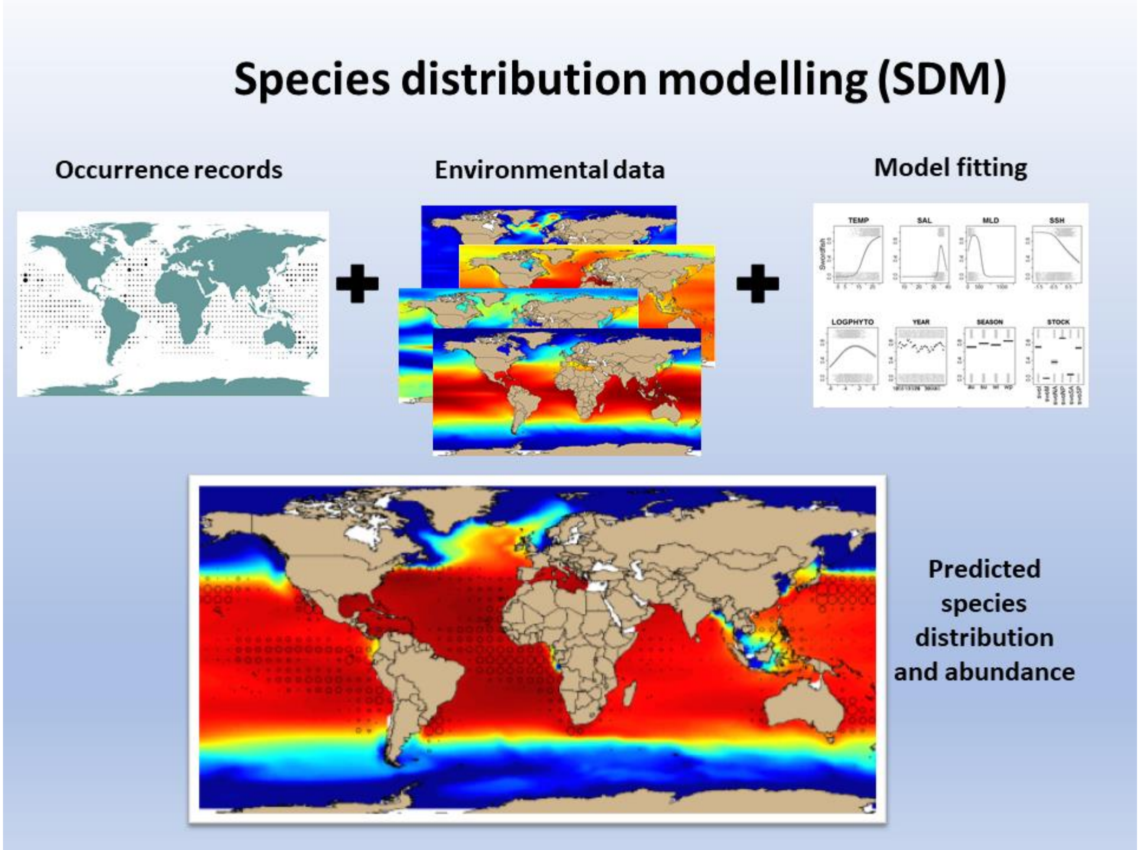


Figure 0.9: *Species distribution models (SDMs) building process.*

Short-time forecasts ranging from seasonal (3 months) to decadal (5-10 years) are now a reality (Payne *et al.*, 2017) and this is an interesting timescale for resource managers (Hollowed *et al.*, 2013). However, predictive skill beyond a few years remains low in many parts of the global ocean (Meehl *et al.*, 2014). Improvement of marine ecological forecasting will require a better understanding of the relationship between marine ecology and climatology in one hand and between science and end-users in the other (Payne *et al.*, 2017).

In fisheries, the scientific advice is commonly based on single species stock assessment set fisheries quotas (Hilborn & Walters, 1992). Nowadays, ecosystem information is being incorporated into traditional stock assessments (**Figure 0.10**) (Dolan *et al.*, 2015; Hollowed *et al.*, 2013; Schmidt *et al.*, 2019). Efforts have been made to improve modeling for dynamical forecasting, including species distributions and ecosystem models to support the management of human activities and conservation efforts, as well as, to develop and implement dialogue between data producers, data users, producers of intermediate products and end-users. In summary, attempts to link fisheries observations, and capacity development in a comprehensive ocean observing framework that allows all monitoring actors to work together, maximizing benefits of efforts have been conducted (Schmidt *et al.*, 2019).

Here, General Additive Models (GAMs), Size Spectrum models (SS) and Dynamic Bioclimatic Envelope Models (DBEM) were described due to their particular interest and used in this thesis.

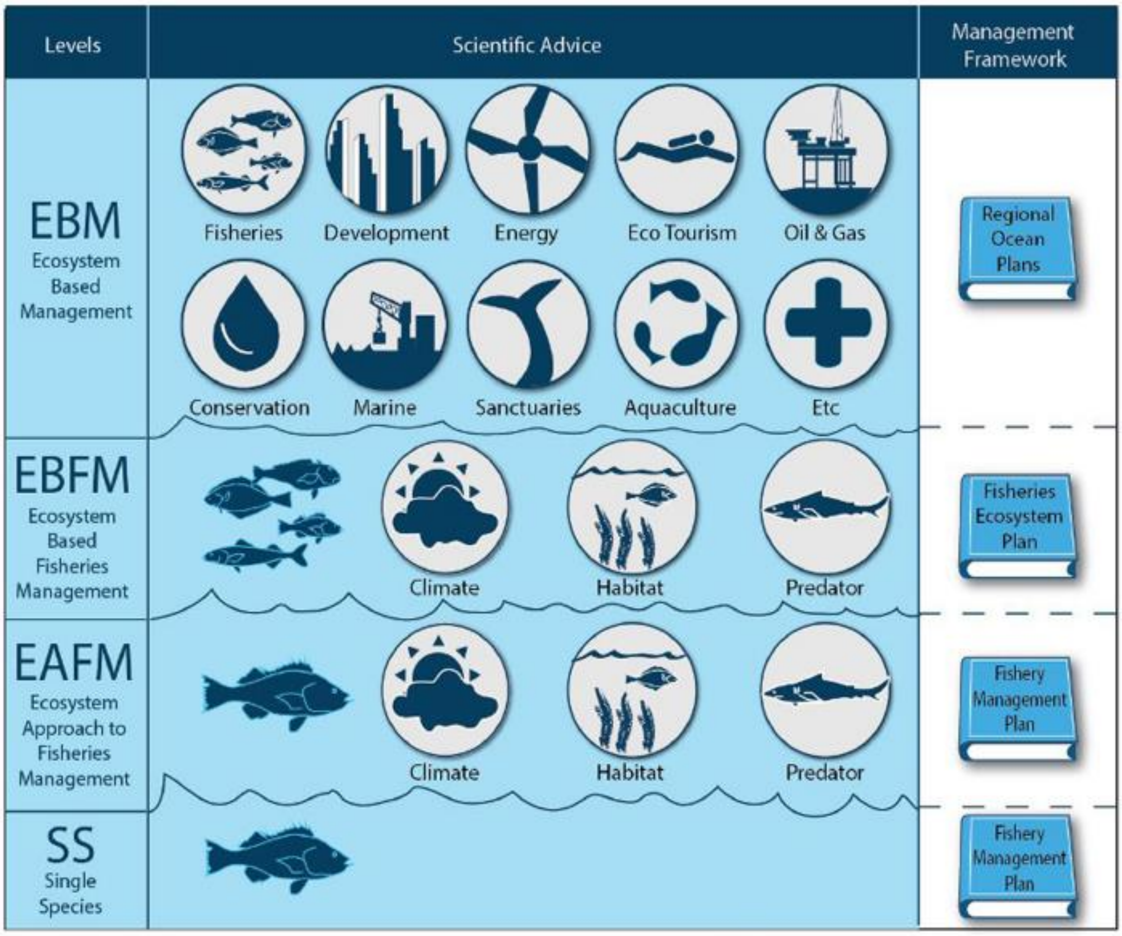


Figure 0.10: From single stock to Ecosystem-Based Management – The paradigms of EM, building upwards from single-species management, to EBM. Scientific advice and the sectors of management build with each level, as well as the management framework. Key differences between ecosystem approaches to fisheries management (EAFM) and EBFM is that the later considers the trade-offs of multiple species, as opposed to a stock within a fishery, and EBFM takes a more coordinated approach to management using strategic planning documents like fishery ecosystem plans. Source from Schmidt et al. (2019) adapted from Dolan et al. (2015).

0.4.1. General Additive Models (GAMs)

The advance in regression analysis due to the Generalized Linear Models (GLM) and Generalized Additive Models (GAM) was an important statistical development of the last 30 years (Guisan *et al.*, 2002). GAMs are a generalized linear model with a linear predictor involving a sum of smooth functions of covariates (Guisan *et al.*, 2002; Hastie & Tibshirani, 1990; Wood, 2012; Wood, 2017) which uses a link function to establish a relationship between the mean of the response variable and a 'smoothed' function of the explanatory variable(s) (Guisan *et al.*, 2002). The model allows us to deal with non-linear and non-monotonic relationships between the response and the explanatory variable(s) (Guisan *et al.*, 2002; Wood, 2017). GAMs are used to construct different species distribution models due to their ability to handle non-linear data structures which can help in the development of ecological models that better represent the underlying data, and hence increase our understanding of ecological systems (Guisan *et al.*, 2002).

The two-step methodology described in Borchers *et al.* (1997) for horse mackerel (*Trachurus trachurus*) was adapted here for different pelagic species (such as anchovy, tuna, and swordfish). In the study cases where species occurrence or abundance data were from fisheries (tuna and swordfish), some adaptations were needed in order to introduce them in the model. The following steps to build a species distribution model with GAMs are described:

i) **Input data:** Fishery catch data are problematic for building reliable SDMs because the observed absences (strata with fishing effort but no catches), when existing, are restricted to the fishing area. Thus, in our model the pseudo-absences were generated randomly, oceanwide, only excluding points with presence data and balanced with the number of presences in each particular year following Barbet-Massin *et al.* (2012), Elith and Leathwick (2009), Guisan and Theurillat (2000) and Iturbide *et al.* (2015). In cases where data come from scientific surveys and absence records are available, pseudoabsences generation is not needed.

ii) **Model fitting, variable selection:** In order to fit unimodal response curves for the environmental variables (according to the ecological niche concept of Hutchinson (1957)) and to avoid overfitting, degrees of smoothness ("k" values) were set equal or less than three. GAMs were built using the "mgcv" package in R-language (Wood, 2012) after removing all the records with missing values. *Dredge* function of 'MuMIn' R-package was used to generate a set of models with combinations (subsets) of terms in the global model (Barton, 2016), with rules for model inclusion based on lowest AIC

(Akaike Information Criterion), which means a better fit (Bruge *et al.*, 2016; Guisan & Zimmermann, 2000; Sakamoto *et al.*, 1986).

a. **Model I: Presence/absence (PA) model**

   The first step is to fit the presence/(pseudo)absence (PA) model to the species occurrence assuming a binomial error distribution with a logit link function.

b. **Model II: Abundance (AB) model**

   The second step is to fit the abundance model (AB) for non-zero observations using the log-transformed abundance as a response variable assuming Gaussian error distribution and identity link. In fishery catch data, Catch-Per-Unit-Effort (CPUE) has been used as a proxy of species abundance.

c. **Final model:**

   The expected abundance (of CPUE) is calculated as the product of the first and second models (PA * AB) after back-transforming the logarithm from the abundance model to the original abundance (or CPUE) scale.

iii) **Habitat-suitability maps:** Habitat preference models are plotted to visually analyze the accuracy of the distribution obtained comparing it with other studies. Model results are represented in the geographical space i.e. the habitat suitability map. In this two-step framework, there are two model outputs; binary results where sites are classified as presences or absence and continuous results where a probability of occurrence is given.

iv) **Model evaluation:** The presence/(pseudo)absence model was validated using the cross-validation method (Burnham & Anderson, 2003), with k-fold equally sized sub-datasets (Hijmans *et al.*, 2013). For instance, k = 5, which is 80% of randomly selected observations to validate the fit of the remaining (i.e., 20%). We followed the two threshold selection criteria of Jiménez-Valverde and Lobo (2007) to convert the species probability of presence to either presence (above the assigned value) or absence (below the threshold). The first criteria selected the threshold for which the sensitivity (true predicted presences) was equal to the specificity (true predicted absences). The second criteria followed the maximization of the sensitivity plus specificity. The confusion matrix accuracy assessment (VanDerWal *et al.*, 2012) is used to evaluate how reasonable was the discrimination of the presences and absences in the PA model. Area under the curve (AUC) values range between 0.5 (random sorting) and 1 (perfect discrimination) and is estimated over the presences and absences estimated by the model and the presences and pseudo-absences randomly generated. Accuracy in the abundance model is calculated by comparing predictions with observations using the *R*-squared value and contrasted with the overall explained deviance. A large difference between both values would indicate overfitting (Villarino *et al.*, 2015).

v) **Model projection:** To estimate the future impact of climate change on fish occurrence and relative abundance, GAM projections for the mid and the end-of-the-21st-century were compared with predictions for the reference period (present).

0.4.2. SS-DBEM

This modeling approach which integrates the species based Dynamic Bioclimatic Envelope Model (DBEM) (Cheung *et al.*, 2008a; Cheung *et al.*, 2011; Cheung *et al.*, 2008b; Cheung *et al.*, 2009a; Cheung *et al.*, 2013b; Cheung *et al.*, 2016; Cheung *et al.*, 2009b) with the size-spectrum approach (SS) (Jennings & Blanchard, 2004; Jennings & Collingridge, 2015; Jennings *et al.*, 2008) (hereafter called SS-DBEM) was firstly developed by Fernandes *et al.* (2013). This approach provided spatially and temporally resolved predictions of changes in species' size, abundance and catch potential with consideration of population dynamics, dispersal (larval and adults) and ecophysiology (Cheung *et al.*, 2008a; Cheung *et al.*, 2011; Cheung *et al.*, 2008b; Cheung *et al.*, 2009a; Cheung *et al.*, 2013b) and account for the effects of ecological interactions which determines resource limits in a given geographical area and, therefore, the biomass of that species that can be supported in this area (**Figure 0.11**). The new algorithm developed describe the resource competition between different species co-occurring in a cell by comparing the energy (in biomass) that can be supported in the cell (estimated with the SS model) with the energy demanded by the species predicted to inhabit the given cell (estimated with the DBEM model) (Fernandes *et al.*, 2013). The algorithm is divided into a first initialization stage where competition parameters are estimated; and a recurrent stage where the competition parameters are used to resolve conflicts between energy (biomass) demands and biomass that can be supported.

Size-based equilibrium model uses established principles in macroecology, life history theory and food web ecology to predict total fish abundance, production, distribution and size structure of target species in an unexploited ecosystem (Jennings & Blanchard, 2004; Jennings & Collingridge, 2015; Jennings *et al.*, 2008). Macroecology studies the relationship between organisms and their environment at large spatial and temporal scales, such as the pattern of abundance, distribution, and diversity of species (Brown, 1995; Gaston & Blackburn, 2000; Gaston & Blackburn, 2003). The energy flux rates and magnitudes from primary producers to consumers depend on primary production, transfer efficiency, predator and prey body mass and temperature (Jennings & Collingridge, 2015). Developed by Jennings *et al.* (2008) and improved by Jennings and Collingridge (2015) the size spectrum model estimates numbers and biomass of species in the water column from the surface to the euphotic depth, or the mixed layer depth if this is deeper.

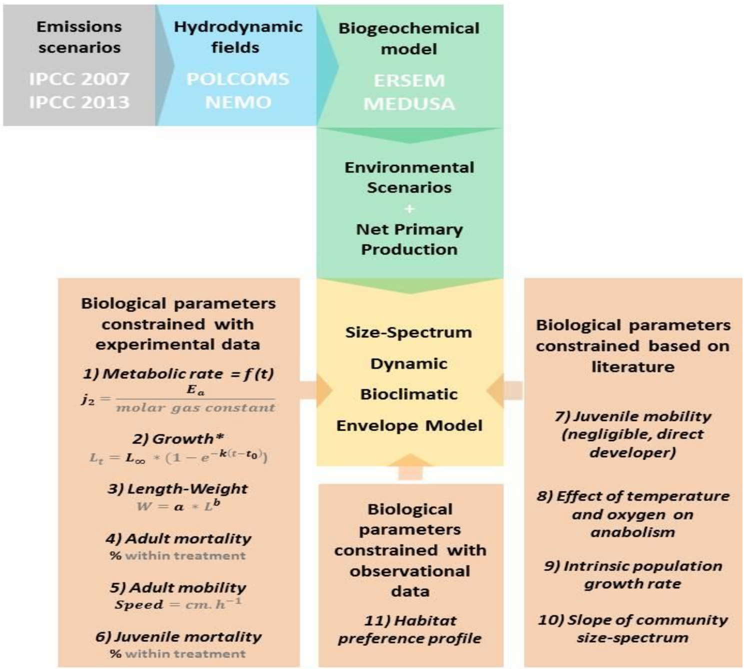


Figure 0.11: Schematic diagram of the SS-DBEM structure, indicating which parameters were estimated based on experimental and observational data, in the present study. Based on Fernandes et al. (2013) and Cheung et al. (2011). Source from the supplementary material of Queirós et al. (2015).

The length of food chains (the number of steps between prey and predator) increases with higher smaller phytoplankton abundance and therefore, carbon export from surface waters decreases. The proportion of primary production available to support consumers at any trophic level is determined by transfer efficiency. The model has been improved to include the effects of varying primary production and temperature on abundance and rates, then, it well suited because it generalizes food web processes with size-based predator-prey interactions that lead to growth and mortality and can be used to assess the effects of additional mortality (such as fishing) on the food web.

The dynamic bioclimatic envelope model (DBEM), developed by Cheung *et al.* (2008b) and later improved (Cheung *et al.*, 2011) and applied (Cheung *et al.*, 2019; Cheung *et al.*, 2009a; Cheung *et al.*, 2013a; Cheung *et al.*, 2009b; Fernandes *et al.*, 2013) was divided in three steps: (i) predict the current distribution of species of interest; (ii) project future changes in distribution and relative abundance of the species; and (iii) project future changes in potential catch. The initial distribution used on DBEM as those used by the Sea Around Us Project (http://www.seaaroundus.org/topic/species/default.aspx) derived from an algorithm of Close *et al.* (2006). Data were obtained from public databases, mainly FishBase (www.fishbase .org) and SeaLifeBase (www.sealifebase.org) and estimates of the relative abundance of a species on a 30’ latitude x 30’ longitude grid of the world ocean were obtained. Future species distributions were projected simulating changes in the environmental parameters such as temperature, oxygen content (represented by O_2 concentration), and pH (represented by H^+ concentration) which affect the growth of marine fish and invertebrates. The model algorithm was derived from the von Bertalanffy growth function (VBGF; von Bertalanffy (1951)) and depends on the difference between available oxygen and oxygen demand for maintenance. The estimated catch potential (both in the past and in the future) is the result of simulating the exploitation of the resource at an ideal Maximum Sustainable Yield (MSY) level, taking into consideration the change in ecosystem productivity over time (and forced by the climate change in the future) (Cheung *et al.*, 2018). The MSY is defined as the highest average theoretical equilibrium catch that can be continuously taken from a stock under average environmental conditions (Hilborn & Walters, 1992).

0.5. Detection and attribution of shift causes

Historical trend analysis of species distribution might be limited due to the nature of the raw data used (Chust *et al.*, 2014b). When data have non-homogeneous spatial and temporal coverage (e.g. most fishing data, historical collections), the conventional estimators such as the abundance-weighted average (AWA) indices (e.g. CoG or distribution boundaries), may confound changes in the distribution of sampling effort with changes in species distribution (Thorson *et al.*, 2016). Data from research surveys are considered more homogeneous and consistent to use in historical trend analysis. Nevertheless, in some cases, scientific survey data do not have homogeneous spatio-temporal coverage (e.g. Bruge *et al.* (2016), Chust *et al.* (2014b)), due to sampling distribution variations from year to year. Attempts have been made to correct this bias, and an example applied to copepods can be found in Chust *et al.* (2014b). Using simulated data, Thorson et al. (2016) formalized the approach and proposed to calculate the shift distribution estimators using a spatio-temporal model (STM) to reconstruct the species distribution instead of observed abundance data. The STM approach estimates the expected density of the population within the spatial domain based on available data and as a function of the spatial (longitude and latitude) and temporal (year and season) factors (Thorson *et al.*, 2016). This approach has several benefits in comparison with conventional estimations of raw data as it allows the use of different sources of data and can account for changes in spatial distribution of the sampling effort (Thorson *et al.*, 2016). This methodology allows to disentangle shifts due to an heterogeneous sampling or sampling bias and the correct attribution of the changes associated with a changing climate from other drivers is important for the implementation of effective harvest and management strategies and for addressing associated socio-economic impacts, mainly in countries which are highly dependent on oceanic resources (Hobday & Evans, 2013).

0.6. Hypothesis and objectives

This study aims to gain an understanding of the global biogeographical patterns of marine communities, mainly pelagic species such as anchovy or top predators (tuna, swordfish) and its response to a changing climate.

The **working hypothesis** has been defined as:

> ***"Climate change and ocean warming affect marine species and it is expected to continue impacting in the future. Disturbances in the habitat of pelagic species provoke poleward shifts, changes in abundance, phenological changes of their biological processes and decreasing body size. These changes affect the fisheries of coastal countries, the economy, and animal protein supply".***

Due to the relevance of studied target species (both ecologically and economically), information about past trends and future projections are important. Historical trends (in spatial distribution and abundance) have been analyzed, as well as future changes have been projected. Overall, the Ph.D. thesis aimed to answer the following **questions**:

1- How climate change has affected the marine pelagic fish species distribution and abundance in the last decades?

2- Which are the suitable habitats of anchovy, tuna, and swordfish?

3- How climate change is expected to affect the marine pelagic fish species distribution and abundance in the future under climate change scenarios?

4- How the tuna abundance and distribution changes could affect the catches of different countries?

5- Has climate change affected the body size of top predators and how is it going to affect in the future?

In order to test the working hypothesis and answer previous questions, the main **objectives** of this Ph.D. thesis were to:

1- Develop marine pelagic fish species distribution models.
2- Analyze historical trends in marine pelagic fish species distribution and abundance through the last decades using long time-series.
3- Analyze the main potential drivers triggering marine species shifts.
4- Develop a methodological framework to disentangle the reasons behind those historical trends.
5- Project future environmental conditions and analyze expected changes in marine pelagic fish species distribution and abundance.
6- Estimate impacts in main commercial tuna species catches inside coastal countries Exclusive Economic Zones.
7- Use the ecosystem-based model to predict future distribution and abundance of top predators and their changes in size due to fishing effort and climate change.

To address these objectives, and analyze climate change impacts over pelagic species, different models and statistical tools have been applied in both, local and global datasets. Species distribution models also called habitat or niche-based models have been developed associating known presence locations of the target species with the characteristics of their environment to predict their potential geographical distribution. Habitat models are usually multivariate and are based on the ecological niche concept of Hutchinson (1957) which defined the niche as the variety of environmental conditions for which the organism is best suited, and the competition is minimized.

0.7. Structure of the thesis

Beyond this **General Introduction** in the topic which aimed to provide some insights on the concepts that will be discussed during the chapters, the main body of the thesis is structured in 4 chapters (**Chapters 1-4**) followed by a **General Discussion** and **Conclusions**.

In the **General Introduction**, the state of the art of physical changes due to anthropogenic climate change and impacts on pelagic species life traits, distribution, abundance, and fisheries has been developed in order to understand the context where this Ph.D. is framed. Subsequently, the studies conducted in order to answer the above mentioned overarching questions and to achieve the main objectives are presented. Although chapters are related, these specific investigations are divided into four chapters and comprise the main body of the Ph.D. thesis. Following the format of the scientific publications, each chapter is formed by an introduction to contextualize the research, material and methods used to achieve the objectives followed by the results, a brief discussion, and conclusions. The main subjects of each chapter are described below:

Chapter 1 examines changes in historical trends and future distribution of anchovy spawning in the Bay of Biscay due to climate change. For that purpose, the historical evolution of the anchovy spawning was analyzed using species distribution models and spatio-temporal reconstruction approaches. Phenological changes were also analyzed using the gonadosomatic index, which is considered a reliable proxy of spawning time. Future distribution of anchovy under the RCP8.5 climate change scenario was also developed. The results obtained added valuable knowledge about habitat preferences of Bay of Biscay anchovy's population and expected sea surface warming impacts mainly in spawning.

Chapter 2 assesses the large-scale distribution of tuna species in a warming ocean. Despite the relevance of tuna in the global economy and the future supply of food, a global-scale study addressing the historical changes of the tuna habitat and providing future distributions based on climate change projections for all major commercial species is lacking. In this chapter, the effects of environmental conditions on the worldwide distribution of six tuna species between 1958 and 2004 and projected changes by mid and end-of-the-century under climate change were investigated. Changes in tuna habitat within countries' exclusive economic zones (EEZ) were also analyzed to assess the potential impact for those countries. The findings may be relevant for tuna stock management and an important contribution to understanding the potential impacts of climate change on fisheries and fishing nations.

Chapter 3 explores the possible drivers behind species historical shifts. A new framework to disentangle the reasons behind species distribution changes is described, which may be applied to any species. In this particular case, the framework was tested with the worldwide distributed main billfish species, the swordfish. This chapter helps to elucidate different drivers affecting species and to avoid wrong attributions.

Chapter 4 described changes in the top predator community under different climate and fishing effort scenarios. The tool to address this study is the ecosystem-based model SS-DBEM which includes population dynamics, dispersal (larval and adults) and ecophysiology to provide spatially and temporally resolved predictions of changes in species' size, abundance and catch potential, therefore, the biomass of that species that can be supported in this area. Changes in species sizes and abundance were analyzed in both, historical and future periods and a generalized decrease in body size was found for tuna, billfish, and direct competitors. Body size of the largest fishes decreases with to highest fishing pressure and worse climatic scenarios.

After describing the four chapters, a discussion together with the limitations has been developed in the **General discussion** section, followed by the main of this Ph.D. thesis summarized in the **General conclusions** section. In the **References** section, all studies and researches references cited along all this Ph.D. thesis are provided.

CHAPTER 1

Historical trends and future distribution of anchovy spawning the Bay of Biscay

1. CHAPTER 1

Historical trends and future distribution of anchovy spawning in the Bay of Biscay

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Historical trends and future distribution of anchovy spawning in the Bay of Biscay

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1.1. Introduction

Global climate change is unequivocal and since 1950, atmospheric and oceanic temperatures have risen steadily (IPCC, 2013; Rhein *et al.*, 2013). Temperatures in the upper layers of the ocean (0-75 m) have shown an increase of 0.11 ± 0.02º C per decade over the period 1971 to 2010, causing an increase of 4% in stratification (IPCC, 2013; Rhein *et al.*, 2013). Climate change has a significant impact across all marine ecosystems, latitudes and trophic levels (Cheung *et al.*, 2013b; Poloczanska *et al.*, 2013). As a response to ocean warming, species shift biogeographic ranges and/or alter phenology (seasonal biological phenomena in relation to climatic conditions) to accommodate temperature changes and maintain their thermal niches (Poloczanska *et al.*, 2013; Richardson *et al.*, 2012). A poleward migration of geographical boundaries of different marine species is expected with an increase in the catch potential in high latitudes and a decrease in many tropical and subtropical regions (Cheung *et al.*, 2009b). Some warm-water fish species have been reported to be expanding their northern distribution limits and accelerating the general latitudinal movement detected for past decades, e.g. Atlantic mackerel (*Scomber scombrus*), Atlantic cod (*Gadus morhua*), bib (*Trisopterus luscus*), blue whiting (*Micromesistius poutassou*), Norway pout (*Trisopterus esmarkii*) and scaldfish (*Arnoglossus laterna*) (Beare *et al.*, 2004; Bruge *et al.*, 2016; Lenoir *et al.*, 2011; Montero-Serra *et al.*, 2015; Perry *et al.*, 2005). Substantial local population extinctions are projected by 2050 under climate change scenarios, particularly in subpolar and tropical regions and semi-enclosed seas such as the Mediterranean Sea (Cheung *et al.*, 2009b).

Small pelagic fish dynamics are often related to environmental fluctuations (Borja *et al.*, 2008; Checkley *et al.*, 2009) and respond rapidly to climate variability (Montero-Serra *et al.*, 2015). Therefore, they can be good biological indicators of climate-driven changes in marine ecosystems (Peck *et al.*, 2013). The European anchovy (*Engraulis encrasicolus,* Linnaeus 1758) is a small pelagic fish with fast growth, high mortality and fecundity (Motos, 1996) and a short life cycle with a maximum lifespan of 4 years (Motos, 1996; Petitgas *et al.*, 2012; Uriarte *et al.*, 2016). This species is distributed across the eastern North and Central Atlantic and range from NW Africa in the south to the North Sea and the Baltic Sea in the north including Mediterranean Sea, Black Sea and Azov Sea (Reid, 1966). European anchovy presents a wide distribution but with differentiated populations often related to local features such as upwellings, bays and estuaries (Zarraonaindia *et al.*, 2012). One of these populations is located in the Bay of Biscay (BB). This anchovy population selects stable habitats related to river plumes, with the Adour and Gironde estuary zones constituting key areas (Koutsikopoulos & Le Cann, 1996; Sagarminaga *et al.*, 2004), and shelf edge fronts and oceanic eddies due to their higher primary production (Motos *et al.*, 1996). The anchovy spawning peak generally occurs during a period of rapid environmental changes. This peak can be initiated by changes in daylight, changes in winds, decreases in freshwater runoff, or warming of atmospheric and seawater temperatures (which vary between 12ºC at the end of winter and 20ºC at the beginning of summer in the BB) (Koutsikopoulos & Le Cann, 1996; Sanz & Uriarte, 1989). The spawning season occurs between March and August (Motos, 1996) starting in the south-east and moving gradually north- and westward (Planque *et al.*, 2007). There are two different spawning areas: coastal and oceanic (Motos, 1996; Uriarte *et al.*, 1996). Costal spawning areas are characterized by high primary production, strong stratification, and stability influenced by river plumes. Anchovy spawning in these areas are small and mostly of 1-year-old (Ibaibarriaga *et al.*, 2013; Sagarminaga *et al.*, 2004; Uriarte *et al.*, 1996). The oceanic spawning areas, which are along the continental slope and have no influence of continental freshwaters (Uriarte *et al.*, 1996), are used by bigger and older anchovies to spawn (Motos, 1996; Uriarte *et al.*, 1996). The spawning timing is different for young and adults. In April, the larger/older anchovy starts to spawn and it is followed by smaller/younger anchovy which prefers slightly higher temperature (Lucio & Uriarte, 1990). The peak of the spawning activity (when most fish present are actively spawning) occurs in May (Sanz & Uriarte, 1989), and it is associated with temperature between 14 and 18ºC (Montero-Serra *et al.*, 2015; Motos *et al.*, 1996; Portner & Peck, 2010; Sagarminaga *et al.*, 2004).

In the Bay of Biscay, the sea surface temperature warmed at a rate of 0.26 ± 0.03ºC per decade between 1982 and 2014 (Costoya *et al.*, 2015), having differential seasonal rates of changing (faster decrease from September to November than warming from April to June). The duration of the warm season (period between first and last day in which sea surface temperature exceeded the 75th percentile temperature) increased between 6 and 14 days per decade on average (Costoya *et al.*, 2015). As a response to this sea warming, changes in some fish abundance were observed during the last decade of the 20th century and the first decade of the 21st century (Poulard & Blanchard, 2005), but have not been reported for the BB anchovy population. We hypothesize that changes in phenology and abundance of the BB anchovy population might have occurred in the last few decades or are expected for the future in response to these environmental variations.

The main objective of this study is to assess the effect of recent sea warming and the impact of climate change on the spatio-temporal spawning distribution of anchovy in the Bay of Biscay. Specific objectives are: 1) to analyze trends in the distribution and phenology of the anchovy in the Bay of Biscay and to identify the main ocean-climatic factors determining the spawning of this species; 2) to build a species distribution model of anchovy egg abundance based on its ecological niche; and 3) to project the distribution model under climate change scenarios to assess expected changes in its abundance.

1.2. Material and methods

1.2.1. Study zone

The study zone is the Bay of Biscay, an open oceanic bay located in the northeast of the Atlantic Ocean (**Figure 1.1**). It has a complex hydrological regime and weather pattern, both of which show spatial and temporal heterogeneities (Costoya *et al.*, 2015; Koutsikopoulos & Le Cann, 1996; Valencia *et al.*, 2004). The BB is characterized by an average weak ocean circulation, the presence of cyclonic and anticyclonic eddies, a poleward flow along slope driven by wind and density gradients, tidally induced currents over the continental shelf and freshwater runoff and river plumes formed in the mouth of the Gironde and Loire estuaries (Koutsikopoulos & Le Cann, 1996). The sea surface temperature shows a latitudinal gradient during the summer period and important freshwater runoffs from the Adour and Gironde estuaries (Koutsikopoulos & Le Cann, 1996; Valencia *et al.*, 2004).

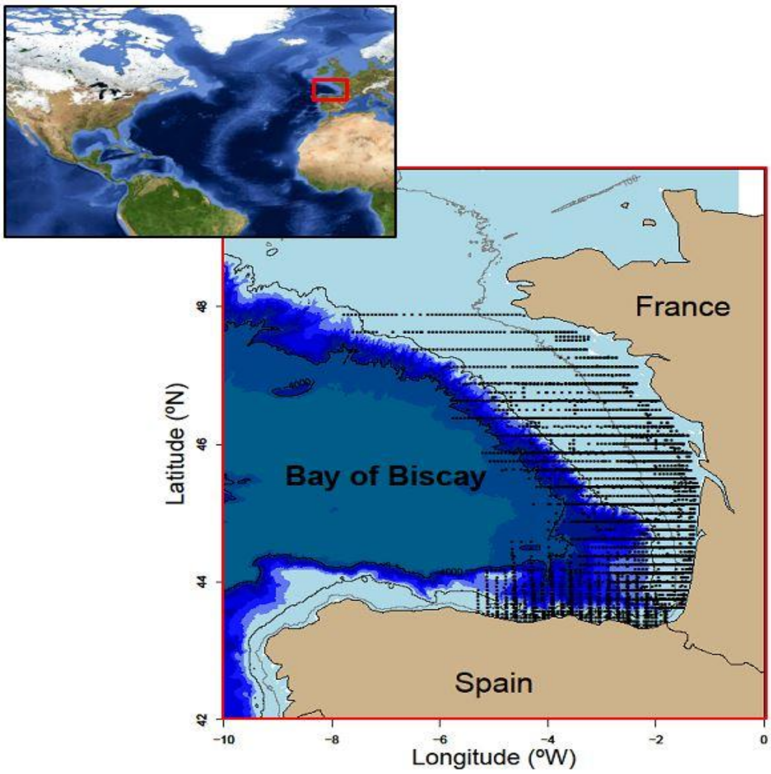


Figure 1.1: Study area and stations of the vertical hauls (PairoVET) that could be performed during the surveys (Santos et al., 2016). Bathymetry with 100, 200 and 4000 m isobaths are also represented.

1.2.2. Biological data

Two sources of data for the European anchovy population of the Bay of Biscay were used in this study. On the one hand, egg and adult data have been collected annually during the BIOMAN surveys (BIOMass of Anchovy, Santos *et al.* (2016)) between 1989 and 2015 (**Figure 1.2**). The objective of these surveys is the estimation of the spawning stock biomass by applying the Daily Egg Production Method (DEPM) (Lasker, 1985) and improving the knowledge of the spawning environment (Santos *et al.*, 2016). On the other hand, additional adult biological samples have been collected annually from the commercial catches landed in the Basque Country during the fishing season from the same time series.

1.2.2.1. Anchovy eggs data

BIOMAN surveys were carried out between May and the first half of June, to coincide with the peak of the spawning period. The area covered by BIOMAN was the wide French continental shelf-oriented S-N from 43.30 to 47.88º N, and the narrow Spanish shelf-oriented E-W from 1.22 to 7.78º W which corresponds to the main spawning area of anchovy (**Figure 1.1**). Limits of the sampling zone varied between years and the criteria for defining them is a continued absence of eggs in consecutive sampling stations. Sampling stations were located every 3 nautical miles (nm) along transects perpendicular to the coast and separated 15 nm. The adaptive sampling method is helped by the use of near-real-time sampling with CUFES (Continuous Underway Fish Egg Sampler, Checkley *et al.* (1997)) explained in Santos *et al.* (2016) and was routinely applied all along vessel tracks every 1.5 miles at 3 m depth aside from the deck. In areas of high egg abundances or where historically high egg production is found (as in the river plumes), additional transects separated by 7.5 nm are completed. This leads to gain in precision (i.e. reducing variance) regarding egg counts and more detailed egg spatial distribution. Following the same criteria, distance between stations along transects changed from 3 to 6 nm when eggs were absent, particularly when moving towards offshore areas. A vertical plankton haul was used for egg sampling, using a CALVET type "PairoVET" net with a 150 µm mesh (Smith *et al.*, 1985). The maximum sampled depth was 100 m or 5 m above the sea-bed in shallower waters. The net was equipped with digital flowmeters (G.O. 2030) for determining the amount of water passing through the net (Santos *et al.*, 2011). A total of 13,732 PairoVET hauls were conducted between 1989 and 2015. At the end of the collection, plankton samples were preserved immediately in 4 % formaldehyde buffered with sodium tetraborate and after 6 h fixation, all eggs were sorted out on board. Anchovy eggs, which are easily distinguished by their characteristic oval shape, were identified and counted. The number of eggs per haul was converted to density (eggs m^{-2}) using flowmeter readings and maximum sampled depth (Smith & Richardson, 1977).

In order to study the spatial and temporal distribution of anchovy eggs, abundance values for each 0.1º x 0.1º resolution squares were estimated. For that purpose, the arithmetic means of values for each square were calculated. The data were analyzed in two forms: Presence/Absence (PA, 1=presence, 0=absence, binomial form) and Density (ED, eggs m^{-2}), with logarithmic transformation.

1.2.2.2. Anchovy adult data

The information on adult parameters was provided from: i) pelagic trawls carried at the same time as the anchovy egg sampling during BIOMAN surveys, with size, weight, sex and age data recorded between 1990 and 2014, with gaps in 1993 and 1996, and ii) ANEBIO (ANchovy BIOlogical data) dataset, collected using samples of commercial anchovy catches from which length, weight, gonadal weight, sex, maturation, and age were recorded between 1986 and 2015 (without information for 2004 and between 2007 to 2009 due to the closure of the fishery) (**Figure 1.2**).

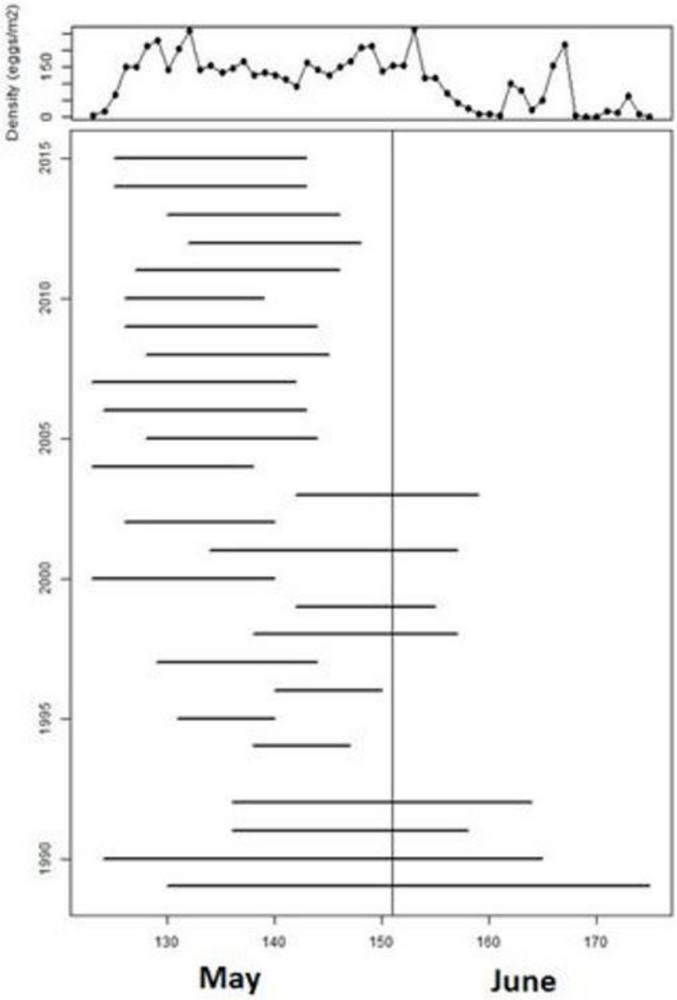


Figure 1.2: *BIOMAN survey times for different years and egg density (egg m-2) average for each Day of the Year.*

1.2.3. Environmental data

Oceanographic data from BIOMAN sampled stations were collected using a CTD (Conductivity, Temperature, and Density) profiler. The variables used for modeling were sea surface temperature (SST, which was recorded at each station), and sea surface salinity (SSS, recorded at every third station in the first year and every station thereafter). A reanalysis of environmental data was also used to extrapolate the model to all the Bay of Biscay. With those environmental data, we were able to model with higher spatial resolution in shallow coastal waters, where global climate models are inadequate (Richardson *et al.*, 2012). The Atlantic-Iberian Biscay Irish Ocean Physics Reanalysis data (a. k. a. NEMO reanalysis) use the NEMO model for the period 2002-2014 with a 1/12º spatial and monthly temporal resolution. The variables used were SST, SSS, and Mixed Layer Depth (MLD) averages for May and June. Monthly means and standard deviations were calculated for BIOMAN and NEMO reanalysis data to estimate the variation between the two sources and ensure that we were not introducing noise in the model (**S. Table 1.1** in **Appendix A**). BIOMAN SST and SSS data were used as the environmental conditions of the spawning period peak to build the model. For the projection of the Bay of Biscay, we used the NEMO reanalysis environmental data. May and June averaged chlorophyll-a (Chl-a) concentrations were used as a proxy for phytoplankton abundance. These data were sourced from various satellite sensor data sets (SeaWIFS, MODIS, MERIS, and VIIRS) between 2002 and 2014 (available from GlobColour at http://hermes.acri.fr/) and with 4 km spatial resolution. Bathymetry data from the NOAA database was extracted using the '*marmap'* R package (Pante & Simon-Bouhet, 2013) with 0.1º x 0.1º spatial resolution.

NCEP Global Ocean Data Assimilation System (GODAS) data for a 0.333º x 1º latitude-longitude grid between 1989 and 2015 were also used to relate with biological indices. Bilinear interpolation was performed to obtain a higher resolution grid (0.5º x 0.5º) (Bruge *et al.*, 2016).

1.2.4. Gonadosomatic index (GSI) and the yearly spawning peak

The gonadosomatic index (GSI) is an indirect approach to evaluate the reproductive status (Brewer *et al.*, 2008) and has been used as an indicator of reproductive activity and peak spawning periods (Kreiner *et al.*, 2001). GSI, a ratio of gonad weight to total body weight, was calculated using the equation of Bougis (1952):

$$GSI = \frac{Gonad\ weight}{Total\ body\ weight}$$

The GSI was computed only for female individuals collected from BIOMAN and ANEBIO described above and some measurements were removed based on the maximum values of length reported in Fishbase (200 mm, http://www.fishbase.org/). Data for January, February, October, November, and December were not included in GSI trend analysis due to the low number of samples. Data from the year 1986 were also discarded because of the scarcity of samples. The logarithm of the gonadosomatic index (GSI) was modeled by means of a Generalized Additive Model (GAM, Wood (2017)) as a function of an interaction between the day of year (D) and year (Y) (to be able to analyze the phenology changes throughout years) and total anchovy length (L) (due to the correlation between the size and spawning capacity of the anchovies):

$$\log(GSI) \sim te(D, Y) + s(L),$$

where *te* is a tensor product that represents the interaction between D and Y which is forced to the cyclic for D, and *s* is a smooth function. We used the 'mgcv' package implemented in the R language (Wood, 2017) for this purpose. Using predicted GSI data from the model, the spawning peak was calculated as the day of the year with the maximum GSI value and the duration was estimated as the time past between the days of the year when the fitted GSI values of the curve exceeds 0.036, a threshold for which individual anchovy females are mature with a 99% certainty (from an *ad hoc* maturity logistic model fitted to the DEPM survey data based on histological analysis). The spawning peak, duration of the spawning and the maximum GSI value trends were evaluated along time, excluding years without monthly data, i.e. 1999, 2000 and 2007. The correlation with different environmental variables that could potentially affect the timing of the spawning peak was analyzed. Yearly anomalies for the average of the months previous to spawning peak (February-May) were estimated for SST, SSS, MLD, and Chl-a as a proxy of phytoplankton.

1.2.5. Spawning distribution models

Anchovy egg distribution in the Bay of Biscay was modeled using Generalized Additive Models (GAMs) based on the method described in Bruge *et al.* (2016) for mackerel (*Scomber scombrus*) in the North-East Atlantic. Egg Presence/Absence (PA) and Density (ED, for non-zero observations) were modeled separately and subsequently combined following the methodology described in Borchers *et al.* (1997) for horse mackerel (*Trachurus trachurus*):

1. The first step was to fit the PA model using the presence/absence of anchovy eggs as a response variable and a binomial error distribution with a logit link function. *Dredge* function of 'MuMIn' R-package was used to generate a set of models with combinations (subsets) of terms in the global model (Barton, 2016), with rules for model inclusion based on lowest AIC (Akaike Information Criterion), which means a better fit (Bruge *et al.*, 2016; Guisan & Zimmermann, 2000; Sakamoto *et al.*, 1986). The confusion matrix accuracy assessment (VanDerWal *et al.*, 2012) was also used to evaluate how reasonable was the discrimination of the presences from the absences through sensitivity (true predicted presences) and specificity (true predicted absences) estimation. The occurrence probability was converted to Pres/Abs by adjusting the threshold obtained using an optimization method based on the maximization of sensitivity plus specificity criteria (Jiménez-Valverde & Lobo, 2007). Overall accuracy provides the proportion of either true positive or true negative predictions.
2. The second step was to fit the egg density model using log-transformed ED as a response variable and Gaussian error distribution only on squares where there were anchovy eggs. We used the same variable predictors selected in the PA model. Predicted ED was conserved in the final model only if it was predicted as a presence in the PA model. In the case of the PA model predicting the absence of eggs, ED would be 0.

3. The last step was the validation of the constructed presence/absence model using the cross-validation resampling method (Burnham & Anderson, 2003). This method is based on the division of datasets (in *k* equally sized groups following the *k*-fold partitioning method (Hijmans *et al.*, 2013)) which are used to fit the model and the subsequent validation. We used *k*=5 in order to use 80% of randomly selected observations to fit the model and the remaining 20% to validate it. Accuracy, which provides the proportion of either true positive or true negative predictions, was calculated by comparing predictions against observations with the squared-R. This value was compared with the overall explained deviance and a large difference between both values would indicate overfitting.

1.2.5.1. Spawning reconstruction model (1989-2015)

In order to analyze the trends between 1989 and 2015 in spawning and disentangle the potential drivers, a spawning distribution model using only spatio-temporal variables was built following the steps defined previously. The spawning reconstruction model was built in order to avoid bias in species distribution due to a non-uniform distribution of sampling in space and time (Bruge *et al.*, 2016; Chust *et al.*, 2014a). The predictors used were the year (to reconstruct the temporal pattern), log-transformed bathymetry (LogBathy, as a descriptor of geographical attachment to the continental shelf) and latitude (as the spatial term) (Bruge *et al.*, 2016). The population center of gravity (as the mean location of the individuals that compose the population (Bez & Rivoirard, 2001), in this case of the total egg density) and 5% and 95% percentiles (P5 and P95, estimated as weighted quantiles) were calculated in order to identify the main drivers on the position of the gravity center. P95 gives essential information on the anchovy egg distribution because the Bay of Biscay is limited by land in the south and east. SST trends for May and June and the average of both months (as the proxy of the temperature in the peak of spawning) were also evaluated, considering the averaged boundaries of the spawning area. Another driver analyzed was density-dependent population dynamics. To address this, the correlation between the gravity center latitude and the total daily egg production estimated from the DEPM (Santos *et al.*, 2016) for each year was calculated.

1.2.5.2. Spawning niche model

With the aim to analyze the current spawning niche of the Bay of Biscay anchovy population, a model including environmental variables was built following the same steps as in the reconstruction model. Individual GAMs were previously built in order to analyze the response curves and the deviance explained of the anchovy eggs by different environmental variables (Thuiller *et al.* (2004)). GAMs were built for BIOMAN and NEMO reanalysis-SST and SSS (for which each point we have a measure of the variable), for NEMO reanalysis-MLD, for Hermes chlorophyll-a concentration and NOAA bathymetry, as well as log-transformed data for the last two variables (LogChla and LogBathy). In order to fit unimodal response curves and avoid overfitting (according to the ecological niche concept), degrees of smoothness ("k" values) were set equal or less than 3 (Burnham & Anderson, 2003; Hastie & Tibshirani, 1990). BIOMAN environmental data were used for building individual GAM-s between anchovy eggs densities and environmental variables, and for the validation of the model. For the extrapolation of the model, NEMO reanalysis environmental data were used. Raw data for anchovy eggs were also represented in order to compare modeled and observed egg distribution patterns.

1.2.6. Future projections under climate change scenarios

Using the spawning distribution model built in the previous step, future projections for the anchovy population were conducted for the mid (2040-2059) and the end-of-the-21st-century (2080-2099) under the RCP8.5 scenario of the Fifth Assessment Report of the Intergovernmental Panel on Climate Change (IPCC5). RCPs (Representative Concentration Pathways) are greenhouse gas concentration trajectories. The RCP8.5 is the highest-carbon-emission scenario (936 CO_2 ppm by the end of the century), which prescribes a continuous increase in greenhouse emissions that results in a 2.6°C to 4.8°C global atmospheric warming and a ~2ºC ocean surface warming (top 100 m) by the year 2100 (IPCC, 2014e). Projections of oceanographic variables (SST, SSS, and MLD) under RCP8.5 were extracted from two sources: 1) the Max Planck Institute's Ocean Circulation Model (MPIOM) with a 0.5º x 0.5º spatial and monthly temporal resolution (**Table 1.1**), 2) the average of 16 IPCC5 models that contain a biological module (hereinafter Ensemble) with a mean ~1º spatial resolution (Cabré *et al.*, 2015). For the IPCC Ensemble, only end-of-the-century projections are studied, e.g. differences between years (2080-2099) and (1980-1999). Note that the resolution along coastal zones is low in both projections. The global sea surface temperature increase calculated as the average of these 16 IPCC5 climate models is 2.51±0.59ºC (Cabré *et al.*, 2015). Chl-a was not used as a variable in future anchovy egg modeling because of the low correspondence between its distribution in biogeochemical models at the reference period and that of NCEP reanalysis.

The niche-based model used 2006-2020 data as the reference period and 2080-2099 as the end-of-the-century period and 2040-2059 for the mid-century. Future ocean boundary forcings are created by adding a change in different parameters to simulated present-day forcings (Holt *et al.*, 2010; Tinker *et al.*, 2016). Different parametrizations in the formulation of the models could have as a consequence, biases between present climate simulations and reanalysis or observations and also in future climate model simulations (Zahn & von Storch, 2010). Many methods were proposed to overcome this issue, but a common simple method usually used is the so-called "Delta method" (Holt *et al.*, 2010; Zahn & von Storch, 2010), which is based on a constant shift of the mean, maintaining present observations distributions. The expected effect of climate change was calculated as the difference between the averages in 2080-2099 (or 2040-2059) and 2006-2020 for each variable. Subsequently, this average difference was added to each grid cell in the NEMO reanalysis variable. Therefore, future projections of climatology are estimated based on historical climatic conditions (observations between 2002 and 2014) and change signal (delta) as follows:

$$Future\ projections_{(2080-2099)} = Historical\ conditions_{(2002-2014)} + Delta$$

where

$$Delta = RCP8.5_{(2080-2099)} - Reference\ conditions_{(2006-2020)}$$

The spawning niche model was then applied to the reference and the future periods, which were compared by means of a difference between the two periods. Additionally, individual-variable models were conducted in order to analyze which variable triggers the main change in egg density and distribution by the end of the century.

Table 1.1: Different change delta values ± standard deviation estimated for the Bay of Biscay used to get future environmental conditions. SST in ºC, SSS in PSU and MLD in meters.

	Mid-of-the-century (2040-2059)			End-of-the-century (2080-2099)		
	SST	**SSS**	**MLD**	**SST**	**SSS**	**MLD**
MPIOM	0.52±0.28	-0.30±0.13	-7.48±8.31	1.51±0.71	-0.57±0.35	-12.40±12.84
Ensemble				2.27	-0.59	-35.83

1.2.7. Comparison between the Center of Gravity for Past and Future

The CoG was used to evaluate the impacts of climate change on the anchovy spawning distribution. A comparison between the CoG in future projections under RPC8.5 conditions and present was also conducted. Annual latitude and longitude locations of the percentiles 5% (P5) and 95% (P95) of the egg density (ED) were also computed and variation rate was estimated in kilometers per decade. In order to estimate the overall ED, we summed the ED of the whole BB (for both present and future projections) and used it as a proxy of total egg production. Thus, we estimated the ED difference between end-of-the-century conditions and present conditions.

1.3. Results

1.3.1. Changes in spawning between 1987 and 2015

1.3.1.1. Gonadosomatic index and the relationship with environmental variables

The gonadosomatic index showed a rapid increase between March and May and a decrease at a slower rate from May to September (**Figure 1.3**). The peak of spawning was in May with GSI greater than 0.08 (8% of the bodyweight corresponding to gonads), whilst out of the spawning period (i.e. end of August to March), these values did not exceed 2% on average. The fitted GAM of the GSI shows two peaks (around 1993 and 2010) with a general increasing pattern along years (**Figure 1.4**). Yearly predicted GSI curves showed differences between years in both, amplitude and duration (**Figure 1.5**). The peak of the spawning advanced significantly (p-value < 0.0001) at a rate of 5.5 days per decade with the main change between 2003 and 2015 (**Figure 1.6**). The beginning and end of the spawning period also showed changes in time. Until 1998 the spawning period became wider (started earlier and finished later). Then, until 2006 it was reduced up to similar values than the beginning of the series but showed a delay at the end of the spawning period. From 2008 onwards there seemed to be a shift along time, with both the peak and the spawning period occurring earlier. The observed spawning peak occurs before the maximum of temperature and chlorophyll-a (**S. Figure 1.1a, d** in **Appendix A**), after the main salinity peak and before the second one (**S. Figure 1.1b** in **Appendix A**), and after the maximum

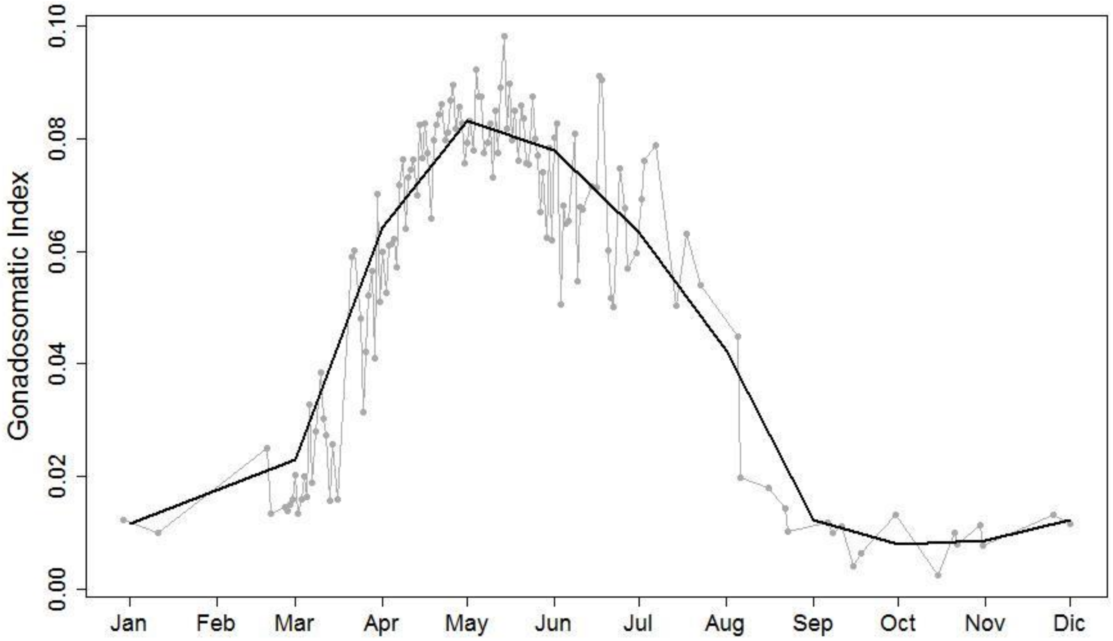


Figure 1.3: Gonadosomatic Index means for each Day of the Year (grey line) and means for months (black line) calculated for time series years (1987-2015).

of MLD (**S. Figure 1.1c** in **Appendix C**). The correlation with a set of environmental variables which could potentially affect the timing of spawning peak, only showed a significant negative correlation with chl-a (p-value = 0.03515) and no correlation with SST (p-value = 0.2478), SSS (p-value = 0.1345) and MLD (p-value = 0.3243). It means that when the anomaly of chlorophyll-a concentration is positive, the spawning peak anomaly is negative and advances on time (occurs earlier in the year).

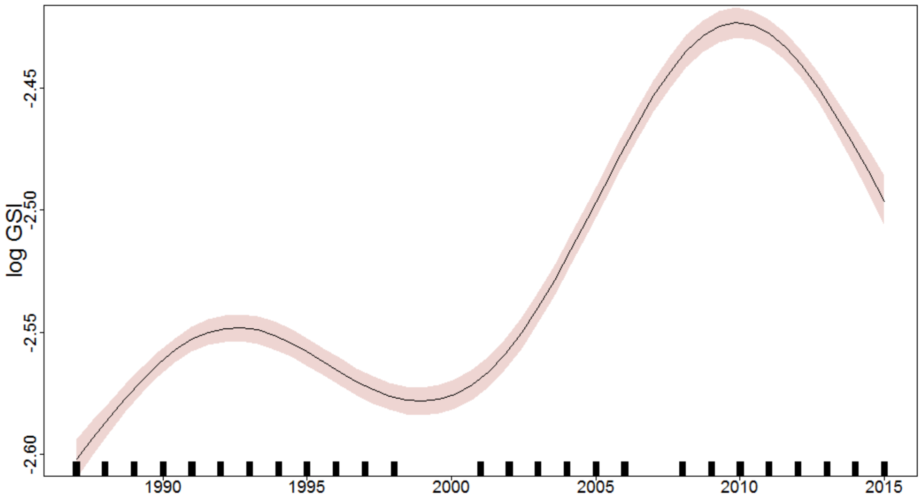


Figure 1.4: Log-transformed GSI response curve through years.

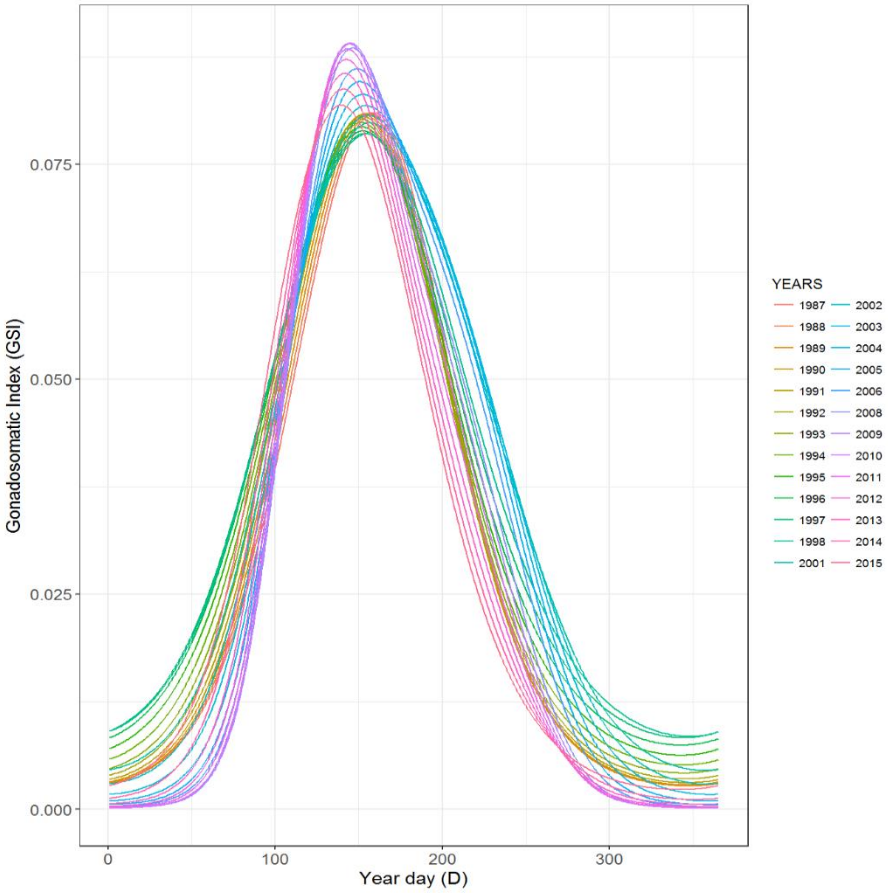


Figure 1.5: Anchovy GSI yearly spawning cycle (GSI per day of the year) along time series (1987-2015).

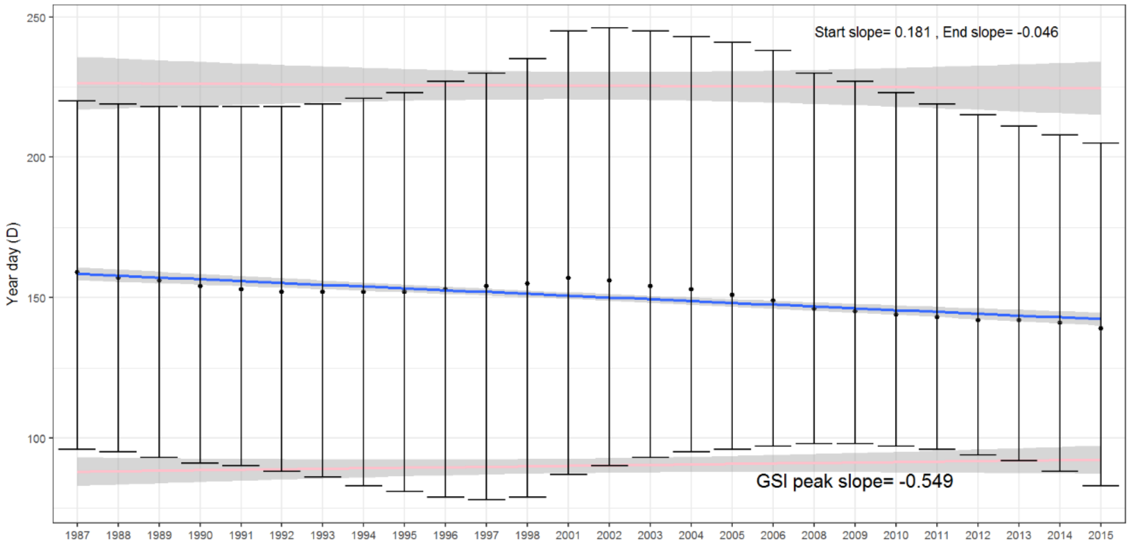


Figure 1.6: Day of the Year when the beginning, the peak and the end of the spawning occur between 1987 and 2015. Smooth curves estimated for the beginning and the end (in pink) and peak (in blue) of the spawning period are also plotted.

1.3.1.2. Spawning reconstruction model (1989-2015)

Total egg production of the BB anchovy showed a large decrease between 2001 and 2005 when the stock collapsed and the fishery was closed (**Figure 1.7**). After that, a rapid recover occurred until 2010, when the fishery was opened again. Total egg production did not show a statistically significant linear trend (p-value=0.4816) from 1989 to 2015. The spawning reconstruction model had AUC (Area Under the Curve), sensitivity and specificity of 0.73, 0.77 and 0.70 respectively. The P95 of the raw ED observations and the spawning spatio-temporal reconstruction model did not change significantly between 1989 and 2015 (p-value = 0.1904 and 0.6427 respectively, **Figure 1.8a**). Sampling effort CoG in 2015 was 70 ± 35 km further north than in 1989 and the north boundary (P95), 113 ± 56 km (**Figure 1.8b**). The sampling effort CoG shift was found to be significant (p-value < 0.001) with an increase of 27.0 ± 1.33 km/decade. Both percentiles (5%, P5 and 95%, P95) shift northward along time (p-values = 0.0003 and 0.0008, respectively), with a north limit shift of 43.8 ± 2.2 km/decade. However, the analysis of the anchovy egg abundance showed a non-significant northward shift of 5.9 km/decade for the P95 in the reconstructed model and 18.1 km/decade estimated with the raw data.

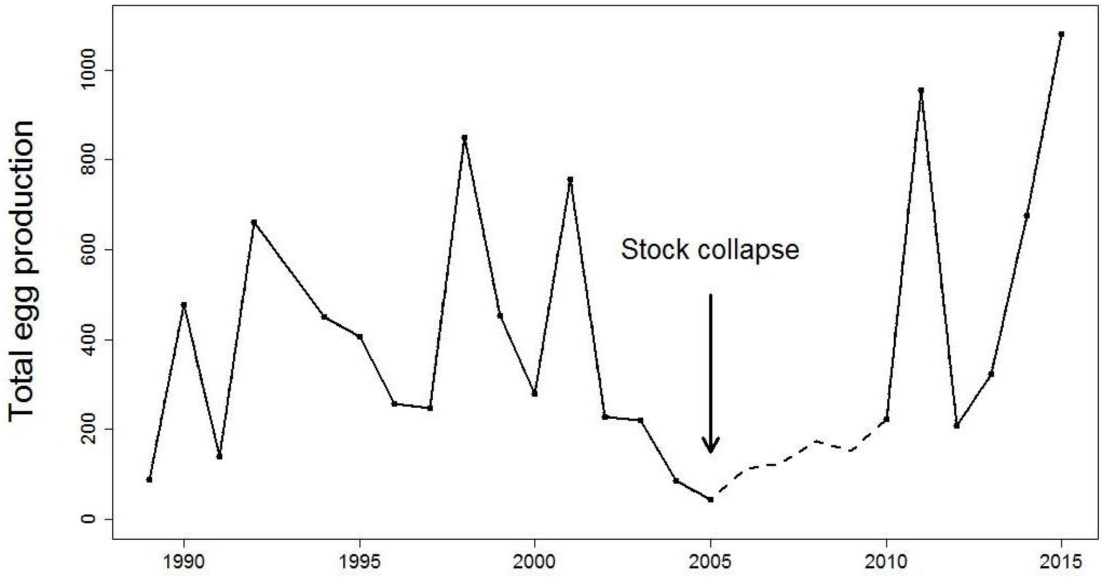


Figure 1.7: The Bay of Biscay anchovy total egg production between 1989 and 2015 time series. anchovy stock collapse and recover years when fishery was closed (in dotted lines).

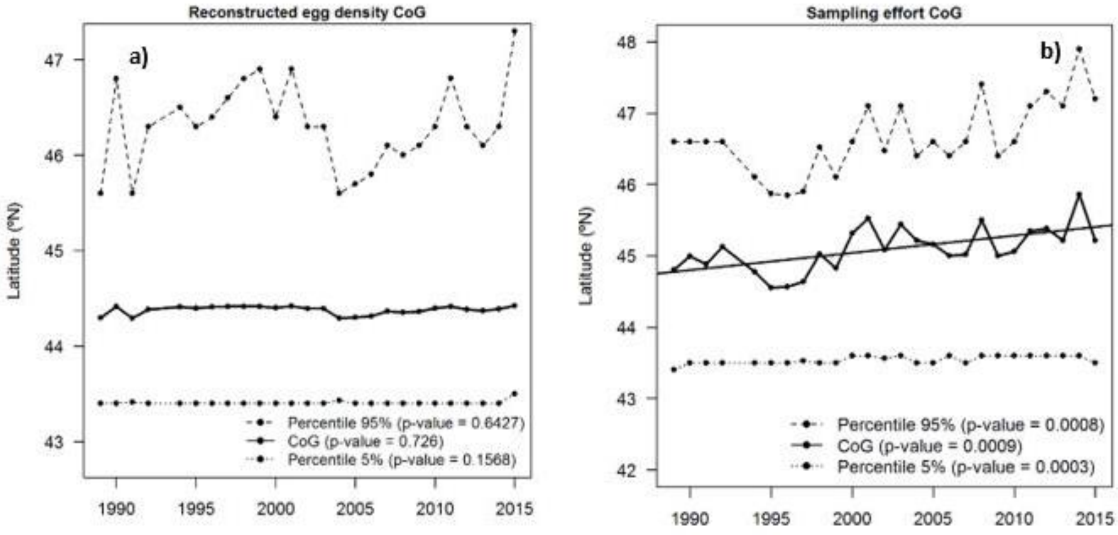


Figure 1.8: Latitudinal shift of the a) reconstructed spawning distribution models Center of Gravity and percentiles 5 and 95 and b) sampling effort between 1989 and 2015.

Anchovy spawning latitudinal CoG and P95 were statistically correlated with total egg production (both p-value < 0.0001, **Figure 1.9**) but not with GODAS sea surface temperature. GODAS data sea surface temperature showed a statistically significant increase of 0.59 ºC between 1989 and 2015 (0.23 ºC /decade, p-value = 0.0416) over the period of May-June in the sampled area (**S. Figure 1.2** in **Appendix A**).

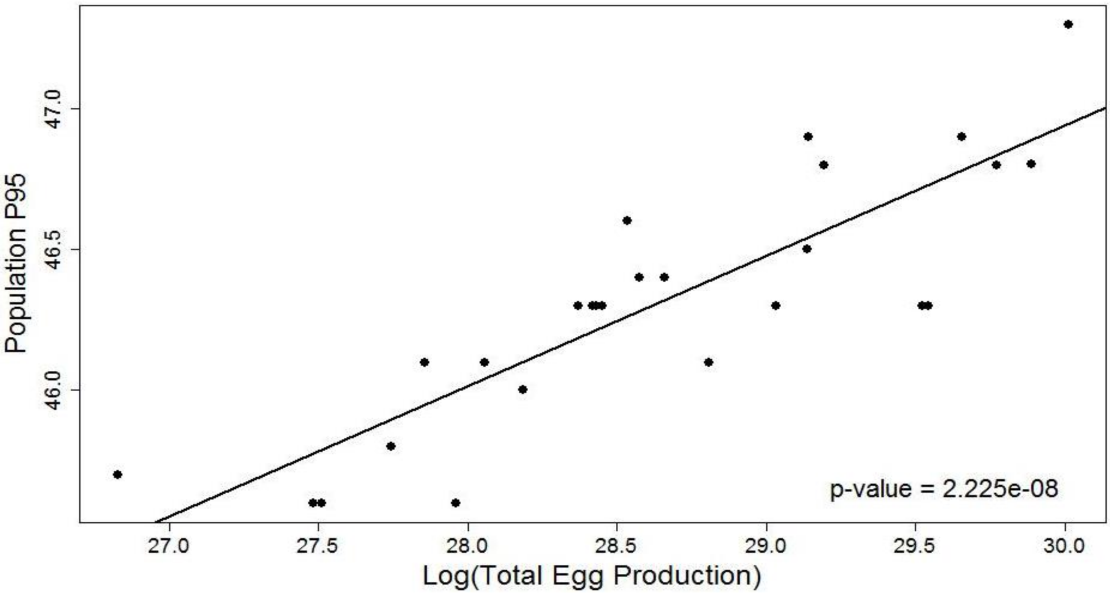


Figure 1.9: Correlation between anchovy eggs distribution P95 (north boundary) and the logarithm of the total egg production.

1.3.2. Spawning niche model

Environmental variables used for building the anchovy egg spawning distribution model after selection with *dredge* were SST, SSS, MLD, chl-a, and LogBathy. Different deviance explained can be seen in **Table 1.2.** Geographical position was also introduced in the model with a bivariate smooth (*s*(latitude, longitude)). The model with all these environmental variables explained 48.4 and 58.1% of the deviance for the PA and ED models, respectively. The Presence/Absence habitat model had an AUC, sensitivity, and specificity of 0.835, 0.855 and 0.815, respectively. The R-squared of the egg density model cross-validation (46.5%) was close to the deviance explained (58.1%) therefore this model was not considered overfitted. **Figure 1.10** shows response curves from the PA (**a**) and ED (**b**) models, whilst **Figure 1.11a and b** show egg observations and habitat model or anchovy spawning distribution model in the present. Different models were built (**Table 1.3**) and the total anchovy egg abundances were compared with mid- and end-century projections. In all those models, chl-a was excluded as previously explained. The model with all variables except chl-a, explained 48% (PA) and 57.8% (ED).

Table 1.2: Deviance explained in % for different variables in PA (presence/absence) and ED (log-transformed density) models. n is the number of samples used in the model.

Variables	GAMs	PA (%)	LogED (%)	n
SST (BIOMAN)	s (SST, k=3)	23.50	25.00	1020
HR SST	s (HRSST, k=3)	19.20	28.80	1171
SSS (BIOMAN)	s (SSS, k=3)	10.60	15.40	887
HR SSS	s (HRSSS, k=3)	9.36	14.70	1171
HR MLD	s (HRMLD, k=3)	20.80	27.50	1171
Chlorophyll-a	s (Chla, k=3)	1.77	3.40	1202
Log(Chla)	s (LogChla, k=3)	2.05	3.17	1202
Bathymetry	s (Bathy, k=3)	4.13	7.11	1175
Log(Bathy)	s (LogBathy, k=3)	6.00	9.00	1175
Lat	s (Lat)	6.08	8.30	1202
Long	s (Long)	31.4	43.20	1202
Lat, Long	s (Lat,Long)	41.1	55.30	1202

Table 1.3: All different model combinations built with their deviance explained for Presence/Absence (PA) and log-transformed density (logED), total anchovy egg abundance (eggs) in the Bay of Biscay for different periods and change rate between mid- and end-of-the-century and present. Importance (SST) is the projected total anchovy egg abundance where the only variable which was changed for future values was SST and others were fixed to current values. The same for SSS and MLD.

Total egg production	PA (%)	LogED (%)	PRESENT	MIDCENT	FUTURE	Midcent Change rate	Future Change rate
+ s(Lat,Long)							
All variables	48.0	57.8	80,076	125,984	211,854	1.57 x	2.66 x
Importance (SST)			80,076	88,341	114,341	1.10 x	1.43 x
Importance (SSS)			80,076	101,356	125,752	1.27 x	1.57 x
Importance (MLD)			80,076	84,241	86,935	1.05 x	1.09 x

1.3.3. Projections of anchovy spawning under the climate scenario

Under the RCP8.5 climate change scenario, the MPIOM model projects the following changes in the spawning area for the mid (2040-2059) and end of the century (2080-2099) with respect to the present (2006-2020): an increase in SST of 0.52 ± 0.28 ºC and 1.51 ± 0.71 ºC, a decrease in salinity of 0.30 ± 0.13 PSU and 0.57 ± 0.35 PSU, and a decrease in mixed layer depth of 7.48 ± 8.31 m and 12.40 ± 12.84 m, respectively. SST, SSS, MLD and log-transformed bathymetry were the chosen variables in the final model. Chlorophyll-a concentration was not selected in future models due to the low resolution and reliability of the projections in coastal areas.

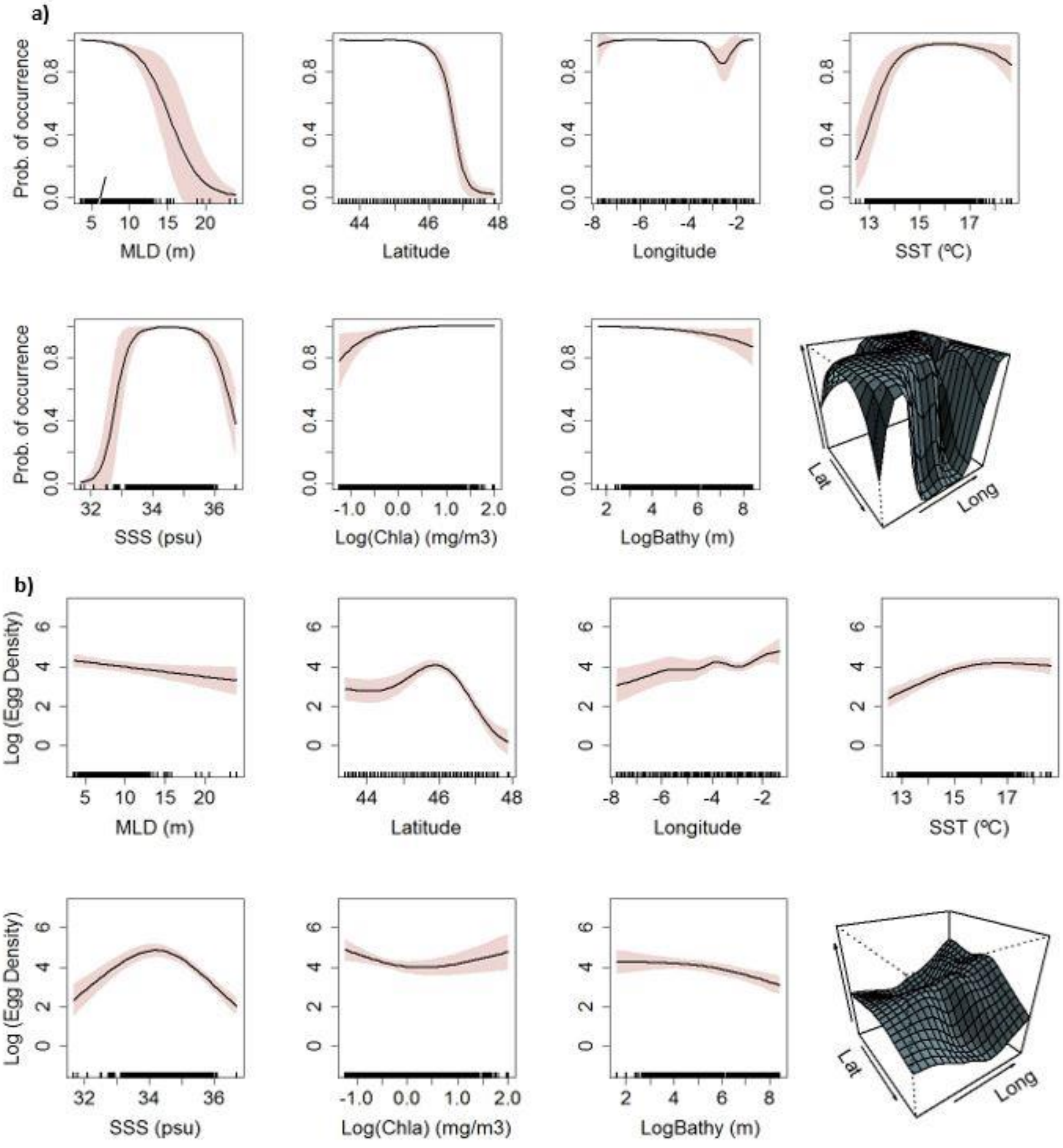


Figure 1.10: a) Egg Presence/Absence (dev. expl.=48.4%) and b) egg Log Density responses curves (dev. expl.=58.1%) for MLD, Latitude, Longitude, SST, SSS, LogChla and LogBathy and relation between coordinates.

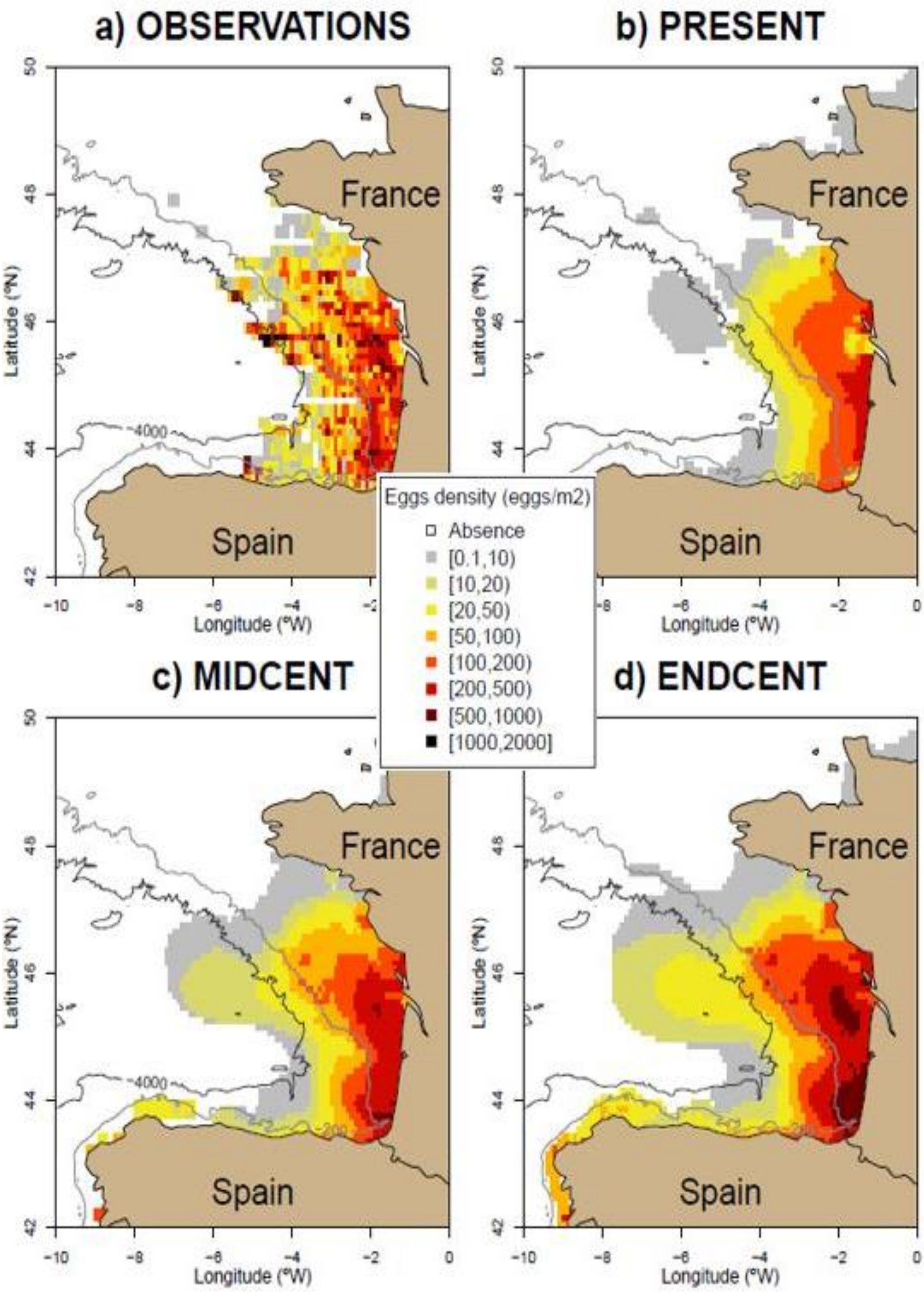


Figure 1.11: Egg abundance models in the Bay of Biscay for a) observations, b) present habitat model (2002-2014), c) mid-century (2040-2059) and c) end-of-the-century (2080-2099). Variables selected in present model are: Latitude, Longitude, MLD, SSS, SST and Chl-a. Chl-a is not used in mid-and end-of-the-century models. 200 and 4000 m isobaths are also represented to see continental shelf slope.

The density of anchovy eggs is projected to increase by mid-century (**Figure 1.11c**) and to increase even more by the end of the century (**Figure 1.11d**). The highest abundances appeared close to the coast, associated with river plumes. However, an expansion of the spawning area occurred over time. It is predicted an increase in the spawning area in 7.8 % (32,313 km^2) and 16.4% (67,793 km^2) for mid- and the end-of-the-century. Total egg abundance was predicted to be 1.57 times higher by mid-century compared to the present in the Bay of Biscay (rising from 80,076 eggs in the present to 125,984 in 2040-2059, **Figure 1.11 b, c**), and 2,66 times higher by the end of the century (211,854 eggs in 2080-2099, **Figure 1.11 b, d**). The center of gravity (CoG) of the egg density is expected to shift 15.6 km southward and 6.5 km eastward by the mid-century and 24 km northward and 1.5 km westward for the end-of-the-century.

Three different models were considered changing one by one the variables (SST, SSS, and MLS) to future values in order to explore which of the variables was the most influential with regards to future projections. SSS was found to be the variable that projected the highest increase in egg abundance. The total egg abundance in the BB projected by the SSS model multiplied 1.27 (1.57) times the present value for mid- (end-of-the-century) (**S. Figure 1.3c, d** in **Appendix A**). The second most important variable was SST, which when projected as the sole variable, projected a 1.10 (1.43) times higher egg abundance (**S. Figure 1.3a, b** in **Appendix A**), whilst MLD projected the lowest abundance increase with 1.05 (1.09) times by mid- (end-of-the-century) (**S. Figure 1.3e, f** in **Appendix A**). Most suitable zones in the three models were found in river plumes (Adour, Gironde, and Loire).

1.4. Discussion

1.4.1. Spawning seasonality and historical trends

The gonadosomatic index showed a strong seasonal pattern with a marked peak between May and June and a sexual resting period between September and February. Some individuals showed an early GSI increasing in March and all of them showed a decrease by September, being the spawning period between April and July-August (depending upon the year). The result is rather consistent with that of Sanz and Uriarte (1989), although in some years it is longer as spawning may reach mid-August.

Phenology changes were found between 1987 and 2015 in BB anchovy, with an advance of 5.5 days per decade in the spawning peak. The duration and peak of the spawning period showed inter-annual fluctuations probably related to changes in environmental factors (Millán, 1999; Petitgas *et al.*, 2013). The peak occurred during the transition between the cold and winter mixing conditions and the warm and stratified summer water conditions (Motos, 1996). In this case, the negative and statistically significant correlation between the anchovy spawning peak and chlorophyll-a support the hypothesis where the spawning peak shows an advance when the phytoplankton abundance increases, as a bottom-up process influencing egg production. The phytoplankton abundance is directly related to zooplankton which is a key trophic level for anchovy feeding. This result agrees with Somarakis *et al.* (2004) who associated earlier spawning peak with areas of high productivity and favorable adult feeding conditions. In other small pelagic species (i.e. mackerel), earlier spawning peak was found as a result of other variables such as temperature increase (Jansen & Gislason, 2011).

The high GSI inter-annual variability corresponds to large individual differences in gonad development. While the highest gonadal weights occurred during the spawning period, the lowest body weights were recorded towards the end of the spawning period (in autumn). This agrees with the studies carried out for anchovy in other areas. For European anchovy in the Bay of Cádiz, Millán (1999) found a more extended and delayed spawning peak (between June and August) and a resting period between November and February, while Regner (1996), reported July as the period of highest GSI for the Adriatic anchovy. The historical increase in GSI from 1989 to 2015 results from a significant increase in relative gonadal weight. Batch fecundity (the number of viable eggs usually released by a serial spawner in a pulse of spawning) is linearly related to ovary free bodyweight (Santos *et al.*, 2016; Sanz & Uriarte, 1989). Instead, the idea of continued feeding during the spawning period is suggested and energy requirement for spawning would then be satisfied by food intake (Dubreuil & Petitgas, 2009; Somarakis *et al.*, 2004). Ovarian-weight is negatively affected by poor environmental conditions and it is reflected by a lower and fluctuating GSI (i.e. Millán (1999)). In the same manner, Motos (1996) stated that the spawning period peak coincides with maximum values of zooplankton biomass, which suggests that good conditions and food availability can increase gonadal weight and also influence batch fecundity along with spawning frequency (Hunter & Leong, 1981). This has been observed for Adriatic anchovy, where egg abundance fluctuates with primary production (Regner, 1996). Anchovies, sardines, and sprats are characterized by high plasticity in their reproductive characteristics and have the ability to respond rapidly to environmental changes (Alheit, 1989). Changes in fishing intensity could also affect phenology although the population was heavily fished before its collapse in 2005. The fishery was closed from 2005 to spring 2010 and no evidence of changes in phenology was found related to this event.

A high correlation was found between the latitude of the anchovy P95 and the total eggs. This supports the hypothesis that northern boundary variability is affected by the overall population (Somarakis *et al.*, 2004). Due to inter-annual variability of the spawning dynamics, the area contracts or expands according to the overall size of Bay of Biscay population, with eggs spreading over all the Bay in high abundance years (Santos *et al.*, 2016). As the basin hypothesis explains (MacCall, 1990), populations represent the optimal areas for reproduction, being restricted to more favorable spawning areas when the abundance is low. Conversely, fish tend to spread over a larger area when the biomass per area exceeds a threshold, in order to avoid intra-specific interactions (i.e. trophic competition and/or egg cannibalism) (Somarakis *et al.*, 2004). Indeed, the northern limit moved further in the years when the egg production was higher. The Bay of Biscay is limited by land in the East and South, so the eggs expand to the West, but more to the North where they have the French continental shelf. In the future, the expansion of the distribution area will be probably due to this expected increase in egg production.

1.4.2. Future projections of spawning activity

According to the RCP8.5 greenhouse gas emission scenario, substantial increases in anchovy egg density (or egg production) and spawning area are expected. The total number of anchovy eggs in the BB is expected to be 2.66 times higher by the end-of-the-century compared with the present, with a 16.4% northwestward expansion of the spawning area due to geographical constraints imposed by the Cantabrian and the French coast in the south and east. A lesser increase of egg density (1.57 times), and expansion of spawning area (7.8%) are estimated by the mid-century as well. Such estimated increase in anchovy egg density is lower than, for instance, the interannual fluctuations of anchovy total egg production (which can vary by an order of magnitude, **Figure 1.7**) (Alheit *et al.*, 2010; ICES, 2016; Taboada & Anadón, 2015), but this variation is also influenced by fleet dynamic and management.

The expansion of the spawning area with a slight northward shift expected for the future, agree with Ibaibarriaga *et al.* (2007), who predict a northern expansion of the species distribution under climate change scenarios. Other studies conducted on a larger spatial scale (North Atlantic and Mediterranean Sea) obtained a substantial northward shift of the distribution of anchovy and a more extended anchovy potential habitat (Lenoir *et al.*, 2011). This quantitative difference is hence due to the different areas analyzed, and the strong geographical attachment of the Bay of Biscay anchovy spawning to the coast and river plumes. Anchovy has a density dependence selection of the spawning area (Motos *et al.*, 1996; Santos *et al.*, 2016). In years with high adult abundance, spawning occurred in most of the coastal area with higher intensity in the main river plumes but not all the potential oceanic area was occupied by larger and older anchovies. In years with low adult abundance, spawning is practically restricted to the principal spawning areas associated with the Estuaries of Gironde, Adour, and Bidasoa, in the SE region of the Bay of Biscay. Those places seem to form a refuge that maintains minimal sustaining conditions for this anchovy population even in adverse environmental conditions (Motos *et al.*, 1996). This population is part of a species with a larger distribution range, and probably tolerate wider environmental ranges than those that are in the Bay of Biscay.

In a recent study conducted by Raybaud *et al.* (2017), an increase in the probability of the occurrence was expected in the northern areas and also in the Bay of Biscay, hence, in agreement with our results. The study of Raybaud *et al.* (2017) was based on projecting the occurrence probability of anchovy adults under SST change scenarios. Although our study is focused only on the Bay of Biscay, our model is based on different climatic changes (not only SST) and provides egg density data collected in a yearly scientific survey (not only occurrence probability), which is important for fisheries management.

Projected changes in fisheries are more complex than simply northward shifts of species distributions, abundance changes or earlier spawning peaks (Bruge *et al.*, 2016; Burrows *et al.*, 2011). Egg abundance fluctuations are correlated with changes in temperature, salinity, primary production and zooplankton abundance, some of them with a one-year lag (Regner, 1996). Our results showed that not all environmental variables analyzed (sea temperature, salinity, and mixed layer depth) affect future projections equally. However, when modeled one by one, all the variables result in an increase in egg abundance in the future.

Temperature, which interacts with other stressors operating at large scales, is considered the main force driving changes in marine ecosystems (Montero-Serra *et al.*, 2015; Portner & Peck, 2010). However, in this study, the sea surface water warming was found to be the variable that results in a second higher projected increase in anchovy egg abundance after sea surface salinity. It would be expected that the temperature window for anchovy eggs would remain tolerable (Ibaibarriaga *et al.*, 2007) and probably more favorable despite climate change even if narrower.

Motos *et al.* (1996) hypothesized a link between anchovy presence and the freshwater runoff originating in river plumes, such as the Adour and Garonne rivers in the BB. However, the anchovy spawning habitat is found in a very wide salinity range, so it is more associated with coastal areas rather than with a given salinity (Reid, 1966). The Gironde estuary used to be an occasional spawning site in the past, but it has become a recurrent anchovy spawning center in the present (Bellier *et al.*, 2007). The Loire river, which is located 250 km northward and has the same freshwater discharge and seasonal dynamics, did not support any anchovy population in 1996 (Koutsikopoulos & Le Cann, 1996). Nevertheless, eggs have been recently found in BIOMAN surveys in this area (Santos *et al.*, 2016) and consequently, Loire river plume appears as a suitable zone to support high egg densities in both future models (mid- and end-of-the-century) and one-by-one-forced environmental variable models. In salinity-based model projections, total egg abundance is higher than temperature-based projections and most of the anchovy egg abundance is found in river plumes, being the Loire, a candidate spawning zone.

MPIOM global model for future projections estimates freshwater inputs as the difference between precipitation and the sum of evaporation, river runoff and glacier melting (which most of the time is not taken into account). Precipitation is the only parameter that is simulated and river runoff is used as an observed monthly mean of the largest 50 rivers of the world (Marsland *et al.*, 2003). Considering only the most important rivers worldwide, the rivers runoff resolution might be low at a local scale, hence the projections are not probably incorporating the salinity spatial heterogeneity in BB due to precipitation differences at each basin.

Anchovy spawning is also related to the mixed layer depth such that a higher egg abundance is found in larger haline stratified conditions (shallow MLD) (Planque *et al.*, 2007). River discharge increases the water column stratification since freshwater decreases upper layer density and suppresses mixing (revision in Costoya *et al.* (2015)). In our anchovy spawning habitat model, the mixed layer depth is used as a proxy of water column (haline and thermal) stratification. MLD-importance model projections are the lowest with an increase of 1.02 (1.05) times the present egg abundance in the mid- (end-) of-the-century. Global climate change models project the MLD to be 7 (12) m shallower due to ocean warming and subsequent water column stratification. Although the MLD decrease is mostly due to an increase in the water column temperature in the projections, the model is not able to distinguish it from the haline stratification although it could resemble freshening from changed river plume conditions. We assumed in our model that thermal mixed layer depth is a good representation of the mixed layer depth because SST explained slightly more MLD deviance (35.1%) than salinity (25.5%) and halo- and thermo-cline depth did not differ (**S. Figure 1.4a, b** in **Appendix A**). There is a substantial stratification increase (MLD decrease) across the whole region that is larger in open-ocean than in coastal zones and throughout the year (Holt *et al.*, 2010). This could explain the larger projected expansion of anchovy eggs across the study area in the MLD-model than others. The same pattern was recorded in 2003 when a wide area was covered in spawn and this was related to the stronger stratification caused by an anomalously intense solar heating (Bellier *et al.*, 2007).

These three variables (SST, SSS, and MLD) are not the only ones controlling the spawning habitat. The multi-model average across 16 IPCC5 models shows up to a 30% decrease in primary and export production globally by the end of the 21st century with respect to the historical value (Cabré *et al.*, 2015) although some specific areas such as the northern European sea (the Barents Sea), the Baltic Sea and Black Sea, show an expected increase in primary production (3–15%)

(Chust *et al.*, 2014a). Other studies project higher reductions in plankton biomass (reduce to less than a half, Schmittner (2005)) due to a decrease in the strength of the Atlantic Overturning Circulation (Collins *et al.*, 2013; Meehl *et al.*, 2007). However, zooplankton production is not expected to change proportionally to primary production, triggering changes in the trophic ratio (zooplankton biomass divided by phytoplankton biomass) in the future and a slight restructuring of the food web (Chust *et al.*, 2014a). Some latitudinal shifts are also expected. Copepod community is expected to shift poleward 8.7 km per decade on average, with a 12-13 day earlier phenological peak predicted by the end-of-the-century (Villarino *et al.*, 2015). We built the model and projected under the worst climate change scenario (RCP8.5) assuming that the environmental variables that most affect anchovy spawning are SST, SSS, and MLD. We did not include climatic multi-decadal variability drivers such as the North Atlantic Oscillation (NAO) or the Atlantic Multidecadal Oscillation (AMO) and other biological variables in our models and assumed that ecological relationships (inter- and intra-specific interactions) will remain similar in the future, which is a limitation of our projections. We also assume that changes in other physical drivers such as wind will be reflected in our model environmental variables. Furthermore, systematic differences in climate sensitivity and response between species or life-stages can desynchronize ecological interactions (Thackeray *et al.*, 2016).

The small pelagic functional group has a keystone position in marine ecosystems and coastal economies worldwide due to its role to sustain both predators and fisheries directly and indirectly (Pikitch *et al.*, 2014). In the past, studies focused on disentangling the effects due to the climate from fishing pressure. Recently, the interest has shifted to the interaction between both drivers and the change in sensitivity (strength of the relationship between biotic and climatic variables) (Macías *et al.*, 2014). Climate-induced changes can collapse some stocks, particularly those that are on the southern edge of species distributions (Beaugrand *et al.*, 2008). Brander (2007) suggested that a reduction of fishing mortality would decrease climate-induced impacts because overfishing is probably acting in synergy with climate forcing. Climate change impacts could also be positive, increasing new fishery opportunities (Cheung *et al.*, 2009b; Hobday, 2010) as it is the case for the Bay of Biscay anchovy, where this and other studies at larger geographical scales suggest that can be favored by recent trends in climate change.

General Circulation Models are able to represent many physical processes that drive large-scale climate change, but they are limited in their representation of coastal areas (Tinker *et al.*, 2016). Downscaling data from global climate models to smaller areas (Holt *et al.*, 2012) is hence crucial to obtain accurate climate projections at regional (Chust *et al.*, 2014a). Besides, ecological niche-based models have to be able to approach the complete curve of environmental predictors to be valid (Thuiller *et al.*, 2004). With all these limitations, modeling the spawning habitat and spawning activity along with available environmental information and projections to the future could be the low-cost first step to designate potential spawning fish habitats (Schismenou *et al.*, 2008).

1.5. Conclusions

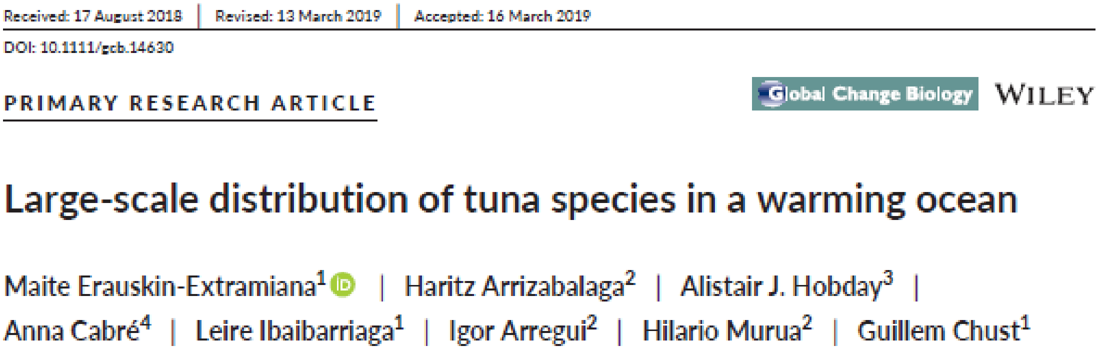
This study showed that anchovy spawning peak advanced at a rate of 5.5 days/decade and a general increase of GSI from 1987 to 2015 in the Bay of Biscay. These changes might be associated with changes in phytoplankton abundance. Moreover, the spawning area expands/contracts depending on the total egg production during this period. Ocean warming and climate change effects are expected to intensify during the 21st century triggering an overall egg abundance increase and an expansion of the anchovy spawning distribution. Since the anchovy habitat is closely related to river plumes such as Adour and Garonne, other large river mouths, such as the Loire, might be colonized in the future. Our projections aim to inform the local fishing community and managers concerning future potential scenarios to develop management plans taking climate change into consideration. Our study suggests that climate change will increase the suitable spawning habitat and the egg production of anchovy in the Bay of Biscay and hence the anchovy population, although more research should focus on monitoring spawning trends, and exploring other potential drivers, adaptive strategies and phenology responses in order to reduce uncertainties in the projections.

CHAPTER 2

Large-scale distribution of tuna species in a warming ocean

2. CHAPTER 2:

Large-scale distribution of tuna species in a warming ocean



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Large-scale distribution of tuna species in a warming ocean

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2.1. Introduction

Fisheries contribute to subsistence and food security for many countries. They provide wild protein resources, generate employment, promote economic growth, and comprise important renewable resources (Bell *et al.*, 2009; Gillett, 2000). Pelagic species, including both small pelagic fishes and large tunas, comprise the largest proportion (21%, 19.6 million tons) of global catches (including crustacean, mollusks, and freshwater fishes) (FAO, 2016). The annual catch of tuna and tuna-like species reached about 7.7 million tons in 2014 (FAO, 2016) and represents an economically important contribution to many nations (Brill & Hobday, 2017). The most economically important tuna species are referred to as principal market tunas and are caught by industrial pelagic fisheries around the globe (FAO, 2011). These principal market tunas include albacore (*Thunnus alalunga*), Atlantic bluefin tuna (*T. thynnus*), bigeye tuna (*T. obesus*), Pacific bluefin tuna (*T. orientalis*), southern bluefin tuna (*T. maccoyii*), yellowfin tuna (*T. albacares*), and skipjack tuna (*Katsuwonus pelamis*). Catches of principal market tunas reached 4.9 million tons in 2016 (ISSF, 2018). The total adult biomass of tuna has been estimated to decline by 49% between 1954 and 2006 (Juan-Jordá *et al.*, 2011), and this decline has been attributed to intensive exploitation (Worm & Tittensor, 2011).

Climate change has a significant impact across all marine ecosystems, latitudes and trophic levels (Scheffers *et al.*, 2016) with many studies showing global warming effects on species distribution and abundance (Burrows *et al.*, 2011; Cheung *et al.*, 2013b; Pecl *et al.*, 2017; Richardson *et al.*, 2012), as well as phenology (Asch, 2015; Poloczanska *et al.*, 2013; Poloczanska *et al.*, 2016). Climate change is predicted to lead to a re-distribution of the global catch potential with a 30–70% increase in high-latitude regions and a 40% decrease in the tropics (Cheung *et* *al.*, 2009b). Increases in the proportion of tropical tuna in sub-tropical regions between 1965 and 2011 were related to ocean warming (Monllor-Hurtado *et al.*, 2017). Due to the socio-economic value of tuna species, understanding and predicting responses to global climate change are a priority for the scientific community to assist in the design of effective fishery management to ensure the sustainability of tuna populations and, hence, the development of the human societies depending on them (Barange *et al.*, 2018; Hobday *et al.*, 2017). Recently, Arrizabalaga *et al.* (2015) described the global habitat preferences of commercially valuable tuna but did not explore historical or future changes in these distributions. Other regional, single ocean or single species efforts have projected tuna distribution and tuna population responses to climate change (Bell *et al.*, 2013b; Christian & Holmes, 2016; Druon *et al.*, 2017; Dueri *et al.*, 2014; Lehodey *et al.*, 2013; Michael *et al.*, 2017). For example, studies on Pacific Ocean skipjack project significant changes in their abundance and spatial distribution (reduction in most tropical waters and expansion in higher latitudes) in the future (Dueri *et al.*, 2014; Dueri *et al.*, 2016; Lehodey *et al.*, 2013). It has also been predicted that the distribution of tuna will be affected by changes linked to physiological characteristics. For example, a decrease in oxygen concentration is expected to compress the vertical habitat of tuna in the water column (Mislan *et al.*, 2017). In general, regional and local studies have used a variety of approaches, with knowledge gaps for most of the large pelagic species, such as critical environmental conditions (Trenkel *et al.*, 2014) making them difficult to compare in absence of a common baseline (Arrizabalaga *et al.*, 2015). In the case of tunas, habitat studies covering their worldwide distribution are required to address global management issues and facilitate the integration of Ecosystem Approach to Fisheries Management (EAFM) in a consistent way across tuna Regional Fishery Management Organizations (RFMOs) (Arrizabalaga *et al.*, 2015; Juan-Jordá *et al.*, 2018). This is particularly important in the case of tunas because they are widely distributed and highly migratory species (Arrizabalaga *et al.*, 2015; FAO, 2011, 2014b) playing ecologically important roles in many regions due to their top-down influence on the ecosystem structure (Cox *et al.*, 2002; Sibert *et al.*, 2006).

Despite the relevance of tuna in the global economy and the future supply of food (Mullon *et al.*, 2017), a global-scale study addressing the historical changes of the tuna habitat and providing future distributions based on climate change projections for all major commercial species is lacking. Here, we investigate the effect of environmental conditions on the worldwide distribution of six tuna species between 1958 and 2004 and projected changes by mid- and end-of-the-century under climate change. We also analyze changes in tuna habitat within countries' Exclusive Economic Zones (EEZ) to assess the potential impact for those countries. The findings will be relevant for tuna stock management and will contribute to understanding the potential impacts of climate change on fisheries and fishing nations.

2.2. Material and Methods

2.2.1. Fishery data

Six of the seven most commercial tuna species were considered in this study (the temperate species - albacore, Atlantic and southern bluefin tunas, and the tropical yellowfin, bigeye, and skipjack tunas). Japanese fleet pelagic longline fishing catch and effort data were used in developing the distribution models because of their extended spatio-temporal coverage. Atlantic (AO), Indian (IO) and Pacific (PO) Ocean Japanese longline catch and effort data were obtained from the five relevant tuna RFMOs, i.e. International Commission for the Conservation of Atlantic Tunas (ICCAT, www.iccat.int), Indian Ocean Tuna Commission (IOTC, www.iotc.org), Western and Central Pacific Fisheries Commission (WCPFC, www.wcpfc.int), Inter-American Tropical Tuna Commission (IATTC, www.iattc.org) and Commission for the Conservation of Southern Bluefin Tuna (CCSBT, www.ccsbt.org), with the exception of WCPFC where fleet-specific information and skipjack catches were not available (Arrizabalaga et al., 2015). Nominal Catch Per Unit Effort (CPUE, tuna tons per 1000 hooks) between 1958 and 2004 was calculated as the ratio of catch (tons) to the number of hooks, with the exception of SBT as catch data were in number of individuals rather than as biomass and only available from 1965 onwards. Although the spatio-temporal resolution was heterogeneous between data sources, all CPUE were averaged by season and at 5ºx5º spatial resolution. Our dataset has some limitations. CPUE was assumed to be a proxy for fish relative abundance and we acknowledge potential issues with this assumption (e.g. Schirripa *et al.* (2017)), and that longline gear is not efficient gear for catching skipjack tuna, as its catchability is very low. However, the longline method catches a wide range of species in a consistent way over a vast spatial scale and time (Arrizabalaga *et al.*, 2015); thus, its main strength is the consistency during time and space for the most commercially valuable tuna species worldwide and it remains the best data source for our analyses. Beyond some data inaccuracies in specific locations, our approach is consistent and the longline fishery data is suited to the objectives of the study since we use a single fishing gear, which represents a “common baseline” for all the species observations. Other gears (e.g. purse seine or bait boat, which do target skipjack tuna), show a much more limited spatial and temporal distribution. Furthermore, the persistent suitable habitat for longline fishing is contained within the tropical and temperate latitudes which seem consistent with the global latitudinal habitat preferences displayed by the top six tuna target species, which are among the main target species of longliners in the high seas (Ortuño-Crespo *et al.*, 2018).

2.2.2. Historical and future environmental data

Historical environmental data (1958-2004) were obtained from the PISCES biogeochemical model (Pelagic Interaction Scheme for Carbon and Ecosystem Studies, Aumont and Bopp (2006)). This model is derived from the Hamburg Model of Carbon Cycle version 5 (HAMOCC5) (Aumont *et al.*, 2003) and simulates the lower trophic levels of marine ecosystems (plankton), the biogeochemical cycles of carbon and the main limiting nutrients (Aumont *et al.*, 2015). Based on the analysis of Arrizabalaga *et al.* (2015), the following variables were used to characterize the environmental preferences of tunas: sea surface temperature (SST, in ºC), sea surface salinity (SSS, in PSU), sea surface height anomaly (SSH, in m) and mixed layer depth (MLD, in m) as abiotic environmental variables, and phytoplankton (log(phyto), in log(mmol/m^3)) as biotic factor. All environmental variables were averaged to the same degree square (5º x 5º) and temporal (season) resolution as the fishery data.

Projections of oceanographic variables for the reference period (1980-1999), mid (2040-2059) and the end-of-the-21st-century (2080-2099) were extracted from the average of 16 IPCC AR5 (Fifth Assessment Report of the Intergovernmental Panel on Climate Change) models that contain a biological module (called Ensemble) with a mean ~1º spatial resolution (Cabré *et al.*, 2015). We considered the highest greenhouse gas concentration scenario (RCP8.5 with 936 CO2 ppm by the end-of-the-century) of the IPCC AR5 (IPCC (2013)) among the four scenarios considered; RCP8.5 is usually used as “business as usual” scenario for the purposes of estimating the worst consequences of climate change. We implemented the Precautionary Approach which represents “caution in advance”. When assessing risk management responses, given the uncertainty of occurrence of any of the IPCC scenarios, the worst scenario should be an important consideration by policymakers. On the other hand, the results for the rest of the scenarios will be contained in the worst scenario, just with the change attained latter. By the end-of-the-century, this business as usual scenario projects a global average increase of temperature and SSH (2.23ºC and 0.16 m, respectively), and a decrease of MLD, SSS, and phytoplankton (18.7 m, 0.24 PSU and 0.16 mmol/m^3, respectively).

2.2.3. Tuna distribution models

2.2.3.1. Generalized additive models

Species distribution models (SDM) associate species occurrence or abundance with environmental conditions (Elith *et al.*, 2006; Guisan & Zimmermann, 2000). SDM of tuna was constructed by modeling tuna CPUEs in relation to environmental conditions using Generalized Additive Models (GAMs) (Hastie & Tibshirani, 1990; Wood, 2012; Wood, 2017). GAMs were selected as they enable the fit of non-linear responses for a wide range of statistical distributions. The two-step methodology described in Borchers *et al.* (1997) for horse mackerel (*Trachurus trachurus*) and for anchovy in the first chapter, was adapted here for tuna catch and effort data. Tuna catch data are problematic for building reliable SDMs because the observed absences (strata with fishing effort but no catches) are restricted to the fishing area. Thus, in our model the pseudo-absences were randomly generated through time and space, only excluding points with presence data and balanced with the number of presences in each particular year following Barbet-Massin *et al.* (2012), Elith and Leathwick (2009), Guisan and Theurillat (2000) and Iturbide *et al.* (2015). In the case of Atlantic bluefin tuna, pseudo-absences were limited to the Atlantic Ocean and the Mediterranean Sea, while in the case of southern bluefin tuna they were limited to the southern hemisphere. Due to the lack of fishery data in the western and central Pacific for skipjack, no pseudo-absences for this species were generated in this area. The first step was to fit the presence/pseudo-absence (PA) model to the tuna occurrence assuming a binomial error distribution with a logit link function. The second step was to fit the abundance model (AB) for non-zero observations using the log-transformed Catch Per Unit Effort (CPUE) as a response variable assuming Gaussian error distribution and identity link. The expected CPUE was calculated as the product of the first and second models (PA * AB) after back-transforming the logarithm of the CPUE from the abundance model to the original CPUE scale. In order to fit unimodal response curves for the environmental variables (according to the ecological niche concept of Hutchinson (1957)) and to avoid overfitting, degrees of smoothness ("k" values) were set equal or less than three. GAMs were built using the "mgcv" package in R-language (Wood, 2012) after removing all the records with missing values.

Three fixed factors (Year, Season and Stock) and their interactions were also added to the full model to correct for the spatial and temporal changes in abundance and/or catchability. The Stock factor also corrects for potential differences in the way the tuna RFMOs data are gathered, which might affect average CPUE values (Arrizabalaga *et al.*, 2015; Schirripa *et al.*, 2017).

2.2.3.2. Model selection and validation

The best model selection was conducted using the *dredge* function of the 'MuMIn' R-package (Barton, 2016). This function generates a subset of models with different combinations of variables of the global model and selects the one with the lowest AIC (Akaike Information Criterion) (Bruge *et al.*, 2016; Guisan & Zimmermann, 2000; Sakamoto *et al.*, 1986).

The presence/pseudo-absence model was validated using the cross-validation method (Burnham & Anderson, 2003), with *k*-fold equally sized sub-datasets (Hijmans *et al.*, 2013). We used *k*=5, i.e. 80% of randomly selected observations to validate the fit of the remaining (i.e. 20%). We followed the two threshold selection criteria of Jiménez-Valverde and Lobo (2007) to convert the species probability of presence to either presence (above the assigned value) or absence (below the threshold). The first criteria selected the threshold for which the sensitivity (true predicted presences) was equal to the specificity (true predicted absences). The second criteria followed the maximization of the sensitivity plus specificity.

The confusion matrix accuracy assessment (VanDerWal *et al.*, 2012) was used to evaluate how reasonable was the discrimination of the presences and absences in the PA model. Area Under the Curve (AUC) values range between 0.5 (random sorting) to 1 (perfect discrimination) and were estimated over the presences and absences estimated by the model and the presences and pseudo-absences randomly generated. Accuracy in the abundance model was calculated by comparing predictions with observations using the R-squared value and contrasted with the overall explained deviance. A large difference between both values would indicate overfitting (Villarino *et al.*, 2015).

2.2.4. Historical trend analysis

In order to analyze the tuna species' habitat changes between 1958 and 2004, we predicted the worldwide distribution annually according to the selected model and using the yearly aggregated environmental data for each particular year. The Gravity Center (GC) of the tuna distribution, as the mean location of the stock biomass (Bez & Rivoirard, 2001) and 5, 20, 80 and 95% percentiles (P5, P20, P80, and P95) of the location weighted by the relative abundance were calculated in order to identify trends in the distribution of tunas' populations and their shifts (considering significant a p-value < 0.05). P5, P20, P80, and P95 provide information on the northern and southern distribution limits in both, past and future. Abundance changes were also estimated as the difference between the relative abundance average for the last and first five years of the time series in each latitude.

2.2.4.1. Distribution and climatic indices

The potential correlations between climatic indices and the distribution GC changes were studied to test the hypothesis that population distribution changes were due to oscillations of global climatic indices instead of climate change. The climatic indices used (from https://www.esrl.noaa.gov/psd/gcos_wgsp/Timeseries/) were: Southern Oscillation Index (SOI), North Atlantic Oscillation (NAO), Pacific/North American teleconnection pattern (PNA), Arctic Oscillation (AO), Southern Annular Mode (SAM), Trans Polar Index (TPI), Pacific Decadal Oscillation (PDO), Dipole Mode Index (DMI) and North Pacific Index (NP). The correlation between the GC and the yearly average of each climatic index was calculated in both spatial axes (latitudinal and longitudinal) but only with those indices considered to affect the distribution area of each stock.

2.2.5. Future projections and changes

To estimate the future impact of climate change on tuna distribution and relative abundance, GAM projections for the mid (2040-2059) and the end-of-the-21st-century (2080-2099) were compared with predictions for the reference period (1980-1999). For each species, model projections were performed at each level of each of the fixed factors and then averaged. These averages represent the spatial distribution and relative abundance of tuna at each location, given an average abundance and catchability condition.

2.2.5.1. Expected changes in Exclusive Economic Zones (EEZs)

The potential abundance changes (in CPUE, tonnes per 1000 hooks) averaged per grid cell for all the species under future climate change was estimated within the exclusive economic zones (EEZs) for all coastal countries. EEZ data (from http://www.marineregions.org) delimit the 200 nautical miles boundary from each coast (Flanders Marine Institute, 2018). As the spatial resolution in coastal areas was low in projection models, we only analyzed those countries with data in more than 30% of the grid-cells inside the EEZ. The averaged relative abundance within EEZs was estimated for the reference period and the future, and changes were calculated as the difference between both periods.

2.3. Results

2.3.1. Tuna distribution models

Selected tuna distribution models explained between 35.5% (southern bluefin tuna) and 62.4% (skipjack tuna) of the deviance during the reference period (**S. Table 2.1** in **Appendix B**).

Most of the models included all the environmental and fixed factors but not all fixed factors interactions (**S. Table 2.1, S. Figure 2.1a, b** in **Appendix B**). The models showed good predictive power (**S. Table 2.2** in **Appendix B**) with an AUC between 0.784 (albacore tuna) and 0.838 (Atlantic bluefin tuna) for PA model, sensitivity between 0.796 (S. bluefin) and 0.882 (yellowfin), specificity between 0.724 (albacore) and 0.806 (A. bluefin) and R-squared values between 0.34 (Atlantic bluefin tuna) and 0.74 (yellowfin tuna).

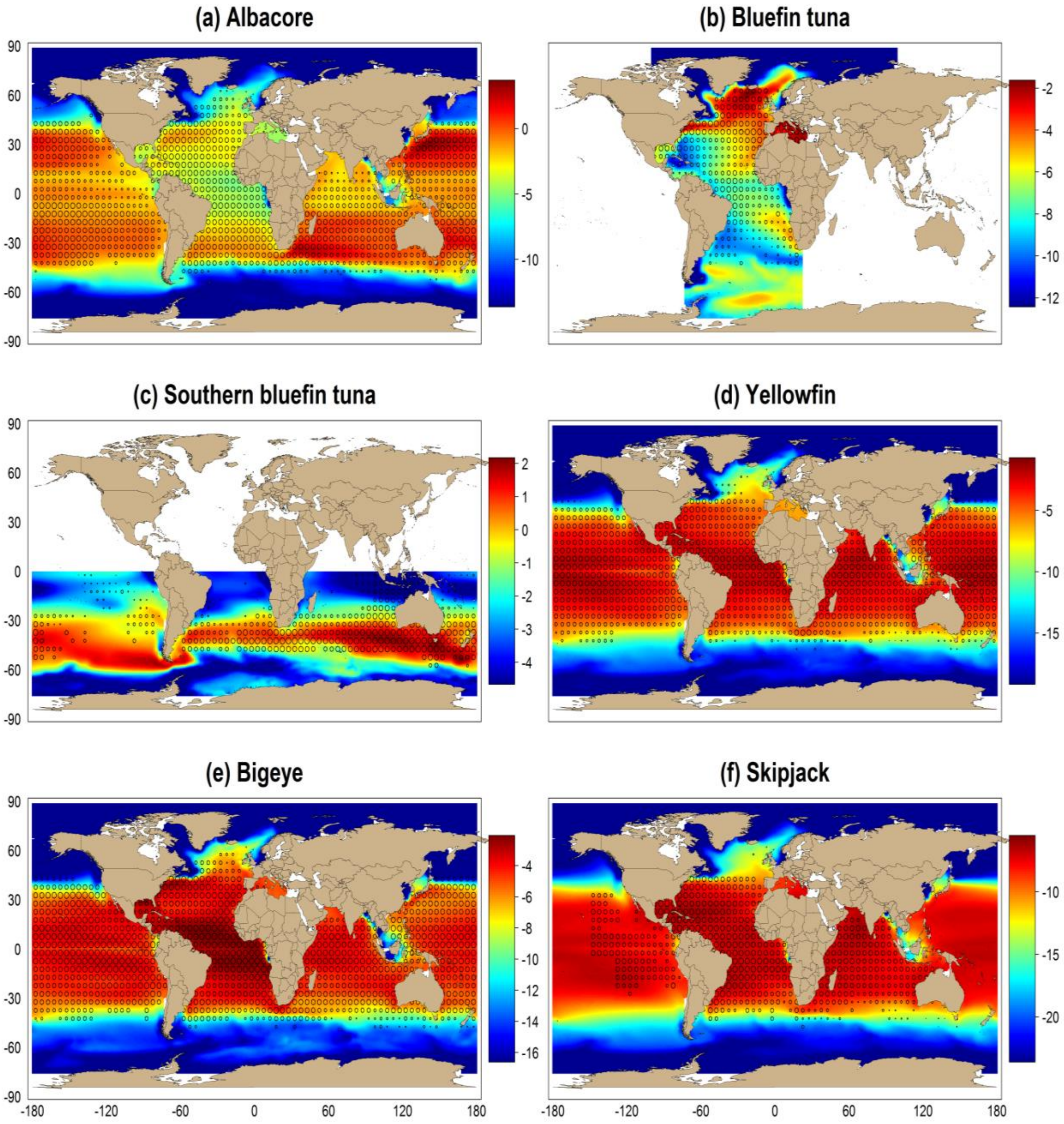


Figure 2.1: Global distribution of tuna species: (a) Albacore tuna, (b) Atlantic bluefin tuna, (c) Southern bluefin tuna, (d) Yellowfin tuna, (e) Bigeye tuna, and (f) Skipjack tuna. Relative abundances (in tons per 1,000 hooks) are represented on a log-transformed scale. Notice the different scales for different species. The black circles represent the raw log-transformed CPUE data and the size is proportional to the value. Circles are not present in the West Pacific in skipjack due to the lack of catch data.

Global tuna relative abundance is represented in **Figure 2.1.** Albacore tuna was distributed between 60 ºS to 60ºN worldwide with larger relative abundances in the temperate waters of Indian and Pacific oceans (**Figure 2.1a**). Lower abundances were associated with high productive areas (such as main upwelling zones) or equatorial areas. Atlantic bluefin tuna mainly appeared north of 35ºN in the North Atlantic Ocean and in the Mediterranean Sea (**Figure 2.1b**). Other areas in the south Atlantic off the west coast of South Africa and Namibia, and in the Southern Ocean show presence. The west Africa area was fished during the first years of the time series (mainly in the 1960's), with the last observation in 1998. Since then, no Atlantic bluefin have been caught with longlines in the southern hemisphere. Southern bluefin tuna appeared between 30 and 60ºS with the highest abundances south of Australia, New Zealand, and South America (Chile and Argentina) (**Figure 2.1c**). High abundances were predicted south of the East Pacific Ocean where there was the absence of fishery data. Between Australia and some Indo-Pacific islands, where southern bluefin catch data were available, very low abundances were predicted by the model. Yellowfin and bigeye tunas were distributed between the equator and the subtropics in three main oceans (Pacific, Indian and Atlantic) with higher abundances of yellowfin in the equatorial areas and between 20ºS and 20ºN in the Atlantic Ocean for bigeye (**Figure 2.1 d and e**). Very low or null abundances were predicted in the central Indo-Pacific region. The potential presence of both species was predicted in the Mediterranean Sea although there was no catch data there. Skipjack tuna showed a similar distribution to yellowfin and bigeye tunas (**Figure 2.1f**).

2.3.2. Past distribution and trend analysis

Historic tuna habitat and relative abundance showed important changes between 1958 and 2004 (**Figure 2.2, Figure 2.3 and Table 2.1**). Modeled albacore latitudinal habitat gravity center (GClat) showed significant (p-value < 0.05) poleward shifts in all the stocks (**Figure 2.3a, c, d, h, i, j and Table 2.1**) with the highest change in North Atlantic Ocean (28.8 km per decade). The distribution limits shifted significantly poleward except in the South Pacific and in the Mediterranean Sea, which involves an expansion of the distribution area. Relative abundance in recent years decreased significantly (up to 50%) in the most productive area for longline between 10 and 30º N and slightly between the equator and 25º S (**Figure 2.2**). A smaller increase occurred in the first 10º of the northern hemisphere and in the northern and southern boundaries (30-40º N and 25-35º S). The longitudinal shifts (GClon) were less pronounced (**Table 2.1**). North Atlantic and Mediterranean stocks shifted eastward while in the South Atlantic shifts were to the west. The Atlantic bluefin tuna habitat GClat shifted northward significantly in the West Atlantic Ocean (p-value<0.001) but this change was not significant in the eastern Atlantic

Ocean (p-value=0.07) (**Figure 2.3e, g and Table 2.1**). In both stocks, the northern limit shift further north was highly significant which means that Atlantic bluefin habitat became more suitable at higher latitudes and had not a significant shift in longitude. The relative abundance of bluefin increased slightly in all the northern hemisphere (0-60º N) in recent years (**Figure 2.2**). The southern bluefin tuna habitat GC shifted northward towards the equator significantly (p-value < 0.001) between 1965 and 2004. In the 1960s and 1970s, southern bluefin tuna GC shifted to the pole (southward) and it was not until the 1980's when it started shifting towards the equator (**Figure 2.3k and Table 2.1**). Both limits (northern and southern) shifted northward and hence, the relative abundance in recent years decreased south of 25ºS (**Figure 2.2**). Yellowfin tuna habitat GClat shifted significantly to the south in the Pacific and Indian Oceans (both p-value<0.001) but no trend was found in the Atlantic Ocean (p-value=0.87) (**Figure 2.3b, f, j, l and Table 2.1**). The largest change occurred in the eastern Pacific Ocean at a rate of 26.6 km per decade. In general, both limits shifted southward in the Pacific and Indian Ocean but poleward in the Atlantic. A significant westward shift was found in the east Pacific stock, the opposite of the eastward shift of the west Pacific stock. The abundance in recent years increased in all latitudes except for a small decrease between 6 and 10ºN (**Figure 2.2**). In contrast to yellowfin, bigeye tuna habitat GClat shifted significantly to the north-west in the Atlantic Ocean (p-value=0.019) and south-west in the Indian Ocean. Pacific tuna stocks showed no significant trends (p-values=0.2 and 0.65 for east and west, respectively) (**Figure 2.3b, l and Table 2.1**). The distribution limits shifted poleward in the Atlantic Ocean (but only significantly in the northern hemisphere), while no trends were found in the Pacific. Bigeye tuna relative abundance increased in recent years through its distribution range, especially between the equator and 60ºN (**Figure 2.2**). Skipjack tuna stocks showed different responses to environmental changes around the world: north and east shifts in the West Atlantic, southward shifts in the east and west Pacific and Indian stocks (p-value=0.046, <0.001 and <0.001 respectively), and no significant shift in the east Atlantic (p-value=0.29) (**Figure 2.3b, e, g, j, l and Table 2.1**). An eastward shift is also found in the western Pacific. The distribution limits did not show a trend, with a different pattern depending on the stock. Changes in the mean abundance per latitude were minor, varying between $-4.3e^{-5}$ to $4.4e^{-5}$ tons/1000 hooks CPUE change (**Figure 2.2**).

In summary, 20 out of 22 stocks have shifted poleward, as represented by their gravity center and/or one of their distribution limits. All temperate tuna habitats shifted significantly poleward (northward in the northern hemisphere and southward in the southern hemisphere), except southern bluefin tuna which moved to the north. Tropical tunas, distributed around the equator, showed opposing shifts in their distribution limits, hence, they were less affected in their GC. They generally shifted southward in the Pacific and Indian Oceans but northward in the Atlantic Ocean. Overall, 91% of the stocks shifted poleward during the study period, representing 89% of the temperate and 92% of tropical tunas. On average, the distribution limits (P80) shifted poleward 6.5 km per decade in the northern hemisphere and 5.5 km per decade in the southern hemisphere.

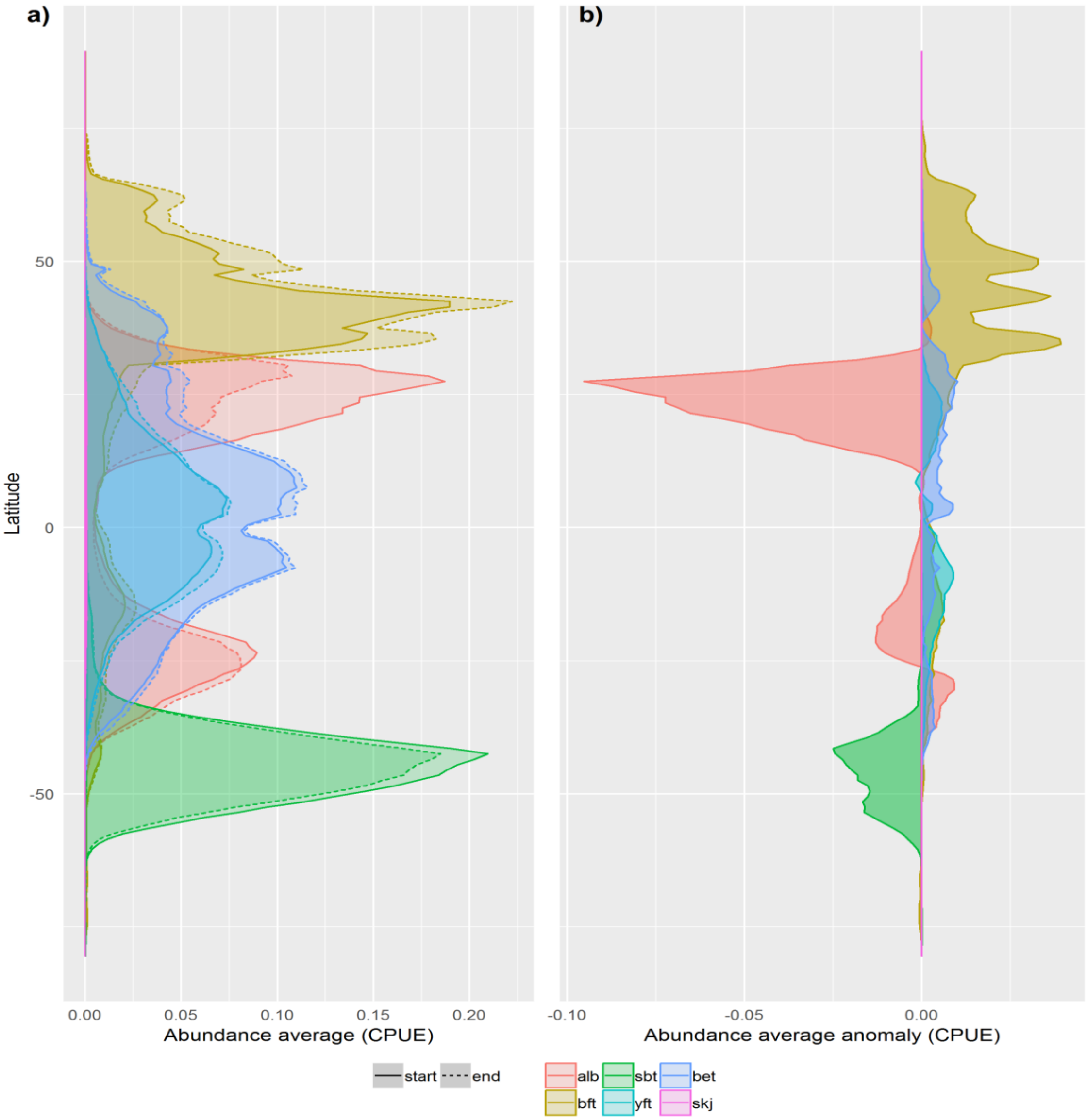


Figure 2.2: Changes in abundance (in tons per 1,000 hooks and 10 individuals per 1,000 hooks in the case of S. bluefin) between past (1958–1963 and 1965–1970 for S. bluefin) and recent (1999–2004) period. (a) Average abundance per latitude for the two periods; (b) abundance anomalies estimated as the difference between past and recent periods for six tuna species: alb = albacore tuna, bft = A. bluefin tuna, sbt = S. bluefin tuna, yft = yellowfin tuna, bet = bigeye tuna, and skj = skipjack tuna.

2.3.2.1. Relation with climatic indices

The analyses between latitudinal GC changes in tuna stocks and climatic indices showed very few significant correlations (**S. Table 2.3** in **Appendix B**). Only 20.5% of the latitudinal changes were related to climatic indices and only 10.3% in the case of longitudinal shifts.

2.3.3. Future tuna projections

2.3.3.1. Distribution and changes in abundance

Future projections of tuna habitat under the RCP8.5 climate change scenario showed similar patterns for the mid- and the end-of-the-century, but our results projected higher changes by 2080-2099, with respect to the reference period (1980-1999). In general, most of the species are projected to expand their northern and southern boundaries (**Table 2.2**) increasing the relative abundance in the limits of their distribution (**Figure 2.4 a, b, c and e**) while tropical tunas as skipjack and yellowfin are projected to increase abundance in their core tropical areas and eastward in the Pacific Ocean (**Figure 2.4 d and f**). However, a decrease of abundance in the most western equatorial Pacific for both skipjack and yellowfin tuna is projected.

Our results projected that the relative abundance of albacore tuna increases in the distribution limits of the Indian and Pacific Oceans, but decrease in temperate areas around South Africa, south of Japan and Taiwan and northeast of Australia (**Figure 2.4a**). The gravity center for the future moves southward for the southern hemisphere stocks (South Atlantic, South Pacific, and Indian) and northward for the northern hemisphere stocks (North Atlantic and North Pacific), except in the Mediterranean Sea where albacore do not show a clear trend (**Table 2.2**). Albacore tuna expand their northern and southern limits and decrease in temperate areas (**Figure 2.4a**). In all the stocks an eastward shift is projected by 2100 (with the highest rate in the North Atlantic) except in the Mediterranean Sea (**Table 2.2**). Atlantic bluefin tuna decrease in most of the current North Atlantic distribution area and increase slightly in the most northern areas of the Atlantic Ocean such as around Svalbard and Jan Mayen Islands (**Figure 2.4b**). The western Atlantic bluefin stock is impeded by landmasses with regard to expansion northward, but the eastern bluefin stock extends its northern distribution limit by the end-of-the-century. Both stocks shift eastward with a higher rate in the eastern Atlantic. The model also projects that the habitat improves in high southern latitudes, where no occurrences have been observed, shifting the west Atlantic bluefin stock southward.

The relative abundance of the southern bluefin tuna increases towards their southern limit by mid-century but it decreases in most of the historical distribution area (**Figure 2.4c**). By the end-of-the-century (2080-2099), the relative abundance decreases in most of the changes, the latitudinal GC shifts slightly southward by mid-century and northward by the end-of-the-century. For both time periods, a westward shift is projected. The southern boundary shifts northward by 2080-2099.

*Table 2.1: Change in Gravity Center (GClat, in latitudinal and GClon in longitudinal degrees per year), North (N) and South (S) limits estimated with percentiles 95 (P95), 80 (P80), 20 (P20) and 5 (P5) for the six tuna species between 1958 to 2004 except in the case of southern bluefin tuna (S. bluefin) which was between 1965 and 2004. P-value < 0.001 is represented by '***', p-value between 0.001 and 0.01 with '**', and p-value >0.01 and < 0.05 by '*'.*

Graphic	**Species**	**Stock**	**Ocean**	**GClon**	**GClat**	**limN (P80)**	**limN (P95)**	**limS (P20)**	**limS (P5)**
a	Albacore	albNP	North Pacific	0.038	0.014*	0.027***	0.016*	0.003	-0.03**
b	Bigeye	betEP	East Pacific	-0.005	-0.004	0.005	0.009	-0.017*	-0.02**
	Skipjack	skjEP	East Pacific	0.001	-0.007*	-0.003	0.01	0.003	-0.014*
	Yellowfin	yftEP	East Pacific	-0.021**	-0.024***	-0.015*	0.004	-0.034***	-0.005
c	Albacore	albSP	South Pacific	0.01	-0.023***	-0.043***	-0.035**	-0.011	-0.01*
d	Albacore	albNA	North Atlantic	0.036***	0.026***	0.045***	0.035***	0.013	-0.043***
e	A. bluefin	bftW	West Atlantic	-0.007	0.05***	0.018***	0.072**	0.036	0.035***
	Skipjack	skjWA	West Atlantic	0.016***	0.011**	0.012**	0.015**	0.017*	0.002
f	Bigeye	betA	Atlantic	-0.011*	0.011*	0.023**	0.017***	-0.002	-0.005
	Yellowfin	yftA	Atlantic	-0.014	-0.001	0.019**	0.005	-0.013*	-0.042**
g	A. bluefin	bftE	East Atlantic	-0.017	0.009	0.038***	0.025***	0.003	0.005
	Skipjack	skjEA	East Atlantic	0.003	0.007	0.037*	0.013*	-0.009	-0.009
h	Albacore	albSA	South Atlantic	-0.018**	-0.008*	0.000	-0.013	-0.012*	0.000
i	Albacore	albM	Mediterranean	0.008*	0.003**	0.001	0.000	0.007	0.004*
j	Albacore	albI	Indian	-0.031**	-0.021***	-0.023***	-0.011	-0.037***	-0.014**
	Bigeye	betI	Indian	-0.021***	-0.011***	-0.002	0.000	-0.011	-0.035***
	Skipjack	skjI	Indian	-0.005	-0.016***	-0.002	-0.001	-0.019**	-0.017**
	Yellowfin	yftI	Indian	-0.003	-0.017***	-0.005	-0.003	-0.022***	-0.037***
k	S. bluefin	sbt	Southern	0.011	0.009***	0.009	0.028***	0.006	0.01*
l	Bigeye	betWP	West Pacific	0.023	0.002	0.009	-0.029***	0.01	-0.017*
	Skipjack	skjWP	West Pacific	0.016*	-0.008***	-0.01*	-0.012*	-0.008	-0.006
	Yellowfin	yftWP	West Pacific	0.046***	-0.02***	-0.011*	-0.03***	-0.013*	-0.004

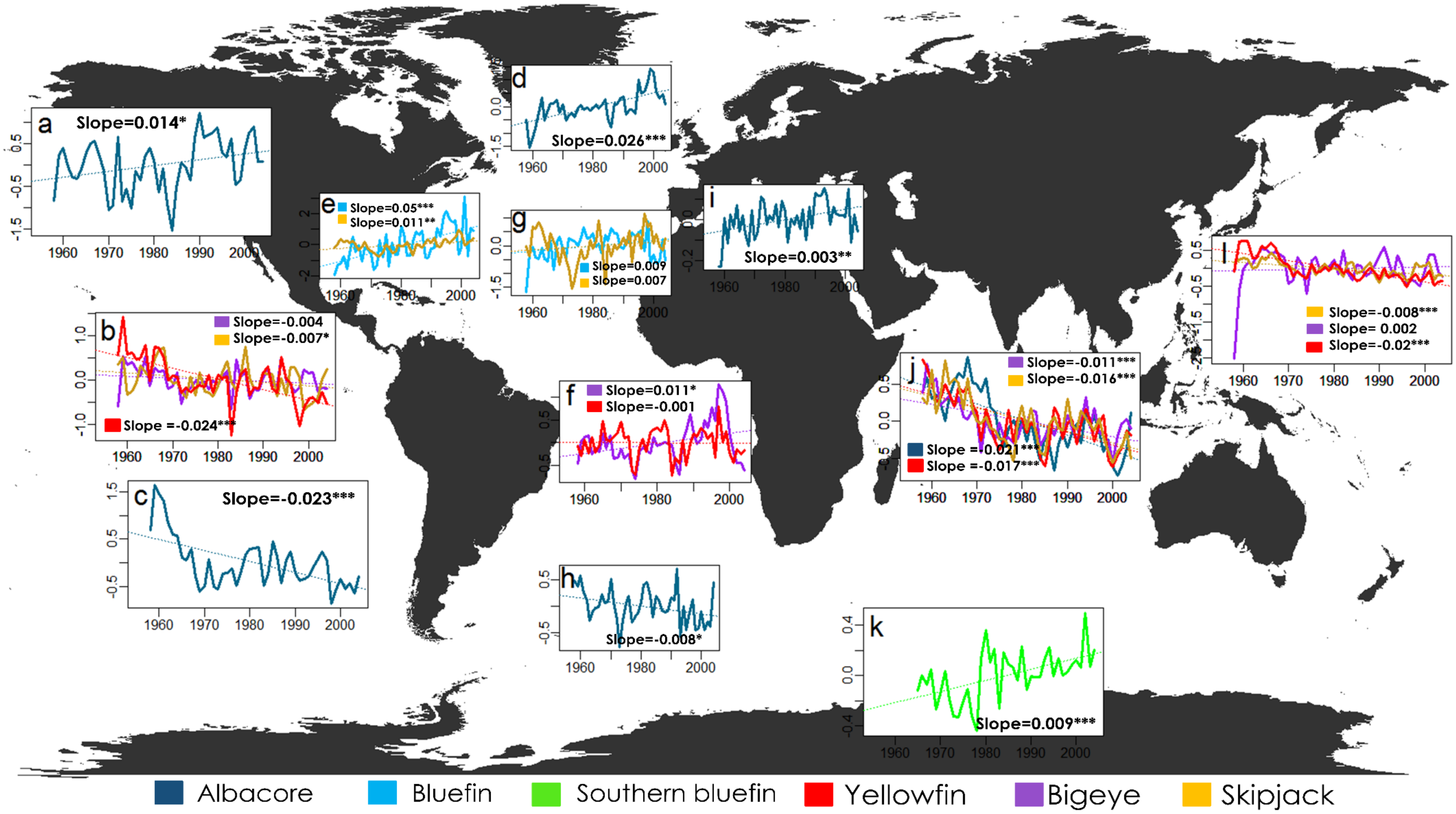


Figure 2.3: *Historical trends for the habitat of 22 tuna stocks' gravity center anomalies (in latitudinal degrees).*

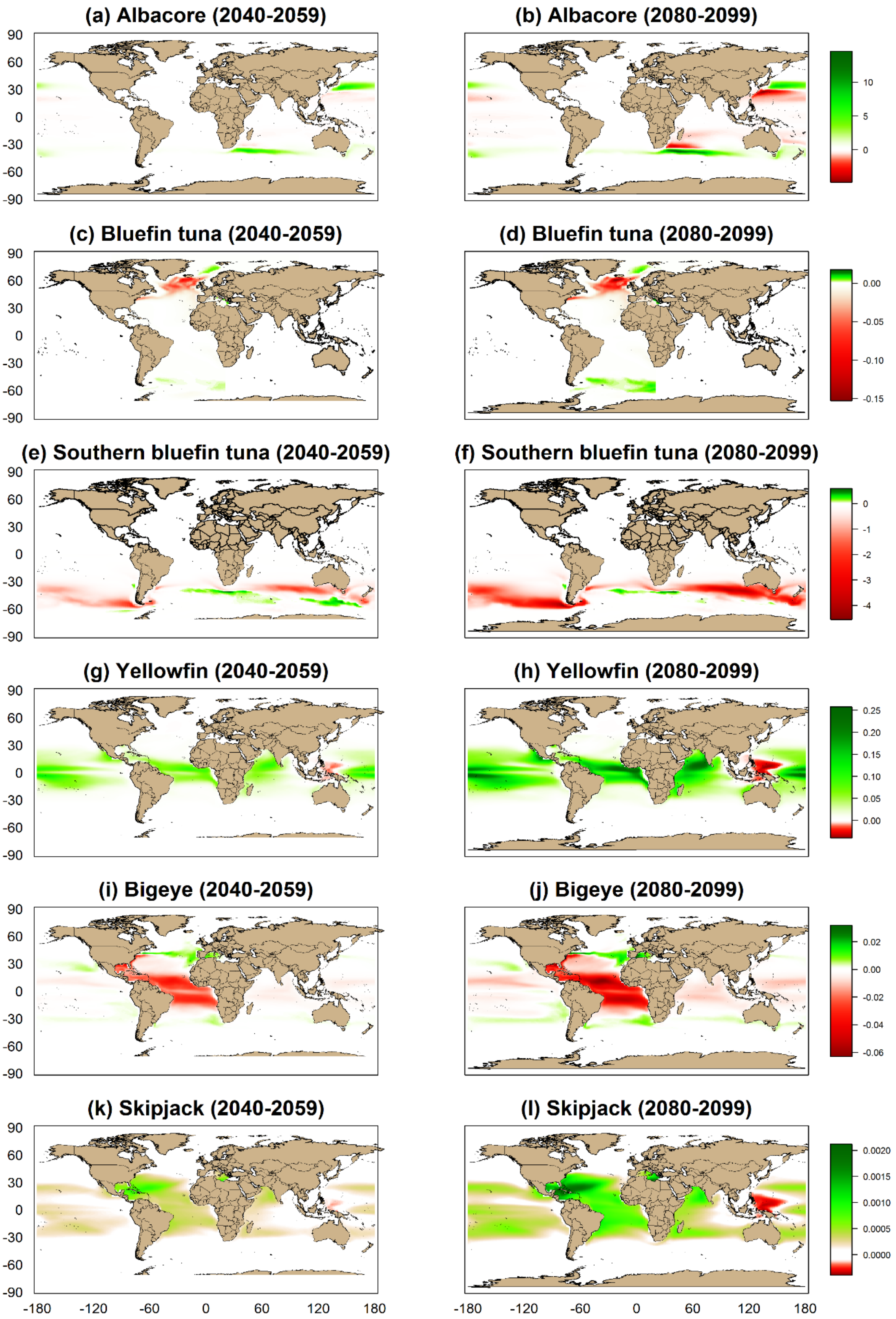


Figure 2.4: *Gains and losses in relative abundance (in tons per 1,000 hooks, except for SBT, in number of individuals per 1,000 hooks) for mid-(left column, a, c, e, g, i and k) and end-of-the-century (right column, b, d, f, h, j, l).*

Yellowfin tuna increase in most of their distribution area, with the highest changes projected for the equatorial areas of the Atlantic, Indian and Central Pacific Oceans (**Figure 2.4d**). However, the abundance is projected to decrease north of Papua New Guinea and east of the Philippines. The yellowfin tuna GClat shifts southward in the west Pacific and Atlantic, while northward in the eastern Pacific and Indian Oceans. Overall, both, the yellowfin and bigeye tuna shift eastward except in the Indian Ocean where a westward shift is projected for both periods (2040-2059 and 2080-2099). The spatial distribution of bigeye tuna is projected to change most in the Atlantic Ocean and less so in the Pacific and Indian Oceans (**Figure 2.4e**). The relative abundance decreases in the equatorial and tropical areas, but increases in the subtropical zones, especially in the northeast Atlantic and in the southeast Atlantic off South Africa and Namibia. The GClat for all bigeye stocks, except in the Atlantic Ocean in 2040-2059, shifts to the south and all the stocks expand their distribution areas. The relative abundance of skipjack tuna increases in most of the distribution area, especially in the western Atlantic Ocean, the Caribbean Sea, and the Bermuda region, similar to yellowfin (**Figure 2.4f**). Southward shifts occur in the Pacific and Indian Oceans and northward in the Atlantic Ocean. Expansions of the eastern Pacific, western Pacific, Indian, and eastern Atlantic stocks distribution areas are projected to occur by the mid-century. A contraction of the distribution is projected for the western Atlantic and western Pacific stocks by the end-of-the-century. Most of the stocks shift to the east except in the Indian Ocean and the western Atlantic.

Table 2.2: Gravity Center anomalies (GClat, in latitudinal and GClon in longitudinal degrees), North (N) and South (S) limits estimated with percentiles 95 (P95) and 5 (P5) for the six tuna species for mid- (2040-2059) and the end-of-the-century (2080-2099) related to the reference period.

Species	Stock	Ocean	GClon	GClat	N	S	GClon	GClat	N	S
Albacore	albI	Indian	0.38	-2.44	-3	-1.5	1.42	-4.78	-6.5	-2.5
	albM	Mediterranean	3.12	-0.65	-0.38	-1.87	-0.97	0.39	-0.5	1.4
	albNA	North Atlantic	3.34	1.97	2.98	1.5	7.49	3.2	4.84	2.23
	albNP	North Pacific	0.48	1.67	1.5	3.5	1.77	2.74	1.5	5.5
	albSA	South Atlantic	1.09	-2.5	-5.28	-1	2.65	-4.45	-9.28	-1.5
	albSP	South Pacific	0.32	-2.84	-5	-2	1.12	-4.98	-10	-3
Bigeye	betA	Atlantic	1.64	0.42	1.5	-2.21	3.47	-0.11	1.79	-2.75
	betEP	East Pacific	0.5	-0.41	1.85	-1.16	1.82	-1.74	2.3	-2.05
	betI	Indian	-0.28	-1.14	-0.11	-1.74	-0.16	-2.49	-0.89	-0.55
	betWP	West Pacific	1.98	-0.34	2.46	-2.34	4.08	-2.57	2.11	-3.01
A. bluefin	bftE	East Atlantic	11.65	-3.14	1.03	-14.74	14.36	-14.28	6.38	-33.46
	bftW	West Atlantic	0.51	-10.67	-0.35	8.01	6.87	-47.29	12.43	4.4
S. bluefin	sbt	Southern	-2.58	-0.63	-1	0	-5.93	2.29	3	0.5
Skipjack	skjEA	East Atlantic	1.65	1.51	5.2	-3.9	0.76	0.15	8.95	-6.99
	skjEP	East Pacific	0.21	-0.04	43.89	-3.33	0.83	-0.75	35.46	-6.92
	skjI	Indian	-0.93	-0.81	-0.65	-3.33	-1.58	-1.2	3.17	-7.38
	skjWA	West Atlantic	-0.44	0.68	-18.08	-4.59	-0.84	1.02	-11.92	-9.46
	skjWP	West Pacific	1.53	-0.18	5.68	-2.28	3.56	-1.21	-29.94	-5.48
Yellowfin	yftA	Atlantic	1.33	-0.27	0.08	-0.41	3.28	-1.13	-3.42	-0.05
	yftEP	East Pacific	0.06	0.18	0.5	0.3	0.99	0.38	1.39	-0.04
	yftI	Indian	-1.44	0.23	0.06	-0.44	-2.65	0.5	0.06	-0.46
	yftWP	West Pacific	1.83	-0.09	0.5	-0.5	3.96	-0.88	1.5	-1.5

2.3.3.2. Tuna abundance changes in the Exclusive Economic Zones

Our results projected important changes in tuna abundance in EEZs in the future (**Figure 2.5, Table 2.3 and S. Table 2.4** in **Appendix B**). All species except albacore, have the same trend for mid- and the end-of-the-century, with greater magnitude by the end. Albacore is projected to increase by 6% by 2050 then decreases by 6% by 2100, relative to the reference period. The relative abundance of albacore tuna decreases in most EEZs, except for some countries located close to its distributional limit. Both bluefin species (Atlantic and Southern) are projected to have the greatest depletion, reaching 60% in the case of Atlantic bluefin tuna by the end-of-the-century. Northern countries such as Norway, Greenland, Iceland, Canada, the United Kingdom, and Ireland have the greatest projected depletion in Atlantic bluefin tuna abundance in the future, with higher decreases by the end-of-the-century. Similarly, the abundance of southern bluefin tuna in the southern hemisphere countries' EEZ is projected to decrease. Bigeye tuna is projected to decrease in all EEZs, except in EEZs for a few high latitude northern and southern hemisphere countries such as Norway, Iceland, Canada, Argentina, Chile, New Zealand, South Africa, and some Northeast Atlantic countries (e.g. Portugal, Spain, France) where the abundance is projected to slightly increase. Skipjack and yellowfin tunas are the only species that are projected to significantly increase in the future (yellowfin is the most favored species almost doubling its relative abundance by 2100), despite the projected decrease in EEZs of a few countries such as Indonesia, Malaysia, Micronesia, Palau, Philippines, and Taiwan.

Table 2.3: Change in abundance (%) within EEZs for the mid- and the end-of-the-century in relation to the reference period for each tuna species.

Species	Mid-century (2040-2059)	End-century (2080-2099)
Albacore	6.58	-6.38
Bluefin tuna	-42.62	-62.62
Southern bluefin tuna	-22.87	-45.9
Yellowfin	43.37	92.12
Bigeye	-18.4	-34.84
Skipjack	27.05	57.36

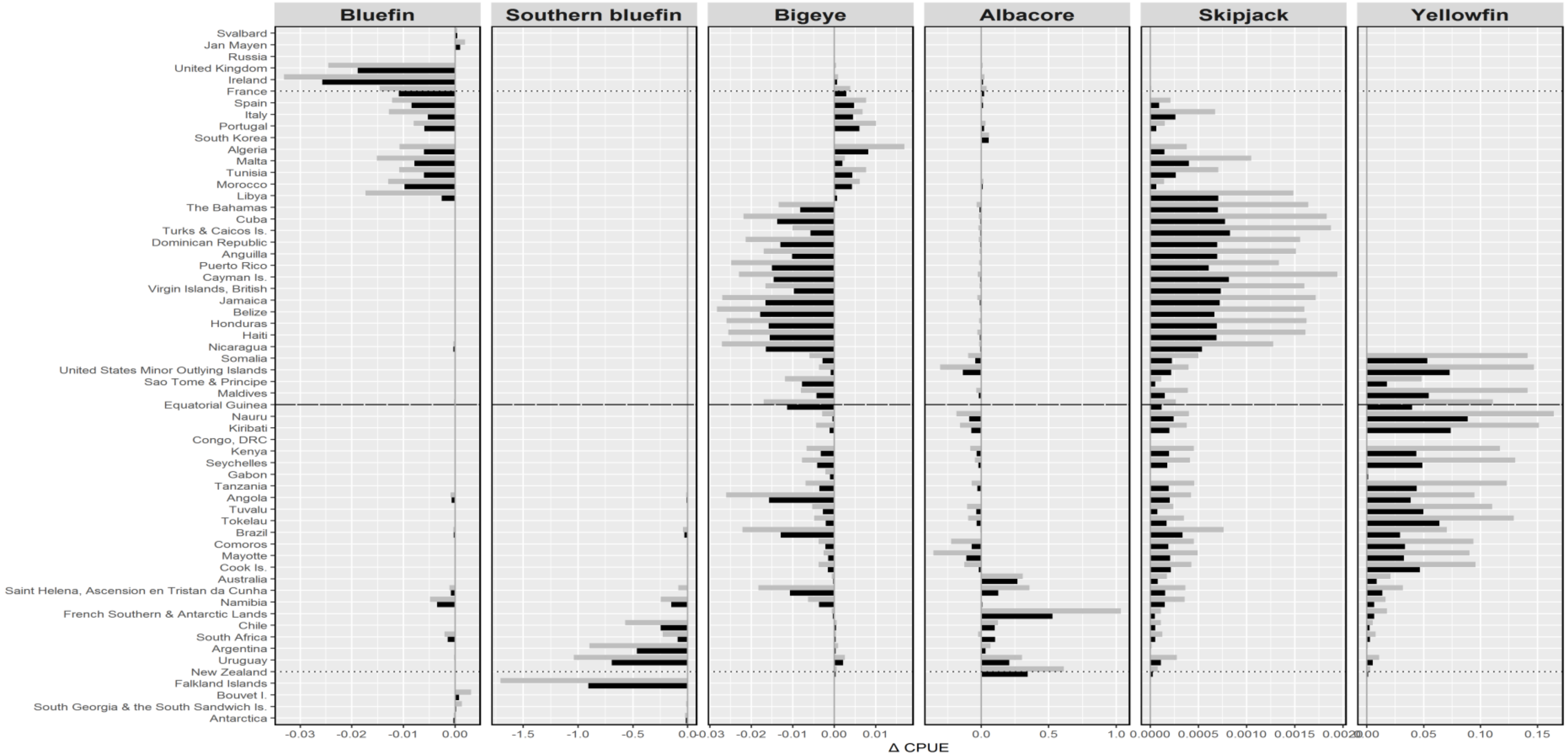


Figure 2.5: Changes in abundance (in CPUE units, tons per 1,000 hooks or individuals per 1,000 hooks in the case of southern bluefin tuna) for the main 10 countries or territories per species with the highest projected changes in the EEZs for mid-century (2040–2059) compared with the reference period (1980–1999). In order to reduce the number of locations such that names can be read, and the latitudinal patterns of changes can be visualized, a set of 10 unique countries with the highest change was selected for each species. If a country was already selected for one species, the next highest unique country for that species was selected and so on, until a unique top 10 list was selected. Across the six species, a total of 60 countries are shown here. Countries are ordered per mean latitude of the EEZ and dotted lines represent the equator (0°) and both 45° parallels (north and south). Numerical values for all countries are shown in Table S4

2.4. Discussion

Tuna habitat as modeled here has shifted poleward over the 1958-2004 period and is projected to continue shifting under climate change, with potentially important consequences for fisheries in coastal states and the countries that depend on them. We estimated a poleward shift in the suitable habitat of 89% of the temperate and 92% of the tropical tuna stocks between 1958 and 2004. Southern bluefin tuna was an exception as it shifted equatorward after 1980. For the same period, a decrease in the relative abundance of albacore was found between 10 and 40º N and 5 and 25º S. Southern bluefin also decreased its relative abundance in most of the latitudes.

We used Japanese longline fleet data because it has been the most consistent fleet fishing in all the oceans for the longest period of time. However, the catchability and availability of skipjack tuna for the Japanese fleet are very low, as seen in the low CPUE values, hence our model projected very small differences between tropical, subtropical and temperate waters habitat for skipjack. Moreover, the Japanese longline fleet catch mostly large fish of all species and the projected distributions should thus be considered as a proxy for the adult population.

Our method, based on the combination of presence/pseudo-absence and abundance models (AB), improved the prediction of the tuna habitat distribution and the relative abundances worldwide compared to the previous method by Arrizabalaga *et al.* (2015) although the deviance explained in the AB model is always slightly lower than in Arrizabalaga *et al.* (2015) due to the limitation that we imposed to the degree of smoothness (k=3). Our method has improved the species distribution models where presence data were not available (e.g. in areas where fish were not observed such as close to the poles).

2.4.1. Tuna distribution models and their reliability

In recent decades, species distribution models have been improved and applied to ecological problems on many species at different spatial and temporal scales (Robinson *et al.*, 2011). However, there are still some limitations to the development of SDM. For instance, predictive modeling of species distribution relies entirely on the assumption of environmental equilibrium between the biotic entities and the physical characteristics of their environment (Guisan & Theurillat, 2000). Our approach also assumes such equilibrium. Nevertheless, most studies that use SDMs neglect the time dimension to construct the model, thus, the cases where it is non-equilibrium in the environment triggers a direct bias in the species response curve. We used a long time-series dataset (47 years of tuna catch and effort data), therefore, the model covers a wide range of situations between environment and species occurrence, which improves the reliability of the species response curve. Fixed factors and their interactions were included in the CPUE model to correct for changes in abundance and/or catchability of tuna by the Japanese fleet (Arrizabalaga *et al.*, 2015). As in the study by Reygondeau *et al.* (2012), where tuna and billfishes were found rarely on continental shelves due to low spatial resolution (5 x 5 degree), coastal results need to be interpreted carefully in our global study. We partially avoided this problem by including results only for those countries with more than 30% of the cells with data within their EEZs. Only longline catch data were included in our model, so an important part of tuna catches is not represented in our models, especially for skipjack tuna that are caught largely by purse seine and, to a lesser extent, pole and line gears (Arrizabalaga *et al.*, 2012). In addition, our model is two-dimensional because it does not incorporate the depth distribution changes which could be important as fishes could change their vertical distribution, moving to deeper waters in response to ocean warming (Dueri *et al.*, 2014; Dulvy *et al.*, 2008; Perry *et al.*, 2005). Although the reliability of our models is high (deviances explained vary between 34.5 and 74.1% and AUC values of 0.784 and 0.838), the projections assume only the relationship between environmental variables and adult tuna distribution. Not all possible environmental variables which may affect tuna distribution were included in the model. For example, other variables such as oxygen (Gilman *et al.*, 2016; Lehodey *et al.*, 2011; Mislan *et al.*, 2017), pH (Lehodey *et al.*, 2011; Lehodey *et al.*, 2017; Nicol S *et al.*, 2016; Yokoyama *et al.*, 2004) or currents (Lehodey *et al.*, 2011) are potential influences on the cellular physiology, survival or condition during early life stages. Nevertheless, the geographic distribution of the species depends not only on their environmental tolerance but also on their thermoregulatory capacity (Brill, 1994; Lehodey *et al.*, 2011), dispersal capacity and biological interactions (Peterson *et al.*, 2011) such as predation (Guisan & Thuiller, 2005), intraspecific or interspecific competition, trophic relationships, and population dynamics. In addition, different responses to climate change impacts can desynchronize ecological interactions (Thackeray *et al.*, 2016). Furthermore, the mortality due to fishing, and recruitment process may have an important impact on the total biomass of the species – such mechanisms have been included in some regional models (e.g. Lehodey *et al.* (2013), Lehodey *et al.* (2018), Senina *et al.* (2016), Senina *et al.* (2018)). On a global scale, fishing and recruitment mechanisms are more complicated to include and remain a subject for future analysis when modeling the population shifts due to climate change.

2.4.2. Past distribution and abundance changes

We found a poleward shift in the suitable habitat of 20 out of 22 tuna stocks between 1958 and 2004. Some 89% of temperate tuna stocks shifted poleward but southern bluefin tuna was the exception as it shifted equatorward after 1980. In the same period, 92% of the tropical tunas shifted poleward to the south in the Pacific and Indian Oceans and poleward to the north in the Atlantic Ocean, except for yellowfin and eastern skipjack where no significant trends were observed. Similarly, Monllor-Hurtado *et al.* (2017) observed that tropical tunas (bigeye, yellowfin, and skipjack) longline catches decreased significantly in tropical waters and increased in sub-tropical waters from 1965 to 2011 due to a poleward shift in response to ocean warming. Atlantic bluefin tuna was captured in waters of east of Greenland in 2012, likely due to a combination of warm temperatures and mackerel immigration (MacKenzie *et al.*, 2014). Recently had also been demonstrated the prevailing influence of the Atlantic Multidecadal Oscillation (AMO) and how the climatic variability can modulate the distribution and abundance of this species (Faillettaz *et al.*, 2019). For many other fish species, the movement of the populations in the last decades has been associated with the latitudinal shift of their habitats (Beare *et al.*, 2004; Bruge *et al.*, 2016; Montero-Serra *et al.*, 2015; Perry *et al.*, 2005). Consistent with this movement, the species composition in marine fisheries has changed due to climate change; the dominance of warmer water species has increased at higher latitudes and the proportion of subtropical species has decreased in the tropics (Cheung *et al.*, 2013b). Range contractions and abundance declines have also been recorded for larger tuna and billfish species (Worm & Tittensor, 2011).

Fewer tuna stocks shifted longitudinally (10 out of 22), moving westward in the Indian, East Pacific, and South Atlantic oceans and eastward in the north, west and east Atlantic, Mediterranean and West Pacific. Some studies related the longitudinal shift of skipjack with climatic indices such as El Niño Southern Oscillation (ENSO) in the Pacific (Lehodey, 2001; Lehodey *et al.*, 1997) and a long-term eastward shift is projected to the central-eastern Pacific (Bell *et al.*, 2013a). Our study considered the six species at global scale, which may explain the low correlation between longitudinal stock shifts and climatic indices (see section 2.4.1) such as El Niño in the Pacific.

The species distribution models can predict occurrence probability in areas where the species has not been observed or caught. For example, favorable habitat is projected for Atlantic bluefin tuna in the South Atlantic Ocean (below 45º S), and likewise for yellowfin and bigeye tunas in the Mediterranean Sea. This suggests that the environmental conditions (limited to those studied in this analysis) in these areas are favorable for those species, but for some reason, they do not occupy them. In contrast, the SDM models can also predict low occurrence or absence where a species has been observed due to low longline CPUE (e.g. southern bluefin tuna) or where the model cannot discriminate between areas of high/low habitat suitability due to low contrast in the CPUE signal (e.g. low skipjack catchability of the Japanese longline). In the case of southern bluefin tuna, for example, there has been little Japanese longline fishery in the spawning ground in tropical waters of south of Java and off the northwest coast of Australia since 1960s (Grewe *et al.*, 1997) which could have affected the relationship between the environment and subsequent habitat suitability projections of the model (i.e. low suitability or absence whereas some catches are observed). We also found a poleward shift between 1965 and 1979 for southern bluefin tuna and a subsequent northward shift that is difficult to explain, as it is not related to climate variability (i.e. climate indices). Additional climate change investigation for this species is warranted.

Concerning habitat changes, the less suitable habitat was found mainly for albacore and southern bluefin tunas over the last 50 years. Juan-Jordá *et al.* (2011) found the highest population declines for temperate tunas throughout the period 1954-2006 and these changes were attributed to their high exploitation level. However, the habitat losses described in this paper might have also contributed to these declines. We found an increase in suitable habitat for yellowfin, bigeye, and Atlantic bluefin tunas and a small change in skipjack tuna habitat between 1958 and 2004. Some studies estimated that the tropical tunas are fished down to approximately maximum sustainable levels, which prevents further sustainable expansion of catches in these fisheries (Juan-Jordá *et al.*, 2011). However, a significant increase in tuna fisheries occurred in the 1970's due to the expansion of global fisheries and the development of new offshore fishing grounds (FAO, 2011). The improvement of the suitable habitat during the last decades for these species might have also partially contributed to this expansion.

2.4.3. Future projections and implications for fishing countries

Future projections under different climate change scenarios are crucial to anticipate the impacts on populations of target species (Dueri *et al.*, 2014; Lehodey *et al.*, 2013), the changes in predator-prey relationships, the impacts on human services and fisheries (Bell *et al.*, 2013b; Cheung *et al.*, 2013b; Cheung *et al.*, 2009b; Dueri *et al.*, 2016), and to identify the most vulnerable nations (Allison *et al.*, 2009; Barange *et al.*, 2018).

Although models are useful tools to project future trends and expected impacts, they also have limitations. We are estimating the future potential distribution and relative abundances solely due to environmental change, but other processes that are not included in the model such as population and fisheries dynamics and trophic interactions. These components are important since they can amplify the warming signal throughout the food web (Chust *et al.*, 2014a; Kwiatkowski *et al.*, 2018). We only projected changes in tuna habitat for the RCP8.5 IPCC AR5 climate change scenario, but changes for other scenarios (RCP 2.6, 4.5 and 6.0) are expected to be similar until around 2050 when they diverge (Hoegh-Guldberg *et al.*, 2014; IPCC, 2013). Tuna habitat projections for the end-of-the-century for other climate scenarios are likely to be between the values estimated for mid- and end-of-the-century in our models (Smith *et al.*, 2011). In addition, and according to the IPCC AR5 (IPCC, 2013), all RCP scenarios are equally likely to occur. The confidence of a projected variable is related to the variable or parameter studied and the period in which the projections are made rather than with the climate change scenario chosen. In addition, as an average of 16 models is used for our projections (ensemble), a homogenization of the species distribution pattern can occur relative to using only one model or focusing in one ocean, which may also reduce apparent relationships to climate drivers such as ENSO.

Temperate tunas and bigeye are expected to decrease at low latitudes and shift poleward. Tropical tunas such as yellowfin and skipjack are projected to increase in relative abundance in the equatorial areas of the main oceans. Our projections, showing that skipjack potential habitat will increase in the future, partially agree with Senina *et al.* (2016), who projected different future situations depending on the model (from a 50% decrease to no change in abundance due to the compensation between the increasing biomass in the tropics and decreasing biomass in the equatorial warm pool). Recent work by Senina *et al.* (2018) projected an overall decrease of yellowfin and skipjack in many Pacific Islands EEZ's by 2050, while our results suggest an increase in most EEZs. This disagreement is likely explained by the differences in the modeling approaches in both studies, such as i) the number of IPCC ensembled models used for projections (16 in our model vs 4 in Senina *et al.* (2018)), ii) selected environmental parameters considered in the models (i.e. oxygen and pH were not considered in our models), iii) the source of fishery data used in the models (only longline, focused mostly on large individuals, in our model vs various fishing gears targeting a wider range of sizes), iv) modeled variable (CPUE in our model vs biomass) and v) the spatial resolution (oceanwide in our model vs Pacific basin scale in Senina *et al.* (2018). However, our results are in agreement with Lehodey *et al.* (2013) and Dueri *et al.* (2014) who projected a slight increase of skipjack abundance in the Western Central Pacific Ocean until 2050 followed by a decrease after 2060. They also projected that the habitat becomes more favorable in the Eastern Pacific Ocean and in higher latitudes, while the western equatorial warm pool would become less favorable for spawning, which agrees with our results. According to our analysis, Atlantic bluefin tuna abundance is projected to decrease across most of its geographical range and to expand northward by the end-of-the-century. This is in agreement with Muhling *et al.* (2017b) who projected temperature-induced reductions in tropical and sub-tropical Atlantic and an improvement in subpolar habitat suitability. This redistribution has implications for spawning and migratory behaviors, and availability to fishing fleets (Muhling *et al.*, 2017b). This northward shift might allow fishing in more northern latitudes (MacKenzie *et al.*, 2014) but also the southern Atlantic habitat is projected to improve. In the past, this species occurred also in the southern Atlantic, until the “habitat bridge” linking both hemispheres was interrupted in the late 1960s (Briscoe *et al.*, 2017; Fromentin *et al.*, 2014). The projected improvement in southern Atlantic habitat might only result in Atlantic bluefin tuna reappearance if the tropical habitat bridge is restored. Similarly, southward shifts are expected for 14 other large pelagic species (including tunas) for the east and west Australian coast for the end-of-the-century with a decrease in their distribution area (Hobday, 2010).

These shifts have implications for fishing countries. A redistribution of global catch potential is expected under climate change scenarios, increasing on average 30–70% in high-latitude regions and decreasing up to 40% in the tropics (Cheung *et al.*, 2009b). The strong interactions between fishing and climate require management to adapt the fishing mortality to guarantee sustainable populations, stabilize catches and profits and reduce collateral impacts on marine ecosystems (Brander, 2007; Juan-Jordá *et al.*, 2011). This occurs when only abundance is expected to decline in the future, but when future projections involve changes in distribution (with gains and losses in suitable habitat areas), there is also a potential for increases in tuna population size (Hobday, 2010).

Many of the countries that are more vulnerable to the impacts of climate change on their fisheries are also the poorest and are located in the tropics (Allison *et al.*, 2009; Barange *et al.*, 2018; Barange *et al.*, 2014). The greatest impacts are projected over the nations of South and Southeast Asia, Southwest Africa (from Nigeria south to Namibia), Peru and some tropical small-island developing states (Barange *et al.*, 2014). These fisheries-dependent developing nations rely on their fisheries sector in terms of wealth, food and employment, and they have limited capacity to invest in climate adaptation (Allison *et al.*, 2009; Barange *et al.*, 2014). Changes in catch potential and composition have direct implications for coastal fishing communities and this emphasizes the need to develop adaptation plans to minimize the impacts of global climate change on the economy, local fisheries and food security in many countries (Barange *et al.*, 2018; Cheung *et al.*, 2013b). Efforts to adapt to climate change should be planned, including adaptation to possible redistribution and decrease/increase of abundance of target species. Additional measures or actions taken in response to climate change should complement and strengthen the overall governance and sustainable use of marine resources (Barange *et al.*, 2018). Tuna is an important source of protein in many countries and the expected increase in their abundance for Pacific nations, as well as other countries, is a possible solution to fill the anticipated gap in protein (Allison *et al.*, 2009; Bell *et al.*, 2015; Gillett *et al.*, 2001). However, other studies such as Senina *et al.* (2018) project that climate change will both positively and negatively affect tuna abundance in Pacific Islands EEZs’ by 2050, with decreasing abundance in the west and slightly increasing abundance in the eastern Pacific. The catch decreasing would result in less revenue from license fees for the Pacific Island countries (unless practical ways can be found to increase the value of catches, Bell *et al.* (2018b)). Nevertheless, the tuna catches in those countries might be enough for domestic food security, especially if management plans are oriented to reallocate more of the tuna caught within the EEZ for supplying local consumption.

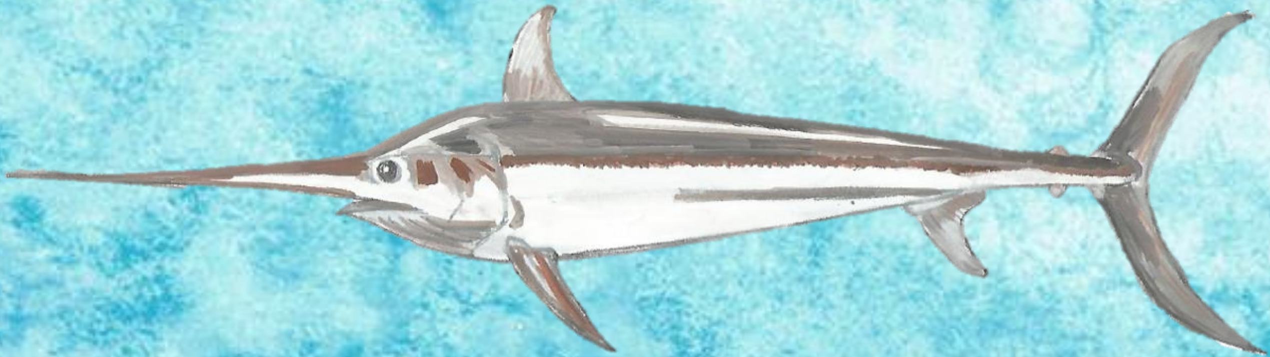
The average catches for all the temperate tuna species (albacore, Atlantic and southern bluefin) and the tropical bigeye are expected to decrease in the future in tropical EEZs, but to increase in the countries located in the boundaries of the suitable area. In contrast, catches for other tropical tuna species (yellowfin and skipjack) are expected to increase in most of the tropical EEZs. However, a large amount of tuna catches corresponds to high seas, which by 2012 and together with billfishes, represented 9.3% of global annual marine fisheries catches (FAO, 2014b; Juan-Jordá *et al.*, 2011). In addition, a persistent suitable habitat for longline occurs within the tropical and temperate latitudes in the high seas, which is consistent with the global latitudinal patterns of the six tuna species (Ortuño-Crespo *et al.*, 2018). Nevertheless, high seas catch affect different fleets and our analysis was limited to countries EEZ. Our results are consistent with Bell *et al.* (2013b), with 82.4% agreement in the trend in skipjack abundance within EEZs of Pacific Island countries and territories (PICTs) (**S. Table 2.5** in **Appendix B**). The level of agreement with skipjack tuna abundance changes in PICTs projected by Senina *et al.* (2018) is lower (67.5%), probably due to the differences between the models and data sets as explained above (**S. Table 2.5** in **Appendix B**). They estimated changes for 2050 and 2100 relative to the 20-years average from 1980-2000 under the A2 emissions scenario (slightly lower emissions levels than the RCP8.5 in IPCC AR5, Rogelj *et al.* (2012)). We projected a decrease in skipjack tuna in the Palau EEZ for both periods, while Bell *et al.* (2013b) expected an increase by 2050 and a decrease by 2100. The other exceptions were the Solomon Islands and Papua New Guinea where our model projected an increase in abundance and Bell *et al.* (2013b) projected a decrease. Changes in catch potential estimated by Cheung *et al.* (2009b) based on 1066species showed similar latitudinal patterns for temperate tunas and bigeye in our study. They expected gains in some high-latitude countries/regions in the northern hemisphere while losses in many tropical and subtropical countries/regions. The highest catch potentials were projected for the northern Atlantic Ocean countries such as Norway, Greenland, and Iceland with an increase of 18–45%, followed by the northern Pacific Ocean (Alaska and Russia) with 20%. In contrast, the catch potential from most other EEZ countries (most of them in tropical and subtropical regions) diminish, with the largest decrease projected in Indonesia (Cheung *et al.*, 2009b).

Changes in the distribution of tuna in different countries may have implications for global food security and strongly impact many tropical communities, which are strongly dependent on local fishing resources (Allison *et al.*, 2009; Bell *et al.*, 2018c; Cheung *et al.*, 2009b). Thus, the generation of knowledge in the most vulnerable countries to climate change is an important research task. Further analysis should focus on the local impacts that the distribution and abundance changes of tunas have on small fisher communities and the adaptation mechanisms needed to diminish those impacts. Such adaptation strategies could involve shifts in fishing areas, changes in target species, and/or changes in fishing agreements (Barange *et al.*, 2018) and must be developed in partnership with affected nations.

CHAPTER 3

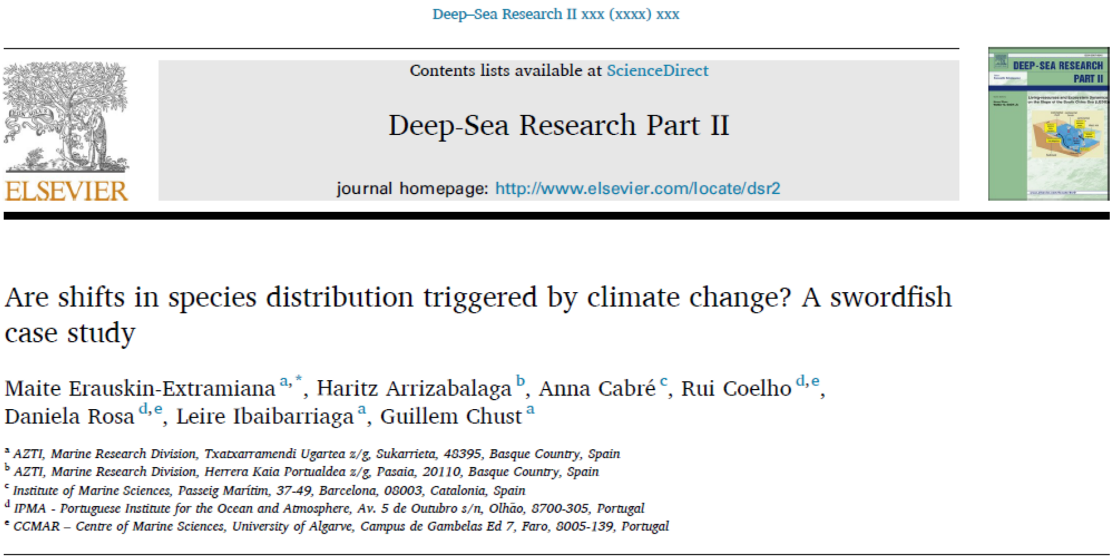
Are shifts in species distribution triggered by climate change?

A swordfish case study



3. CHAPTER 3:

Are shifts in species distribution triggered by climate change? A swordfish case study



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Are shifts in species distribution triggered by climate change? A swordfish case study

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3.1. Introduction

Global climate change is redistributing life on Earth (Pecl *et al.*, 2017). The most evident response of species to climate stimuli are the shifts in geographic distribution in order to track preferred environmental conditions (Bruge *et al.*, 2016; Burrows *et al.*, 2011; Monahan & Tingley, 2012; Pecl *et al.*, 2017; Randin *et al.*, 2009). Generally, poleward distribution shifts towards higher latitudes are being recorded globally (IPCC, 2014c; Poloczanska *et al.*, 2016; Portner & Peck, 2010). On land, some species are moving to cooler, higher elevations (Chen *et al.*, 2011; Kelly & Goulden, 2008; Wilson *et al.*, 2005). In the ocean between 81-83% of all observations for the distribution, phenology, community composition, abundance, and demography are consistent with the expected impacts of climate change (Poloczanska *et al.*, 2016) moving to colder waters and greater depths (Dueri *et al.*, 2014; Dulvy *et al.*, 2008; Perry *et al.*, 2005). Different species respond at different rates and varying degrees. As a consequence, key interactions among species are often disrupted and new interactions are developed (Pecl *et al.*, 2017).

Species distribution models (SDM), also called habitat or niche-based models (Anderson *et al.*, 2002), associate known presence locations of the target species with the characteristics of the environment to predict their potential geographical distribution (Elith *et al.*, 2006; Guisan & Zimmermann, 2000). In recent years, predictive modeling of species distribution has become an increasingly important tool to address various issues in ecology, biogeography, evolution and more recently, in conservation biology and climate change research (reviewed in Guisan and Thuiller (2005)). Specifically, habitat predictions present opportunities for quantifying spatio-temporal distribution changes while accounting for sources of natural climate variation (Champion *et al.*, 2018). Common approaches to detect species range shifts investigate the geographic center of the population's distribution or Center of Gravity (CoG), distribution limits and area occupied (Thorson *et al.*, 2016; Woillez *et al.*, 2009).

Historical trend analyses of species distribution might be limited due to the nature of the raw data used (Chust *et al.*, 2014b). When data have non-homogeneous spatial and temporal coverage (e.g. most fishing data, historical collections), the conventional estimators such as the abundance-weighted average (AWA) indices (e.g. CoG or distribution boundaries), may confound changes in the distribution of sampling effort with changes in species distribution (Thorson *et al.*, 2016). Data from research surveys are considered more homogeneous and consistent to use in historical trend analyses than catch or collection data (Green & Green, 1979). However, in some cases, scientific survey data do not have homogeneous spatio-temporal coverage (e.g. Bruge *et al.* (2016), or data in chapters 1 and 2), due to variations in the spatial distribution of sampling through time. Attempts have been made to correct this bias, and an example applied to copepods can be found in Chust *et al.* (2014b). Using simulated data, Thorson et al. (2016) formalized the approach and proposed to calculate shifts using a spatio-temporal model (STM) to reconstruct the species distribution instead of using observed occurrence or abundance data. STM approach estimates the expected density of the population within a spatial domain based on available data and as a function of spatial (longitude and latitude) and temporal (year and season) factors (Thorson *et al.*, 2016). Changes in distribution estimators of the STM, such as the CoG of the population were analyzed; the average location in the latitude of the species for each unit of time (e.g. year) weighted by the species abundance measured at each location (Bez & Rivoirard, 2001). This approach has several benefits in comparison with distribution estimations based on occurrences as it allows the use of different sources of data and can account for changes in spatial distribution of sampling effort (Thorson *et al.*, 2016).

In this paper, we propose a framework that helps to disentangle the causes of the species shifts by analyzing the climate impacts and correcting for the sampling effort bias in data. We developed a framework to ascertain whether the changes in the spatial distribution of species are due to habitat changes, fishing activity or other ancillary factors. The framework is based upon the analyses and comparison of historical trends in species distribution latitudinal shifts among raw data (sampling effort, observed species occurrence and abundance) and species distribution based on the habitat model and the spatio-temporal reconstruction of the population abundance. In the proposed framework, species distribution estimated from raw data (occurrence or abundance) could be used only in those cases in which the sampling (or fishing) effort is homogeneous with time. When the distribution of fishing effort changes with time, a spatio-temporal reconstruction is needed to correct for bias caused by sampling and will be used to estimate those changes and to disentangle the reasons behind them.

We applied this new framework to swordfish (*Xiphias gladius*, Linnaeus, 1758). This species was selected because it has a wide distribution from tropical to cold waters of all oceans, including the Mediterranean Sea (Chow *et al.*, 1997; Nakamura, 1986). It is divided into six stocks for management purposes (Mediterranean Sea, swoM; Indian Ocean, swoI; North Atlantic, swoNA; South Atlantic, swoSA; North Pacific, swoNP and South Pacific, swoSP) which can have different responses to environmental changes. For each swordfish stock, we applied the defined framework to identify the historical shifts of the center of gravity of the stock distribution from 1958 to 2004 and the potential drivers of these changes. Subsequently, we projected the future distribution for the mid (2040-2059) and the end-of-the-21st-century (2080-2099) under the RCP8.5 climate change scenario, which is the highest greenhouse gas concentration scenario with 936 CO2 ppm by the end of the century (IPCC, 2013).

3.2. Material and methods

3.2.1. Detection and attribution of species shifts

Based on previous works (Chust *et al.*, 2014b; Thorson *et al.*, 2016), we developed a framework for analyzing shifts in the species distribution, and to ascertain if such shifts were habitat-driven (see **Figure 3.1**). To test whether distribution shifts along time are due to changes in the habitat conditions, we computed the latitudinal CoG for the following five different raw data historical time-series and model-based reconstructions (observed species presence/absence and abundance, sampling effort, predicted spatio-temporal and habitat model, **Figure 3.1**). Temporal trends in CoG were assessed by fitting a regression model (in this case and for swordfish we used a linear model) and testing whether the trend coefficients are significantly different from zero. The trend analyses in CoGs were estimated from the five different data described in detail below:

1) *Sampling effort*: presences and real absences of the sampling at each location each year. In our case we considered the fishing locations to represent sampling effort.
2) *Raw observed population occurrence:* only species presences (or positive catch data) were considered.

3) *Raw observed population abundance*: only species positive occurrence data weighted, or abundance were considered (for instance, CPUEs in the case of fisheries catch data).
4) *Habitat or niche-based model:* this model represents the environmental habitat preference of the species. It is built using environmental variables and the CoG trends estimated from this model represent the shift in species distribution and abundance only due to environmental changes (changes in their habitat).
5) *Spatio-temporal reconstruction model (STM)*: this model predicts species distribution and abundance based on spatial and temporal variables. Due to possible changes in sampling (fishing effort), target species occurrences and/or abundances (catches in the case of fishing data) need to be analyzed as a function of year, latitude and longitude to account for changes in the distribution of effort through time (Chust *et al.*, 2014b; Thorson *et al.*, 2016). This approach estimates the expected density of the population in all locations within a spatial domain defined by the available data. Using General Additive Models (GAMs), the essential component to reconstruct the spatio-temporal species distribution is a bivariate smooth term allowed to change yearly, *s(long, lat, by=year)*. In the case of swordfish, specifically, the spatio-temporal reconstruction used additional terms to improve the model and account for population differences: season, stock (a term included to account for differences between swordfish populations) and their interactions. The environmental variables are included in the model to improve its accuracy. However, to prevent environmental trends affecting the distribution trends of the reconstructed species model, environmental variables were averaged for the overall period and introduced as a constant habitat trough time.

In the proposed framework (**Figure 3.1**), if sampling CoG estimated from raw data had no significant trend because there are no changes in sampling effort in space and time, then, historical trend estimated from the occurrences (positive records) of the species are considered representative of changes in population distribution. However, we also estimate the CoG trend of the STM and compare this with the raw data to detect possible inconsistencies between both trends. The spatio-temporal CoG should match the observed CoG, otherwise, the model could be unreliable, probably due to scarcity of data and/or inappropriate model fitting and it should be revised. By contrast, if there is a trend in the CoG of sampling, we cannot rely on the CoG of observed presence data and we need to look at the reconstructed CoG from the STM. To ascertain the causes of the trends in population from STM, both are compared with the habitat model trend. In cases where CoG trends estimated from habitat model and STM are statistically significant and have the same sign (positive or negative), this potentially indicates niche tracking. In the situation where the CoG trend of STM is substantially different from that of the habitat model, the population shift is due to other causes not related to environmental changes. Therefore, there is no niche tracking.

In some cases, the variation of CoG through time (e.g. STM) might not be linear but can covary with the CoG of another model (e.g. habitat). With the aim of obtaining more information which helps to disentangle the nature of each trend and its causes, the correlation matrix between the CoG of models and data was estimated. The matrix shows the magnitude and sign of the correlation between different trends and therefore, the relation between them that sometimes is lost in the linear trends.

We used Generalized Additive Models (Hastie & Tibshirani, 1990) to model habitat preferences and reconstruct the spatio-temporal distribution of swordfish. Prior to model building, we tested for collinearity between explanatory variables by calculating variance inflation factors (VIF) (Zuur AF *et al.*, 2009), where any variable > 5 were excluded, repeating the process until all variables had < 5.

A two-step approach, as described in Borchers *et al.* (1997) for horse mackerel (*Trachurus trachurus*), in chapter 1 for anchovy (*Engraulis encrasicolus*) and in chapter 2 for main commercially tuna species, was adapted and used here for swordfish. Two models were built, namely: 1) the presence/pseudo-absence (PA) model, assuming a binomial error distribution with a logit link function to estimate the relative probability of occurrence, and 2) an abundance model (AB) using log-transformed positive CPUE observations as response variable, assuming Gaussian error distribution and identity link, which was used to predict abundance conditional on the positive presence of swordfish. The conditional abundance predictions is the product of the relative probability of occurrence from the PA model and the relative abundance estimated from the AB model (PA * AB) after back-transforming the logarithm of the CPUE to the original CPUE scale. Real absences are limited to the area fished, and there is no information out of these areas. Therefore, we generated pseudo-absences as presences. Barbet-Massin *et al.* (2012) recommend the use of a large number (e.g. 10,000) of pseudo-absences with equal weighting for presences and absences when using regression techniques (e.g. generalized additive model). Thus, we generated the same number of pseudo-absences as presences (Barbet-Massin *et al.*, 2012) randomly distributed worldwide (Iturbide *et al.*, 2015). In addition, the fixed factors, namely year, season and stock as well as their interactions up to third order were considered in the model, to separate the environmental effects from those due to potential changes in catchability, abundance, or differences in data collection and/or reporting between different tRFMOs (Arrizabalaga *et al.*, 2015; Schirripa *et al.*, 2017).

Model selection was conducted using the *dredge* function of the 'MuMIn' R-package (Barton, 2016). This function generates a subset of models with different combinations of variables of the global model and selects the one with the highest deviance explained with the lowest number of variables based on the AIC (Akaike Information Criterion) (Guisan & Zimmermann, 2000; Sakamoto *et al.*, 1986). Model validation for presence/pseudo-absence was conducted with a k-fold cross-validation procedure (Burnham & Anderson, 2003), using k=5 equally sized sub-datasets (Hijmans *et al.*, 2013), whereas the R-squared value was calculated between the observations and predictions for the abundance model. For the PA model, a ROC (Receiver Operating Curve) analysis was undertaken with the calculation of the AUC (Area Under the Curve). The threshold for the cut-off point was selected for which the sensitivity (true predicted presences) was equal to the specificity (true predicted absences) (Jiménez-Valverde & Lobo, 2007), and used to convert the calculated model probabilities into either presence or absence categories (above or below the threshold, respectively). Accuracy in the PA model was evaluated with the confusion matrix accuracy assessment (VanDerWal *et al.*, 2012). For both models (PA and AB), the deviance explained was analyzed and reported and Analysis of the Variance (ANOVA) was also conducted to see the most important variables.

3.2.2. Case of study: swordfish

Swordfish is the most widely distributed species of billfish, occurring in tropical, subtropical and temperate waters from 45º N to 45º S (Palko *et al.*, 1981; Sakamoto *et al.*, 1986). Swordfish are large, reaching lengths of 3 m (Collette, 1995) and weighing 650 kg (Nakamura, 1986), highly migratory (FAO, 1994) and predatory fishes. It is an important fisheries target and by-catch species (Ward & Elscot, 2000) and it is considered as Least Concern (LC) by the IUCN Red List, although the population abundance is decreasing (Collette *et al.*, 2011). This species has shown a 28% decline over a three-generation (20 year) period (Collette *et al.*, 2011). Some assessments carried out in recent years seem to indicate that total and spawning biomass are above levels that would maintain maximum sustainable yield (MSY), including in the Pacific Ocean (Hinton *et al.*, 2005; Kolody *et al.*, 2006), North Atlantic (ICCAT, 2017) and Indian Ocean (IOTC, 2017). Other indicators, such as average size or catch rates in certain areas and fisheries, have raised concerns about fishery sustainability (Abascal *et al.*, 2009). Most of the uncertainty associated with the assessments of swordfish is attributable to the scarce information on the biology of the species, such as on stock-recruitment relationships, mortality, age-at-first-maturity, and stock structure (Abascal *et al.*, 2009).

Swordfish longline catch and effort data for the Atlantic, Indian and Pacific Oceans were obtained from four tuna Regional Fisheries Management Organizations (tRFMOs) (Arrizabalaga *et al.* (2015), specifically: International Commission for the Conservation of Atlantic Tunas (ICCAT, www.iccat.int), Indian Ocean Tuna Commission (IOTC, www.iotc.org), Western and

Central Pacific Fisheries Commission (WCPFC, www.wcpfc.int), and Inter-American Tropical Tuna Commission (IATTC, www.iattc.org). Only catch data from the Japanese fleet was used in the subsequent analyses because it is the main fleet that has operated consistently worldwide since the late 1950s and has an extended spatio-temporal coverage. The only exception was the case of the WCPFC where fleet specific information was not available. Catch (tonnes) and effort (number of hooks) data were obtained from 1950 to 2012, except for the eastern Pacific where data were only available until 2004. Nominal Catch Per Unit Effort (CPUE, swordfish tonnes per 1000 hooks) between 1958 and 2004 was calculated as the ratio of catch (tonnes) to the number of hooks, which was then used as a proxy of relative fish abundance. Catch data were aggregated to the broadest resolution (by season and 5º x 5º degree spatial resolution) because the spatio-temporal resolution between sources of data was heterogeneous.

3.2.3. Environmental data

Historical environmental data were obtained from the PISCES biogeochemical model (Pelagic Interaction Scheme for Carbon and Ecosystem Studies; Aumont and Bopp (2006)). The following environmental variables were considered: sea surface temperature (SST in ºC), sea surface salinity (SSS in PSU), sea surface height (SSH, in m), mixed layer depth (MLD, in m) and log-transformed phytoplankton concentration (log(phyto) in mmol m^{-3}). All the environmental variables were averaged to the same spatial (5º x 5º) and temporal (season) resolution as the fishery data.

Data for future oceanographic conditions were extracted from the average of 16 models in the Fifth Assessment Report of the Intergovernmental Panel on Climate Change (IPCC AR5; IPCC5), which contain a coupled biogeochemical model (hereinafter Ensemble) with a mean ~1º spatial resolution (Cabré *et al.*, 2015). The variables used for future predictions were the same as for the swordfish model (SST, SSS, SSH, MLD, and phytoplankton). Swordfish habitat distribution and relative abundance projections were conducted under the highest greenhouse gas concentration scenario (RCP8.5 with 936 CO_2 ppm by the end of this century) of the AR5 IPCC (2013) for the mid (2040-2059) and the end-of-the-21st-century (2080-2099). This climatic scenario was selected because it is the "business as usual" scenario, assuming current emission practices, for the purposes of estimating the worst consequences of climate change.

3.2.4. Future projections and changes

To study the future impact of climate change on swordfish distribution and relative abundance, projections of the habitat model for the mid (2040-2059) and the end-of-the-21st-century (2080-2099) were compared with estimates for the reference period (1980-1999).

Future projections were performed at each level of each of the fixed factors (year, season and stock) and then averaged to represent the spatial distribution and relative abundance of swordfish at each location, given an average abundance and catchability condition.

3.3. Results

3.3.1. Swordfish distribution models

Since not enough collinearity was found between environmental variables (SST= 1.46; SSS= 1.28; log(phyto)= 1.25; SSH= 1.08 and MLD= 1.31), all of them were included in the model. The Presence/pseudo-Absence (PA) and Abundance (AB) habitat models explained 43.05% and 38.03% of the total deviance of the occurrence and relative abundance of swordfish, respectively (**Table 3.1**). The number of pseudo-absences randomly generated were weighted with the number of presences (60,273). Model cross-validation indicates that the predictive power of the PA model is high with an AUC mean (± standard deviation) of 0.816±0.003, a sensitivity of 0.863±0.002 and a specificity of 0.769±0.003. The threshold value to convert the estimated model probabilities into either presence or absence categories was 0.57. For the AB model, an R-squared averaged value of 0.33±0.3 was obtained. The final PA model selected included all the variables except the three-way interaction and the season:year interaction, while the abundance model included all the variables (**Table 3.1**). The ANOVA showed that in the PA model, the temperature was the most important variable (**S. Table 3.1a** in **Appendix C**). However, in the AB model, the most important variable was the phytoplankton (**S. Table 3.1b** in **Appendix C**). The STM showed higher deviance explained in both the PA and AB models (52.2% and 54.0% respectively) than the habitat model. Accordingly, the STM cross-validation values were higher (AUC of 0.844±0.004, for a sensitivity of 0.893± 0.003 and a specificity of 0.796±0.007, and an R^2 of 0.46±0.04), with a threshold value to convert occurrence probabilities into presence or absence lower than in the habitat model (0.52). The ANOVA in the STM showed the same pattern as in the habitat model; the temperature was the main variable in the PA model (**S. Table 3.1c** in **Appendix C**), while in the AB model it was the phytoplankton followed by the temperature (**S. Table 3.1d** in **Appendix C**).

GAMs identified clear ranges in certain environmental variables that defined the presence/absence and/or abundance of the swordfish niche model. For instance, the probability of swordfish presence below 15ºC is low, while swordfish abundance showed a maximum at 20-25ºC. Salinity explained more of the distribution of swordfish presence (PA model) than of abundance. Higher swordfish abundance was observed at increasing mixed layer depth values and decreased as sea surface height anomalies became positive. Swordfish presence was maximum at medium values of phytoplankton concentration, but abundance continued increasing at higher values. The response curves of both models differ in their shape for each variable (**S. Figure 3.1** in **Appendix C**).

The combination of PA and AB habitat models provides the swordfish distribution with its environmental preferences (**Figure 3.2a**). The model suggests a higher probability to find larger concentrations of swordfish in the Atlantic, based on its environmental characteristics, compared to other oceans. Optimum swordfish habitat is generally between 45ºS and 45ºN, except in the North Atlantic where it extends farther north, up to 60ºN, and appears in areas with major primary productivity (i.e. upwelling areas in the west coast of Africa, Iberian Peninsula and South and North America). The highest abundances in the STM were found in tropical areas at around the Greenwich meridian, in the Atlantic Ocean and in the Southeast Pacific (**Figure 3.2b**).

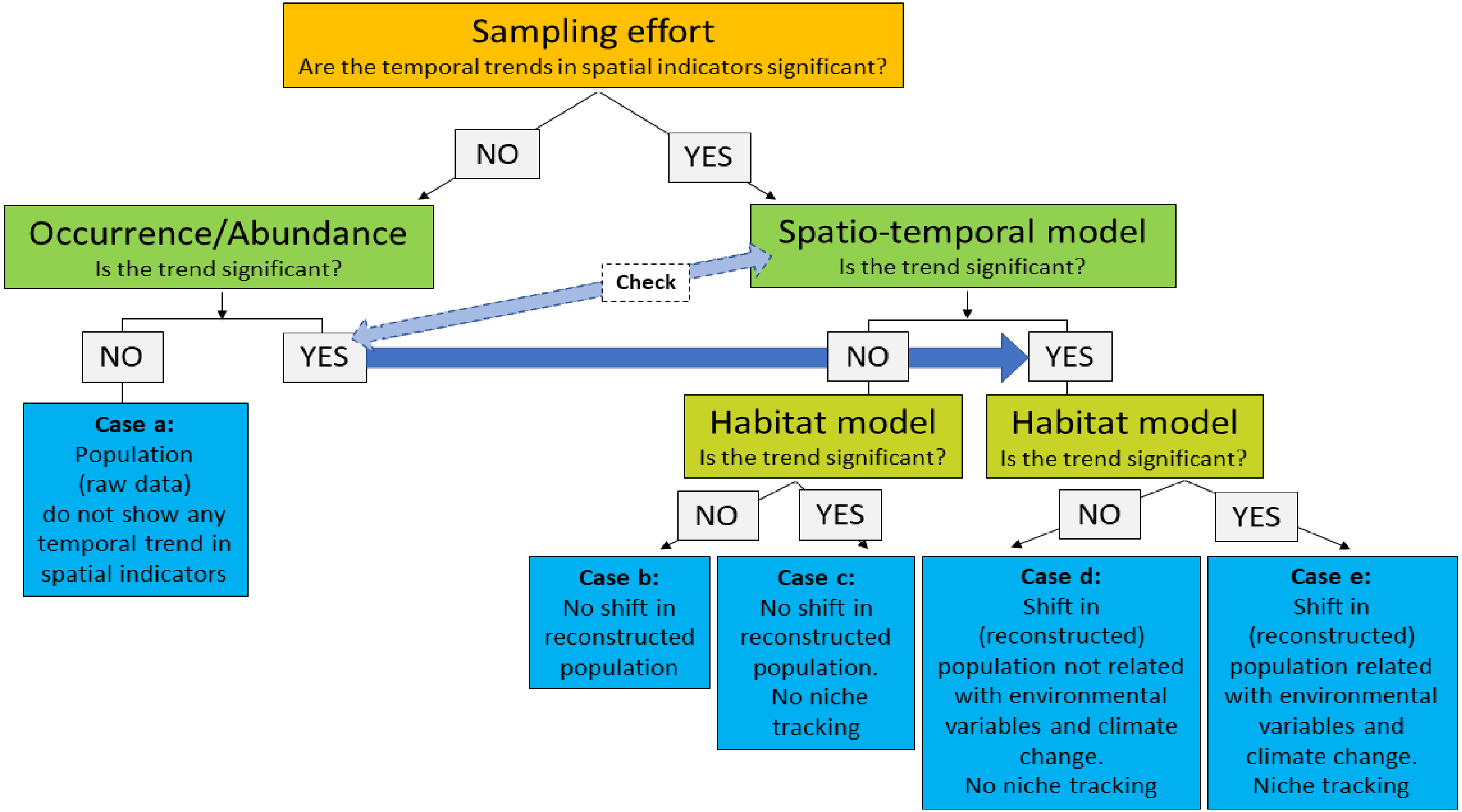


Figure 3.1: Framework detection/attribution of the different factors affecting species historical shifts. The flow diagram arrows represent the direction to follow. The dashed arrow represents the recommendation of comparing the raw data center of gravity with the spatio-temporal reconstruction model CoG.

Table 3.1: *Swordfish distribution presence/pseudo-absence (PA) and relative abundance (AB) for habitat and spatio-temporal models summarized. The "+" sign represents variables and interactions that were introduced in each model. In the STM, the longitude and latitude change year by year.*

	(Intercept)	log(phyto)	(lon, lat,by=year)	mld	sal	ssh	temp	season	stock	year	season:stock	season:year	stock:year	season:stock:year	dev.expl
PA Habitat	-2.79	+		+	+	+	+	+	+	+	+		+		43.05
AB Habitat	-5.03	+		+	+	+	+	+	+	+	+	+	+	+	38.03
PA STM	-3.14	+	+	+	+	+	+	+	+	+	+	+	+	+	52.2
AB STM	-5.52	+	+	+	+	+	+	+	+	+	+	+	+		54.00

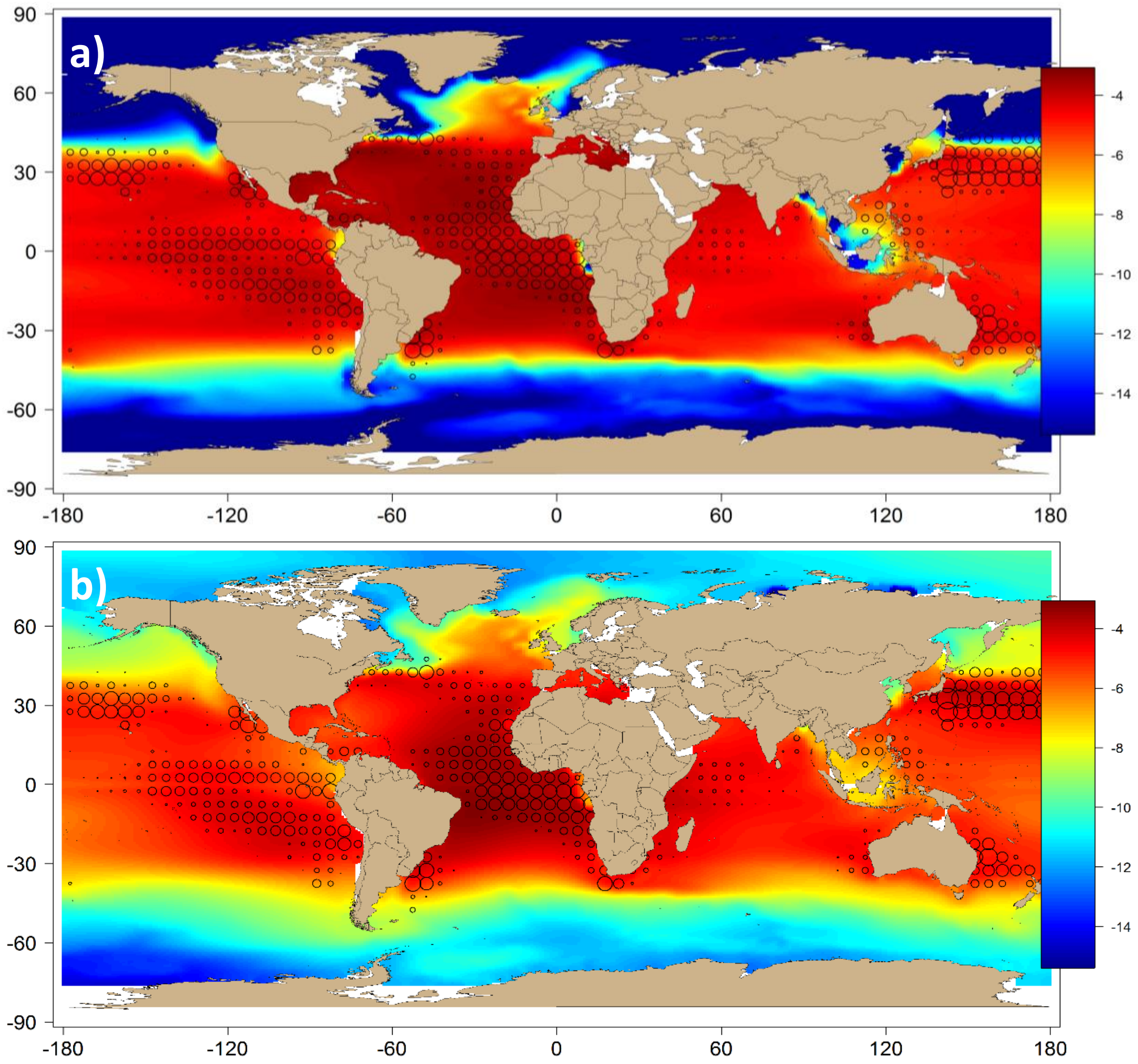


Figure 3.2: a) Swordfish habitat distribution model (in natural logarithmic scale) for the reference period (1980-1999). Black circles represent the raw data (CPUE observations). The size of the circles is proportional to the CPUE which units are tons per 1000 hooks. b) Spatio-temporal model representation (in logarithmic scale) for the reference period (1980-1999). In both maps, white areas represent lack of environmental data.

3.3.2. Detection and attribution of swordfish shifts

Historical time-series trend analysis showed high variations in the center of gravity along the 1958-2004 period (**Figure 3.3**) with different responses in the sampling effort and swordfish stocks (**Table 3.2**). The correlation matrix between different historical trends for each stock showed that historical trends of the STM and habitat are highly correlated in most of the stocks except in the North Atlantic (**Figure 3.4**).

The time-series trends and correlations were analyzed under the framework proposed in **Figure 3.1** to ascertain whether the species shifts are due to changes in habitat conditions, fishing activity or other factors. Fishing effort shifted significantly in the Indian Ocean (IO), as well as the swordfish's population and abundance CoG and the habitat, which shifted significantly southward. Hence, we should look at the STM, which did not shift significantly; therefore, it is assumed that there is no shift in the Indian Ocean (IO) stock. Its habitat displaced around 6 times slower (31 km decade-1) than fishing effort (206 km decade-1) and swordfish population (178 km decade-1) and abundance (173 km decade-1). However, the STM and habitat are highly correlated (**Figure 3.4**), which suggests that the interannual shift variability of the population distribution tracks its habitat.

In the Mediterranean Sea (MS), there was no fishing effort bias, thus, population raw data trends should be reliable. Swordfish in the MS moved significantly southward (77.7 km decade^{-1}), as well as the habitat, which shifted 5.5 km decade^{-1}. This indicates that the species followed its habitat preference; therefore, there might be a niche tracking in the MS. Nevertheless, historical trends in the MS need to be analyzed carefully due to the overall scarcity of data.

In the North Atlantic (NA), the Japanese fleet moved farther north at a rate of 368 km decade^{-1} between 1958 and 2004. As the fishing effort could mask the real trend of the population, the STM is analyzed. The STM indicated no linear trend, but CoG varies strongly through the time. This variation was not caused by environmental changes because there were neither significant habitat changes nor the correlation between habitat and STM.

In the South Atlantic (SA), there were no significant shifts in fishing effort or population even though habitat had changed. However, fishing effort and population are highly correlated, as in the case of STM and the habitat. In the SA case, the variation in CoG cannot be well captured by linear trends and correlations needed to be analyzed suggesting an interannual variation following environmental changes.

In both hemispheres of the Pacific Ocean (PO), the fishing effort shifted significantly southwards at around 50 km decade^{-1}, meaning that the trend of population distribution might be affected by sampling bias. The habitat shifted southward only for the north Pacific (NP, at a rate of 19 km decade^{-1}). There was no niche tracking in the Pacific Ocean's stocks. In the NP, there was no swordfish shift. However, the habitat and the STM are highly correlated, while in the south (SP), the population shifted southward due to other reasons not related to the environment (there was no significant trend of the habitat). The STM and the habitat are highly correlated in the SP, which suggests that the interannual distribution shift variability of the population tracks its habitat. The population was affected by fishing effort biases and the real trend was masked (no shift was observed in raw data analysis but there was a shift in the STM). The highest shift rate in population was estimated for the abundance in the SP, with a southward rate of 237 km decade^{-1}.

*Table 3.2: Shifts in latitudinal center of gravity (kilometers per decade) of the five different raw data and model-based historical time-series: fishing (sampling) effort, population presences, abundance, habitat model and spatio-temporal reconstruction model. The interpretation of the results is provided according to the framework developed in Figure 1. P-value < 0.001 is represented by '***', p-value between 0.001 and 0.01 with '**', and p-value >0.01 and < 0.05 by '*'.*

Ocean	Stock	Sampling effort	Occurrence	Abundance	Spatio-temporal	Habitat	Interpretation
Indian	swoI	**-207.1***	-179.2***	-173.7***	**-34.5**	-31.2***	Indian stock population is affected by the fishing effort bias, then, we look at the spatio-temporal reconstruction model. Swordfish has no significant trend in the Indian ocean although it has the same sign of the significant habitat shift. There is no niche tracking according to linear trends. **Case c in Figure 3.1**.
Mediterranean	swoM	**-22.3**	**-77.9***	**-145.8*****	**5.6**	**-5.6*****	Mediterranean stock shift might follow environmental changes. There is no fishing effort bias, so we can trust the raw data linear trends. There is niche tracking but the result needs to be analyzed carefully due to scarce data. **Case e in Figure 3.1**.
North Atlantic	swoNA	**369.6*****	125.8	114.7	**-3.3**	-3.3	North Atlantic stock had no northward shift according to the spatio-temporal reconstruction model. **Case b in Figure 3.1**.
North Pacific	swoNP	**-52.3***	-105.8***	-50.1	**-51.2**	-18.9*	North Pacific stock is affected by fishing effort bias which masks the real trend of the population. There is no change in the spatio-temporal model although there is a significant habitat shift based on linear trends. **Case c in Figure 3.1**.
South Atlantic	swoSA	**76.8**	**79.0**	**135.8**	**40.1**	-13.4*	South Atlantic stock had no significant shift (population), although the niche shifted significantly southward. As there is no fishing effort bias, the population trend is analyzed. **Case a in Figure 3.1**.
South Pacific	swoSP	**-47.9***	-6.7	-237.1***	**-39.0***	**-2.2**	South Pacific stock shifted southward due to reasons not related to environmental changes and masked by sampling effort as the linear trends suggested. **Case d in Figure 3.1**.

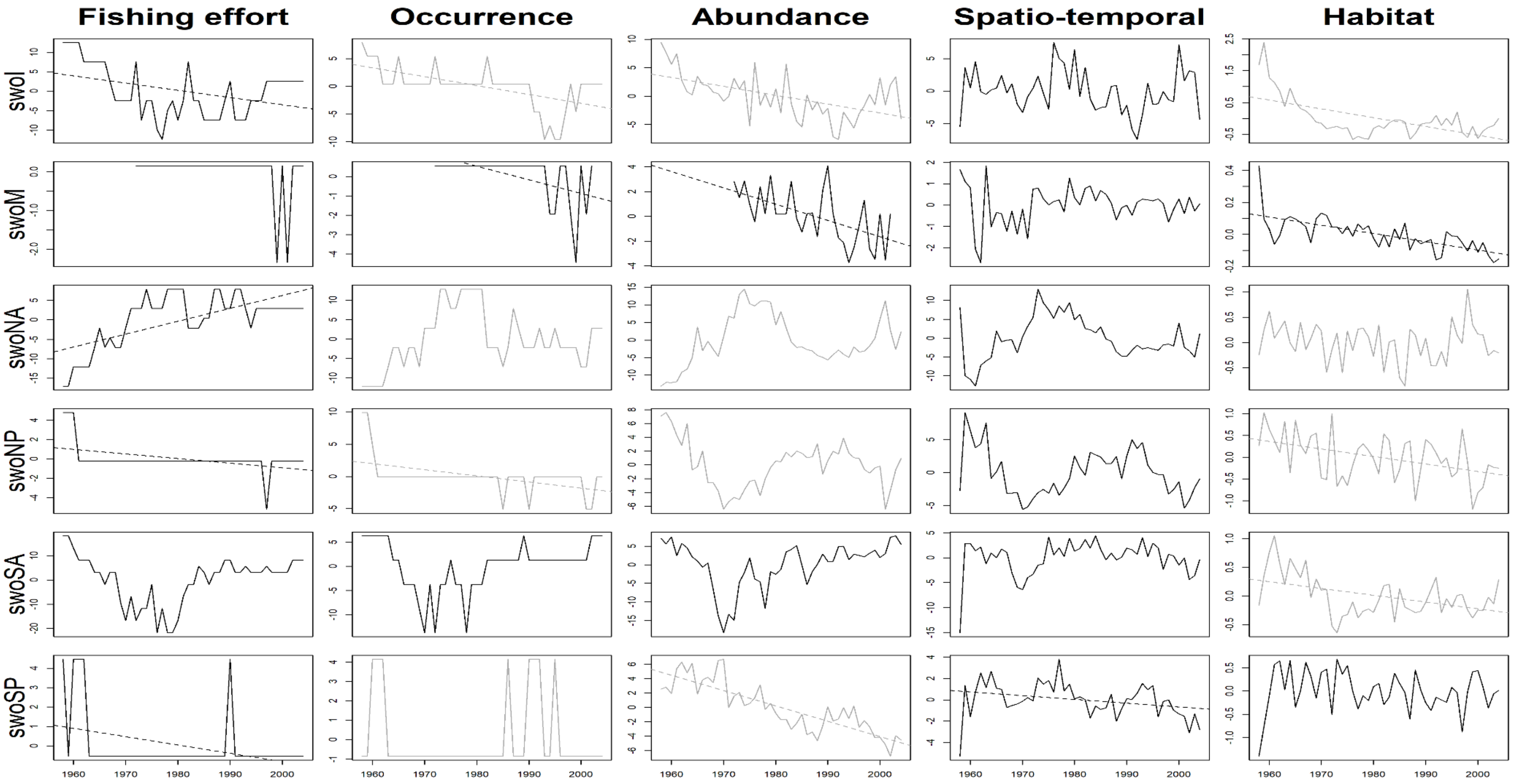


Figure 3.3: Latitudinal center of gravity anomalies (in degrees) per year of the five different raw data and model-based historical time-series: fishing (sampling) effort, occurrence, abundance, spatio-temporal reconstruction model and habitat model. Each row corresponds to stocks by region: swoI, Indian; swoM, Mediterranean Sea; swoNA, North Atlantic, swoNP, North Pacific; swoSA, South Atlantic and swoSP, South Pacific. The dashed line represents the significant trend of the time series (p<0.05). The black color represents that it is analyzed in the flow diagram from Figure 1 while the grey color represents the historical trend but it is not analyzed following the framework.

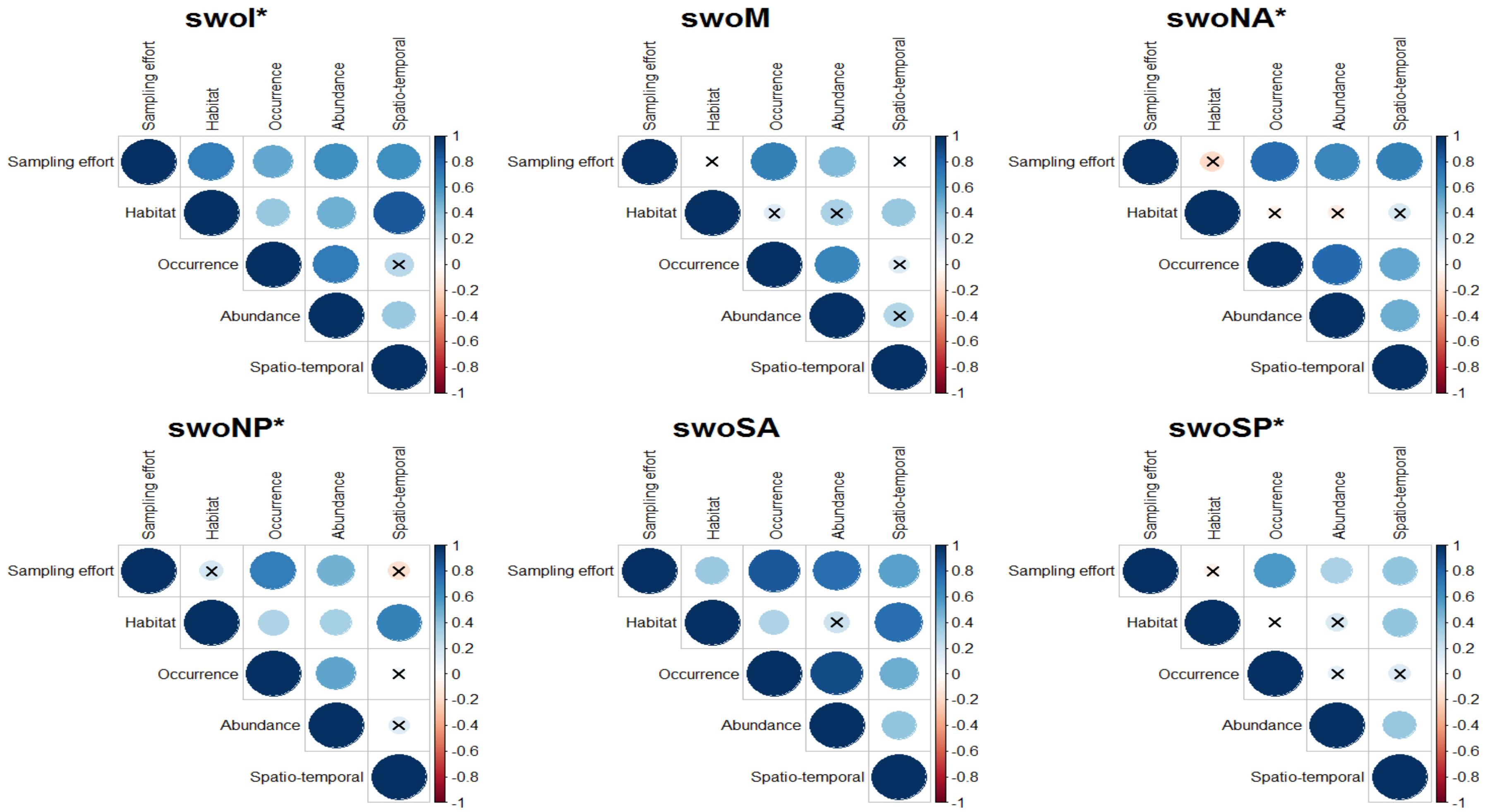
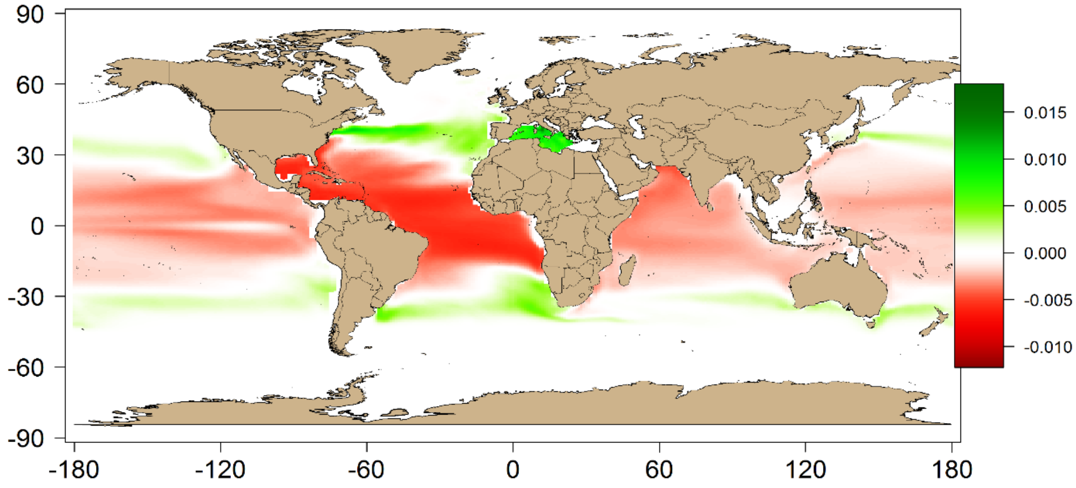


Figure 3.4: Correlations per stock between historical trends of sampling (fishing) effort, habitat, occurrence and abundance, and the spatio-temporal reconstruction. "×" represents the non-significant correlations. Blue colors represent positive correlations and red represents negative correlations. The "" after the stock name means that this stock has a significant sampling (fishing) effort trend, then, there was a sampling (fishing) effort bias.*

3.3.3. Future projection and changes

Future projections of swordfish habitat showed an increase of the relative abundance in its northern and southern boundaries (Figure 3.5) and a decrease in the equatorial area within all the oceans under the RCP8.5 climate change scenario. The habitat conditions for the swordfish seem to improve in the Mediterranean Sea as well as the Iberian Peninsula and Morocco, south of Australia, the north of New Zealand, west of Chile, South Africa, and east of Argentina. The highest decrease is expected in the equatorial Atlantic Ocean. Changes for mid- and the end-of-the-century show the same trend, with a decrease of 9.2% the total CPUE by 2050, but higher impacts were projected for the end-of-the-century with an overall decrease of 21.5%.

a) Mid-century (2040-2059)



b) End-century (2080-2099)

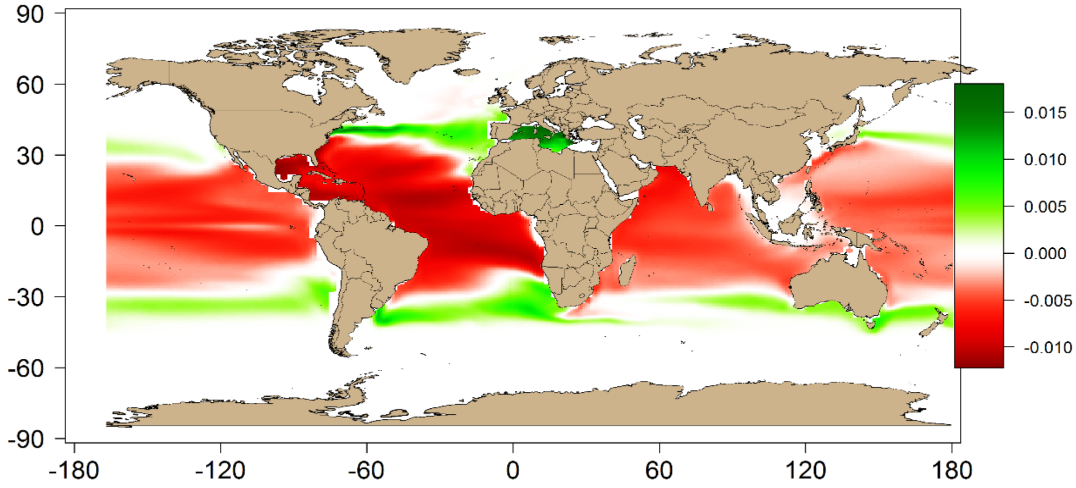


Figure 3.5: Expected changes on swordfish CPUE (Catch-Per-Unit-Effort) for a) mid-century (2040-2059) and b) end-of-the-century (2080-2099), relative to the reference period (1980-1999). (in logarithmic scale) for the reference period (1980-1999). In both maps, white areas represent lack of environmental data.

3.4. Discussion

Good understanding of the impacts of climate change and fisheries' on marine ecosystems is very important to predict species behavior and develop management plans (Currie et al., 2019). However, it is a complex process and different efforts have been made to disentangle the causes of species shift (Currie et al., 2019; Thorson et al., 2017; Thorson et al., 2016). A start point would be to understand their spatio-temporal changes during the study period to guide the interpretation of observed distribution changes (Currie et al., 2019). Thorson et al. (2016) improved on linear regressions of CoG in terms of error estimation but they could not disentangle the reasons behind the species shifts. Thorson et al. (2017) separated changes due to temperature, size-structure and unknown, while Currie et al. (2019) suggested that relationships between distributional shifts, metrics of fishing intensity and climate should be starting within the statistical framework and therefore applied a novel two-step approach to identify fish distribution trends from trawl surveys within a spatio-temporal delta modeling framework.

In this study, we developed a new framework to analyze the historical trends of the distribution of a population to ascertain if the reasons for the stocks' shifts were habitat-driven. However, the linear trend of the CoG may not account for other processes that affect the temporal variability of the species distribution. The correlation between different historical trends can be more informative than the linear trend results and needs to be carefully and complementary analyzed. Importantly, this new framework is potentially useful for any time series of species spatial distribution. In this particular case study, where swordfish has a worldwide distribution and the stocks' division lines are related to the management more than with biological factors, only one model was fit for all the stocks. However, in other case studies where subpopulations are highly isolated with weak gene flow, a fit model for each stock could be more appropriate.

Following the developed framework, we found a latitudinal shift in 2 out of 6 swordfish worldwide stocks between 1958 and 2004 (Mediterranean and South Pacific stocks) and found that the swordfish species does not always track its most suitable, shifting habitat. The Mediterranean stock was the only stock that shifted significantly while tracking its habitat. The shift in the Mediterranean was southward instead of poleward. The Mediterranean is a small, semi-enclosed sea with a relatively long longitudinal gradient but low latitudinal gradient. The MS warmed everywhere between 1958 and 2006, but slightly more in the southern area (Mariotti, 2010). This is probably the main reason explaining that swordfish habitat shifted southward, as species would follow their niche.

The STM showed that only the South Pacific stock shifted poleward significantly, although the linear trend analysis did not show a niche tracking. The positive correlation between the CoG and habitat preference suggested that the change in population distribution might be due to environmental variability. The shift patterns of swordfish observed in the PO suggest limited or null connectivity between both hemispheres and different regions although some individuals appear to move between tropical waters (e.g. from Vanuatu to French Polynesia and New Zealand) indicating greater connectivity than previously thought (Evans et al., 2014).

In the IO, genetic diversity detected at the regional scale was not significantly higher than that detected at the local scale, so the SW IO functions as a unique population, even though some discrete genetic differences could possibly indicate the presence of a second genetic pool in the northern part of that ocean (Muths et al., 2009). In contrast, in the overall Indo-Pacific region, four different stocks were suggested by Lu et al. (2006): an area off northern Madagascar, the Bay of Bengal, and the rest of the Indian Ocean, and western Pacific. Thus, different subpopulations' divisions can be found depending on the ocean.

For many other fish species, the latitudinal population shifts in the last decades have been associated with their habitat (Beare et al., 2004; Bruge et al., 2016; Montero-Serra et al., 2015; Perry et al., 2005). The spatio-temporal reconstruction allowed avoiding sampling biases (in this case fishing effort bias) and a better understanding of the behavior of the species. The fishing effort in the North Atlantic moved northward at a rate of 369 km per decade. This may be due to changes in the dynamics of the fishing fleets, such as changes from targeting tropical tunas in the tropics to bluefin tuna in higher temperate latitudes, or due to the bluefin tuna regulations introduced mostly in the last decades that have caused changes in behavior of the fleets and also affect catch rates of other species such as swordfish (ICCAT, 2017; Ijima & Yokawa, 2017). Our framework helps to disentangle the causes of the species shifts (analyzing the climate impacts and correcting for the sampling effort bias in data).

The potential application of the current methodology to derive proxies for relative habitat size needs fishery catch data from fleets with large coverage, such as the Japanese. There is a long history of Japanese longline activities in all oceans, and the presence of swordfish has been detected in a wide range of latitudes and longitudes (Aquamaps, 2016). However, even when disentangling a single fleet catch data with broad coverage, the results could still be affected by potential differences in their practice across oceans. To be able to include potential changes in the fleet dynamic between oceans, catchability, abundance, or differences in data collection, fixed factors as *year*, *season* and *stock*, and their interactions, were included in the model (Arrizabalaga et al., 2015). Long time-series were used to build the model (47 years) to ensure that long-term variations were detected (Reygondeau et al., 2012). Nevertheless, possible relative habitat size changes in the future might be limited by the assumptions of our model. Another consideration is that CPUE was used as a proxy of abundance, but this is also a relative measure and can be confounded with the dynamic of the fleets. Following the same approach as in Chapter 2, the nominal CPUE was used, having been estimated as the division of the sum of the seasonal catches by the sum of the seasonal effort for each geographical cell for the entire study period.

Other limitations of the model are the lack of the vertical dimension (no depth is introduced) or biological factors. This is important because the preferent depth of swordfish has been determined to be above the thermocline (Collette, 1995) and a higher stratification of the water column in the future could change the depth distribution. Besides, the swordfish availability to longline fleets is influenced by temporal and spatial variability in their vertical distributions (Evans et al., 2014) with important implications for abundance indices estimations derived from catch data (Maunder & Punt, 2004; Maunder et al., 2006).

In addition, we present the first study that models the worldwide habitat distribution and relative abundance of swordfish and estimates the projected changes in abundance and distribution. There have been some previous studies with regional distribution models, namely in Brazil (Hazin & Erzini, 2008), in the Atlantic Ocean (Goodyear et al., 2017), in the Pacific Ocean (Bigelow et al., 1999), in the Mediterranean (Damalas et al., 2007; Tserpes et al., 2008), and off the Chilean coast (Silva et al., 2015). With a two-step method that combines Presence/pseudo-Absence and Abundance models, we estimated the changes in the swordfish habitat distribution and its associated relative abundance during the second half of the 20th century and projected into the future with the worst climatic scenario conditions (RCP8.5).

Swordfish may demonstrate behavioral responses at different oxygen concentrations, and individuals may be limited by the amount of time they are capable to bear low concentration conditions (Evans et al., 2014). In addition, prey species might distribute themselves vertically because of different oxygen tolerances and thermoregulation (Brill, 1994; Seibel, 2011), thereby affecting the vertical distribution of swordfish (Evans et al., 2014). Adults are opportunistic feeders, foraging for their food from the surface to the bottom over a wide depth range (Nakamura, 1997), so they may be able to adapt to predate other prey. Nonetheless, other life processes such as spawning, intra- or interspecific interactions, such as predation (Guisan & Thuiller, 2005) or competition, and long-distance migrations associated with more favorable conditions can be desynchronized due to the different responses of species or life stages to climate change (Evans et al., 2014; Patterson et al., 2009; Thackeray et al., 2016).

3.4.1. Future projections and changes

Overall, the relative abundance of swordfish is projected to decrease by 9.2% in 2050 and 21.5% by 2100. However, an increase is projected in the northern and southern boundaries of the distribution throughout all oceans. The highest increases are expected in the Atlantic Ocean, mainly in the Mediterranean Sea where the largest abundances are projected in the western area. Mitochondrial DNA analysis revealed that despite the high migration of swordfish between the Mediterranean Sea and the Atlantic Ocean across the Strait of Gibraltar, little genetic exchange occurs between populations, with a high degree of differentiation found between the Mediterranean and the Atlantic Ocean populations (Kotoulas *et al.*, 1995). Thus, the increase in the relative abundance expected in the Mediterranean must be supported by the local population.

Other areas with an increase in the habitat suitability component of CPUE in the future will be the South Atlantic Ocean, south of Australia, north of New Zealand, east of Japan, central Chile and the border between California (United States) and Baja California (Mexico). CPUE loses are projected in equatorial areas of all oceans, mainly in the Atlantic and Caribbean Sea. As their condition of highly migratory species (FAO, 1994), batch spawners (Murua & Saborido-Rey, 2003) and opportunistic feeders of different types of fish, crustaceans, and squids (Young *et al.*, 2006), swordfish will probably acclimatize to the environmental changes and shift following their habitat preference in order to dwell in the best environmental conditions.

However, future swordfish CPUE projections should be taken as general trends due to the high uncertainty in fisheries scenarios. The models assume, for instance, that fishing season and effort will be kept constant. In addition, current models do not account for the evolutionary responses of marine populations so that there is still uncertainty in future biodiversity predictions. Marine populations might be adapting to global changes through the modification of traits including life history and physiology. Recent studies have shown that life-history traits of fish stocks have evolved in response to fishing and global warming (Crozier & Hutchings, 2014; Jorgensen *et al.*, 2007), and this has potential repercussions on fisheries production and economic yield that need to be investigated further (Eikeset *et al.*, 2013). New models should include the evolutionary and physiological responses and ecosystem interactions and improve the framework to be able to ascertain other reasons that cause a change in the distribution and abundance of the target species.

CHAPTER 4

The influence of climate change and fishing pressure in top predators’ body size

4. CHAPTER 4:

The influence of climate change and fishing pressure on top predators' body size

4.1. Introduction

4.1.1. Climate change on marine ecosystems and fisheries

Climate change is a relatively recent stressor over marine ecosystems and fisheries (Brander, 2010), determining the past and future distributions of biodiversity with impacts in fishermen communities, resources managers, economies and human society in general (Burrows *et al.*, 2011; Cheung *et al.*, 2009b; Hobday *et al.*, 2015; Karp *et al.*, 2019; Pecl *et al.*, 2017; Peterson *et al.*, 2002; Weng *et al.*, 2015). Under climate change scenarios, the propagation of a hydroclimatic signal can be amplified up the plankton food web (Chust *et al.*, 2014a), causing biomass declines at higher trophic levels (Lotze *et al.*, 2019). Lotze *et al.* (2019) estimated that the mean global animal biomass will decrease by 5% (±4% SD) under low emissions and 17% (±11% SD) under high emissions, with an average 5% decline for every 1 °C of warming. In addition, projected biomass declines will be primarily driven by increasing temperature and decreasing primary production.

Species and marine communities may respond to thermal change in a complex and unexpected manner (Friedland *et al.*, 2018; Hollowed *et al.*, 2019). Friedland *et al.* (2018) suggested that the spatial distributions of lower trophic level organisms are less responsive to thermal change because of their ability to integrate seasonal thermal changes, while the responses of higher trophic level species depend on both, the availability of lower trophic level organisms and environmental conditions. Therefore, the different responses may be linked to the organism's capacity to adapt to novel thermal regimes.

Climatic shifts, understood as a permanent shift in the spatial distribution of a species or stock from its historical region to a new region or habitat (Karp *et al.*, 2019) due to climate change, have been implicated as major causes of fluctuations in marine fish diversity and abundance in both pelagic and demersal assemblages (review in Genner *et al.* (2010)). However, other factors (e.g. fishing, habitat degradation, trophic dynamics) may also cause shifts (Bell *et al.*, 2014). Changes in fisheries productivity (referred to as the total biomass or number of fish individuals that a stock can produce and relates to how much it can theoretically support) directly affect the stock assessment and management process (Karp *et al.*, 2019). Changes in productivity may be cyclical oscillating from years to decades or unidirectional (as is expected with climate change), where the productivity is not expected to return to its original state in the foreseeable future (Karp *et al.*, 2019). To understand the combined effects of fishing and climate change over life-history parameters of stocks is an important but ignored priority (Perry *et al.*, 2010; Planque *et al.*, 2010).

4.1.2. Impacts on body size

Ecosystem size structures tend to be highly regular decreasing in abundance with size according to a power-law distribution. This power-law relationship, known as the abundance-size spectrum, describes the expectation of a high abundance of small individuals and few large organisms (Heneghan *et al.*, 2019). However, changes in size distribution has been recorded (Audzijonyte *et al.*, 2016; Baudron *et al.*, 2014; Cheung *et al.*, 2013a; Daufresne *et al.*, 2009; Genner *et al.*, 2010) and decreasing body size has been proposed as the third universal ecological response to increasing temperatures together with the shift of species ranges and the seasonal shifts in life cycle events (Cheung *et al.*, 2013a; Daufresne *et al.*, 2009). The physiology behind the response is well established for ectotherms inhabiting aquatic environments and it is often based on the temperature-size rule (Atkinson, 1994): the tendency for increased juvenile growth (faster approach towards asymptotic size) and developmental rates combined with the decreased adult body size ($L\infty$) at higher temperatures. As higher temperatures decrease the aerobic capacity, individuals with smaller body sizes have a reduced risk of oxygen deprivation. Different mechanisms (physiological and evolutionary) could produce this theoretically predicted and empirically observed life-history pattern but both of them have similar consequences such as a decrease in body size, increase in proportion of small-sized species, young age classes and earlier maturation (Audzijonyte *et al.*, 2016; Daufresne *et al.*, 2009). For example, a decrease in body size of six of eight commercial fish species in the North Sea was recorded over 40 years period due to 1–2 °C increase in water temperature, resulting in a yield-per-recruit of these stocks by an average of 23% (Genner *et al.*, 2010).

4.1.3. Top predators

Ocean warming impacts mentioned above, together with the negative influence of sustained fishing over the reproductive capacity of many populations (Genner *et al.*, 2010), affected to multiple species, even to some historically abundant marine species that are now economically or biologically extinct (Reynolds *et al.*, 2005). Fishing has reduced and locally extirpated populations of predatory fishes, such as top predators (Jennings & Kaiser, 1998). Fisheries mainly focus on fishing larger individuals within populations, which usually are slow-growing, late-maturing and long-lived species with low rates of potential population increase (Jennings *et al.*, 1999). The empirical evidence suggests that species with those characteristics (such as top predators) are the best predictors of vulnerability to fishing (Reynolds *et al.*, 2005). Large species reductions do not have a consistent effect on the abundance and diversity of their prey; therefore, a greater decline has been recorded for large fish than in smaller ones due to fishing effort, and those species can be the least resilient to chronic fishing pressure (Jennings & Kaiser, 1998). As a consequence of overharvesting top predators, cascading density-dependent effects on other trophic levels may occur, with broader ecosystem-level implications (Frank et al., 2005; Myers et al., 2007).

Tuna and billfishes are considered top predators due to their top-down influence on the ecosystem structure, where they play a very important ecological role (Cox *et al.*, 2002; Hinman, 1998; Sibert *et al.*, 2006). Both tunas and billfishes are highly migratory (FAO, 1994) and broadly distributed, inhabiting a wide range of environments from low nutrient tropical waters to productive sub-polar seas (Muhling *et al.*, 2017a). They have the ability to maintain body temperature elevated (endothermy) (Block, 1991). As a consequence, they are able to inhabit highly productive seasonal feeding grounds, dealing with high changes in temperature (dropping below 10ºC) (Block & Stevens, 2001; Brill *et al.*, 1999; Holland, 1990). While tunas have long fascinated marine scientists' and their importance has promoted further researches, the billfishes have received far less study.

Tuna species comprise an annual catch of around 7.5 million tonnes (FAO, 2016, 2018) and represent an economically important contribution to many nations (Brill & Hobday, 2017) particularly in developing countries (Fernandes, 2018; Lauria *et al.*, 2018). Billfishes are considered as by-catch in longline fishing generally reducing their abundance more than that observed for the targeted tuna species, thus, they are vulnerable to exploitation effects (Kitchell *et al.*, 2006). However, the economic importance of angling for billfishes substantially exceeds their ecological role as predators and the hypothetical removal of billfishes evoked a more rapid response, but with little effect on food web structure (Kitchell *et al.*, 2006).

The ability to move away from unsuitable habitats due to the high mobility and migratory behavior and the plasticity in spatial habitat use of many pelagic fish species, makes the determination of climate change impacts a complex problem (Hobday & Evans, 2013). There are some studies about how climate change has been affecting and will affect tuna species, and to a lesser extent to billfishes. Most of efforts have been focused on monospecific models (Chust *et al.*, 2019; Dueri *et al.*, 2014; Lehodey *et al.*, 2017; Lehodey *et al.*, 2018; Senina *et al.*, 2018; Senina *et al.*, 2016) or multispecific models for some regions or oceans (Lehodey *et al.* (2008); Fu *et al.* (2019) chapter 2 of this thesis). Some global studies have been conducted using correlative models to predict main commercial tuna species suitable habitats (Arrizabalaga *et al.*, 2015)and the biogeochemical provinces (distribution of tuna and billfishes in ecoregions) were defined to describe the spatial distribution, main environmental drivers and species composition of each community detected (Reygondeau *et al.*, 2012).

4.1.4. Modeling high trophic levels

Modeling strategies for predicting the potential impacts of climate change on the natural distribution of species have often focused on the characterization of a species' bioclimate envelope but it has been criticized arguing that there may be many factors other than climate that play an important part in determining species distributions and the dynamics of distribution changes (Pearson & Dawson, 2003). Different models were developed with the same aim of introducing many of the biological and physical processes that occur in the ocean and which affect the entire ecosystem and species which inhabit there as well as to resolve the mechanistic connections between environmental variability and upper trophic level dynamics (Fulton, 2010; Travers *et al.*, 2007). Models of low trophic levels, which represent mainly the plankton community through functional groups are well suited for exploring environment effects on ecosystems whereas high trophic level models, mostly species-based, can be used for assessing fishing effects. Coupling both models to build end-to-end models that quantify the propagation of simultaneous fishing and climate effects down and up the food web is complicated (Fulton, 2010; Travers *et al.*, 2007).

Some of those ecosystem models are the Dynamic Bioclimatic Envelope Model (DBEM, Cheung *et al.* (2009a)) which combines a dynamic bioclimate envelope model with a population growth model; SEAPODYM (Bell *et al.*, 2013a; Lehodey *et al.*, 2013; Lehodey *et al.*, 2010) which is based on advection-diffusion-reaction equations, and considers population dynamics of target (exploited) species in relation to age-specific habitats and APECOSM (Dueri *et al.*, 2014), a mechanistic numerical model incorporating environmental variables, metabolic rates and behavioral responses of fish among others. Using those models as a tool, hundreds of species were analyzed together in order to elucidate the main patterns of expected changes under different scenarios (Cheung *et al.*, 2008b; Cheung *et al.*, 2009b). Due to the ecologically and economically important and life-history traits of tuna and billfishes, how climate change and fishing pressure have affected their distribution, abundance and body size and how they will do it in the future is very important from an ecosystem perspective.

The objective of this chapter is to analyze the potential changes in the body size of top predators under future scenarios of climate change and fishing pressure. Climate change has been considered in terms of GHG (Greenhouse Gas) emissions (different RCPs), and fishing scenarios were defined by the Maximum Sustainable Yield -MSY-. Projections of body size under both, climatic and fishing scenarios have not yet been conducted for high trophic levels. In contrast with previous literature, the model SS-DBEM has been selected in the present study (described below) given the large number of mechanisms that it considers. This model combines multiple approaches described above (e.g. envelop, growth, dispersion, and size-spectrum) for multiple species. Therefore, this is the first study that applies the combination of those two models to predict distribution, abundance and body size changes in high trophic level marine fish species (top predators). In addition, the biological parameters used in the model were updated and defined specifically for the target species of this study by conducting an extended literature review.

4.2. Material and methods

A multi-species model combining a species-based bioclimate envelope model with size-based trophic model was used (Fernandes *et al.*, 2013) to explore the potential impacts of climate change and fishing of target species of tuna species (albacore, Atlantic bluefin tuna, southern bluefin tuna, yellowfin, and skipjack) and billfish (swordfish). Bioclimate envelope models have already been used to predict the redistribution of both terrestrial and aquatic species (Cheung *et al.*, 2009b; Jones *et al.*, 2012; Pearson & Dawson, 2003). Those models consist of two main components: (1) species' habitat suitability spatially, and (2) spatial population dynamics of target species. Population dynamics include population growth, movement, and dispersal of adult and larvae, as well as the ecophysiological effects of temperature, oxygen, and pH on body size, growth, mortality, and reproduction (Cheung et al., 2013b). The size-based equilibrium model (Jennings & Collingridge, 2015; Jennings *et al.*, 2008) draws on established principles in macroecology, life history theory and food web ecology to predict the global abundance, production, distribution and size-structure of marine consumers and to assess the effects of parameter uncertainty on these predictions.

4.2.1. SS-DBEM

This modeling approach which integrates the species based Dynamic Bioclimatic Envelope Model (DBEM) (Cheung *et al.*, 2008a; Cheung *et al.*, 2011; Cheung *et al.*, 2008b; Cheung *et al.*, 2009a; Cheung *et al.*, 2013b; Cheung *et al.*, 2016; Cheung *et al.*, 2009b) with the size-spectrum approach (SS) (Jennings & Blanchard, 2004; Jennings & Collingridge, 2015; Jennings *et al.*, 2008) (hereafter called SS-DBEM) was firstly developed by Fernandes *et al.* (2013). This approach provided spatially and temporally resolved predictions of changes in species' size, abundance and catch potential with consideration of population dynamics, dispersal (larval and adults) and ecophysiology (Cheung *et al.*, 2008a; Cheung *et al.*, 2011; Cheung *et al.*, 2008b; Cheung *et al.*, 2009a; Cheung *et al.*, 2013b) and account for the effects of ecological interactions which determines resource limits in a given geographical area and, therefore, the biomass of that species that can be supported in this area (**Figure 0.11** in **General Introduction section**). The new algorithm developed to describe the resource competition between different species co-occurring in a cell by comparing the energy (in biomass) that can be supported in the cell (estimated with the SS model) with the energy demanded by the species predicted to inhabit the given cell (estimated with the DBEM model) (Fernandes *et al.*, 2013). The algorithm is divided into a first initialization stage where competition parameters are estimated; and a recurrent stage where the competition parameters are used to resolve conflicts between energy (biomass) demands and biomass that can be supported.

4.2.1.1. Size-spectrum (SS)

Size-based equilibrium model uses established principles in macroecology, life history theory and food web ecology to predict total fish abundance, production, distribution and size structure of target species in an unexploited ecosystem (Jennings & Blanchard, 2004; Jennings & Collingridge, 2015; Jennings *et al.*, 2008). Macroecology studies the relationship between organisms and their environment at large spatial and temporal scales, such as the pattern of abundance, distribution, and diversity of species (Brown, 1995; Gaston & Blackburn, 2000; Gaston & Blackburn, 2003). The energy flux rates and magnitudes from primary producers to consumers depend on primary production, transfer efficiency, predator and prey body mass and temperature (Jennings & Collingridge, 2015). The macroecological model is used to estimate numbers (N) and biomass (B) of consumers at body mass (M) (Jennings & Collingridge, 2015). Developed by Jennings *et al.* (2008) and improved by Jennings and Collingridge (2015) the size spectrum model estimates numbers and biomass of species in the water column from the surface to the euphotic depth, or the mixed layer depth if this is deeper. The assumption of all primary production occurred in this zone was done and all model outputs were depth-integrated and result expressed per unit area.

The length of food chains (the number of steps between prey and predator) increases with higher smaller phytoplankton abundance and therefore, carbon export from surface waters decreases. For those reasons, it is important to establish the size structure of the phytoplankton community which supports consumer production. This size structure of the phytoplankton community was used to estimate the export production or sinking rate. The proportion of primary production available to support primary consumers' production was estimated with the transfer efficiency through the food web which was modified with a multiplier for the relative export fraction which includes all losses of energy from the modeled system. In the model, transfer efficiency determines the relationship between primary consumer production at any higher trophic level. Assuming that body size and temperature determine individual rates of production, biomass, and numbers at the same body mass or trophic level can be estimated, then, it generalizes food web processes with size-based predator-prey interactions that lead to growth and mortality and can be used to assess the effects of additional mortality (such as fishing) on the food web. Fishing effects can be also analyzed defining the selectivity by species and sizes.

4.2.1.2. Dynamic bioclimatic envelope model (DBEM)

The DBEM was divided into three steps: (i) predict the current distribution of species of interest; (ii) project future changes in distribution and relative abundance of the species; and (iii) project future changes in the potential catch.

a. Initial distribution

Initial distributions for tuna and swordfish abundance developed individually in chapters 2 and 3 were introduced in the model. Those initial distributions were built using the Japanese fleet pelagic longline fishing catch and effort data for six of the seven most commercial tuna species and swordfish from the five relevant tuna Regional Fishery Management Organizations (tRFMOs). For further details, see chapters 2 and 3 material and methods sections. Those initial distributions are more accurate than those provided by Sea Around US projects which were initially used since they use a more complete occurrence data and species *ad hoc* distribution modeling.

b. Biological data and species selection

Species' biological parameters information was obtained from FishBase (www.fishbase.org) and Sea Around Us Project, thereinafter SAUP (www.seaaroundus.org). Our study focused on six of the seven most commercial tuna species, swordfish, and their direct competitors. Selected target species were: albacore (*Thunnus alalunga*), Atlantic bluefin (*Thunnus thynnus*), Southern bluefin (*Thunnus maccoyii*), yellowfin (*Thunnus albacares*), bigeye (*Thunnus obesus*), skipjack (*Katsuwonus pelamis*) and swordfish (*Xiphias gladius*). A selection of direct competitor fish species was conducted, avoiding higher taxa groups than species such as families or genera. Direct competitor species’ selection was conducted after the following filtration:

(i) Trophic level (TL): all fish species with an estimated trophic level higher than 4 were selected. Southern bluefin was also introduced as a target species although the TL=3.87.

(ii) Type of habitat: only pelagic species were selected. Due to the selection of species which compete directly with target species, demersal and benthopelagic species were avoided.

(iii) Distribution: species might have a worldwide distribution and not limited to the continental shelf due to the most oceanic distribution of tuna and swordfish. The native range of species was verified in FishBase.

A literature review was conducted, and biological parameters values were updated (see **S. Table 4.1** in **Appendix D**). Von Bertalanffy growth function coefficients from different studies for each species were averaged after discarding the two smallest and highest values found in the literature. FishBase's value was used as an individual source of information and represented by the average of the observations. The trophic levels and maximum Stand Lengths (SL) were updated according to SAUP data (downloaded in January 2019). Smaller species have less mobility than bigger species. Therefore, the mobility coefficient for small species was changed to 250 (cm h^{-1}) and for large species to 300 (cm h^{-1}). We made a differentiation because previously the values were the same for many species independently of their body size and swimming capacity.

Fisheries related parameter values were also updated. Fishing mortality at Maximum Sustainable Yield (F_{MSY}) which was previously estimated by Pauly (1980) using a relationship with the natural mortality was updated. In this study, the F_{MSY} values from Stock Assessment reports were used. In addition, the intrinsic population growth values were estimated as F_{MSY}*4.

c. Environmental data

The global coupled carbon-climate Earth System Models (ESMs) developed over the last several years at the Geophysical Fluid Dynamics Laboratory (GFDL) of the National Oceanic and Atmospheric Administration (NOAA) are the product of an effort to expand upon the capabilities of past GFDL models used to study climate on seasonal-to-centennial time scales (e.g., review in Dunne *et al.* (2012)) and to advance understanding of how the earth's biogeochemical cycles, including human actions, interact with the climate system (Dunne *et al.*, 2012). The ESM2M model, which is the one used into the DBEM model, include the thermocline depth being relatively deep, with a relatively strong El Niño-Southern Oscillation and in general, representing better climate changes relating to surface circulation given its superior surface temperature, salinity, and height patterns, tropical Pacific circulation and variability, and Southern Ocean dynamics.

The environmental factors included in the model were the bottom (average of 15 meters, bottom layer) and surface (integration of 15 m, top layers) temperature (ºC), pH ($[H^+]$), O2 (in mol/kg), salinity (PSU), ice coverage in the cell (%), total net primary production (total of the water column) (g C m-2 d-1), mixing depth layer (m), advection U (m/s) and advection V (m/s).

d. Climatic scenarios

Future species distributions were projected simulating changes in the environmental factors such as temperature, oxygen content (represented by O_2 concentration), and pH (represented by H^+ concentration). Those changes would affect the growth of marine fish and invertebrates. The model algorithm was derived from the von Bertalanffy growth function (VBGF; von Bertalanffy (1951)). Body growth depends on the difference between available oxygen and oxygen demand for maintenance. It is suggested that relative oxygen supply becomes increasingly limiting as fish growth, because of the lower rate of increase in respiratory surface (and hence oxygen supply) relative to that of increase in body size (and hence oxygen demand) (Pauly, 1981; Pauly & Kinne, 2010).

The distribution and abundance of target species from 1970 to 2099 were projected under four climate scenarios representing high-, two medium- and low- range greenhouse gas emissions. Four climate scenarios included: the mitigation scenario with 421 ppm (RCP2.6), the 538 ppm and 670 ppm stabilization experiments (RCP4.5 and RCP6.0), and 936 ppm the business as usual high emission scenario (RCP8.5) by the year 2100 (IPCC, 2013). Changes in environmental parameters such as surface and bottom seawater temperature, oxygen concentration, salinity, net primary production, surface advection, and sea ice concentration were obtained from the Geophysical Fluid Dynamics Laboratory Earth System Model (GFDL ESM2M; Dunne *et al.* (2013)). A common baseline was defined to be able to analyze changes between the combination of the climatic and fishing scenarios. The RCP6.0 climatic scenario was chosen due to the current trend in atmospheric increasing (IPCC, 2019b).

e. Fishing scenarios and parameters

Fisheries related parameter values were also updated. Fishing mortality at Maximum Sustainable Yield (F_{MSY}) which was previously estimated by Pauly (1980) using a relationship with the natural mortality was updated. In this study, the F_{MSY} values from Stock Assessment reports were used. The estimated catch potential (both in the past and in the future) is the result of simulating the exploitation of the resource at an ideal MSY level, taking into consideration the change in ecosystem productivity over time (and forced by the climate change in the future) (Cheung *et al.*, 2018). The MSY is defined as the highest average theoretical equilibrium catch that can be continuously taken from a stock under average environmental conditions (Hilborn & Walters, 1992). The current exploitation status of target species related to the MSY was estimated and fishing effort scenarios were defined by the following multiplying factors: 0.8, 0.9, 1.0, 1,1 and 1,2 (thereinafter 0.8MSY, 0.9MSY, 1.0MSY, 1.1MSY and 1.2MSY). This approach has been used in previous research (Fernandes *et al.*, 2015; Mullon *et al.*, 2016) and current international project protocols (Ferit; Fu *et al.*, 2019; Hansen *et al.*, 2019).

4.2.1.3. Body size distribution changes

The estimation of changes in body size of target species was estimated in two different ways. The first way was to estimate the mean of the size-length frequency distribution derived from the model. The second way to estimate changes in body size through the species was using the ratio between the biomass and the abundance ($ratio = \frac{biomass}{abundance}$). When ratio values are related to a reference period, positive changes (ratio>1) indicate that bigger individuals are expected, while for negative values (ratio<1), smaller individuals are predicted.

4.2.1.4. Size-length frequency distribution by FAO areas

Due to the management importance of the FAO's main fishing areas, which are a classification that divides the oceanic masses of the globe into nineteen fisheries sectors (FAO, 2014a), changes inside each have been considered relevant to this study. Then, changes per each FAO area were estimated.

4.3. Results

4.3.1. Direct competitor species selection

Species selected as direct competitors between them due to trophic level and spatial overlap were the following: wahoo (*Acanthocybium solandri*), common dolphinfish (*Coryphaena hippurus*), Indo-Pacific sailfish (*Istiophorus platypterus*), opah (*Lampris guttatus*), escolar (*Lepidocybium flavobrunneum*), Atlantic blue marlin (*Makaira nigricans*), shortbill spearfish (*Tetrapturus angustirostris*), striped marlin (*Tetrapturus audax*), longbill spearfish (*Tetrapturus pfluegeri*), blackfin tuna (*Thunnus atlanticus*), Pacific bluefin tuna (*Thunnus orientalis*) and longtail tuna (*Thunnus tonggol*). The tuna species out of the main commercially valuable ones comprise smaller catch volumes and their economic interest may be lower. The 19 species of high trophic level fishes were divided in three main groups: (i) tuna; albacore, A. bluefin tuna, southern bluefin tuna, yellowfin, bigeye, skipjack, wahoo, blackfin tuna, Pacific bluefin tuna, and longtail tuna, (ii) billfishes; swordfish, Indo-Pacific sailfish, Atlantic blue marlin, short and long spearfish and (iii) others; common dolphinfish, opah and escolar. Common lengths (in a different color per group) and maximum reported lengths (in grey) can be compared in **Figure 4.1**. Billfish species are mainly the largest top predator species studied here and some tuna species are the smallest.

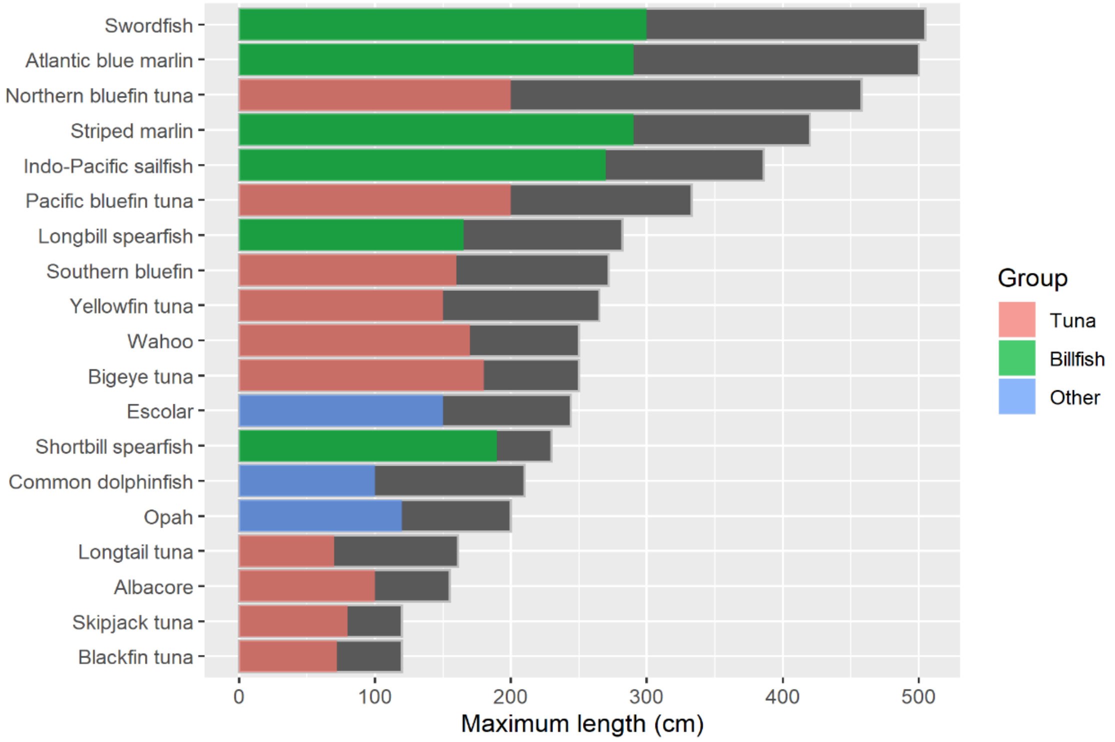


Figure 4.1: Common lengths (in red: tuna, green: billfish and blue: other) and maximum reported lengths (in grey) for selected 19 top predator species.

4.3.2. Biomass and abundance change under different scenarios

The four greenhouse gas emission scenarios predict an increase in the Sea Surface Temperature (in ºC) and a slight increase in Primary Production (change in % related to 2000-2010 period) for the end-of-the-century (**Figure 4.2)**.

The model projects that most of the top predator target species of this study would increase both, the abundance (number of individuals) and biomass (tonnes) under the four climatic scenarios (**Figure 4.3a and b**). Some of the species, such as albacore, swordfish and shortbill spearfish showed a decrease for the end of the century but apart from that, there are no remarkable differences by groups (tuna, billfish and other). However, differences between climatic scenarios are remarkable in most of the species, RCP2.6 scenario predictions becoming much more optimistic than the others.

The RCP6.0 climate and 1.0MSY fishing scenarios ("business as usual") were considered as a baseline in order to obtain an equilibrium scenario representative of a non-fishing hypothetical scenario. Using estimated changes related to this defined baseline (**Figure 4.4a and b**), differences between scenarios were more easily observed and help to elucidate if changes were fishing- or climatic-driven. In some species (Pacific bluefin tuna, Atlantic bluefin marlin, escolar, opah, Indo-Pacific sailfish, striped marlin, longbill, and shortbill spearfish) highest abundance changes were climate-driven, mainly by the end-of-the-century while others (yellowfin tuna, longtail tuna, swordfish, northern bluefin tuna) were mainly fishing-driven. However, some species (such as swordfish, skipjack, and bigeye) showed mixed causes changing the main driver through time (fishing-driven at the beginning and climatic-driven at the end of the time series). Changes in biomass related to the common baseline differ from changes in abundance although trends are similar. Nevertheless, fishing-driven changes are more important in biomass through all the century, becoming more important than climatic-driven changes in some species (striped marlin, Indo-Pacific sailfish).

In contrast to biogeochemical models where the uncertainty increases in the end-of-the-century due to climatic scenarios, uncertainty here showed a variety of patterns. Some species have higher uncertainty at the beginning of the time series (skipjack, bigeye, yellowfin tunas, and swordfish abundance) related to fishing scenarios and others (P. bluefin tuna, shortbill, and longbill spearfish) showed higher uncertainties at the end of the century related with climatic scenarios. However, a variety of combinations can be found, and they do not appear to follow any group patterns.

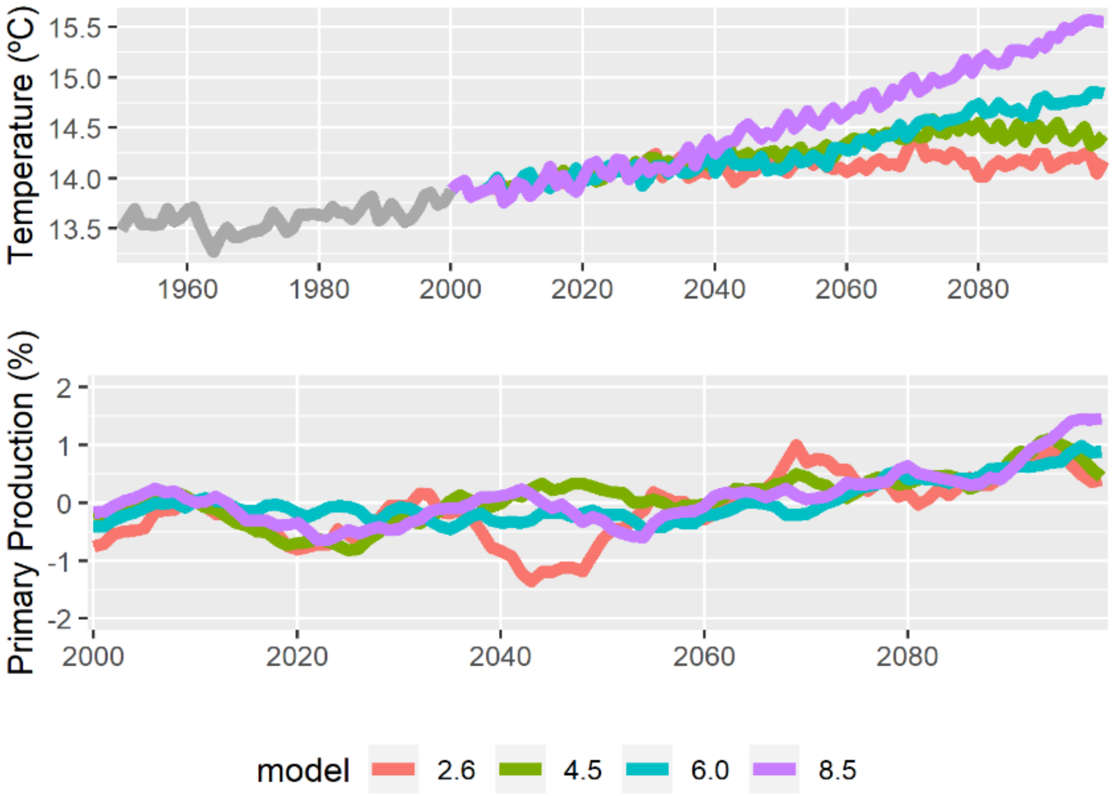


Figure 4.2: (a) Sea Surface temperature (ºC) for the historical period (in grey) and (b) Primary Production change (%) projections by the end-of-the-century under different greenhouse gas emission scenarios (RCP2.6, 4.5, 6.0 and 8.5).

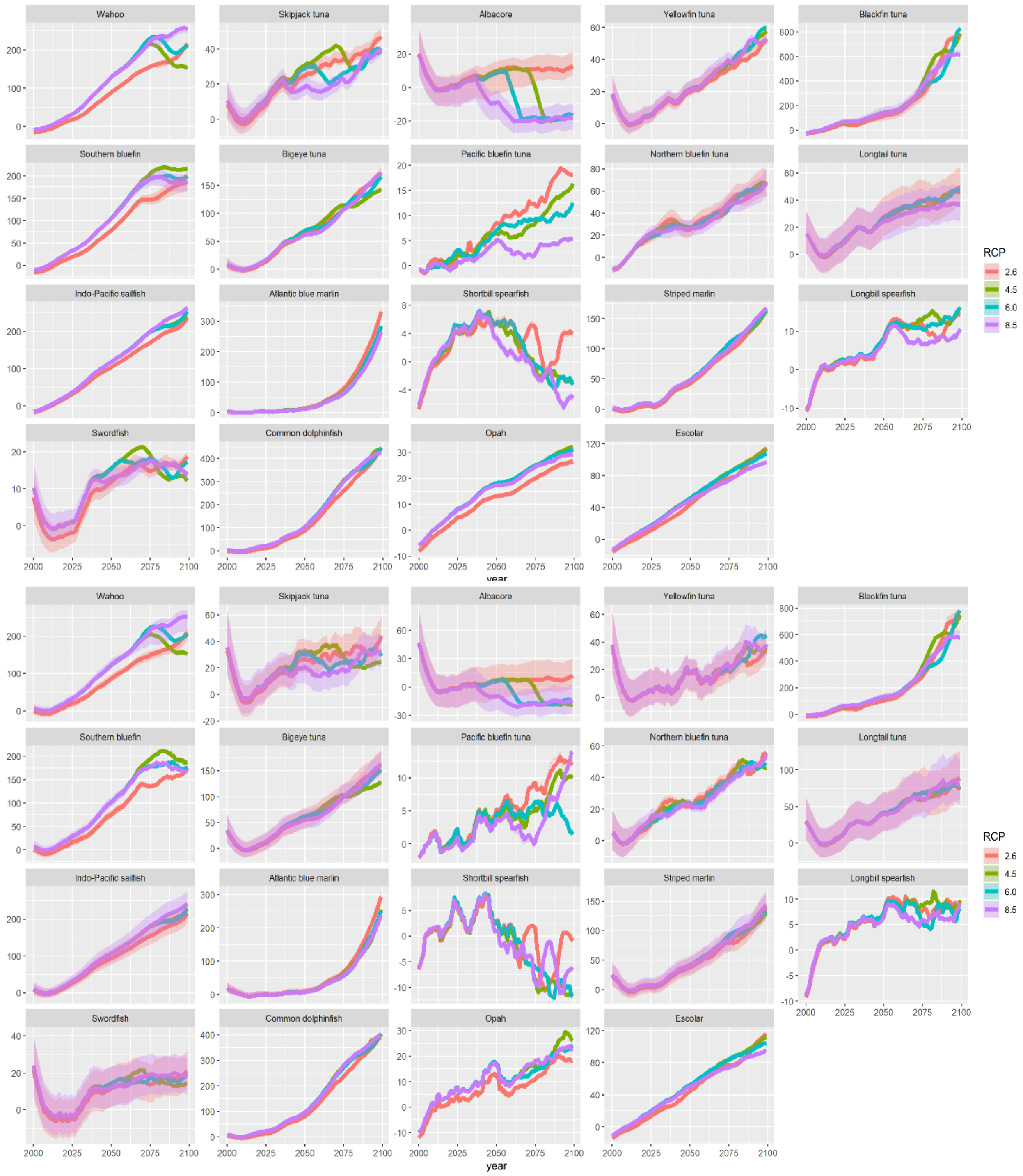


Figure 4.3: (a) Abundance (number of individuals) and (b) biomass change in % related to the reference period (2000-2010) for different climatic scenarios (RCP2.6, 4.5, 6.0 and 8.5). Each envelope is defined by fishing scenarios (0.8MSY and 1.2MSY) and species are ordered by groups (tuna, billfish and other).

Figure 4.4: (a) Abundance (number of individuals) and (b) biomass change proportion related to the business as usual status considered as RCP6.0 and 1.0MSY. Colors correspond to different climatic scenarios (RCP2.6, 4.5, 6.0 and 8.5) and each envelope (shaded area) is defined by fishing scenarios (0.8MSY and 1.2MSY) and species are ordered by groups (tuna, billfish and other).

4.3.3. Size changes under different scenarios

The mean of the size distribution of species individuals and biomass are expected to change under different climatic scenarios (**Figure 4.5a**). The main trend in both, abundance and biomass, is a decrease in size-length distribution when changes are climatic-driven and not large differences can be appreciated between scenarios. Size-length distribution changes due to fishing effort showed (**Figure 4.5b**), on the contrary, higher differences between scenarios. A consistent larger decrease trend across species and both, biomass and abundance, was predicted for averaged sizes-length distribution under higher fishing efforts than lower fishing effort scenarios. The variability between fishing scenarios is much higher than the climatic scenarios. This is the pattern for most of the species such as albacore, A. blue marlin, bigeye,

Figure 4.5: Mean of the size distribution (x axis) per year (y axis) of the abundance (left) and biomass (right) for (a) different climatic scenarios (top) assuming 1.0MSY fishing intensity and (b) different fishing scenarios (down) assuming the RCP2.6 climatic scenario.

longtail, southern bluefin, and blackfin tunas, Indo-Pacific sailfish among others. However, some species average size (escolar, longbill and shortbill spearfish, opah and P. bluefin tuna) seem to be insensitive to different fishing intensities.

4.3.4. Size changes by FAO areas

Positive ratios (biomass divided by the abundance) have been predicted for more optimistic climate and fishing scenarios (Figure 4.6), being RCP2.6 ad 0.8MSY the most positive scenario. Middle climatic scenarios (RCP4.5 and 6.0) with no fishing (1.0MSY) seem to have lower ratio variation, while the most negative changes have been predicted under the highest gas emission scenario (RCP8.5) and with high fishing intensity (1.2MSY). Nevertheless, the worst climatic scenario combined with the lowest fishing effort scenario projected more positive ratios than the combination of no fishing and more benevolent climatic scenarios (1.0MSY-RCP4.5 or 6.0). Therefore, fishing intensities below 1.0MSY could help mitigating climate change impacts. FAO Area 61 (the Northwestern part of the Pacific Ocean), showed the highest variability in ratio changes.

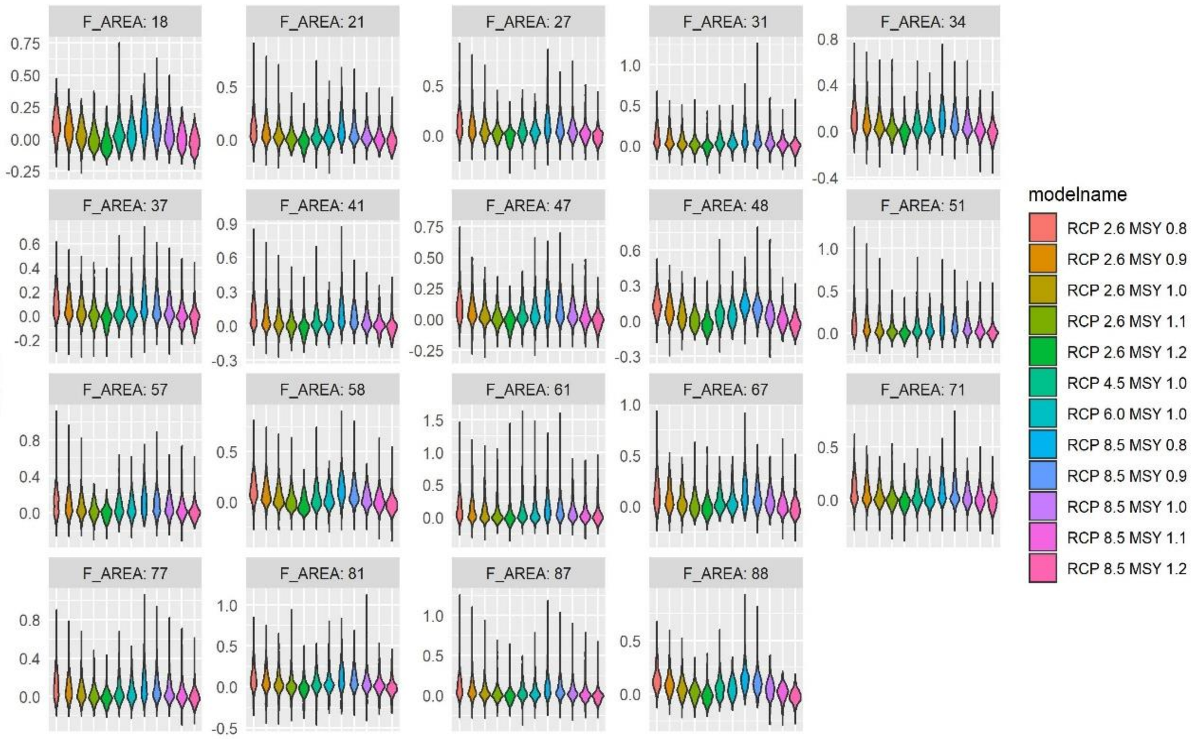


Figure 4.6: *Ratio (the biomass divided by the abundance) change related to the reference period (2000-2010) by each FAO fishing area across the combination of 4 climatic scenarios (RCP2.6, 4.5, 6.0 and 8.5) and five fishing scenarios (0.8, 0.9, 1.0, 1.1 and 1.2MSY).*

4.4. Discussion

4.4.1. Size-length frequency changes under climatic and fishing scenarios

Most of the studies have predicted a generalized decrease in species biomass under future climate and fishing scenarios, mainly for higher trophic levels (Fu *et al.*, 2019; Lotze *et al.*, 2019). Those trends are in contrast with most of the results obtained here where model projections increase in biomass. However, it has to be highlighted that many of these results are based on simple size-spectrum approaches were the authors have stated that the models fail in the highest trophic levels and particularly tuna species (Blanchard *et al.*, 2011; Jennings & Collingridge, 2015). Despite projected increases obtained here are in disagreement with previously published research, some agreements have been found with previous researches, such as predictions for skipjack and yellowfin in **Chapter 2**, where a relative abundance increase was projected under the future RCP8.5 business as usual climatic scenario. Besides, these results and the relative difference with the baseline scenario confirm previous research stating the synergies between climate and fishing impacts over the species size (Fernandes *et al.*, 2017; Queirós *et al.*, 2018).

Species may react differently to climatic and fishing-driven changes; however, a common pattern has been found for the top predators analyzed here; most of them are projected to increase in abundance and biomass but decreasing the averaged body size across all fishing and climatic scenarios. The species abundance (number of individuals) increase could be the consequence of a decrease in body size. Therefore, smaller individuals are predicted in future scenarios. The biomass increase in the highest trophic levels can be driven by the GDFL biogeochemical model which is one of the most optimistic models that can be used for future projections. The averaged sea surface temperature increases in the business as usual RCP8.5 is around 2ºC and lower for the other climatic scenarios. In addition, the maintenance of the global averaged primary production or a slight increase of 1%, may benefit the target species. Both averaged positive changes may be beneficial for tropical and temperate species which can expand their distribution and therefore, shift following their preferent environmental conditions. The propagation of a hydroclimatic signal up the food web can magnify (or depress) the biomass values along one or more trophic pathways through the trophic amplification (or attenuation) (Chust *et al.*, 2014a), and in our case, the results suggest a magnification of the biomass through a trophic amplification. The worldwide distribution (Muhling *et al.*, 2017a), high mobility (Collette & Nauen, 1983; FAO, 1994), high thermal tolerance (Korsmeyer & Dewar, 2001), vertical movements and diving behavior (Block & Stevens, 2001; Brill *et al.*, 1999) the non-highly specific feeding (Collette & Nauen, 1983) of the target species may help in the adaptation of those species to the new environmental conditions.

Overall, abundances and biomasses are predicted to be higher with lower fishing pressure in most of the species, and consequently, lower with higher fishing pressure (Cheung *et al.*, 2017; Travers *et al.*, 2010). However, in some cases, higher fishing pressure predicted higher abundances and biomasses which can be the consequence of a decrease in the intra-specific competition. Lotze *et al.* (2019) conclude that fishing did not alter substantially the effects of climate change but remarked that the inclusion of dynamic scenarios of fishing will be needed in the next model development steps. On contrary, some studies have determined that fishing is a greater stressor than climate change when they are examined individually (Woodworth-Jefcoats *et al.*, 2019). For example, Cheung *et al.* (2017), projected a decrease in global catches under status quo fishing scenario (fishing mortality rate, F, defined as two times F_{MSY}) for both climatic scenarios (RCP4.5 and business as usual RCP8.5) but an increase in abundance and resilience of fish stocks under the cooperative management and high seas closure scenarios (lower fishing pressure). Then, mixed responses have been found in different studies.

Although our results seem to be in disagreement with the general results obtained in other studies, the relative changes and the disentangling between the importance of the climate change effects versus fishing pressure and across different scenarios may provide valuable information for top predators. Similar multispecific and global studies usually are controversial (Cheung *et al.*, 2009a; Myers & Worm, 2003) but they must be contextualized and value their usefulness pointing general patterns and trends.

The reduction in body size or change in the size-length frequency trough time has also been reported (Baudron *et al.*, 2014; Bianchi *et al.*, 2000; Dulvy *et al.*, 2004; Erauskin-Extramiana *et al.*, 2017; Genner *et al.*, 2010; Saenz-Arroyo *et al.*, 2005). This result found for top predators has been defined as the third universal ecological response to increasing temperatures (Cheung *et al.*, 2013a; Daufresne *et al.*, 2009) besides the shift of species ranges toward higher altitudes and latitudes and the seasonal shifts in life-cycle events. This theoretically predicted and empirically observed life-history pattern has been recorded as a decrease in body size, an increase in the proportion of small-sized species, young age classes and earlier maturation (Audzijonyte *et al.*, 2016; Daufresne *et al.*, 2009).

The size spectrum seems detection of the effects of temporal changes in fishing intensity, then, different fishing scenarios may predict changes in size-length frequency distribution. Like many other ecosystem indicators, size-based indicators are sensitive but not specific to fishing impacts and confounding effects may mislead the interpretation of observed change in indicator value (Shin *et al.*, 2005). However, there are evidences of fishing impact in body size distribution. The fishing pressure was related with the steepening in the slope of length spectra, the average weight of individuals and community maximum length of coral-reef fish communities in Fijian islands (Dulvy *et al.*, 2004) and the steepening of the spectrum slope in the North Sea fish community (Rice & Gislason, 1996). Slopes seem to be less sensitive to fishing pressure in tropical regions (Bianchi *et al.*, 2000), where growth is faster (Pauly, 1980). Nevertheless, further modeling and worldwide comparative studies are needed to provide a better understanding of size-based indices and the factors affecting them (Shin *et al.*, 2005).

4.4.2. Model parametrization and limitations for top predators

Most of the biological parameters for main commercial tuna species and swordfish were updated in our model based on the literature, as well as the initial distribution. However, neither new initial distribution nor biological parameters revision was conducted for the direct competitor species. The recruitment equation was also revised to examine if there was any other recruitment equation that best fits the study species because it is a key process in fish population dynamics. Initially, the DBEM model did not consider an explicit stock-recruitment relationship, then, the magnitude of larval recruitment was dependent on pelagic larval duration, ocean currents, and diffusivity (Cheung *et al.*, 2008b). SST has previously been associated with larval development; thus, it is perhaps not surprising that in the months immediately following spawning it appears to influence subsequent recruitment fluctuations (Harford *et al.*, 2015). In 2011, the expected biomass per recruit was determined using a size-based population model, where total larval production was directly proportional to spawning biomass per recruit (Cheung *et al.*, 2011). The recruitment equation was not modified due to the lack of consensus about the best model. In stock assessment, Beverton-Holt and “hockey-stick” recruitment equations (Barrowman & Myers, 2000; Froese, 2008) are commonly used, although Deriso’s General Model (modified to take into account environmental effects) was found as the best spawning stock-environment-recruitment model for north Atlantic albacore recruitment prediction (Arregui *et al.*, 2006). All these examples reveal the difficulty of making correct assumptions in the model. Although the recruitment equations review depicts, they were considered appropriate for selected target species.

As in all ecosystem-based models, some assumptions were made in this study and together with the uncertainties may affect the models' performance (Cheung *et al.*, 2009a). First, the models are based on an equilibrium assumption that depicts species environmental preferences. Second, the models did not consider the potential for phenotypic and evolutionary adaptations of the species. In addition, the interspecific competition algorithm in SS-DBEM does not specify the interactions but the competition was modeled using size considerations. This simplification avoids the difficulties of describing complex species-specific predatory interactions and the assumption that the interactions that are seen today will persist in the future. Furthermore, at the system level, size-based processes account for much of the variation in prey choice and trophic structure (Fernandes *et al.*, 2013). Besides, in the size-spectrum model component, the relationship between log-abundance and log-body size classes in the cell was assumed to be linear for computational performance. However, this assumption can be violated in reality by species' migrations and seasonal fluctuations in primary production (Blanchard *et al.*, 2011; Fernandes *et al.*, 2013).

All assumptions and uncertainties aside, the main strength of these two models combination approach comes from providing spatially and temporally resolved species and size predictions, with full consideration for the effects of ecological interactions (Fernandes *et al.*, 2013). Our model has provided new insight and provides a new tool for further exploring the effects of future climate change and different fishing pressures over ecologically and economically valuable top predator species. The combination of the models includes the size-spectrum but also many mechanisms that other models have not taken into account. In general, similar studies are monospecific or are focused on lower trophic levels. However, this is the first study that applies the combination of those two models to predict distribution, abundance and body size changes in high trophic level marine fish species (top predators). In addition, predictions for higher trophic levels show always larger variability, may be less accurate particularly at higher RCPs, then, results are considered less robust (Jennings & Collingridge, 2015; Lotze *et al.*, 2019).

4.4.3. Further work

Although biological parameters and equations have been revised and updated, the parametrization may need further work, mainly updating direct top predator species parameters. Further work is needed to improve the model and to adapt it for top predators and other high trophic level species. Highlighting the existing barriers for top predators modeling, more tests and examination of the biological equations are needed. Future development of the DBEM will also attempt to incorporate other key biological processes that are likely to be important for target species such as evolution. Besides, the spatial changes may be explored to provide further information about the behavior of the species or their redistribution and shift. This information may be helpful for management plans and/or implementation of an ecosystem approach to fisheries. In addition, predictions have been only conducted for the GDFL biogeochemical model, but the use of a model ensemble is suggested, rather than individual models to be able to estimate and analyze inter-model differences or model spread as an estimate of uncertainty around the projections (Bopp *et al.*, 2013).

Our projections may also be interesting within FISHMIP (Fisheries and Marine Ecosystem Model Intercomparison Project), part of the Inter-Sectoral Impact Model Intercomparison Project (ISIMIP), where heterogeneous models are forced with common Earth System Model (ESM) CMIP5 outputs under prescribed scenarios for historic (from the 1950s) and future (to 2100) time periods to inform understanding of the range of plausible changes in marine ecosystems, and improve the capacity to define and convey strengths and weaknesses of model-based advice on future states of marine ecosystems and fisheries (Tittensor *et al.*, 2018).

GENERAL DISCUSSION

5. GENERAL DISCUSSION

5.1. Habitat modeling and projections of pelagic species

5.1.1. Advantages and limitations of Species Distribution Models (SDM)

The last years have seen an explosion of studies on methodological aspects of SDMs, allowing some considerable progress to be made (Guisan & Thuiller, 2005). A huge amount of modeling tools has become available for modeling species distribution (reviewed in Guisan and Thuiller (2005)) which vary on the type of response variables and predictors. Despite the limitations described above, correlative SDMs are frequently used, and can at least provide initial hypotheses for future distributions and abundance of different species (Bruge *et al.*, 2016; Chust *et al.*, 2014b; Dell *et al.*, 2015; Hartog *et al.*, 2011; Muhling *et al.*, 2011; Robinson *et al.*, 2015b; Villarino *et al.*, 2015).

In recent decades, species distribution models (SDM) and their output habitat suitability maps have been improved and applied successfully to investigate a variety of ecological issues (Guisan & Thuiller, 2005; Robinson *et al.*, 2011). Projections of future conditions from IPCC climate models (Bopp *et al.*, 2013; Collins *et al.*, 2013) are applied to develop habitat models to project future species distributions and abundance. SDM does not usually include population dynamics and fishing impacts. No prior understanding or knowledge is needed about recruitment processes, food web dynamics, dispersal or behavioral mechanisms. The predictive modeling of SDM relies entirely on the assumption of environmental equilibrium between the biotic entities and the physical characteristics of their environment (Guisan & Theurillat, 2000). As both species and environmental data are usually sampled during a limited period of time or/and space, models fitted using these data can only reflect a snapshot view of the expected relationship (Guisan & Thuiller, 2005).

SDM also assume that statistical relationships observed between fish and their environment in the recent past will continue to apply in the future, which may not be a valid assumption. Correlations that have no obvious mechanistic basis may be particularly problematic (Peck *et al.*, 2013). In addition, the assumption that observed species distributions correspond to ecological niches is often overly simplistic (Robinson *et al.*, 2011). The problem with the Hutchinsonian concept of niche, in which most of the SDM is based, is its difficulty to apply to the real world since the number of environmental variables affecting an organism is large (Hardesty, 1975). Results can be more complex than a poleward shift (Hobday, 2010) in the cases where there are barriers to poleward movement, or when other environmental variables apart of temperature can be influential. Many past range shifts have been studied from a single environmental covariate prism, usually temperature. Although temperature-based models can be useful in an exploratory analysis, exclusion of relevant environmental drivers could yield skewed and inaccurate assessments of species responses to climate change. McHenry *et al.* (2019) showed how the inclusion of additional environmental covariates can improve habitat suitability model performance while significantly altering projections of species' future ranges. Their results demonstrate the advantages and importance of incorporating a broader set of environmental variables when projecting marine species range shifts, as a continued focus on ocean temperatures may mask species' vulnerability to climate change. This suggests that where temperature is not physiologically limiting, other variables such as feeding habitat suitability or oxygen limitation may be more important in determining future distributions and that correlative SDMs are usually most reliable when upper and/or lower habitat limits are well known and defined, and present or future conditions approach those limits (Rijnsdorp *et al.*, 2009; Robinson *et al.*, 2015b).

Geographic distribution of the species depends not only on their environmental tolerance but also on their thermoregulatory and dispersal capacity (Brill, 1994; Lehodey *et al.*, 2011), larval survival, juvenile settlement or recruitment, which are most likely to drive stock and population sizes in the longer term and biological interactions (Guisan & Thuiller, 2005; Peterson *et al.*, 2011). All those factors may not be integrated into the simplest SDMs.

Apart from the limitations mentioned above, there are many sources of error, bias, and uncertainty associated with ecological models and climate projections. An important source of uncertainty comes from the environmental forcing used in past reconstructions and future projections (Bopp *et al.*, 2013). Models are constantly improving to decrease the error, but the magnitude of uncertainty can be substantial and is often not considered in impact studies. Regardless of the method or model used to analyze the impacts, some effort should be made to quantify or assess the source of error and/or uncertainties from the climate models. In this context, inter-model difference or model spread has been used as an estimate of uncertainty around the projections (Bopp *et al.*, 2013) and the use of model ensembles is also suggested, rather than individual models. Furthermore, global climate models are not able to accurately project short-medium term natural variability (interannual to decadal-scale environmental variability) (Gupta *et al.*, 2015). In the particular case of fishes, another important source of error is the lack of quantitative data on interaction between species and their environment (Guisan & Thuiller, 2005; Hobday & Evans, 2013; Payne *et al.*, 2017) and the possibility of a biological processes desynchronization (Thackeray *et al.*, 2016).

The development of SDM for marine pelagic fish species was conducted in this thesis in **Chapters 1-3** as the basis to analyze historical and future trends (**questions 1-4, objective 1**).

5.1.2. Mechanistic ecosystem model

Due to the limitations of simple statistical habitat models, ecosystem models have been developed in order to integrate more complex biological processes such as population dynamics, food webs interactions or recruitment. In fisheries, traditional management approaches like single-species stock assessments are still common, but advances in ocean observing technologies and modeling provide the capacity to revolutionize the management of living marine resources, considering changes in the physical environment and interactions between ecosystem elements, including human uses holistically (Schmidt *et al.*, 2019). Ecosystem models are perceived as the way forward, through more complex mechanistic, behavioral or ecological models (Muhling *et al.*, 2017a). The development of more complex ecosystem models has been allowed due to increasing computing power and progress in modeling ocean physical and biogeochemical states (Muhling *et al.*, 2017a). Different models were developed with the same aim of introducing many of the biological and physical processes that occur in the ocean and which affect the entire ecosystem and species which inhabit there.

Models that incorporate biomass, biological functions and population dynamics are often more useful than those which only consider distribution, but robust methods for parameter estimation from historical data are required (Muhling *et al.*, 2017a). Although the understanding of these mechanisms increases through laboratory studies, tagging programs, scientific surveys, and other research efforts, these complex models need an important number of parameters about life cycles and population dynamics, as well as computational power.

Chapter 4 results highlight the limitations of those models for higher trophic levels (**question 5, objective 7**). Although a literature review to update biological parameters value and recruitment equation revision were conducted for the SS-DBEM, results were in disagreement with other studies were a generalized decrease in species biomass under future climate and fishing scenarios were predicted (Fu *et al.*, 2019; Lotze *et al.*, 2019). However, it has to be highlighted that many of these results are based on simple size-spectrum approaches were the authors have stated that the models fail in the highest trophic levels and particularly tuna species (Blanchard *et al.*, 2011; Jennings & Collingridge, 2015). Further work is needed to improve the model and to adapt it for top predators and other high trophic level species. In addition, predictions have been only conducted for the GDFL biogeochemical model, but the use of a model ensemble is suggested, rather than individual models to be able to estimate and analyze inter-model differences or model spread as an estimate of uncertainty around the projections (Bopp *et al.*, 2013).

High trophic level species projection may also be interesting within FISHMIP (Fisheries and Marine Ecosystem Model Intercomparison Project), part of the Inter-Sectoral Impact Model Intercomparison Project (ISIMIP) to inform understanding of the range of plausible changes in marine ecosystems, and improve the capacity to define and convey strengths and weaknesses of model-based advice on future states of marine ecosystems and fisheries (Tittensor *et al.*, 2018).

5.2. Climate change historical and future impacts on marine ecosystems

Most of the marine ecosystems that provide a range of services on which humans depend on have already been affected by climate change. The impacts directly concern fisheries production, carbon sequestration, coastal protection and loss of biodiversity (Brander, 2010). The effects of climate change in heavily exploited species may be stronger than in less exploited or unexploited species (Brander, 2007) due to their higher sensitivity and vulnerability (Brander, 2005; Hsieh *et al.*, 2006) as a consequence of a reduced age structure (Ottersen *et al.*, 2006), and constriction of geographic distributions (Hilborn *et al.*, 2003). The impact of climate change to keystone species (Pauly *et al.*, 1998; Pinnegar & Engelhard, 2008; Pitcher, 2001), which play a very important role in regulating community structure in marine systems (Aburto-Oropeza *et al.*, 2008; Sadovy & Eklund, 1999), can trigger cascading effects and trophic amplification (Chust *et al.*, 2014a; Lotze *et al.*, 2019).

Climate change is one of the most recent stresses that fish stocks have experienced (**Figure 5.1**) after overfishing, pollution, eutrophication, physical destruction of habitats, outbreaks of disease, invasions of introduced species (Jackson *et al.*, 2001) and will likely have progressively greater impacts on marine ecosystems and fisheries. Anticipating and adapting to such changes will help to minimize the disruption to marine ecosystems and to human food supplies (Brander, 2010).

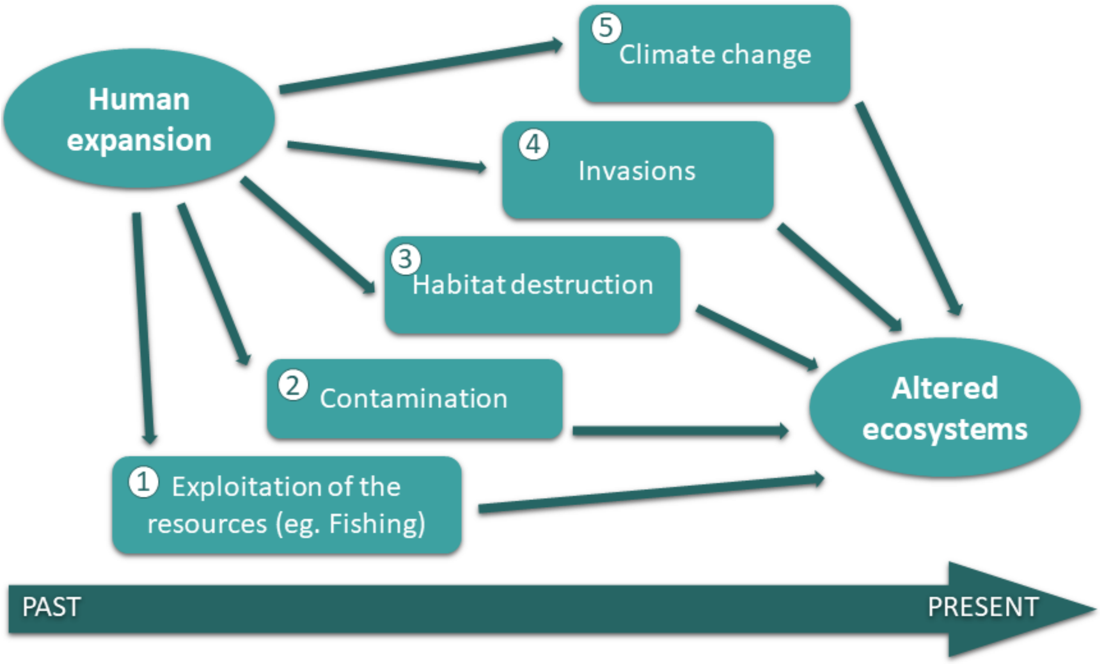


Figure 5.1: The historic development of pressures on fisheries and marine ecosystems due to human expansion. Fishing always preceded other human and climate change disturbances (redrawn from Jackson et al. (2001)).

5.2.1. Impacts

Species respond differently to climate change. Some of them shift to other areas (Brander *et al.*, 2003; Robinson *et al.*, 2015a; Trenkel *et al.*, 2014), colonize them (Huse & Ellingsen, 2008), change their biological functions' timing to adapt to the new characteristics of the environment (Dufour *et al.*, 2010), or in the worst case that they are not able to adapt to environmental changes, local population decline or extinction may occur (Anderson *et al.*, 2013). On land, increasing anthropogenic activities and temperatures negatively impact the capacity of terrestrial taxa to track isotherm shifts in latitude and elevation, suggesting that biotic responses on lands are lagging behind the velocity of climate change, particularly for long-lived taxa and poor-dispersers. On the contrary, in the oceans, the velocity of isotherm shifts interacts synergistically with anthropogenic disturbances and baseline temperatures (Lenoir *et al.*, 2019).

In the case of pelagic species, due to their high mobility (Collette & Nauen, 1983), a shift in their distribution is mainly expected. Shifts in pelagic fish species, principally in large pelagics, have been recorded (Monllor-Hurtado *et al.*, 2017). However, other types of adaptations have also found in other species; an earlier spawning peak (Jansen & Gislason, 2011), change of spawning areas and timing of pre- and post-spawning migration (Lehodey *et al.*, 2015; Trenkel *et al.*, 2014) and/or change in feeding grounds or timing to adjust to shifts in their prey (Corten, 2000; Dufour *et al.*, 2010). Range contractions and abundance declines have also been recorded for larger tuna and billfish species (Worm & Tittensor, 2011). For many other fish species, the movement of the populations in the last decades has been associated with the latitudinal shift of their habitats (Beare *et al.*, 2004; Bruge *et al.*, 2016; Montero-Serra *et al.*, 2015; Perry *et al.*, 2005). Consistent with this movement, the species composition in marine fisheries has changed due to climate change; the dominance of warmer water species has increased at higher latitudes and the proportion of subtropical species has decreased in the tropics (Cheung *et al.*, 2013b).

In **Chapter 1** of this Ph.D., historical trends in anchovy egg production and timing of the spawning were analyzed while in **Chapter 2** and **Chapter 3**, main commercial tuna species, as well as swordfish historical changes in distribution and in abundance were addressed (**question 1, objectives 2-4**). Overall, the results can be divided into two groups. On one hand, the earlier spawning peak of the anchovy in the Bay of Biscay suggested a phenology adaptation to the rising water temperature as well as to the time when phytoplankton and therefore, zooplankton abundance increases (Somarakis *et al.*, 2004). Spatial changes had been related to population dynamics, supporting the hypothesis that northern boundary variability is affected by the population abundance (Checkley *et al.*, 2009; Santos *et al.*, 2016; Somarakis *et al.*, 2004) more than with a poleward shift. The distribution area expands and contracts depending on the total population abundance, restricting to more favorable spawning areas when the abundance is low (MacCall, 1990).

On the other hand, historical poleward shifts were found in most tuna stocks with the highest decrease in habitat suitability for albacore and bluefin tunas. Those results were habitat-driven, while other research attributed tuna populations decline to their high-exploitation level (Juan-Jordá *et al.*, 2011). Following the developed framework applied to swordfish global case, a latitudinal shift in 2 out of 6 swordfish stocks (Mediterranean and South Pacific stocks) was found during the same period. Surprisingly, swordfish does not always track its most suitable, shifting habitat. Then, swordfish stocks shift due to other reasons not related to environmental changes.

The reduction in body size or change in the size-length frequency trough time has also been reported (Baudron *et al.*, 2014; Bianchi *et al.*, 2000; Dulvy *et al.*, 2004; Erauskin-Extramiana *et al.*, 2017; Genner *et al.*, 2010; Saenz-Arroyo *et al.*, 2005) and some studies related the reduction in body size with fishing (Dulvy *et al.*, 2004; Rice & Gislason, 1996). **Chapter 4** results on top predators' body sizes agree with the so-called third universal ecological response to increasing temperatures (Cheung *et al.*, 2013a; Daufresne *et al.*, 2009) together with distribution shifts and phenology changes. In the future, the body size of the largest fishes is expected to decrease under higher fishing pressures and worse climatic scenarios. Changes in body sizes may be mainly driven by fishing but it is not the only driver as we showed; therefore, attribution of changes may be needed carefully (Shin *et al.*, 2005) (**question 5, objective 7**).

5.2.2. The challenge of detection and attribution of trends

In order to obtain a better understanding of the climate change impacts and develop improved management plans, drivers behind species shifts or phenology changes must be identified. It is a complex process and different efforts have been made to disentangle the causes of species shift (Currie et al., 2019; Thorson et al., 2017; Thorson et al., 2016). The most common aim of those studies is to detect species range shifts due to climate change, focusing for instance, on the spatial center of the population's distribution (Center of Gravity, CoG), distribution limits and area occupied (Thorson et al., 2016). For example, Bell et al. (2014) disentangled the changes in biomass CoG due to sea warming and fishing pressure in the Northeast US shelf. However, some wrong attributions can be made due to taxonomic and geographic biases in original data (Schmidt et al., 2019) or correlations that not necessarily imply causality (Van Nes et al., 2015). This issue has been long debated, but in recent years, a powerful new methodological approach has been developed, based on nonlinear state-space reconstruction, that can distinguish causality from spurious correlation in multivariate time series from deterministic dynamical systems (Sugihara et al., 2012; Van Nes et al., 2015).

In **Chapter 3**, a new framework was developed to analyze the historical trends of a population distribution to ascertain if the reasons for the stocks' shifts were habitat-driven. Analyzing the historical trends of the spatial distribution changes, we are able to answer the questions about how climate change has affected the pelagic species distribution and abundance in the last half-century and which were the drivers behind (**question 1, objectives 1, 3 & 4**). The approach helps to disentangle the causes of the species shifts (analyzing the climate impacts and separating the sampling effort bias in data). Importantly, this new framework is potentially useful for any time series of species spatial distribution and can be compared with any driver that can trigger changes in species. Comparisons between the reconstructed spatio-temporal model and parameters that can be affecting the target species' historical trends may inform about which drivers are redistributing or changing the phenology of each species.

5.2.3. Future scenarios

The studies that aim to project pelagic fishes distribution, recruitment and/or abundance have increased in number in the last two decades (Muhling *et al.*, 2017a). Although future projections under different climate change scenarios are crucial to anticipate the impacts on populations of target species (Dueri *et al.*, 2014; Lehodey *et al.*, 2013), changes in predator-prey relationships, the impacts on human services and fisheries (Bell *et al.*, 2013b; Cheung *et al.*, 2013b; Cheung *et al.*, 2009b; Dueri *et al.*, 2016), the identification of the most vulnerable nations

(Allison *et al.*, 2009; Barange *et al.*, 2018), and fisheries status projections are more complex than simply combination of northward shifts of species distributions, abundance changes or earlier spawning peaks (Bruge *et al.*, 2016; Burrows *et al.*, 2011).

Climate projections provide insight about habitat suitability into the likely time in the future while seasonal forecasting is beneficial in helping industries plan ahead to reduce impacts in poor years and maximize opportunities in good years (Hobday *et al.*, 2018). Projections for target species are usually conducted under "the business as usual" RCP8.5 climate change scenario but changes for other scenarios (RCP 2.6, 4.5 and 6.0) are expected to be similar until around 2050, while after that they diverge (Hoegh-Guldberg *et al.*, 2014; IPCC, 2013). However, the sixth phase of the Coupled Model Intercomparison Project (CMIP6) (IPCC, 2019a) output is growing rapidly and will afford a re-examination of important aspects of the climate system. The CMIP6 employs scenarios rooted in socioeconomic trajectories: the shared socioeconomic pathways (SSPs) (O'Neill *et al.*, 2014; Simpkins, 2017) in addition to RCP scenarios from CMIP5.

The projected impacts in anchovy (**Chapter 1**), tuna (**Chapters 2 & 4**) and swordfish (**Chapter 3**) will be discussed below and questions about how climate change is expected to affect the pelagic species distribution, abundance and hence, coastal countries catch in the future under climate change scenarios will be answered (**question 3-5, objectives 5-7**).

The small pelagic functional group has a keystone position in marine ecosystems and coastal economies worldwide due to its role for both, predators and fisheries directly and indirectly (Pikitch *et al.*, 2014). In the past, studies focused on disentangling the climate effects from fishing pressure. Recently, the interest has shifted to the interaction between both drivers and the change in sensitivity (strength of the relationship between biotic and climatic variables) (Macías *et al.*, 2014). Climate-induced changes can collapse some stocks, particularly those that are on the edge of species distributions (Beaugrand *et al.*, 2008). Unlike in many studies where a decline in abundance and/or a poleward shift is projected, an increase in egg production and an expansion of the expanding area is expected for the anchovy in the Bay of Biscay due to environmental changes. A similar expansion of the potential habitat has been projected with an increase in the probability of the occurrence in the northern areas (Lenoir *et al.*, 2011; Raybaud *et al.*, 2017).

In the case of tuna and swordfish, due to their condition of highly migratory species (FAO, 1994), batch spawners (Collette & Nauen, 1983; Murua & Saborido-Rey, 2003) and opportunistic feeders of different kind of fish, crustaceans, and squids (Collette & Nauen, 1983; Young *et al.*, 2006), they are expected to acclimatize to the environmental changes and shift following their preferred habitat in order to dwell in the best environmental conditions. Developed models do not account for the evolutionary responses of marine populations so that there is still uncertainty in future biodiversity predictions, then, only habitat-driven changes were projected.

Two different responses have been projected into the future; temperate tunas, bigeye, and swordfish are expected to decrease at low latitudes and shift poleward increasing the abundance in distribution boundaries, while tropical tunas such as yellowfin and skipjack are projected to increase their relative abundance in the equatorial areas of the main oceans. Both bluefin species (Atlantic and Southern) are projected to have the greatest depletion, reaching 60% in the case of Atlantic bluefin tuna by the end-of-the-century. Only some countries located close to their distributional limit will increase their bluefin abundance as well as albacore. The total relative abundance of swordfish is also projected to decrease in 21.5% by 2100 although some increases supported by the local population are expected in the Mediterranean Sea. Those results align with Lotze *et al.* (2019) who predicted a mean global animal decrease of 17% (±11% SD) under high emissions by 2100 primarily driven by increasing temperature and decreasing primary production. Biomass decrease is expected to be more pronounced at higher trophic levels, through a process known as trophic amplification (Chust *et al.*, 2014a; Lotze *et al.*, 2019). Skipjack and yellowfin tunas are the only species that are projected to significantly increase in the future in agreement with projections from other studies (Lehodey *et al.* (2013), Dueri *et al.* (2014), Muhling *et al.* (2017b), Bell *et al.* (2013b)). The results partially agree with Senina *et al.* (2016) and disagree with future projection in EEZs with Senina *et al.* (2018).

However, most of the predictions are based on the assumption that the state of the ecosystems or species may respond in a smooth, continuous way to environmental changes but when conditions change sufficiently to pass a certain critical threshold, an abrupt transition could occur, with 'early-warning signals' being difficult to detect (Scheffer *et al.*, 2001). Systems may also respond in a non-linear way to gradual change if they have no alternative stable states and those possible future states are not commonly included in projections because there are very difficult to predict in advance.

5.3. Vulnerability and adaptation of the fishery sector to climate change

Climate change and fishing impact synergistically over natural marine resources. Climate change alters the distribution of suitable habitat, forcing organisms to shift their range or attempt to survive under suboptimal conditions, while fishing reduces the abundance of marine populations and truncates their age structure leading to range contractions or shifts (Bell *et al.*, 2014). The vulnerability of different fisheries, fleets, and countries to climate change may vary, depending on their exposure, dependence on fisheries production and their capacity to respond and adapt (Allison *et al.*, 2009; Brander, 2010). Main changes in fisheries due to climate change include (Kalikoski *et al.*, 2019; Muhling *et al.*, 2017a):

- Shifts in fish distribution and migration behavior. Fish populations may move away from historical fishing grounds, crossing management or national boundaries (Ainsworth *et al.*, 2011; Pinsky *et al.*, 2018) and disrupting traditional fishing patterns. For example, abundance decline would be recorded in one area while an increase would occur in another but the true stock abundance may actually remain constant (Link *et al.*, 2011).
- Mobile, large-scale fleets (commercial fleets) will be able to better adapt to the shifts in fish distribution than small-scale, community-based (artisanal) fleets. The ability of fishermen to follow shifting stocks may be limited by the technology available and infrastructure, vessel ranges, fuel costs, and locations of ports (Madin *et al.*, 2012; Pinnegar *et al.*, 2010). Changes in the spatial overlap between fishing fleets and target species could occur.
- Change in species catchability. A shallowing thermocline, or a shoaling of hypoxic sub-surface layers, may constrict large pelagic species towards the surface, increasing their vulnerability to some fishing gears (Lehodey *et al.*, 2011; Stramma *et al.*, 2012).
- Decrease of catches in equatorial and tropical areas and an increase in higher latitudes (Cheung *et al.*, 2009b). Therefore, a tropicalization of the catches may occur (Cheung *et al.*, 2013b), mainly in fishermen communities with a limited capacity to change the spatial distribution of their fishing effort.
- Change in policies, management plans, and regulatory systems to deal with climate change effects that may impact on fishing practices (Karp *et al.*, 2019). In addition, the effectiveness of current management zones and protected marine areas may diminish as fish distributions change and they may have to be reviewed (Pinnegar *et al.*, 2010).
- Alteration of the population dynamics of exploited stocks. Changes in the carrying capacity may affect fishing mortality where historical fishing levels may no longer be sustainable (Brander, 2009; Rijnsdorp *et al.*, 2009).
- Direct impacts have been recorded and more are expected in communities and economies due to changes in dynamics of exploited species as well as the related fisheries. Many communities, mainly in developing nations rely heavily on fisheries for small pelagic fishes, for livelihoods and food security which can be affected (Bell *et al.*, 2013b; Weng *et al.*, 2015).

In **Chapter 2**, changes in main commercial tuna species distribution are estimated for the end-of-the-century due to ocean warming (**questions 3 & 4, objectives 5 & 6**). Overall, equatorial countries will decrease their catchable tuna abundance, while more temperate latitudinal countries' fleets will increase their tuna availability. The average catches for all temperate tuna species (albacore, Atlantic, and southern bluefin) and the tropical bigeye are expected to decrease in the future in tropical EEZs, but to increase in the countries located in the boundaries of the suitable area. Many of the countries that are more vulnerable to the impacts of climate change on their fisheries are also the poorest (Allison *et al.*, 2009; Barange *et al.*, 2018; Barange *et al.*, 2014) and therefore, with most difficulties to adapt to those changes. These developing nations rely on their fisheries sector in terms of wealth, food, and employment, and they have limited capacity to invest in climate adaptation (Allison *et al.*, 2009; Barange *et al.*, 2014). This situation occurs when only the abundance is expected to decline in the future, but, when future projections involve changes in distribution (with apparent abundance decreases in some areas and increases in others), there is also potential for increases in tuna population size (Hobday, 2010), and/or conflicts between coastal countries (Karp *et al.*, 2019). This potential increase is projected for tropical tuna species (yellowfin and skipjack), two species that are expected to increase in most of the tropical EEZs. However, other studies such as Senina *et al.* (2018) project that climate change will both positively and negatively affect tuna abundance in Pacific Islands EEZs depending on the location of the country across the Pacific Ocean. The catch decreasing would result in less revenue from license fees for the Pacific Island countries (unless practical ways can be found to increase the value of catches (Bell *et al.*, 2018c)).

Progressive impacts that interact with each other are mainly expected in fisheries in the future (i.e. linear respond), but marine ecosystems can also respond to changes in physical or biological forces in a nonlinear way (Hsieh *et al.*, 2006). As an example, a major change in species composition, production, and dynamics may take place when a threshold value is exceeded (Brander, 2009). A possible adaptation for reducing the impact of climate change could be to reduce fishing pressure due to the higher sensitivity of exploited species to climate change impacts (Brander, 2007). However, the social aspects of changes in stock productivity and availability must also be considered in future fisheries management (Ommer *et al.*, 2013). The strong interactions between fishing and climate require management to adapt the fishing mortality to guarantee sustainable populations, stabilize catches and profits and reduce collateral impacts on marine ecosystems (Brander, 2007; Juan-Jordá *et al.*, 2011). Efforts to adapt to climate change should be planned, including adaptation to possible redistribution and decrease/increase in abundance of target species.

Three approaches have been suggested to manage shifting species; a reevaluation of the stock identification and/or unit area and an implementation of spatially explicit modeling (Link *et al.*, 2011). Additional measures or actions taken in response to climate change should complement and strengthen the overall governance and sustainable use of marine resources (Barange *et al.*, 2018).

Scientists and managers need to be able to detect changes, understand mechanisms that trigger them, evaluate risks and priorities, developed assessment plans and projections and advice to managers and stakeholders (**Figure 5.2**) (Karp *et al.*, 2019). To ensure the maintenance of living marine resources under changing conditions, traditional methods and assumptions used in the fishery management process need to be adapted to get a more holistic and ecosystem-linked approach to reduce risk of maladaptation (actions, or inaction that may lead to increased risk of adverse climate-related outcomes) for the social-ecological system (IPCC, 2014a; Karp *et al.*, 2019).

In coastal communities where local fisheries are important, and climate change is likely to drastically reduce the sustainability of them, consideration of alternative livelihoods and occupational flexibility for fishermen may help to prevent the collapse of fisheries-dependent communities (Metcalf *et al.*, 2014; Ommer *et al.*, 2013). Besides, other aspects not directly related to effects on fisheries will need to be managed, such as re-negotiations of quotas amongst states and countries, jurisdictional changes, and adjustment of abundance indicators from different regions (McIlgorm, 2010).

Appropriate responses to current and predicted changes in stock distribution and productivity are highly important and it concerns fishery managers which sometimes are led to make controversial decisions, such as changes to allocation, spatio-temporal closures, stock status determinations, and catch limits. Scientist advice should provide the necessary knowledge to evaluate the management action under future scenarios considering population resilience, age structure, and genetic diversity of targeted species (Karp *et al.*, 2019).

In summary, a more precautionary approach to fishery management may be more effective by attempting to preserve as much resilience in exploited populations as possible, rather than trying to control fluctuations, particularly for highly variable small pelagic fishes (Barange & Perry, 2009; Brander, 2009).

Figure 5.2: Climate-ready fisheries management process. Changing climate conditions are represented at the center of the diagram, effects in the biotic community are showed in the next ring out from the center. The outer ring represents the climate-ready fisheries management. Source from Karp et al. (2019).

GENERAL CONCLUSIONS

6. GENERAL CONCLUSIONS

The studies carried out in this Ph.D. thesis (i) have contributed to understanding the environmental preferences of commercially important pelagic fish species and built habitat distribution models, (ii) have provided new insights for climate change impacts in the past and in the future of the target species, and (iii) have added knowledge about the species responses to environmental changes that may help the improvement of fisheries management. The main conclusions of this dissertation are detailed below following the stated overall questions.

***Question 1:* How climate change has affected the marine pelagic fish species distribution and abundance in the last decades?**

Objectives 1-4

1. Climate change has impacted over pelagic fish species and some populations have responded shifting poleward (**Figure 6.1a**), increasing/decreasing their relative abundance (**Figure 6.1b**) and/or changing their phenology (**Figure 6.1d**). Those changes occurred at different rates and intensities, varying also between hemispheres across the same species. Some local population distribution changes have been more related to population dynamics and denso-dependent processes (**Figure 6.1c**) than to warming.

   The correct attribution of changes observed in the target species is challenging. Sampling effort bias and/or spatio-temporal heterogeneous data correction may be the first step before analyzing historical trends. The developed conceptual framework is a roadmap to attribute changes to environmental changes, sampling effort bias or other drivers and can be applied to any species.

***Question 2*: Which are the suitable habitats of anchovy, tuna, and swordfish?**

Objective 1

2. Suitable habitat differs among species, but high trophic level tuna and swordfish showed a latitudinally structured habitat. Tropical tuna and swordfish prefer equatorial waters, therefore warmer waters. Temperate tuna species inhabit higher latitude waters, where the temperature is lower but they still have a wide temperature and other environmental variables (such as salinity) tolerance range. The BB anchovy is part of a species with a larger distribution range, and probably tolerate wider environmental ranges than those that are in the Bay of Biscay. This particular population is very associated with the estuaries of Gironde, Adour, and Bidasoa, in the southeast region of

the Bay of Biscay. These places seem to form a refuge that maintains minimal sustaining conditions for this anchovy population even in adverse environmental conditions.

Question 3**: How climate change is expected to affect the marine pelagic fish species distribution and abundance in the future under climate change scenarios?* ***Objectives 1 & 5

3. Climate change will impact pelagic fish species differently. Some species are projected to shift poleward (**Figure 6.1a**), increasing their abundance in the distribution limits but decreasing in equatorial areas (temperate tuna and swordfish), while others (temperate tuna) seem to increase their abundance due to the beneficial environmental conditions (**Figure 6.1b**). However, other biological or phenological responses can occur that the statistical correlative models are not able to predict. In addition, the 2-dimension model is limited because vertical movements to avoid unsuitable conditions have been recorded in highly mobile species (such as tuna and swordfish). For the BB anchovy spawning, the suitability of the area is expected to improve, increasing the total egg production.

Question 4**: How the tuna abundance and distribution changes could affect the catches of different countries?* ***Objective 6

4. Changes in distribution and relative abundance of main commercial tuna species may affect coastal countries' tuna catches. As a consequence, a redistribution of the catches is expected. Equatorial countries and mainly Pacific Islands are expected to increase tropical tuna species such as yellowfin and skipjack but to decrease all other tuna species. Some few countries, which are located in the temperate tuna species distribution limits, will increase their temperate tuna catches but the rest of higher latitude countries tuna catches will decrease due to climate change.

Question 5**: Has climate change affected the body size of top predators and how is it going to affect in the future?* ***Objective 7

5. Both climate and fishing pressure have affected the body size and size-length frequency distribution of top predators (tuna, billfishes and direct competitors) and they will affect it in the future (**Figure 6.1b)**. Known as the third universal ecological response to increasing temperatures, a decrease of body size of high trophic level species is expected to be impacted by climate change and fishing pressure in the future. The SS-DBEM, the ecosystem-based model used to estimate body size changes in top predators, has been reviewed and updated trying to improve high trophic level species projections but results still need further work.

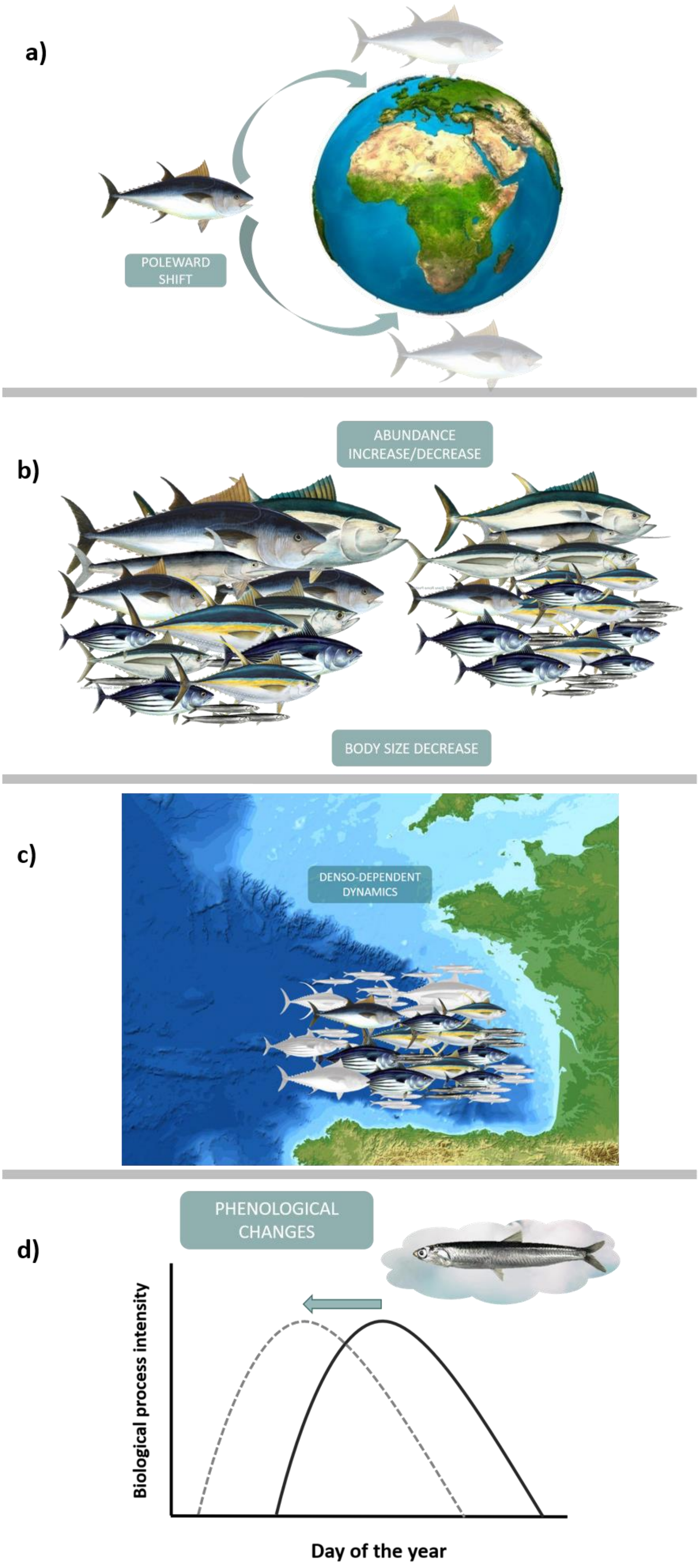


Figure 6.1: *Marine pelagic fish species possible responses to the climate change:*

a) a poleward shift,

b) an abundance increase/decrease and/or body size change,

c) denso-dependent population dynamic fluctuations and

d) phenological changes.

7. THESIS

HYPOTHESIS: *"Climate change and ocean warming affect marine species and it is expected to continue impacting in the future. Disturbances in the habitat of pelagic species provoke poleward shifts, changes in abundance, phenological changes of their biological processes and decreasing body size. These changes affect the distribution of fisheries' activity of coastal countries.*

***THESIS*: "Climate change and ocean warming have provoked a poleward shift of the suitable habitat of some species. Due to the high migratory behavior of large pelagic and rapid respond of small pelagic species to environmental changes, poleward shifts and phenological changes have been recorded. However, not all species studied have followed their environmental preferences and some latitudinal changes were related to population denso-dependent dynamics more than to habitat change. In addition, the correct attribution of species changes is challenging because different drivers often covary. Under the worst climatic and fishing effort scenarios, further species distribution, abundance as well as body size alterations are projected. Consequently, a redistribution of tuna catches is expected, impacting on coastal countries for which fishing is an important activity".**

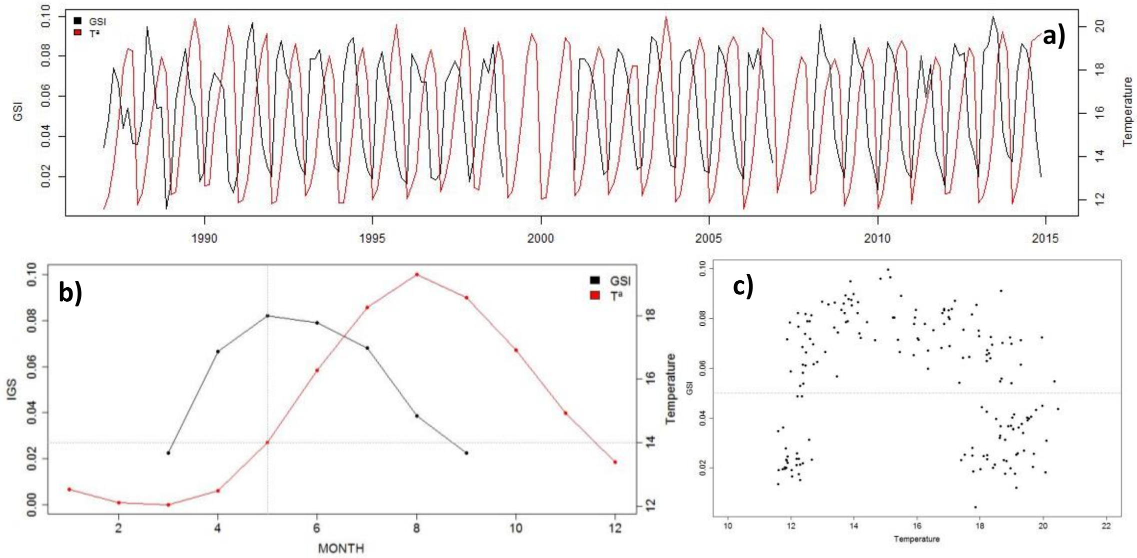
APPENDICES

APPENDICES

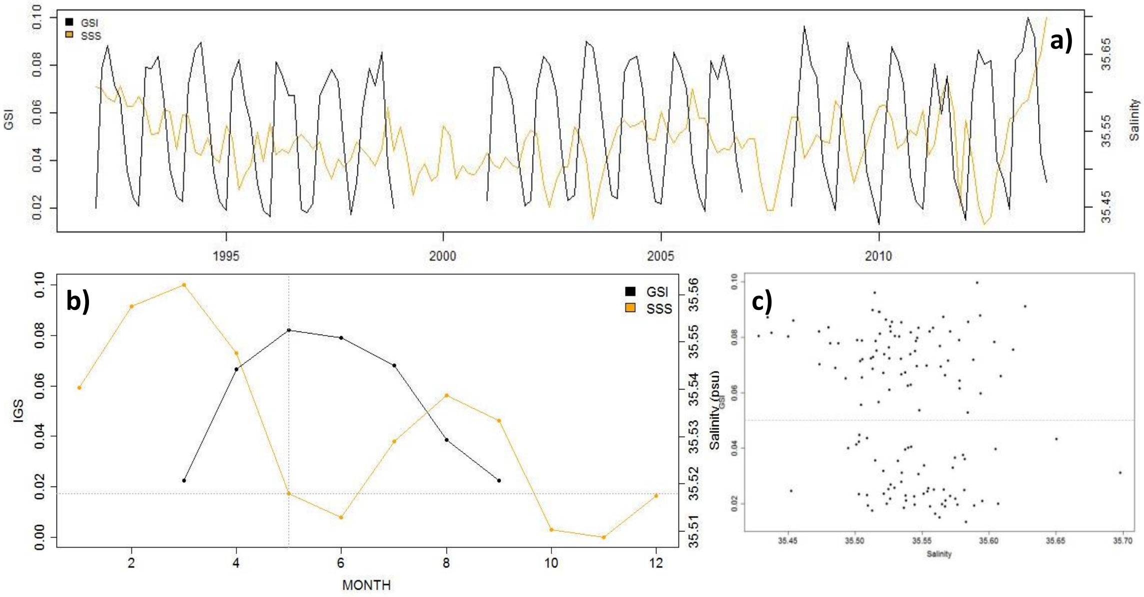
APPENDIX A

S. Table 1.1. Means and standard deviation (sd) of BIOMAN surveys (BIO-) and NEMO reanalysis (NEMO-) environmental data for the Bay of Biscay.

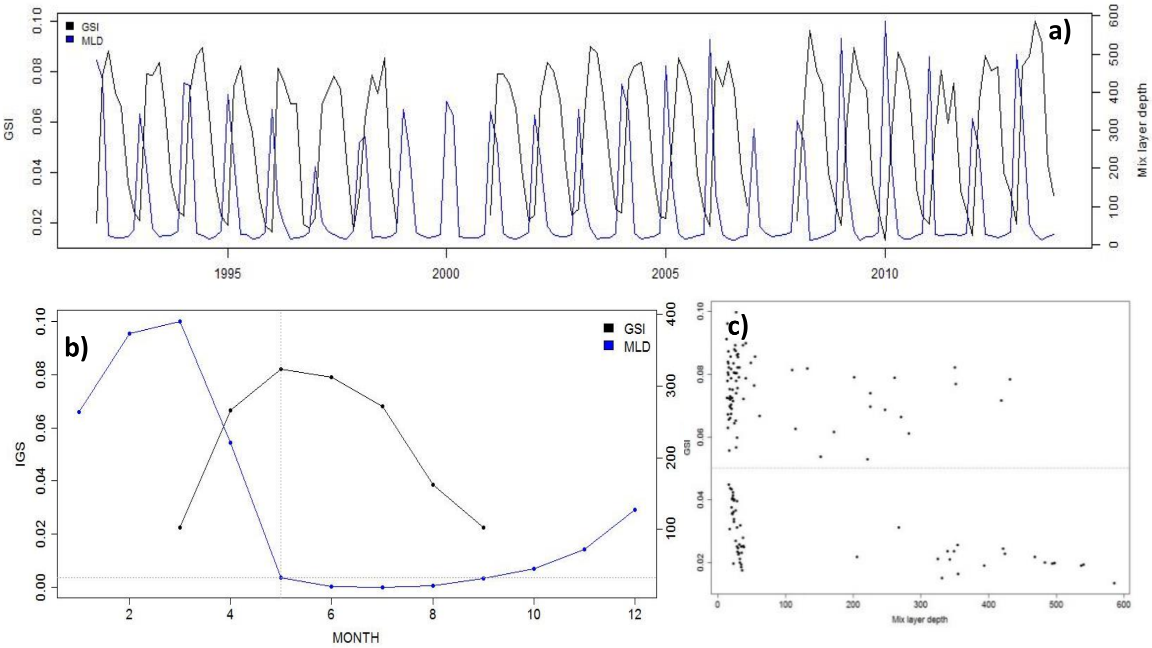
	BIO-SST (ºC)	BIO-SSS (psu)	NEMO-SST (ºC)	NEMO-SSS (psu)	NEMO-MLD (m)	sd-SST (ºC)	sd-SSS (psu)
May	15.51	34.92	15.25	34.81	8.71	±0.18	±0.08
June	17.57	34.85	18.11	34.47	6.57	±0.39	±0.27



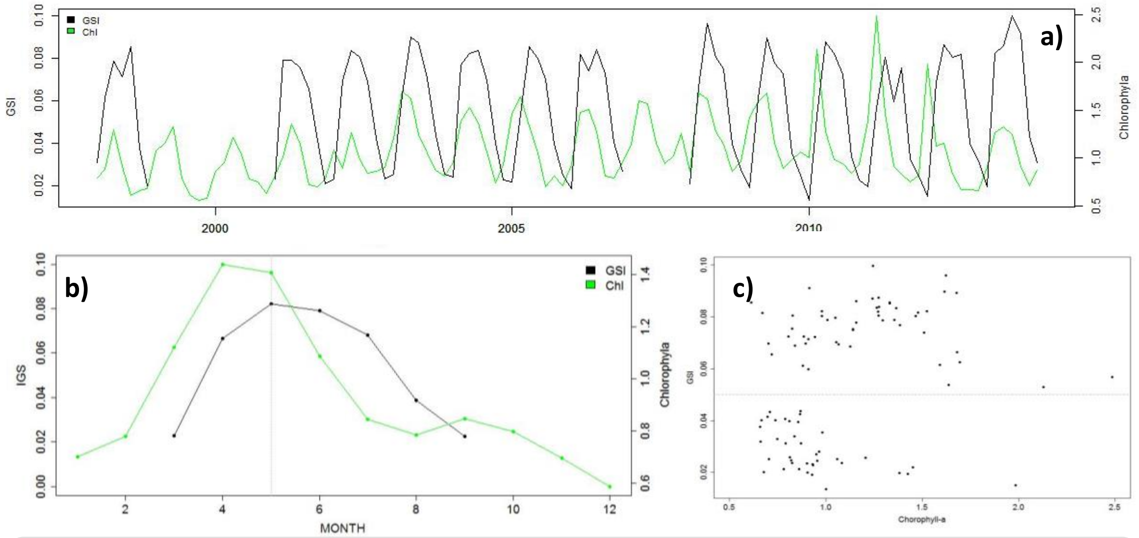
S. Figure 1.1: GSI and SST relationship: a) Time-series, b) scatter plot and c) monthly average. GSI is in black line and SST in red.



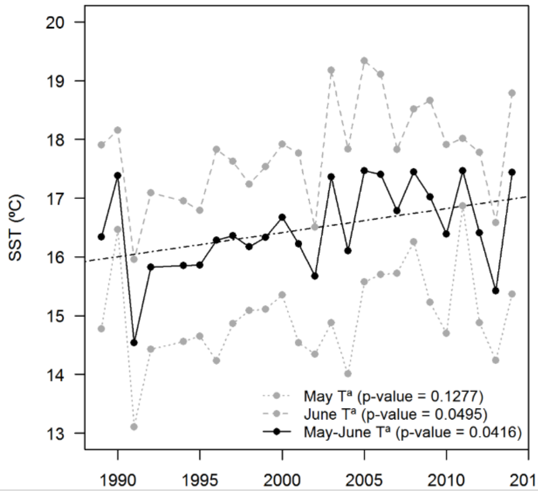
S. Figure 1.2: GSI and SSS relationship: a) Monthly average, b) scatter plot and c) time-series. GSI is in black line and SSS in orange line.



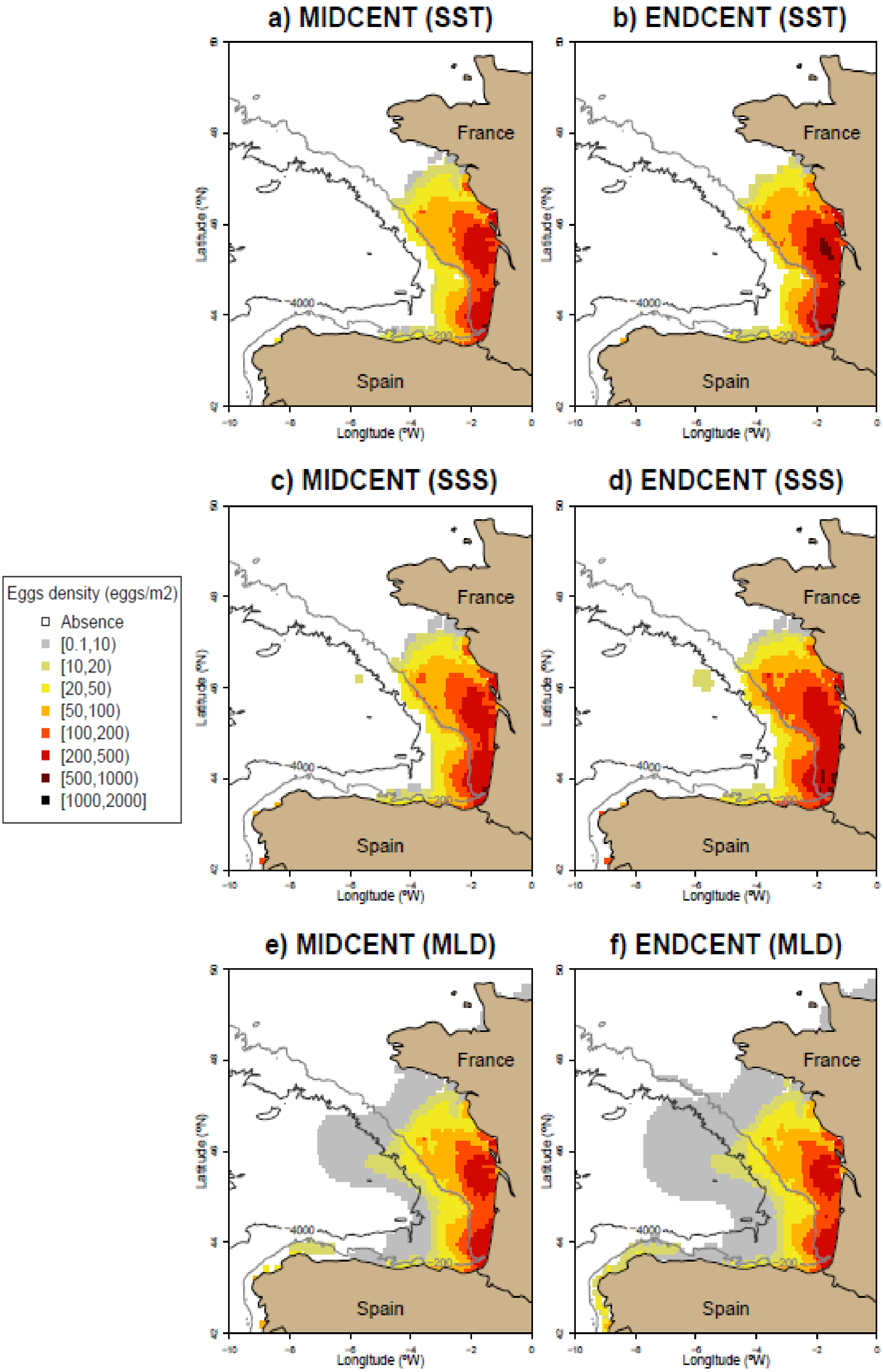
S. Figure 1.3: GSI and MLD relationship: a) Monthly average, b) scatter plot and c) time-series. GSI is in black line and MLD in blue line



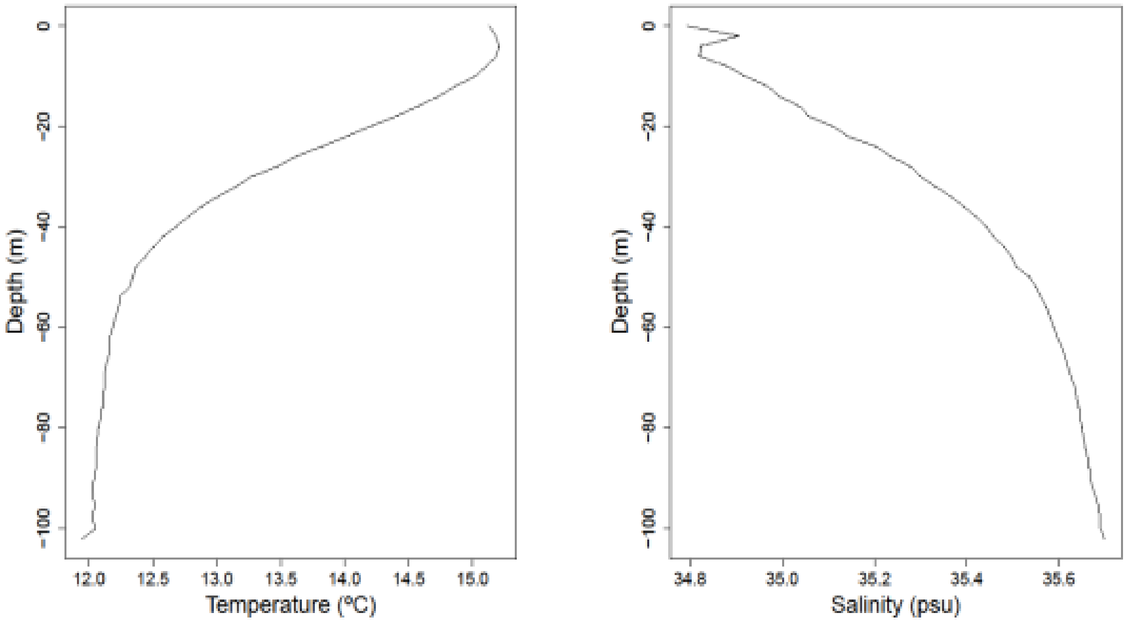
S. Figure 1.4: GSI and Chl-a relationship: a) Monthly average, b) scatter plot and c) timeseries. GSI is in black line and Chl-a in green line



S. Figure 1.5: Sea surface temperature from GODAS for the spawning area (Bay of Biscay) over the period May-June 1989-2015.

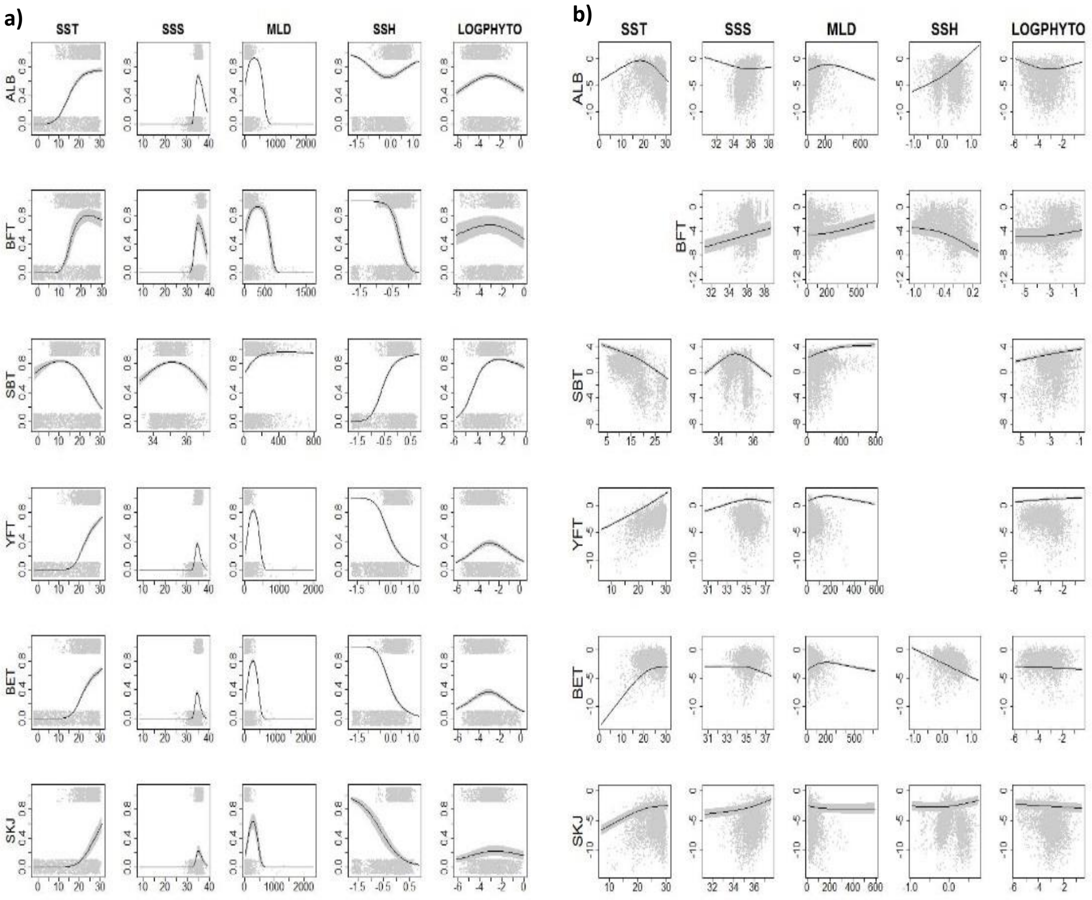


S. Figure 1.6: *Future projections changing only one of the environmental variables to future conditions and using others as a constant (importance): a) SST, b) SSS and c) MLD.*



***S. Figure 1.7**: Averaged CTD profiles of a) temperature and b) salinity of BIOMAN 2015 surveys.*

APPENDIX B

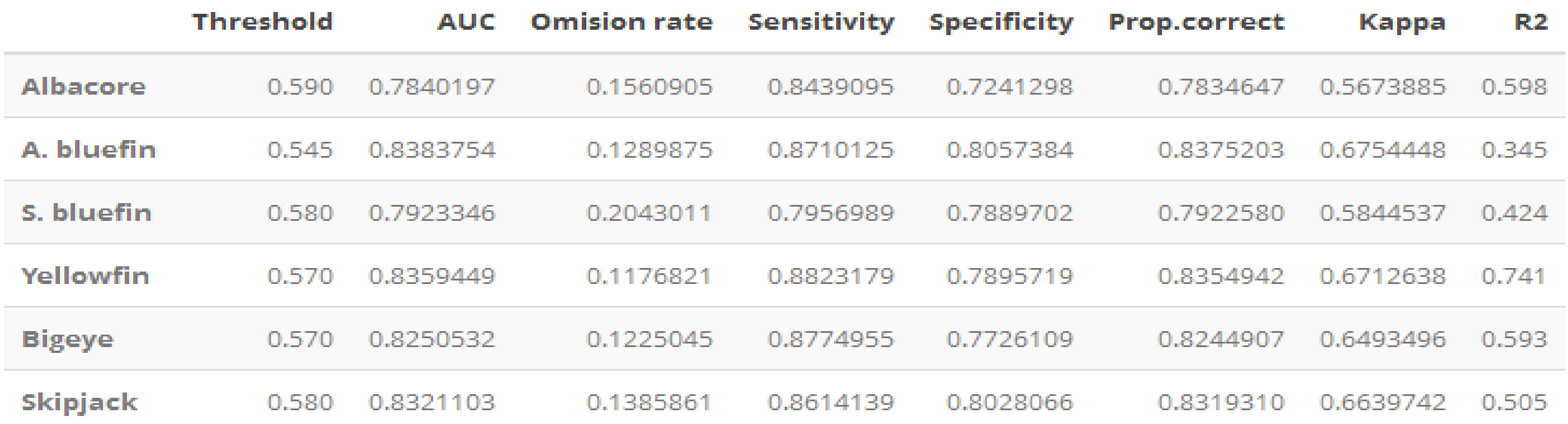


S. Figure 2.1: Response curves of a) Presence/pseudo-absence (PA) and b) ABundance (AB) models for the six-tuna species (in rows: alb=albacore, bft=A. bluefin, sbt=S. bluefin, yft=yellowfin, bet=bigeye and skj=skipjack tunas) and different variables (in columns: SST=Sea Surface Temperature, SSS=Sea Surface Salinity, MLD=Mixed Layer Depth, SSH= Sea Surface Height and Logphyto=log-transformed phytoplankton concentration).

S Table 2.1: Summary of the selected models (presence/pseudo-absence and abundance) with the environmental parameters, fixed factors and the interactions selected, and the deviance explained (%) by each of them.

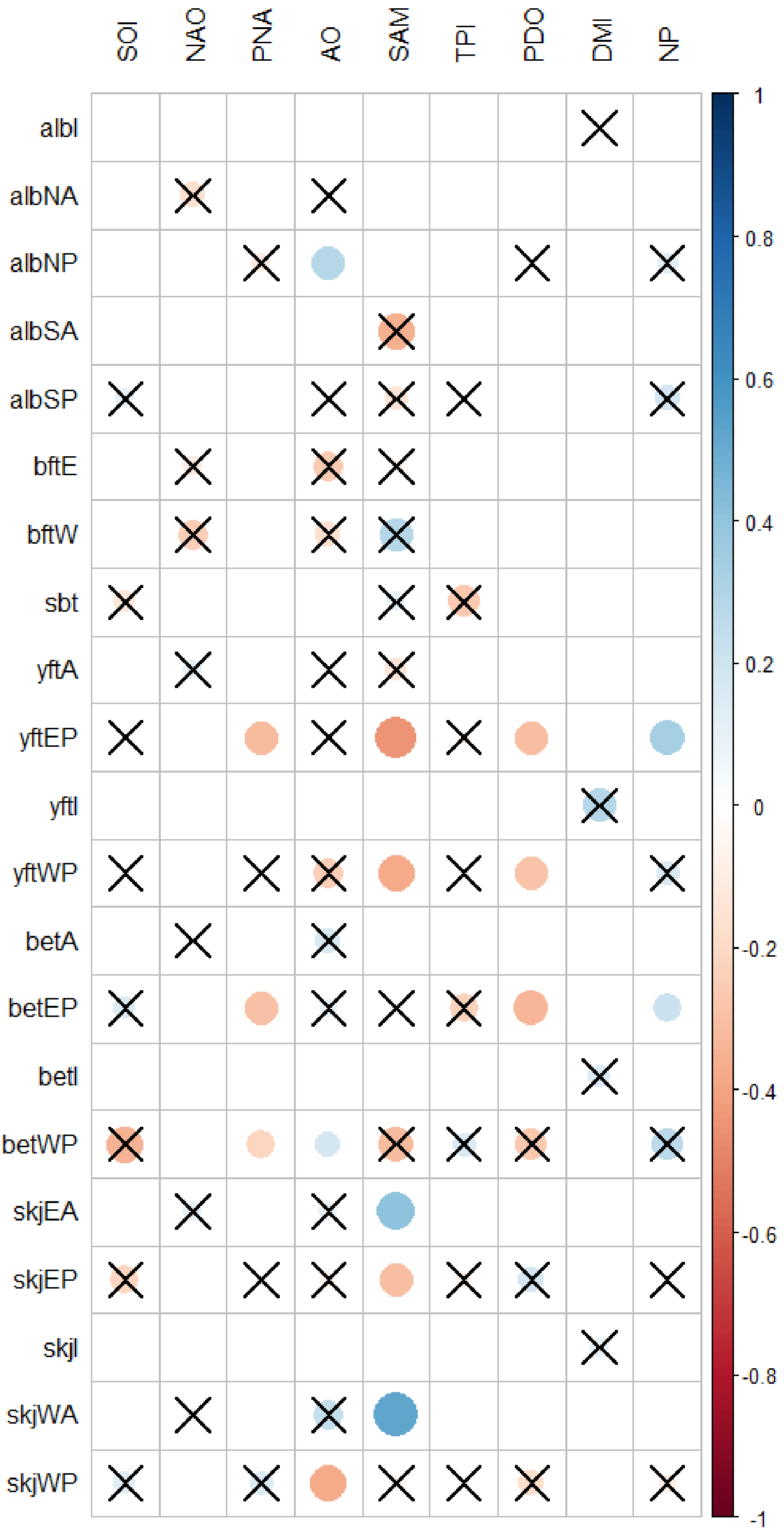
Species	Model	(Intercept)	s(logphyto, k = 3)	s(mld, k = 3)	s(sal, k = 3)	s(ssh, k = 3)	s(temp, k = 3)	season	stock	year	season:stock	season:year	stock:year	season:stock:year	dev.expl
Albacore	PA	-2.4815944	+	+	+	+	+	+	+	+	+		+		36.98
	AB	-4.2214996	+	+	+	+	+	+	+	+	+		+		51.76
Bluefin tuna	PA	-2.9385521	+	+	+	+	+	+	+	+	+		+		43.67
	AB	-3.2971680	+	+	+	+		+	+	+	+	+	+		47.36
Southern bluefin tuna	PA	-0.7008228	+	+	+	+	+	+		+					35.54
	AB	0.3391786	+	+	+		+	+		+		+			52.62
Yellowfin	PA	-5.0097227	+	+	+	+	+	+	+	+	+		+		48.21
	AB	-2.5428113	+	+	+		+	+	+	+	+	+	+	+	49.02
Bigeye	PA	-4.5675182	+	+	+	+	+	+	+	+	+		+		45.75
	AB	-2.3488877	+	+	+	+	+	+	+	+	+	+	+	+	41.78
Skipjack	PA	-3.0985859	+	+	+	+	+	+	+	+	+		+		47.16
	AB	-5.7934399	+	+	+	+	+	+	+	+	+	+	+	+	62.41

S. Table 2.2: Model validation. Columns 1-7 (Threshold-Kappa) are related with PA models and column 8 (R^2) with abundance models.



	Threshold	AUC	Omision rate	Sensitivity	Specificity	Prop.correct	Kappa	R2
Albacore	0.590	0.7840197	0.1560905	0.8439095	0.7241298	0.7834647	0.5673885	0.598
A. bluefin	0.545	0.8383754	0.1289875	0.8710125	0.8057384	0.8375203	0.6754448	0.345
S. bluefin	0.580	0.7923346	0.2043011	0.7956989	0.7889702	0.7922580	0.5844537	0.424
Yellowfin	0.570	0.8359449	0.1176821	0.8823179	0.7895719	0.8354942	0.6712638	0.741
Bigeye	0.570	0.8250532	0.1225045	0.8774955	0.7726109	0.8244907	0.6493496	0.593
Skipjack	0.580	0.8321103	0.1385861	0.8614139	0.8028066	0.8319310	0.6639742	0.505

S. Table 2.3: Correlation significances (p-value) between tuna stocks changes in latitudinal GCs' and different climatic drivers: SOI (Southern Oscillation Index), NAO (North Atlantic Oscillation), PNA (Pacific/North American teleconnection pattern), AO (Artic Oscillation), SAM (Southern Annular Mode), TPI (Trans Polar Index), PDO (Pacific Decadal Oscillation) and DMI (Dipole Mode Index) and NP (North Pacific Index).



***S. Table 2.4**: Excel file with six tuna species abundance changes (in absolute values and in %) for mid- and the end-of-the-century.*

Country	Albacore 2050	Albacore 2100	Bluefin 2050	Bluefin 2100	Southern bluefin 2050	Southern bluefin 2100	Yellowfin 2050	Yellowfin 2100	Bigeye 2050	Bigeye 2100	Skipjack 2050	Skipjack 2100
Algeria	0,0006	-0,0041	-0,0060	-0,0108	-	-	0,0027	0,0065	0,0082	0,0169	0,0001	0,0004
American Samoa	-0,0527	-0,1410	-	-	-0,0086	-0,0134	0,0400	0,0901	-0,0016	-0,0033	0,0002	0,0003
Angola	-0,0025	-0,0047	-0,0007	-0,0008	-0,0094	-0,0138	0,0387	0,0945	-0,0157	-0,0260	0,0002	0,0004
Anguilla	-0,0043	-0,0126	-0,0001	-0,0001	-	-	0,0122	0,0171	-0,0102	-0,0170	0,0007	0,0015
Antarctica	0,0000	0,0000	-0,0003	-0,0002	-0,0173	-0,0227	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000
Antigua & Barbuda	-0,0040	-0,0107	-0,0001	-0,0002	-	-	0,0161	0,0287	-0,0132	-0,0224	0,0006	0,0012
Argenti-	0,0309	0,0678	0,0000	0,0000	-0,4621	-0,8966	0,0003	0,0009	0,0004	0,0010	0,0000	0,0000
Aruba	-0,0062	-0,0127	-0,0004	-0,0004	-	-	0,0326	0,0637	-0,0224	-0,0393	0,0004	0,0010
Australia	0,2675	0,3072	-	-	-0,3125	-0,7571	0,0087	0,0209	-0,0003	-0,0006	0,0001	0,0002
Barbados	-0,0050	-0,0103	-0,0002	-0,0002	-	-	0,0478	0,1080	-0,0241	-0,0446	0,0003	0,0007
Belize	-0,0036	-0,0109	-0,0001	-0,0001	-	-	0,0231	0,0329	-0,0179	-0,0283	0,0007	0,0016
Benin	-0,0015	-0,0033	-0,0001	-0,0001	-	-	0,0497	0,1505	-0,0081	-0,0106	0,0002	0,0004
Bermuda	-0,0375	-0,1116	-0,0001	-0,0002	-	-	0,0046	0,0058	-0,0060	-0,0118	0,0004	0,0010
Bonaire, Saint-Eustasius, Saba	-0,0047	-0,0100	-0,0009	-0,0011	-	-	0,0188	0,0352	-0,0162	-0,0283	0,0004	0,0008
Bouvet I.	0,0000	0,0000	0,0008	0,0031	-0,0036	-0,0077	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000
Brazil	0,0053	-0,0068	-0,0002	-0,0003	-0,0288	-0,0417	0,0292	0,0704	-0,0129	-0,0221	0,0003	0,0008
Ca-da	0,0003	0,0009	-0,0022	-0,0027	-	-	0,0001	0,0002	0,0001	0,0004	0,0000	0,0000
Cape Verde	-0,0043	-0,0100	-0,0030	-0,0040	-	-	0,0109	0,0232	-0,0151	-0,0267	0,0003	0,0007
Cayman Is.	-0,0087	-0,0252	0,0000	0,0000	-	-	0,0291	0,0381	-0,0146	-0,0230	0,0008	0,0019
Chile	0,0992	0,1247	0,0001	0,0002	-0,2464	-0,5712	0,0026	0,0052	0,0004	0,0006	0,0001	0,0001
Christmas I.	-0,0664	-0,1282	-	-	-0,0014	-0,0020	0,0037	0,0060	-0,0028	-0,0048	0,0000	0,0000
Clipperton Island	-0,0341	-0,0578	-	-	-	-	0,0275	0,0784	-0,0026	-0,0044	0,0001	0,0003

Cocos Is.	-0,0796	-0,1569	-	-	-0,0039	-0,0054	0,0078	0,0180	-0,0037	-0,0066	0,0000	0,0000
Colombia	-0,0070	-0,0130	-0,0004	-0,0005	-	-	0,0162	0,0281	-0,0132	-0,0219	0,0003	0,0008
Comoros	-0,0696	-0,2234	-	-	-0,0202	-0,0317	0,0335	0,0937	-0,0021	-0,0037	0,0002	0,0005
Congo, DRC	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000
Cook Is.	-0,0170	-0,1255	-	-	-0,0223	-0,0420	0,0468	0,0957	-0,0016	-0,0038	0,0002	0,0004
Costa Rica	-0,0163	-0,0253	-	-	-	-	0,0043	0,0141	-0,0024	-0,0036	0,0000	0,0000
Cote d'Ivoire	-0,0023	-0,0044	-0,0003	-0,0004	-	-	0,0805	0,2135	-0,0208	-0,0343	0,0003	0,0006
Cuba	-0,0070	-0,0191	0,0000	0,0000	-	-	0,0213	0,0260	-0,0138	-0,0219	0,0008	0,0018
CuraÃ§ao	-0,0068	-0,0140	-0,0003	-0,0004	-	-	0,0350	0,0717	-0,0218	-0,0380	0,0004	0,0009
Dominica	-0,0051	-0,0105	-0,0001	-0,0002	-	-	0,0346	0,0773	-0,0210	-0,0367	0,0004	0,0008
Dominican Republic	-0,0063	-0,0176	0,0000	0,0000	-	-	0,0221	0,0379	-0,0130	-0,0213	0,0007	0,0016
Ecuador	-0,0389	-0,0680	-	-	-0,0203	-0,0267	0,0083	0,0251	-0,0012	-0,0021	0,0000	0,0001
Equatorial Guinea	-0,0017	-0,0031	-0,0001	-0,0002	-0,0013	-0,0020	0,0399	0,1109	-0,0113	-0,0170	0,0001	0,0003
Falkland Islands	0,0010	0,0030	0,0000	0,0000	-0,9055	-1,7082	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000
Faroe Is.	0,0035	0,0073	-0,0314	-0,0411	-	-	0,0001	0,0001	0,0001	0,0004	0,0000	0,0000
Fiji	-0,0125	-0,2166	-	-	-0,0289	-0,0474	0,0155	0,0430	-0,0019	-0,0030	0,0001	0,0003
France	0,0225	0,0402	-0,0109	-0,0146	-	-	0,0009	0,0011	0,0029	0,0038	0,0000	0,0000
French Guia-	-0,0049	-0,0110	-0,0001	-0,0002	-	-	0,0622	0,1551	-0,0181	-0,0329	0,0003	0,0006
French Polynesia	0,0083	-0,0842	-	-	-0,0488	-0,0930	0,0337	0,0700	-0,0009	-0,0029	0,0002	0,0005
French Southern & Antarctic Lands	0,5282	1,0341	-	-	-0,2432	-0,5529	0,0064	0,0178	-0,0003	-0,0006	0,0000	0,0001
Gabon	-0,0002	-0,0004	0,0000	0,0000	0,0000	0,0000	0,0013	0,0016	-0,0011	-0,0022	0,0000	0,0000
Gha-	-0,0022	-0,0044	-0,0002	-0,0003	-	-	0,0798	0,2184	-0,0194	-0,0304	0,0002	0,0005
Greenland	0,0000	0,0000	-0,0018	-0,0020	-	-	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000
Gre-da	-0,0066	-0,0134	-0,0001	-0,0002	-	-	0,0467	0,1103	-0,0202	-0,0362	0,0003	0,0007
Guadeloupe	-0,0043	-0,0097	-0,0001	-0,0002	-	-	0,0245	0,0515	-0,0174	-0,0302	0,0004	0,0010

Guatemala	-0,0260	-0,0464	-	-	-	-	0,0462	0,1380	-0,0018	-0,0026	0,0002	0,0004
Guinea-Bissau	-0,0024	-0,0046	-0,0008	-0,0010	-	-	0,0325	0,0783	-0,0237	-0,0377	0,0004	0,0009
Guya-	-0,0044	-0,0095	-0,0002	-0,0003	-	-	0,0515	0,1282	-0,0214	-0,0375	0,0003	0,0006
Haiti	-0,0109	-0,0272	0,0000	0,0000	-	-	0,0328	0,0546	-0,0156	-0,0256	0,0007	0,0016
Heard I. & McDold Is.	0,0000	0,0000	-	-	0,0265	-0,0125	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000
Honduras	-0,0045	-0,0165	-0,0001	-0,0001	-	-	0,0305	0,0411	-0,0158	-0,0260	0,0007	0,0016
Iceland	0,0018	0,0035	-0,0279	-0,0417	-	-	0,0000	0,0001	0,0002	0,0004	0,0000	0,0000
India	-0,0293	-0,0600	-	-	-	-	0,0325	0,0872	-0,0024	-0,0043	0,0002	0,0004
Indonesia	-0,0578	-0,1029	-	-	-0,0007	-0,0010	-0,0013	-0,0030	-0,0017	-0,0028	0,0000	-0,0001
Ireland	0,0145	0,0231	-0,0257	-0,0331	-	-	0,0002	0,0003	0,0007	0,0009	0,0000	0,0000
Italy	0,0007	-0,0031	-0,0053	-0,0128	-	-	0,0016	0,0033	0,0045	0,0068	0,0003	0,0007
Jamaica	-0,0104	-0,0291	0,0000	0,0000	-	-	0,0363	0,0573	-0,0166	-0,0270	0,0007	0,0017
Jan Mayen	0,0001	0,0004	0,0010	0,0019	-	-	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000
Japan	0,4805	-1,2167	-	-	-	-	0,0096	0,0194	-0,0005	-0,0011	0,0001	0,0002
Kenya	-0,0342	-0,0801	-	-	-0,0259	-0,0392	0,0435	0,1171	-0,0033	-0,0067	0,0002	0,0005
Kiribati	-0,0734	-0,1571	-	-	-0,0256	-0,0437	0,0739	0,1514	-0,0011	-0,0043	0,0002	0,0004
Liberia	-0,0021	-0,0039	-0,0003	-0,0004	-	-	0,0834	0,2218	-0,0235	-0,0391	0,0003	0,0006
Libya	-0,0020	-0,0051	-0,0026	-0,0174	-	-	0,0013	0,0026	0,0007	0,0006	0,0007	0,0015
Madagascar	-0,1365	-0,5360	-	-	-0,0520	-0,0874	0,0222	0,0605	-0,0009	-0,0017	0,0002	0,0005
Malaysia	-0,0075	-0,0103	-	-	-	-	-0,0001	-0,0001	0,0000	0,0000	0,0000	0,0000
Maldives	-0,0168	-0,0362	-	-	-0,0058	-0,0080	0,0546	0,1414	-0,0043	-0,0080	0,0002	0,0004
Malta	-0,0009	-0,0041	-0,0079	-0,0151	-	-	0,0014	0,0030	0,0020	0,0025	0,0004	0,0010
Marshall Is.	-0,0672	-0,1535	-	-	-	-	0,0400	0,0605	-0,0038	-0,0088	0,0001	0,0001
Martinique	-0,0052	-0,0108	-0,0001	-0,0002	-	-	0,0387	0,0860	-0,0212	-0,0380	0,0004	0,0008
Mauritius	-0,1411	-0,4692	-	-	-0,0363	-0,0603	0,0234	0,0609	-0,0016	-0,0033	0,0002	0,0004
Mayotte	-0,1096	-0,3528	-	-	-0,0181	-0,0294	0,0328	0,0902	-0,0014	-0,0026	0,0002	0,0005

Mexico	-0,0041	-0,0399	-0,0008	-0,0009	-	-	0,0279	0,0615	-0,0048	-0,0091	0,0003	0,0006
Micronesia	-0,0581	-0,1322	-	-	-0,0192	-0,0290	0,0211	0,0105	-0,0044	-0,0090	0,0000	-0,0002
Montserrat	-0,0051	-0,0108	-0,0001	-0,0001	-	-	0,0275	0,0608	-0,0192	-0,0322	0,0004	0,0009
Morocco	0,0115	0,0150	-0,0098	-0,0130	-	-	0,0030	0,0061	0,0043	0,0061	0,0001	0,0001
Mozambique	-0,0761	-0,2692	-	-	-0,0275	-0,0456	0,0265	0,0765	-0,0021	-0,0036	0,0002	0,0005
Myanmar	-0,0143	-0,0244	-	-	-	-	-0,0003	-0,0005	-0,0003	-0,0004	0,0000	0,0000
-mibia	0,0081	0,0051	-0,0035	-0,0048	-0,1483	-0,2475	0,0067	0,0165	-0,0037	-0,0063	0,0002	0,0004
-uru	-0,0880	-0,1822	-	-	-0,0228	-0,0368	0,0888	0,1645	-0,0004	-0,0029	0,0002	0,0004
New Caledonia	0,0329	-0,3421	-	-	-0,0649	-0,1140	0,0143	0,0347	-0,0010	-0,0020	0,0002	0,0003
New Zealand	0,3431	0,6119	-	-	-0,5933	-1,3147	0,0013	0,0033	0,0003	0,0006	0,0000	0,0001
Nicaragua	-0,0066	-0,0147	-0,0003	-0,0004	-	-	0,0261	0,0444	-0,0165	-0,0271	0,0005	0,0013
Nigeria	-0,0010	-0,0019	-0,0001	-0,0001	-	-	0,0306	0,0925	-0,0082	-0,0111	0,0001	0,0002
Niue	-0,0276	-0,2300	-	-	-0,0295	-0,0552	0,0225	0,0530	-0,0016	-0,0031	0,0002	0,0004
Norfolk I.	0,4313	-0,2226	-	-	-0,2353	-0,4202	0,0074	0,0173	0,0005	0,0003	0,0002	0,0004
Northern Mari-- Islands-Guam	-0,2356	-0,6565	-	-	-	-	0,0184	0,0271	-0,0019	-0,0038	0,0001	0,0001
Norway	0,0011	0,0025	-0,0025	-0,0046	-	-	0,0000	0,0000	0,0000	0,0001	0,0000	0,0000
Oman	-0,0221	-0,0610	-	-	-	-	0,0228	0,0676	-0,0001	-0,0004	0,0003	0,0006
Pakistan	-0,0264	-0,0580	-	-	-	-	0,0196	0,0506	-0,0012	-0,0028	0,0003	0,0008
Palau	-0,0717	-0,1446	-	-	-	-	-0,0087	-0,0275	-0,0041	-0,0069	-0,0001	-0,0003
Papua New Guinea	-0,0608	-0,1372	-	-	-0,0134	-0,0202	0,0420	0,0596	-0,0021	-0,0053	0,0001	0,0001
Paracel Islands	-0,1460	-0,2733	-	-	-	-	-0,0008	-0,0032	-0,0010	-0,0017	0,0000	-0,0001
Philippines	-0,1561	-0,3803	-	-	-	-	-0,0002	-0,0055	-0,0016	-0,0027	0,0000	-0,0001
Pitcairn Is.	0,0523	-0,0556	-	-	-0,0800	-0,1433	0,0095	0,0167	-0,0015	-0,0037	0,0003	0,0005
Portugal	0,0207	0,0307	-0,0060	-0,0080	-	-	0,0035	0,0076	0,0060	0,0101	0,0001	0,0002
Puerto Rico	-0,0059	-0,0150	-0,0001	-0,0001	-	-	0,0232	0,0424	-0,0151	-0,0248	0,0006	0,0013
Reunion	-0,1350	-0,6858	-	-	-0,0598	-0,1026	0,0189	0,0477	-0,0007	-0,0016	0,0002	0,0005

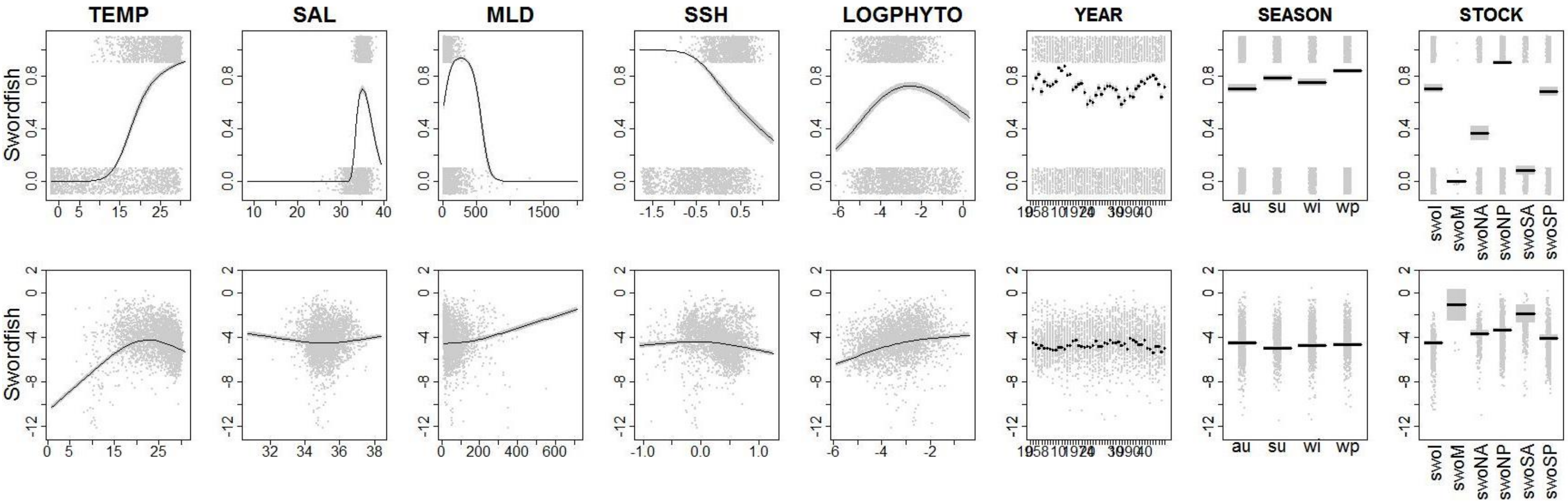
Russia	0,0004	0,0016	0,0000	0,0000	-	-	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000
Saint Hele-, Ascension en Tristan da Cunha	0,1267	0,3586	-0,0008	-0,0011	-0,0056	-0,0854	0,0138	0,0319	-0,0107	-0,0183	0,0002	0,0004
Saint Vincent and the Gre-dines	-0,0065	-0,0136	-0,0001	-0,0001	-	-	0,0515	0,1187	-0,0207	-0,0380	0,0003	0,0007
Samoa	-0,0528	-0,1276	-	-	-0,0060	-0,0084	0,0325	0,0799	-0,0018	-0,0034	0,0001	0,0003
Sao Tome & Principe	-0,0009	-0,0016	0,0000	-0,0001	-0,0001	-0,0002	0,0178	0,0484	-0,0078	-0,0119	0,0001	0,0001
Senegal	-0,0035	-0,0069	-0,0014	-0,0018	-	-	0,0175	0,0427	-0,0186	-0,0294	0,0004	0,0008
Seychelles	-0,0212	-0,0475	-	-	-0,0147	-0,0216	0,0490	0,1304	-0,0041	-0,0078	0,0002	0,0004
Sierra Leone	-0,0017	-0,0032	-0,0004	-0,0005	-	-	0,0771	0,1924	-0,0272	-0,0458	0,0003	0,0007
Solomon Is.	-0,0435	-0,1019	-	-	-0,0072	-0,0102	0,0298	0,0514	-0,0027	-0,0056	0,0001	0,0001
Somalia	-0,0434	-0,0969	-	-	-0,0307	-0,0469	0,0533	0,1414	-0,0029	-0,0060	0,0002	0,0005
South Africa	0,1024	-0,0228	-0,0014	-0,0020	-0,0919	-0,2284	0,0029	0,0078	0,0004	0,0005	0,0001	0,0001
South Georgia & the South Sandwich Is.	0,0000	0,0000	0,0002	0,0013	-0,0077	-0,0125	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000
South Korea	0,0567	0,0588	-	-	-	-	0,0001	0,0001	0,0001	0,0001	0,0000	0,0000
Spain	0,0124	0,0149	-0,0084	-0,0122	-	-	0,0037	0,0077	0,0047	0,0077	0,0001	0,0002
Spratly Islands	-0,0810	-0,1245	-	-	-	-	-0,0012	-0,0021	-0,0004	-0,0005	0,0000	0,0000
Sri Lanka	-0,0289	-0,0649	-	-	-	-	0,0371	0,1006	-0,0038	-0,0067	0,0001	0,0003
St. Kitts & Nevis	-0,0058	-0,0119	-0,0001	-0,0001	-	-	0,0296	0,0653	-0,0196	-0,0327	0,0004	0,0010
St. Lucia	-0,0060	-0,0128	-0,0001	-0,0001	-	-	0,0495	0,1126	-0,0210	-0,0384	0,0003	0,0007
Suri-me	-0,0040	-0,0086	-0,0002	-0,0003	-	-	0,0506	0,1319	-0,0201	-0,0341	0,0002	0,0006
Svalbard	0,0000	0,0003	0,0004	0,0005	-	-	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000
Taiwan	-0,1849	-0,5210	-	-	-	-	0,0029	0,0004	-0,0015	-0,0029	0,0000	-0,0001
Tanzania	-0,0296	-0,0703	-	-	-0,0215	-0,0324	0,0439	0,1229	-0,0036	-0,0069	0,0002	0,0005

The Bahamas	-0,0130	-0,0335	0,0000	0,0000	-	-	0,0086	0,0078	-0,0082	-0,0134	0,0007	0,0016
Timor-Leste	-0,1391	-0,2532	-	-	-0,0016	-0,0020	-0,0028	-0,0070	-0,0021	-0,0033	-0,0001	-0,0001
Togo	-0,0020	-0,0042	-0,0002	-0,0002	-	-	0,0734	0,2058	-0,0147	-0,0231	0,0002	0,0005
Tokelau	-0,0334	-0,0965	-	-	-0,0064	-0,0103	0,0639	0,1293	-0,0021	-0,0049	0,0002	0,0003
Tonga	0,0361	-0,1625	-	-	-0,0400	-0,0723	0,0183	0,0458	-0,0015	-0,0027	0,0002	0,0004
Trinidad & Tobago	-0,0052	-0,0113	-0,0001	-0,0002	-	-	0,0560	0,1312	-0,0215	-0,0400	0,0003	0,0007
Tunisia	0,0003	-0,0030	-0,0060	-0,0108	-	-	0,0018	0,0043	0,0044	0,0077	0,0003	0,0007
Turks & Caicos Is.	-0,0062	-0,0195	0,0000	-0,0001	-	-	0,0113	0,0113	-0,0058	-0,0101	0,0008	0,0019
Tuvalu	-0,0363	-0,1034	-	-	-0,0089	-0,0124	0,0497	0,1101	-0,0027	-0,0053	0,0001	0,0002
United Kingdom	0,0060	0,0110	-0,0189	-0,0245	-	-	0,0001	0,0001	0,0002	0,0004	0,0000	0,0000
United States	0,0180	-0,0627	-0,0085	-0,0128	-	-	0,0056	0,0115	-0,0022	-0,0039	0,0001	0,0002
United States Minor Outlying Islands	-0,1357	-0,3049	-	-	-0,0291	-0,0488	0,0728	0,1469	-0,0009	-0,0036	0,0002	0,0004
United States Virgin Islands	-0,0055	-0,0133	-0,0001	-0,0001	-	-	0,0260	0,0493	-0,0169	-0,0284	0,0005	0,0011
Uruguay	0,2067	0,3023	-0,0001	-0,0002	-0,6929	-1,0382	0,0052	0,0109	0,0021	0,0026	0,0001	0,0003
Vanuatu	-0,0842	-0,2669	-	-	-0,0170	-0,0254	0,0158	0,0410	-0,0022	-0,0036	0,0001	0,0002
Venezuela	-0,0067	-0,0137	-0,0002	-0,0003	-	-	0,0394	0,0864	-0,0217	-0,0379	0,0004	0,0008
Viet-m	-0,0683	-0,1106	-	-	-	-	-0,0004	-0,0007	-0,0002	-0,0003	0,0000	0,0000
Virgin Islands, British	-0,0043	-0,0134	-0,0001	-0,0001	-	-	0,0140	0,0187	-0,0098	-0,0165	0,0007	0,0016
Wallis & Futu-	-0,0542	-0,1228	-	-	-0,0047	-0,0064	0,0262	0,0705	-0,0021	-0,0036	0,0001	0,0002
Western Sahara	0,0060	0,0010	-0,0057	-0,0076	-	-	0,0029	0,0069	0,0002	-0,0003	0,0001	0,0003
Yemen	-0,0322	-0,0789	-	-	-	-	0,0467	0,1349	-0,0012	-0,0029	0,0003	0,0006

S. Table 2.5: Comparison of trends (increase or decrease) in Pacific countries skipjack abundance in the future (2050 mid-century and 2100 end-of-the-century) with Bell et al. (2013b) and Senina et al. (2018).

Country	2050 (our study)	2100 (our study)	2050 (Bell et al. 2013)	2100 (Bell et al. 2013)	2050 (Senina et al. 2018)	2100 (Senina et al. 2018)
New Caledonia	+	+	+	+	+	+
Tonga	+	+	+	+	+	+
Fiji	+	+	+	+	+	+
French Polynesia	+	+	+	+	+	+
Vanuatu	+	+	+	+	+	+
Cook Is.	+	+	+	+	+	+
American Samoa	+	+	+	+	+	+
Samoa	+	+	+	+	+	+
Wallis & Futuna	+	+	+	+	+	+
Solomon Is.	+	+	-	-	-	-
Tokelau	+	+	+	+	-	-
Tuvalu	+	+	+	+	-	-
Kiribati	+	+	-	-	+	-
Papua New Guinea	+	+	+	+	-	-
Nauru	+	+	+	+	-	-
Palau	-	-	+	-	-	-
Marshall Is.	+	+	+	+	-	-

APPENDIX C



S. Figure 3.1: Generalized Additive Models' response curves per environmental variable and fixed factors. Upper row: response curves for presence/pseudo-absence habitat model, and lower row: response curves for relative abundance habitat model. For the Season, the variable levels represented are: au=autumn, su=summer, wi=winter and wp=spring; for the Stock, the levels represented are: swoI=Indian, swoM=Mediterranean, swoNA=North Atlantic, swoNP=North Pacific, swoSA=South Atlantic and swoSP=South Pacific.

APPENDIX D

S. Table 4.1: New biological parameters values after the literature review introduced in the SS-DBEM model. Columns meaning: TaxonKey (species code in the model), TaxonName (scientific name of the species), CommonName (species common name), Von Bertalanffy equation parameters (Linf→ asymptotic size, VBonK→ growth coefficient, t0→ is a value used to calculate size when age is zero), size-length equation (lwA →intercept, lwB→slope), TL (trophic level mean), seTL (trophic level standard error), MaxLenTL (maximum total length) and SLmax (maximum standard length).

TaxonName	CommonName	Linf	VBonK	t0	lwA	lwB	TL	seTL	MaxLenTL	SLmax
Acanthocybium solandri	Wahoo	250.00	0.34	-0.31	0.003	3.190	4.26	0.78	250	227
Coryphaena hippurus	Common dolphinfish	210.00	1.41	-0.07	0.050	2.750	4.37	0.77	210	175
Istiophorus platypterus	Indo-Pacific sailfish	348.00	0.11	-0.87	0.044	2.628	4.50	0.79	386	344
Katsuwonus pelamis	Skipjack tuna	81.30	0.54	-0.88	0.005	3.220	4.43	0.76	120	102
Lampris guttatus	Opah	203.40	0.20	0.00	0.028	3.000	4.22	0.62	200	160
Lepidocybium flavobrunneum	Escolar	203.40	0.08	-1.29	0.010	3.000	4.34	0.67	244	200
Makaira nigricans	Atlantic blue marlin	500.00	0.32	-0.25	0.007	2.960	4.49	0.67	500	410
Tetrapturus angustirostris	Shortbill spearfish	233.40	0.44	-0.21	0.001	3.834	4.50	0.76	230	189
Tetrapturus audax	Striped marlin	420.00	0.26	-0.34	0.017	3.062	4.58	0.76	420	287
Tetrapturus pfluegeri	Longbill spearfish	257.40	0.36	-0.25	0.010	3.000	4.40	0.75	282	248

Thunnus alalunga	Albacore	118.50	0.24	-1.37	0.027	2.800	4.30	0.73	155	136
Thunnus albacares	Yellowfin tuna	175.70	0.43	0.33	0.022	2.981	4.41	0.50	265	231
Thunnus atlanticus	Blackfin tuna	107.90	0.33	-0.39	0.018	3.024	4.35	0.70	120	104
Thunnus maccoyii	Southern bluefin	210.60	0.16	-0.28	0.017	3.060	3.87	0.53	272	228
Thunnus obesus	Bigeye tuna	239.50	0.20	-0.53	0.018	2.902	4.49	0.80	250	205
Thunnus orientalis	Pacific bluefin tuna	303.20	0.10	-0.92	0.010	3.000	4.21	0.55	333	293
Thunnus thynnus	Northern bluefin tuna	313.70	0.11	-0.65	0.023	2.934	4.45	0.78	458	376
Thunnus tonggol	Longtail tuna	144.90	0.32	-0.36	0.010	3.000	4.50	0.54	161	138
Xiphias gladius	Swordfish	269.30	0.10	-1.99	0.008	3.210	4.53	0.80	505	449

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“We protect what we love and

we love what we know”

Jacques Cousteau