Universitat
de les Illes Balears

DOCTORAL THESIS

2023

ECOLOGY AND MANAGEMENT OF THE COMMON DOLPHINFISH (*Coryphaena hippurus*) IN A WARMING MEDITERRANEAN

Vicenç Moltó Seguí

Universitat de les Illes Balears

DOCTORAL THESIS

2023

Doctoral Program in Marine Ecology

ECOLOGY AND MANAGEMENT OF THE COMMON DOLPHINFISH (*Coryphaena hippurus*) IN A WARMING MEDITERRANEAN

Vicenç Moltó Seguí

Director/a: Ignacio Alberto Catalán Alemany

Director/a: Andrés Alonso Ospina Álvarez

Director/a: Francisco Alemany Llodrà

Tutor/a: Guillem Mateu Vicens

Doctor by the Universitat de les Illes Balears

Fotografia: Fernando Garfella Palmer

Als qui admiren els tresors del mar

Acknowledgments / Agraïments / Agradecimientos

Diuen que els agraïments de la tesi és el que tothom proper es vol llegir, i en veritat mostren la part més personal dels anys transcorreguts en aquesta aventura. Aquesta tesi no s'ha desenvolupat com sol ser habitual, com un treball a temps complet a un centre d'investigació, sinó que ja va començar sabent que no la faria a dedicació completa, compaginant amb una altra feina i durant un temps a una altra ciutat diferent del centre d'investigació dels directors de tesi. Això ha fet que s'hagi allargat en el temps i sigui molta gent que m'ha acompanyat, aconsellat i recolzat en aquest camí. Esper que totes aquestes persones es puguin sentir identificades i correspostes en aquestes línies. I si hem deix algú, que m'ho faci saber, almanco farem una cervesa a la nostra salut!

L'agraïment més merescut de la tesi és per als seus directors, i com a director principal a n'Ignasi Catalan. Alguna vegada m'han comparat fer una tesi com si el doctorand fos el patró d'un vaixell que amb la tesi comença a navegar fent-se el seu camí dins el món de la investigació. Hi haurà temporades de calma i els estudis aniran bé, però també algun temporal que farà canviar el rumb de la tesi. Si és així, n'Ignasi ha estat el far, imbatible davant qualsevol adversitat, que ha guiat el camí per a que aquesta tesi arribés a bon port. De tot cor, moltes gràcies per la teva ajuda, constància, dedicació i, sobretot, la teva comprensió quan hi havia altres truis (campanyes, oposicions, etc.) per enmig. Als codirectors de tesi també els hi estic molt agraït. Andrés, per a mi ets el mag de la visualització de dades! De la teva forma de treballar molt metòdica i dels teus coneixements dels quals he après molt. Xisco, tu i jo ja duim un bon camí fet, en el que he anat creixent gràcies als teus coneixements. Tot i que durant aquesta tesi has estat a l'exili de l'ICCAT, has estat present per qualsevol cosa que s'hagi necessitat. Dins aquest paràgraf, vull agrair especialment a en Miquel Palmer, que es pot considerar també un director de tesi tot i que no surti el seu nom a la portada. T'estic molt agraït de tot el que he après gràcies a tu, sobretot d'estadística i resoldre els problemes matemàtics que se'ns han anat plantejant, per els seminaris aquests que surts amb el cervell frit, i per haver suportat la matadura que t'he donat darrere els articles de la tesi. A tots vosaltres, moltes gràcies per fer-me créixer professionalment.

La tesi va arrancar a IMEDEA, i la primera tasca que vaig fer va ser treballar amb els otòlits, un tema que sempre m'havia fet especial il·lusió. Vull agrair especialment a na Sílvia i na Beatriu que m'introduïren dins aquest mon particular de la ciència de pesqueries. També vull agrair als companys de batalletes del dia a dia durant aquells primers mesos a IMEDEA, especialment a nen Guille, que vàrem començar la tesi més o menys plegats i m'hagués agradat continuar junts de principi a fi, i als companys Mario, Àngel i Edu al dia a dia. Guard un especial record dels dies de treball de camp, pescant vaquetes per en Guille, marcant pops a Andratx per en Mario i el repte d'intentar marcar dorados per la tesi, amb aquells jornals de curri d'altura, de la que mai oblidaré l'entrada triomfal a Porto Cristo amb en Pep Alòs i les bones rialles que feim cada vegada que hi pensam!

En relativament poc temps hem va torcar anar-me'n a Murcia, on una bona part d'aquesta tesi l'hem haguda de fer a distància. D'aquella etapa vull agrair als companys i companyes del Centre Oceanogràfic de Murcia que hem van seguir animant a que no la deixés de banda i continués amb esforç per tirar-la endavant, així com la meva ambició professional. I com no pot ser d'altra manera, agrair a tot el grup de col·legues que ens vam fer allà, els companys de pis, companyes de sofriment predoctoral, i tants moments compartits. A tots vosaltres, Judit, Tania, Alejandro, Carmen, Manu, Maridol, Sole, Ana, María, Fon i com no, Mara que ens cuidava com a mare de tots, i de ben segur algú que hem deix, sou grans amistats i sempre és un gust retrobar-nos. Especialment, vull agrair també a Juan Santos, Lucía, Julia i Juantxi, amb vosaltres a Murcia vaig trobar una família!

Tornar a Palma, al Centre Oceanogràfic de Balears i amb la proximitat dels directors de tesi ha permès que recuperés cavalls de força per continuar fins enllestir-la. Al igual que abans, és d'agrair a les companyes i companys del COB el recolzament i ànims rebuts per tirar endavant la tesi. El submarí petit sempre serà el submarí petit, amb tots els que érem un temps abans de la tesi i els que som a dia d'avui. Però especialment, dins el gremi, vull agrair a qui per jo són pilars del dia a dia: Mar Santandreu, Safo, Sergio, Albert, Melissa, Ana, moltes gràcies de bon cor per sempre ser-hi i per ser com sou!

Una gran part d'aquesta tesi ha estat possible gràcies al projecte COPEMED, de FAO (Comissió General de Pesca del Mediterrani). Agraeixo als integrants del Cory-WG com a coautors d'alguns articles de la tesi, i en especial a la seva coordinadora Pilar Hernández, no només per els nombrosos estudis i dades recopilades sobre llampuga en tots aquests anys passats, sinó per permetre'm la oportunitat de treballar-hi, d'integrar-me en el working group, liderar l'article de revisió bibliogràfica i impulsar el treball d'stock assessment. Sobre el treball d'stock assessment, agrair a Rubén Roa, de qui he pogut aprendre d'aquest altre mon dins la ciència de pesqueries i metodologies d'avaluacions d'estoc.

El "consejo de sabios" amb l'alineació Rubén, Fran, Cristian i David, mereix una especial distinció dins aquestes línies, per totes els "consejos" de "ganyaneo", de caixons de cervesa amb gel de laboratori, i també les discussions científiques amb gintònics, que encara que no ho pareixi, n'hi ha hagut de ben interessants.

Unes paraules d'agraïment també han d'anar dirigides a la banda de música de Pollença i les companyes i companys de la música, més que companys és un grup de grans amistats, una de les millors activitats d'esbarjo per jo, que permet defugir moltes vegades de tot el dia de pensar o viure al voltant de la ciència.

La família mereix una de les dedicacions més importants. Faci el que faci, de la família sempre tindré el recolzament incondicional. Mamà, papà no tan sols respectareu el que volia "ser de gran", sinó que ho vau recolzar i gràcies al vostre esforç hem va permetre estudiar-ho i arribar fins aquest punt, juntament amb un pilar de vida que és un germà. Els que ja no hi son, principalment els padrins, tot i no saber que era això "modern, de la biologia" de ben segur estaríeu orgullosos de veure'm arribar a aquest punt. I, per acabar, l'agraïment més carinyós el dec a na Bea, gràcies per suportar aquest esprint final, de ben

segur hauré estat ben mal d'aguantar, i sobretot per mostrar-me una altra manera de gaudir la vida amb el camí que feim junts.

Funding

The research within this thesis has been carried out in the framework of the CERES project (EU 678193), funded by the Horizon 2020 program of the European Union. The project COPEMED (Coordination to Support Fisheries Management in the Western and Central Mediterranean), funded by FAO (Food and Agriculture Organization from the United Nations) has contributed with data and promoted two research articles for the doctoral thesis.

At the beginning of this thesis, I was funded with a predoctoral grant from the Regional Government of the Balearic Islands and the European Social Fund.

List of Manuscripts

The content of this thesis dissertation is a compilation of several original research articles, published or submitted to indexed scientific journals. Each chapter corresponds to one of the research articles listed below.

- Moltó, Vicenç; Hernández, Pilar; Sinopoli, Mauro; Besbes-Benseddik, Amina; Besbes, Raouf; Mariani, Adriano; Gambin, Miriam; Alemany, Francisco; Morales-Nin, Beatriz; Grau, Antoni Maria; Camiñas, Juan Antonio; Báez, José Carlos; Vasconcellos, Marcelo; Ceriola, Luca; Catalán, Ignacio A. (2020). A global review on the biology of the dolphinfish (*Coryphaena hippurus*) and its fishery in the Mediterranean Sea: advances in the last two decades. Reviews in Fisheries Science & Aquaculture, 28(3), 376-420. JCR 2020: Q1. IF: 5.893.

- Moltó, Vicenç; Palmer, Miquel; Polin, Marco; Ospina-Álvarez, Andrés; Catalan, Ignacio A. Submitted to ICES Journal of Marine Science. Improving the inference of spawning phenology from sea surface temperature for a wide-spread large pelagic fish.

- Moltó, Vicenç; Palmer, Miquel; Ospina-Álvarez, Andrés; Pérez-Mayol, Sílvia; Besbes-Benseddik, Amina; Gatt, Mark; Morales-Nin, Beatriz; Alemany, Francisco; Catalán, Ignacio A. (2021). Projected effects of ocean warming on an iconic pelagic fish and its fishery. Scientific reports, 11(1), 1-11. JCR 2021: Q2. IF: 4.996.

- Palmer, Miquel; Álvarez-Ellacuría, Amaya; Moltó, Vicenç; Catalán, Ignacio A. (2022). Automatic, operational, high-resolution monitoring of fish length and catch numbers from landings using deep learning. Fisheries Research, 246, 106166. JCR 2021: Q2. IF: 2.817.

- Moltó, Vicenç; Catalán, Ignacio A.; Ospina-Álvarez, Andrés; Hernández, Pilar; Roa-Ureta, Rubén H. (2022). A multiannual five-fleet generalized depletion model for the stock assessment of the Mediterranean dolphinfish (*Coryphaena hippurus*) fishery. ICES Journal of Marine Science. 79(5), 1481-1496. JCR 2021: Q1. IF: 3.906.

Table of Contents

Summary

The common dolphinfish or mahi-mahi (*Coryphaena hippurus*) is a large pelagic and highly migratory fish distributed in tropical and subtropical waters around the globe. The Mediterranean Sea population supports traditional small-scale fisheries targeting juvenile individuals, based on the use of fish aggregating devices (FADs), mainly in the Balearic Islands, Sicily, Malta and Tunisia, thus being of high importance for local culture and economy. However, in these areas the adults are only observed during the spawning season, suggesting a reproductive migration.

The goal of this thesis is to revise and expand the knowledge on the Mediterranean dolphinfish population, focusing on the effects of a warming Mediterranean. For over two decades, several researchers have conducted invaluable biological and fishery studies on this species in the area. This thesis aims to go one step further, first exploring the effects of environmental drivers on biological and ecological traits, and then using this knowledge to develop novel technologies and methodologies for the assessment of the Mediterranean stock, which remains unassessed at this point.

Among the main results, it can be highlighted that the models incorporating temperature have improved the reproductive traits and growth estimates. Specifically, studies developed in this thesis show that the spawning peak occurs systematically before the annual temperature peak in a wide latitudinal range of dolphinfish populations and that the duration of the spawning is related to the mean annual temperature, allowing us to predict the seasonal spawning patterns from temperature. In addition, a validated temperature-dependent growth model based on juveniles targeted by the artisanal fishery based on FADs has allowed to assess the length at catch of the recruits at the opening date of the fishery under several climate change projections from the Intergovernmental Panel on Climate Change (IPCC) and also under a marine heatwave. Results suggest that in warmer scenarios there might be an increase in the mean size, as well shifts in length distributions with a higher percentage of shorter individuals in long-term climatic projections. These results could be applied both to short-term management actions considering environmental conditions and to mid/long-term management, projecting potential effects under future environmental conditions derived from sea warming.

With regards to the Mediterranean dolphinfish fisheries management, an automated process based on artificial intelligence has been developed to obtain larger amounts of high-resolution fish length data for the fish that are in boxes previously to be sold in the auction. These data will serve to validate previous studies and as input for assessment models opening research avenues that use length distribution as an input variable. A multi-annual five-fleets generalized depletion model, adapted to the fishery dynamics of the countries exploiting this fishery, has also been developed. This method has been adopted by the General Fisheries Commission of the Mediterranean (GFCM) to assess the Mediterranean dolphinfish stock, providing accurate reference points for the first time for this stock. These results also suggest that the stock is not under risk of overfishing,

showing stability in recruitment and exploitation rates, although the precautionary approach suggests not increasing the fishing effort until a quantitative evaluation of the population is available.

Finally, we propose future lines of research, which should focus on mechanistic approaches to understand the environmental relationship with biological and ecological traits across all life stages. Improving the knowledge of environmental requirements for early life stages is also crucial for understanding the sources of early mortality and better-understanding recruitment dynamics, which is also essential to explain capture fluctuations throughout the time series. Furthermore, research on movement ecology is critical to unraveling migratory patterns that determine the dynamic of captures by different countries, their behavior in relation to the FADs and the catch-effort relationship.

Resum

La llampuga o mahi-mahi (*Coryphaena hippurus*) es una espècie considerada gran pelàgic i altament migratòria, distribuïda en aigües tropicals i subtropicals arreu del món. La població del Mediterrani sustenta pesqueries tradicionals d'arts menors dirigides a individus juvenils, basades en l'ús de dispositius concentradors de peixos (capcers), principalment a les illes Balears, Sicília, Malta i Tunísia. Aquestes pesqueries tenen una gran rellevància en la cultura i economia locals d'aquests països. No obstant, en aquestes regions sols s'observen individus adults durant l'època de posta, el que suggereix una migració reproductiva.

El principal objectiu d'aquesta tesi és revisar i ampliar el coneixement de la població de llampuga del Mediterrani, amb especial èmfasi en els efectes de l'escalfament global i fenòmens associats. En les darreres dècades, s'han realitzat nombrosos estudis sobre la biologia i pesqueries d'aquesta espècie a la regió. Aquesta tesi pretén anar un pas enllà explorant en primer lloc els efectes ambientals sobre alguns trets biològics i ecològics de l'espècie i emprar aquest coneixement i generar millors eines per aconseguir una gestió sostenible de l'estoc Mediterrani, que segueix fora una avaluació formal a dia d'avui.

Entre els principals resultats, cal destacar que la incorporació de la temperatura en els models desenvolupats per aquesta espècie ha millorat l'estima dels patrons reproductius i de creixement. Concretament, els estudis desenvolupats en el marc d'aquesta tesi mostren que el pic de posta ocorre sistemàticament amb anterioritat al pic de anual de temperatura en diferents poblacions de llampuga en un ampli rang de latituds i que la duració de la posta està relacionada amb la temperatura mitjana anual, fet que permet predir el patró estacional de posta a partir de la temperatura. A més, un model validat de creixement depenent de temperatura basat en juvenils explotats per la pesqueria ha permès avaluar les talles de captura de reclutes a la data d'inici de la pesqueria sota diferents projeccions de canvi climàtic segons el Panell Intergovernamental sobre el Canvi Climàtic (IPCC) i també d'onades de calor marines. Els resultats suggereixen que en escenaris d'escalfament hi haurà un increment de la talla mitjana i una desviació en la distribució de talles, amb uns percentatges més elevats d'individus de talles més petites en projeccions climàtiques a llarg termini. Aquests resultats són aplicables tant en accions de gestió a curt termini, considerant la variabilitat ambiental, com per a una gestió a mig i llarg termini, al predir els potencials efectes sota condicions ambientals futures derivades de l'augment de temperatura.

Quant a la gestió de les pesqueries de llampuga a la Mediterrània, s'ha desenvolupat un procés automatitzat basat en intel·ligència artificial per a obtenir dades massives en alta resolució de talles individuals dels peixos disposts en les caixes prèviament a la seva venta a la llotja. Aquestes dades serviran per a validar estudis previs, així com per alimentar models d'avaluació pesquera, obrint així noves oportunitats en investigacions que requereixen distribucions de talles com a variable clau. També s'ha desenvolupat un model de depleció generalitzat, multi-anual i multi-flota, adaptat a les dinàmiques de les

pesqueries dels diferents països que exploten aquesta espècie. Aquest mètode s'ha adoptat per la Comissió General de Pesca del Mediterrani (CGPM), permetent avaluar l'estoc de llampuga al Mediterrani, obtenint els primers punts de referència d'explotació per a aquest estoc. Aquests resultats suggereixen que no existeix risc de sobrepesca a l'estoc, mostrant una estabilitat tant en les taxes d'explotació com de reclutament, encara que amb l'enfocament precautori seria recomanable no incrementar l'esforç pesquer fins a disposar d'una avaluació quantitativa de la població.

Finalment, es proposen futures línies d'investigació, que s'haurien de centrar en aproximacions mecanicistes per comprendre les relacions ambientals amb els trets biològics i ecològics de l'espècie en tots els seus estadis vitals. Incrementar el coneixement dels requeriments ambientals per als primers estadis de desenvolupament també resulta crucial per comprendre la mortalitat en les primeres etapes de vida, així com la dinàmica de reclutament, essencial per poder explicar fluctuacions en les captures al llarg de les sèries temporals. A més, investigar sobre l'ecologia del moviment resulta clau per revelar els patrons migratoris, aportar informació per entendre millor les variacions de captures dels diferents països i les relacions entre captura i esforç, així com el comportament de l'espècie envers als capcers.

Resumen

La lampuga, dorado, o mahi-mahi (*Coryphaena hippurus*) es una especie considerada gran pelágico y altamente migratoria, distribuida en aguas tropicales y subtropicales alrededor del mundo. La población del Mediterráneo sustenta pesquerías tradicionales de artes menores dirigidas a individuos juveniles, basadas en el uso de dispositivos de concentración de peces (DCPs), principalmente en las islas Baleares, Sicilia, Malta y Túnez. Estas pesquerías tienen una gran importancia en la cultura y economía local de estos países. Sin embargo, en estas regiones solo se observan individuos adultos durante la época de puesta, lo que sugiere una migración reproductiva.

El principal objetivo de esta tesis es revisar y ampliar el conocimiento de la población de lampuga del Mediterráneo, con especial énfasis en los posibles efectos del calentamiento de los océanos. En las últimas dos décadas se han realizado numerosos estudios sobre la biología y pesquerías de esta especie en la región. Esta tesis pretende ir un paso más allá, explorando en primer lugar los efectos ambientales sobre los rasgos biológicos y ecológicos de la especie y generar nuevas herramientas útiles para la gestión del stock Mediterráneo, que sigue sin evaluación formal a día de hoy.

Entre los principales resultados, la incorporación de la temperatura en los modelos desarrollados para esta especie ha mejorado la estima de los patrones reproductivos y de crecimiento. Concretamente, los estudios desarrollados en el marco de esta tesis muestran que el pico de puesta ocurre sistemáticamente con anterioridad al pico anual de temperatura en distintas poblaciones de lampuga en un amplio rango de latitudes y que la duración de la puesta está relacionada con la temperatura media anual, lo que permite predecir el patrón estacional de puesta a partir de la temperatura. Además, un modelo validado de crecimiento dependiente de temperatura basado en juveniles explotados por la pesquería ha permitido evaluar las tallas de captura de reclutas en la fecha de apertura de la pesquería bajo distintas proyecciones de cambio climático según el Panel Intergubernamental sobre el Cambio Climático (IPCC) y también en olas de calor marinas. Los resultados sugieren que en escenarios de calentamiento podría haber un incremento de la talla media y una desviación en la distribución de tallas, con un porcentaje más elevado de individuos de tallas más pequeñas en proyecciones climáticas a largo plazo. Estos resultados son aplicables tanto en acciones de gestión a corto plazo, considerando la variabilidad ambiental, como para una gestión a medio y largo plazo, al predecir los potenciales efectos bajo condiciones ambientales futuras derivadas del cambio climático.

En cuanto a la gestión de las pesquerías del Mediterráneo, se ha desarrollado un proceso automatizado basado en inteligencia artificial para obtener datos masivos en alta resolución de tallas individuales de los peces dispuestos en las cajas previamente a su venta en lonja. Estos datos servirán para validar estudios previos, así como para alimentar modelos de evaluación pesquera, abriendo así nuevas oportunidades en las investigaciones que requieren distribuciones de tallas como variable esencial. También

se ha desarrollado un modelo de depleción generalizado multianual y multi-flota, adaptado a las dinámicas de las pesquerías de los distintos países que explotan esta especie. Este método se ha adoptado por la Comisión General de Pesca del Mediterráneo (CGPM) permitiendo evaluar el stock de lampuga del Mediterráneo, obteniendo los primeros puntos de referencia precisos para este stock. Estos resultados también sugieren que no existe riesgo de sobrepesca en el stock, mostrando una estabilidad tanto en las tasas de explotación como de reclutamiento, aunque aplicando el enforque precautorio no sería recomendable incrementar el esfuerzo pesquero hasta disponer de una evaluación cuantitativa de la población.

Finalmente, se proponen futuras líneas de investigación, que deberían enfocarse en aproximaciones mecanicistas para entender las relaciones ambientales con los rasgos biológicos y ecológicos de la especie en todos sus estadios vitales. Incrementar el conocimiento de los requisitos ambientales para los estadios tempranos de vida también resulta crucial para comprender la mortalidad en estas primeras etapas de vida, así como la dinámica de reclutamiento, lo que es esencial para explicar fluctuaciones en las capturas a lo largo de las series temporales. Además, investigar en la ecología del movimiento es clave para revelar los patrones migratorios, dar posibles explicaciones a los patrones en las capturas de los distintos países, y las relaciones entre captura y esfuerzo, así como el comportamiento de la especie en relación con los DCPs.

SECTION 1

General Introduction

1. Who? Llampuga, common dolphinfish or mahi-mahi (*Coryphaena hippurus*)

The common dolphinfish (*Coryphaena hippurus*, L. 1758), also known as mahi-mahi or llampuga, lampuga and lampuki in the Mediterranean regions, is a large pelagic species widely distributed in tropical and temperate regions around the world. It comprises highly migratory regional populations which are usually targeted by artisanal professional and sport fisheries, providing significant landings and economic benefits to coastal communities. Given that Chapter 1 of this thesis offers a comprehensive review of the current knowledge on dolphinfish biological traits and the Mediterranean fisheries, this general introduction focuses on the characteristics that make this species an appropriate case study to address the effects of climate change on fisheries. Specifically, the following paragraphs aim to provide the background for understanding the relevance of further research on the environmental effects on this species in the Mediterranean, and to develop new tools for its management.

Dolphinfish primarily inhabit the epipelagic marine ecosystem, which is the upper section of the water column, and hence the more sensitive to temperature variations due to direct solar radiation. The epipelagic habitat is strongly influenced by the atmospheric dynamics and the rotation of the earth, resulting in strong variability due to several processes and structures, such as ocean currents, upwelling, mesoscale gyres or thermoclines (Bigg and Bigg, 2003). Dolphinfish is a thermophilic species with a distribution range defined by the 16ºC isotherm (Palko et al., 1982), and is able to follow isotherms that drive regional migrations (Massutí and Morales-Nin, 1995; Merten et al., 2016, 2014a, 2014b). Its migration behavior is directed toward reaching appropriate spawning habitats and adequate foraging grounds, which are usually characterized by different environmental requirements (Putman, 2018). This species, which occupies a high trophic level has a short lifespan, with a maximum of four years reported (Beardsley, 1967), but an average of fewer than two years (Oxenford, 1999). Its high metabolic rate is supported by an omnivorous diet and voracious behavior, resulting in one of the fastest recorded growth rates for teleost fishes (Oxenford, 1999; Palko et al., 1982). Some of these traits suggest that the population dynamics of this species should be strongly linked to the interannual variability in the environmental conditions, in a similar way as small pelagic fish such as anchovies and sardines.

Given the information mentioned above, and the growing awareness of the impacts of warming seas on fish and fisheries (Free et al., 2019), it is timely and appropriate to analyze the potential effects of changes in sea surface on key characteristics of dolphinfish. While there have been documented cases of changes in the distribution and range extensions of dolphinfish attributable to environmental conditions in distant areas (Norton, 1999; Salvadeo et al., 2020), many questions remain unanswered regarding the environmental effects on the ecology and fisheries of this species, as will be further discussed.

2. Where? The Mediterranean dolphinfish population

The Mediterranean Sea is a semi-enclosed basin adjacent to the Atlantic Ocean, connected with it through the Strait of Gibraltar at its west end, and linked to the Red Sea through the Suez Canal at its southeast, and the Black Sea at its northeast end. Owing to its oceanographic and climatic properties, the Mediterranean Sea has been considered a miniature ocean, and is recognized as a biodiversity hotspot, harboring one of Earth's highest levels of biodiversity (Bethoux et al., 1999; Coll et al., 2010). In addition, the Mediterranean Sea has also been designated as a climate change hotspot (Giorgi, 2006), being more sensitive than open oceans to the impacts of climate change, as those produced by variations in temperature and salinity, among others (Adloff et al., 2015; Bethoux and Gentili, 1999; Durrieu de Madron et al., 2011; Nykjaer, 2009; Schroeder et al., 2016; Shaltout and Omstedt, 2014; Vargas-Yáñez et al., 2008), as well as to extreme events (Darmaraki et al., 2019). These environmental changes have significant effects on the Mediterranean's marine biota, including mass mortality events with notable ecosystem consequences, temperature-mediated diseases, shifts in species distribution, changes in trophic interactions or regimes, and the invasion and expansion of alien species (Cerrano et al., 2000; Coll et al., 2010; Coma et al., 2009; Edelist et al., 2013; Garrabou et al., 2009, 2001; Lazzari et al., 2014; Lejeusne et al., 2010; Marbà and Duarte, 2010; Massuti et al., 2010; Moullec et al., 2019; Raitsos et al., 2010; Sabatés et al., 2006; Vezzulli et al., 2010).

Dolphinfish have been exploited as a fishing resource by Mediterranean coastal communities since ancient times. Currently, the four countries actively involved in this fishery are Spain (only the Balearic Islands archipelago), Italy (mainly in Sicily), Malta and Tunisia. This fishery is one of the most important in the aforementioned countries, representing one of the most landed species in terms of the weight of catches and economic incomes generated (Battaglia et al., 2010; Morales-Nin et al., 2010; Palmer et al., 2017; Quetglas et al., 2016). Dolphinfish is highly valued by these coastal societies, being promoted gastronomically as a seasonal fresh fish product, and targeted both by recreational and professional fishers (Font and Lloret, 2014; Morales-Nin et al., 2005; Venturini et al., 2017).

3. Why? The challenges in the warming Mediterranean

This section aims to briefly summarize the current knowledge regarding the Mediterranean dolphinfish population, highlighting the knowledge gaps that will guide the research objectives of this thesis.

The General Fisheries Commission for the Mediterranean (GFCM), a Regional Fisheries Management Organization (RFMO) under the Food and Agriculture Organization (FAO) of the United Nations, has been promoting research on this fishing resource since the early 1990s. Chapter 1 of this thesis will exhaustively describe the current biological knowledge of the Mediterranean dolphinfish, which is derived from these projects and is schematized in Fig. 1. This research includes several studies on age, growth and reproduction, from which several biological parameters and processes were calculated, including growth rates, length-weight relationships, gonadosomatic indices and fecundity, among others. These results have also been documented in two doctoral theses conducted in Tunisia and the Balearic Islands (Besbes Benseddik, 2017; Massutí, 1997). However, the environmental drivers of these biological processes and the potential effects of environmental changes on them have not yet been studied.

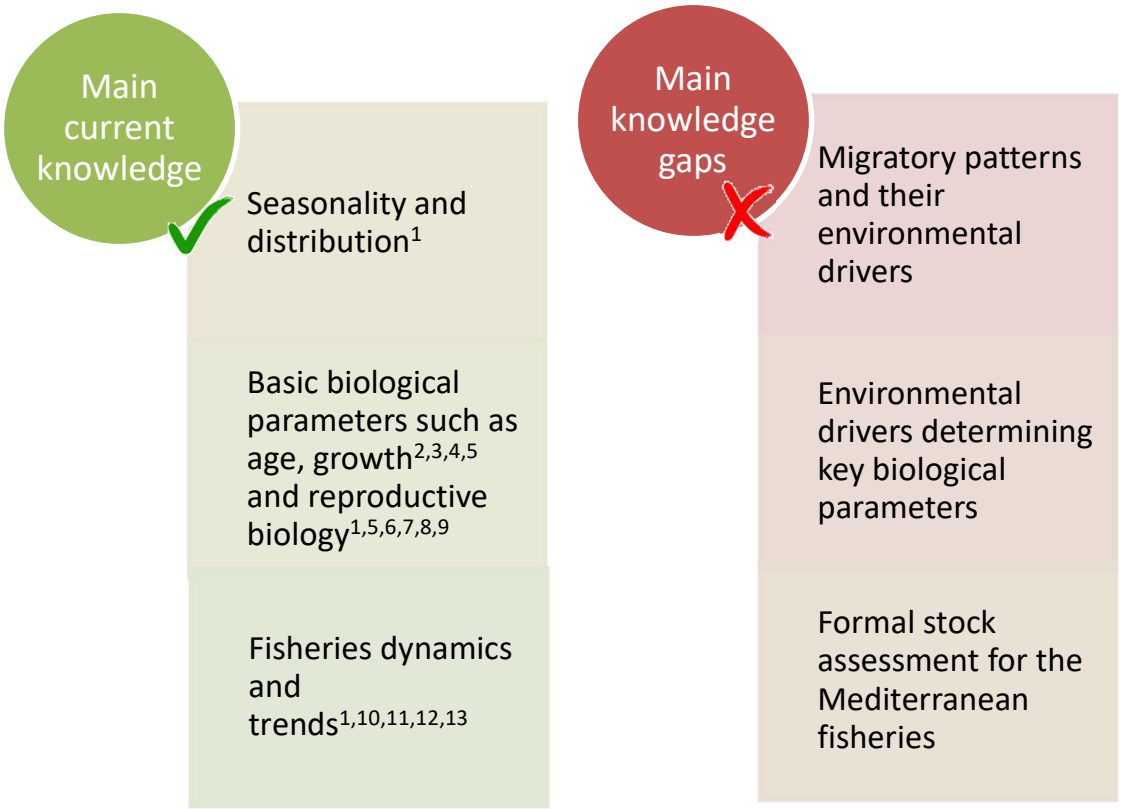

Figure 1. Scheme of the current knowledge and identified gaps of knowledge of the Mediterranean dolphinfish population. The references used in this figure are [1]Massutí and Morales-Nin (1995), [2]Massutí et al. (1999), [3]Morales-Nin et al. (1999), [4]Benseddik et al.

(2011), [5]Gatt et al. (2015), [6]Massutí and Morales-Nin (1997), [7]Potoschi et al. (1999b), [8]Besbes Benseddik et al. (2015), [9]Besbes Benseddik et al. (2019), [10]Potoschi et al. (1999a), [11]Vella (1999), [12]Zaouali and Missaoui (1999), [13]Morales-Nin et al. (2000).

The need for studies on the effects of the environment on the ecology and fisheries of this species is particularly relevant in the face of climate change. One of the major effects of climate change is ocean warming, as oceans absorb most of the energy increase (Cheng et al., 2022; Levitus et al., 2005). This warming has multiple impacts on marine systems, ranging from the species to the ecosystem level (Doney et al., 2012; Hoegh-Guldberg and Bruno, 2010; Poloczanska et al., 2013). As a response to the effects of warming, species are forced to move to their climate niche through changes in three different aspects: space (distribution), physiology and phenology (Bellard et al., 2012).

In the context of fisheries science, phenologies and key physiological processes such as reproduction (spawning), recruitment, growth, and mortality, strongly determine population dynamics and, as a result, the yield of the fishery. Traditionally, only the intrinsic biological characteristics of a specific species (such as age, growth/length, length-weight relationships, etc.) and the fishery dynamics (catch and effort) have been considered in management. However, studies that incorporate the effects of the environment on these processes have increased significantly since the 2000s (Beaugrand and Kirby, 2018; Morrongiello et al., 2012; Walther et al., 2002). It is essential to understand how exploited species respond to environmental changes, and even more so to incorporate future climate projections as they become available, to anticipate the potential impacts of climate change on fisheries and design adaptive management measures.

In addition, to fully comprehend the population dynamics of the Mediterranean dolphinfish, it is necessary to understand not only the relative influence of the environmental factors on basic biological and ecological traits but also on the exploitation dynamics and on the interaction between exploitation and biological factors. This requires obtaining and integrating large amounts of data from different sources. Unfortunately, the speed of this integration is often suboptimal for less economically important fisheries. The Mediterranean dolphinfish fishery is an example of these data-limited fisheries, where the stock is currently unassessed due to a lack of sufficient data, or processing available data, to conduct a formal assessment and determine biological reference points (Fujita, 2021; Newman et al., 2015). Addressing this issue requires gathering basic biological data whose lack impedes the development of stock assessment methods, which can be achieved through the application of new technologies based on automatic processes. Advances in computer power, digitalization and the development of multiple sensors now enable the integration of data at unprecedented levels.

The Mediterranean dolphinfish fishery has received attention from the International Commission for the Conservation of the Atlantic Tunas (ICCAT) and the GFCM in recent years due to the absence of a formal stock assessment. In 2019, the GFCM declared the species a priority and initiated a research program to develop a management plan by 2023 (Recommendation GFCM/43/2019/1). To achieve this goal, it is crucial to improve basic

aspects of the fishery, such as data collection, better definition of effort, and gaining knowledge on the stock structure and movement patterns of the species in the fishing region.

In spite of this progress, gaining a deeper understanding of the ecological traits and their relationship with environmental variability, including climate change, remains a challenge for scientists studying the Mediterranean dolphinfish population. Therefore, the application of new advances in the field of fisheries science is necessary to better manage this resource.

4. Structure of this Thesis

This doctoral thesis is structured into five sections. The first section serves as a general introduction, that provides the context and presents the main objectives, which form the second section. The third section is composed of a series of five chapters that develop the different objectives, each one relatively independent of the others, consisting of research articles published or submitted to indexed journals. As a result, this thesis does not have a common methodology section. Each chapter has its own discussion, but the fourth section provides a general discussion of the results obtained throughout the different chapters. Finally, the fifth section includes the conclusions derived from this thesis.

The third section, which divided into five chapters contains the bulk of the research, as mentioned above, organized into three different research lines. The first one matches with the first chapter, corresponding to an extensive review regarding the state of the art of the common dolphinfish biology, with special attention to the Mediterranean population and fisheries. The two following chapters constitute the second section, aiming to reveal the relationship between environmental factors, including climate change, and the ecology of this species. Finally, the third section include two chapters comprising studies focused on fisheries management aspects of this species. This structure is schematized in Fig. 2, and the different chapters are listed below:

Section 3.1: State of the art of the dolphinfish biology and Mediterranean fisheries.

> Chapter 1: A global review on the biology of the dolphinfish (*Coryphaena hippurus*) and its fishery in the Mediterranean Sea: Advances in the last two decades. Published in Reviews in Fisheries Science and Aquaculture.

Section 3.2: Environmental variability and ecological traits.

> Chapter 2: Improving the inference of spawning phenology from sea surface temperature for a wide-spread large pelagic fish. Submitted to Ecological Modelling.
>
> Chapter 3: Projected effects of ocean warming on an iconic pelagic fish and its fishery. Published in Scientific reports.

Section 3.2: Models and tools for fisheries management

> Chapter 4: Automatic, operational, high-resolution monitoring of fish length and catch numbers from landings using deep learning. Published in Fisheries Research.
>
> Chapter 5: A multiannual five-fleet generalized depletion model for the stock assessment of the Mediterranean dolphinfish (*Coryphaena hippurus*) fishery. Published in ICES Journal of Marine Science.

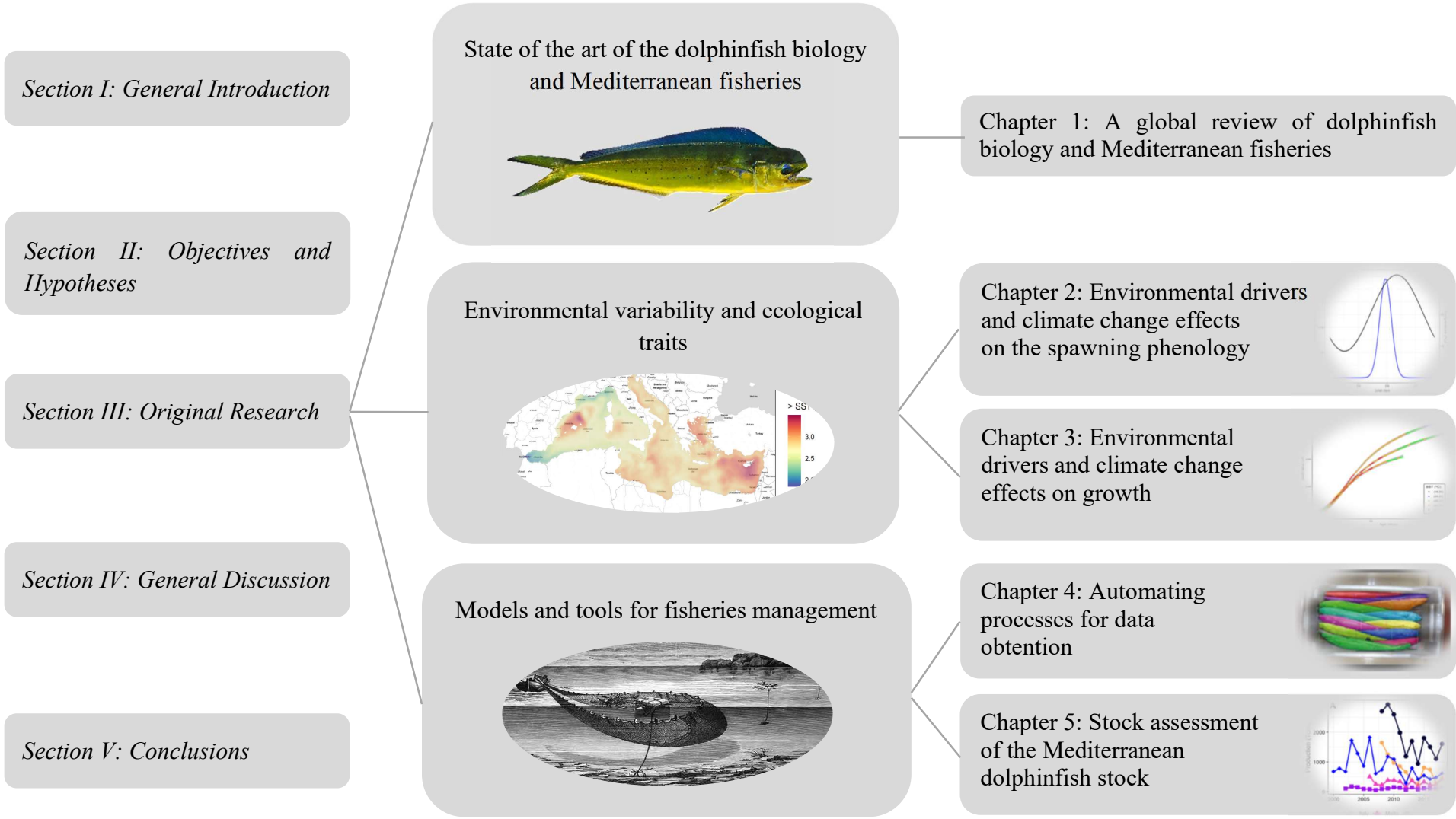

Figure 2: Scheme of the thesis structure with particular detail of the research section.

SECTION 2

Objectives and Hypotheses

The previous section has identified knowledge gaps regarding the Mediterranean dolphinfish population, which will be addressed in this doctoral thesis. The general objectives of this thesis are twofold: first, to advance in our understanding of how environmental drivers, particularly temperature and future thermal scenarios derived from climate change, affect and may affect key biological traits of the Mediterranean dolphinfish population at the physiological level (e.g., growth) and phenology (e.g., spawning). Second, to advance in the development of models and tools to assist in the management of the fisheries in this region. To this end, the specific objectives of this thesis, and the specific research hypothesis raised in each one of them, are as follows:

1) To examine the relationship between environmental structure and variability with respect to spawning phenology.

Specifically, the research hypothesis raised for this objective is:

H_0: There will be no significant shift in the spawning phenology of the dolphinfish population as sea temperatures increase.

H_1: Changes in the annual thermal cycle may affect the spawning phenology of this species.

2) To determine the relationship between environmental variability and the growth patterns of dolphinfish that are targeted by Mediterranean fisheries.

With the following underlying hypothesis:

H_0: Changes in environmental variability, mainly in sea surface temperature, will not significantly affect the growth patterns of the dolphinfish targeted by Mediterranean fisheries.

H_1: Changes in environmental variability, mainly in sea surface temperature, can improve the estimates of dolphinfish growth targeted by Mediterranean fisheries.

3) To develop new models and tools that can improve the management of this species in the Mediterranean.

These hypotheses will be tested through the building and application of statistical approaches of varying complexity to newly generated and existing datasets, the application of new technologies and the development of an extended assessment model for the Mediterranean dolphinfish fishery.

SECTION 3

Original Research

Chapter 1: A global review on the biology of the dolphinfish (*Coryphaena hippurus*) and its fishery in the Mediterranean Sea: advances in the last two decades.

Moltó, Vicenç; Hernández, Pilar; Sinopoli, Mauro; Besbes-Benseddik, Amina; Besbes, Raouf; Mariani, Adriano; Gambin, Miriam; Alemany, Francisco; Morales-Nin, Beatriz; Grau, Antoni Maria; Camiñas, Juan Antonio; Báez, José Carlos; Vasconcellos, Marcelo; Ceriola, Luca; Catalán, Ignacio A.. (2020). A global review on the biology of the dolphinfish (*Coryphaena hippurus*) and its fishery in the Mediterranean Sea: advances in the last two decades. *Reviews in Fisheries Science & Aquaculture*, 28(3), 376-420. DOI: https://doi.org/10.1080/23308249.2020.1757618

Web link: https://www.tandfonline.com/doi/abs/10.1080/23308249.2020.1757618

Chapter 2: Improving the inference of spawning phenology from sea surface temperature for a wide-spread large pelagic fish.

Moltó, Vicenç; Palmer, Miquel; Polin, Marco; Ospina-Álvarez, Andrés; Catalan, Ignacio A. Improving the inference of spawning phenology from sea surface temperature for a wide-spread large pelagic fish. **Submitted** to ICES Journal of Marine Science

Chapter 3: Projected effects of ocean warming on an iconic pelagic fish and its fishery.

Moltó, Vicenç; Palmer, Miquel; Ospina-Álvarez, Andrés; Pérez-Mayol, Sílvia; Besbes-Benseddik, Amina; Gatt, Mark; Morales-Nin, Beatriz; Alemany, Francisco; Catalán, Ignacio A. (2021). Projected effects of ocean warming on an iconic pelagic fish and its fishery. Scientific reports, 11(1), 1-11. DOI: https://doi.org/10.1038/s41598-021-88171-1

Web link: https://www.nature.com/articles/s41598-021-88171-1

Chapter 4: Automatic, operational, high-resolution monitoring of fish length and catch numbers from landings using deep learning.

Palmer, Miquel; Álvarez-Ellacuría, Amaya; **Moltó, Vicenç**; Catalán, Ignacio A. (2022). Automatic, operational, high-resolution monitoring of fish length and catch numbers from landings using deep learning. Fisheries Research, 246, 106166. DOI: https://doi.org/10.1016/j.fishres.2021.106166

Web link:
https://www.sciencedirect.com/science/article/pii/S0165783621002940

Chapter 5: A multiannual five-fleet generalized depletion model for the stock assessment of the Mediterranean dolphinfish (*Coryphaena hippurus*) fishery.

Moltó, Vicenç; Catalán, Ignacio A.; Ospina-Álvarez, Andrés; Hernández, Pilar; Roa-Ureta, Rubén H. (2022). A multiannual five-fleet generalized depletion model for the stock assessment of the Mediterranean dolphinfish (*Coryphaena hippurus*) fishery. ICES Journal of Marine Science. 79(5), 1481-1496. DOI: https://doi.org/10.1093/icesjms/fsac072

Web link:
https://academic.oup.com/icesjms/article/79/5/1481/6581598?login=false

SECTION 4

General Discussion

This general discussion summarizes results and concepts stemming from the different chapters and draws a general picture of what has been learned throughout the thesis, as well as what remains to be known with respect to the ecology and fisheries of dolphinfish in the Mediterranean.

Chapter 1 provides an exhaustive revision of the biological traits of dolphinfish worldwide, with special attention to the Mediterranean population. This review identified a series of knowledge gaps to be addressed, which have been grouped into two sections: i) the lack of knowledge about the relationships between environmental variables and biological traits for the Mediterranean dolphinfish population, as well as on the effects of environmental variability on the population dynamics, and ii) the lack of a formal stock assessment to support management measures for the Mediterranean dolphinfish stock. The new contributions presented in this thesis fill in some of these knowledge gaps, generating new knowledge regarding the ecology of the species in the region and developing useful methodologies for a better management of the stock. Both issues were addressed keeping in mind the potential effects of the rapid warming of the Mediterranean. Therefore, much of the work developed herein tried to unveil the potential effect of temperature on key life history traits.

Chapters 2 and 3 contribute to answering the latter point, analyzing the effects of the sea surface temperature (SST) on reproductive phenology and growth, respectively. These are key biological parameters determining population dynamics, and SST is one of the main environmental drivers. In Chapter 2, we generated a model to predict the fish spawning phenology from temperature. In this model, we related the annual thermal profile with the spawning phenology, which was inferred from two independent sources of data, the gonadosomatic index (GSIs) obtained from different populations in a wide latitudinal range and the hatch-date distribution inferred from otolith readings of different inter-annual cohorts. Our results suggest that the spawning peak occurs consistently before the temperature peak, despite the latitudinal differences, and that the spawning spread (i.e., spawning period) depends on the mean annual temperature. The empirical method developed in this chapter provides a tool to assess the effect of temperature variability on the spawning phenology either in the short term, by considering the inter-annual variations in spawning phenology according to the different annual temperature patterns or marine heat waves, and assessing future changes according to the future climate projections of ocean warming.

In Chapter 3, we developed an individual-based model to relate the growth of this species to the SST experienced and photoperiod at birth. Our model captured well the juvenile dolphinfish growth temperature dependences and allowed us to predict the length at catch distribution of the dolphinfish population at the start of the fishery, which is especially important in a fishery regulated through an established opening of the fishing season. In addition, this model allowed us to project the growth and the length at catch distributions under changing thermal conditions, such as marine heat waves (MHW) and future temperature projections for the end of the current century according to the IPCC scenarios RCP4.5 and 8.5. To account for potential changes in spawning phenology under future

thermal conditions, which could also result in potential changes in length-at-catch distribution, the hatch-date distribution of the dolphinfish population was established according to the model developed in Chapter 2. Our results suggest an increase of 5.1% and 12.8% in fork length according to the RCP4.5 and 8.5, respectively and of 13.2% under the conditions of the 2003 MHW. Similarly, to the previous chapter, this methodology would also allow us a short-term (annual) assessment of any annual cohort growth and length at catch distribution given the annual thermal profile, and to project future growth and length at catch, under modeled future thermal conditions.

Among the limitations of our approaches (Chapters 2 and 3) to relate environmental conditions with biological parameters is that we used phenomenological models to determine the dependencies of these parameters with the spawning phenology and growth, providing only correlational effects within the ranges considered in our studies. Phenomenological models have resulted in useful procedures for capturing and reproducing the environmental effects on the biological traits within certain ranges, such as temperatures experienced within physiologically tolerable ranges and individuals below 65 cm fork length (mostly sexually immature and therefore avoiding energy investment for reproduction). However, both chapters discuss the importance of using a combination of mechanistic models and experiments to better infer causal effects. One example of such models are bioenergetic approaches, such as Dynamic Energy Budgets models (DEBs; Kooijman, 2010; Nisbet et al., 2012). These models are based on energy balances (the main biological processes result from energy flows directed to maintenance, growth and reproduction), providing integrated effects on physiological traits regardless of the life stage. These models require good information on environmental drivers (e.g., food availability) together with metabolic information about the species. At the beginning of the Ph.D., only partial information was available (Kraul, 1989), but as more information becomes available, this avenue is expected to be explored further (Perrichon et al., 2019; Stieglitz et al., 2017).

In addition, both chapters consider fixed juvenile mortality rates within the modeling processes, as no information on variable mortality rates as a function of length is available. Mortality processes strongly affect population dynamics; therefore, variable mortalities can lead to potential biases in our results, especially when conducting projections under future environmental conditions. Variable mortalities can be coupled in our modeling approaches just as this information becomes available, but for now, it is uncertain. Early mortality may be dependent on the larval habitat quality, which for most large pelagic species, including dolphinfish, is determined by relatively small and mesoscale hydrographic structures, such as retention structures, including salinity fronts and eddies (Alemany et al., 2010; Bakun, 2006; Diaz-Barroso et al., 2022; Kitchens and Rooker, 2014; Reglero et al., 2019; Rooker et al., 2012). It is also uncertain how climate change will affect circulation, which is crucial for dispersal and connectivity in early life stages, and therefore can exert strong effects on mortality (Lett et al., 2010; van Gennip et al., 2017; Wilson et al., 2016). As for future projections, considering these effects is nowadays a serious challenge (Hewitt et al., 2020; Richards et al., 2021). Another key component for modeling early life mortality is a correct understanding of predator-prey

relationships (Bailey and Houde, 1989; Hunter, 1981). These relationships are not only spatially unknown for this species, but they can be altered by short and long-term environmental conditions, which in turn influence the spawning phenology, leading to changes in ichthyoplankton assemblages (Asch, 2015; Auth et al., 2018; Genner et al., 2010; Thaxton et al., 2020; Weigel et al., 2021) and also in the way that species interact with their preys (Asch et al., 2019; Durant et al., 2007). Therefore, a better knowledge of larval and early juvenile dynamics is necessary if the population dynamics of this species are to be better understood.

Chapters 4 and 5 make significant contributions to the provision of information and tools for better management of Mediterranean dolphinfish fisheries. In Chapter 4, we developed a model based on artificial intelligence (deep learning) together with a statistical framework to accurately estimate the number of fish and their furcal length before being sold in the centralized auction of Mallorca. Manual sampling is cost-intensive in terms of time and personnel, and can only be conducted occasionally for less economically important fisheries. Automated sampling strategies based on artificial intelligence offer the potential for continuous and more efficient monitoring programs. These solutions also allow richer data collection by sampling most of the landed individuals. This leads to more information-rich data sets, which can be stratified at different levels (e.g., boat-level and geographic-level), providing more detailed information regarding fisheries dynamics. For this particular species, for example, this technique could allow us to study the effect of temperature on the average length at the opening of the fishery or the effect of punctual extreme events on growth, validating the results obtained from Chapter 3.

In Chapter 5 we adapted a generalized depletion model to assess the Mediterranean dolphinfish fishery. These models present the advantage of having low data requirements, and therefore are suitable for data-limited fisheries. However, they highlight the need for tools such as the ones developed in Chapter 4 to obtain basic data from automated sampling, which can provide high-resolution data sets required for feeding the models. Generalized depletion models are suitable for short-lived species, as they can adjust well to the dynamics of high biomass inputs followed by fast depletion rates, which fits the dynamics of the dolphinfish fisheries. In the Mediterranean, there are four FAD fisheries targeting dolphinfish, one for each country fishing area, and dolphinfish also constitute a by-catch from the long-lines fisheries operating in the same open water regions, which we considered as a fifth fishery. These fisheries also have different catch-effort dynamics, which lead to the development of the five-fleet generalized depletion model. Our model allowed us to obtain reference points for the first time for the Mediterranean dolphinfish fisheries. The model estimated a 0.25 $month^{-1}$ natural mortality rate. The instantaneous exploitation rate is over 40% only in a few instances during the peak of catches within the fishing season, which suggests that this stock is not overexploited. Despite the depletion of the sum of annual catches from all FAD fisheries in 2012 (see fisheries dynamics from Chapter 1), regular recruitment rates is fluctuating around 10 million individuals (Chapter 5), suggesting that the stock is not undergoing overfishing. Apart from the generalized drop in catches in 2012, we identified and discussed correlated

fluctuations in catches for the countries placed in the central Mediterranean region identified in Chapter 1, which represents the majority of catches. These fluctuations suggest dynamics of the stock related to environmental factors, such as movements of the stock affecting the captures (Lehodey et al., 2006), or affecting the recruitment pulses (Myers, 1998). A further research line to improve the stock assessment is to incorporate this behavior in the stock assessment methodologies, by integrating environmental variables and or movement information within the analytical processes of the assessment models to better capture abundances and recruitment magnitudes (Chrysafi and Kuparinen, 2015).

Related with the latter point, and connected to previous paragraphs, a major knowledge gap identified in the introduction section was related to the environmental drivers of migration of this species in the Mediterranean. This species is highly mobile and migrates to areas located around the western and central Mediterranean islands in spring to spawn. Juveniles, a few months old, leave these regions after the FADs fishing season, when they reach a certain length. The migratory pathways of adults determine where dolphinfish spawn. Recruitment fluctuations (also reflected in catch trends) are not solely dependent on stock size, but largely on environmental suitability for offspring survival and the movement behavior of juveniles and adults. Therefore, characterizing the environmental factors determining that determine moving behavior is essential to understand stock dynamics, which is particularly relevant in the central Mediterranean (Chapter 1).

In this sense, some movement assumptions had to be made in Chapters 2 and 3. However, we did make an effort to address this gap of knowledge and clarify these issues further. For instance, we attempted to tag adult fish using pop-up archival and remote transmitting tags in late spring, both before and during the spawning season. Unfortunately, these attempts were unsuccessful due to the fact that adults tend to dwell far from the coast and are present in exceptionally low densities, making them difficult to access in our region. Additionally, the size of these tags makes them unsuitable for juveniles. Acoustic telemetry offers the potential for revealing the movement patterns of this species, including migratory pathways and related environmental parameters (Abecasis et al., 2018; Alós et al., 2022; Matley et al., 2022). Additionally, acoustic telemetry could provide useful information for management strategies, such as the environmental requirements of juveniles during the fishing season or the interactions with the FADs, determining catch-effort relationships (Crossin et al., 2017). Accordingly, we have lately started an acoustic tagging program inserted in the European and Balearic Tracking networks (https://trackingfish.com/), which hopefully will help in clarifying the movement patterns of this species at several scales.

In summary, this thesis has expanded the knowledge regarding the Mediterranean dolphinfish ecology, especially in the face of changing climate in a warming region, relating environmental parameters with key ecological traits, such as growth and reproduction. Concerning the management of the Mediterranean stock, this thesis has contributed with new methodologies for basic fisheries data collection based on new technologies, and novel stock assessment methods adapted to the particularities of short-

life species with high abundance fluctuations, which have allowed to provide the first reference points for the Mediterranean dolphinfish stock. Although significant progress has been made, there are still several key issues that need to be addressed. For example, a more comprehensive approach is needed to identify the causal mechanisms involved, to fully understand environmental variability effects on physiology and biological traits. We also need to better understand the sources of early mortality determining recruitment and year-class strength. Additionally, the movement ecology of the Mediterranean population remains an area that requires further study. To tackle these challenges, it will be necessary to invest effort and resources in coupling theoretical, experimental and field studies, such as those conducted within bioenergetic model frameworks. Studies on ichthyoplankton ecology will also be essential to determine the environmental requirements for the survival of early life stages, and implementing technologies such as acoustic telemetry will improve our understanding of movement behavior. Concerning the management measures, mechanisms to explicitly implement environmental factors and movement components to stock assessment models should also be explored for a better assessment of the Mediterranean stock.

SECTION 5

Conclusions

English

- The review of available literature on common dolphinfish biology and ecology and its Mediterranean fisheries shows that, in spite of major advances over the two last decades, major knowledge gaps related to the environment and biological traits relationships remain, as well as highlight the need for a formal stock assessment.
- Sea surface temperature is a crucial environmental driver that influences the spawning phenology of the common dolphinfish across a wide range of latitudes. By using annual surface temperature profiles, it is possible to predict the seasonal spawning pattern of the species in many regions of the world with reasonable accuracy.
- The observed hatch-date frequency distribution inferred from fishery samplings might be biased due to variability in mortality processes and temporal distribution of samplings. Including both natural and fishing mortality rates, fishery constraints such as closures or vulnerable size threshold to the fishery, together with the temperature-dependent growth of the species, allow correcting biases in hatch-distribution estimates.
- The reproductive period of the common dolphinfish consistently occurs between 51 and 63 days before the annual temperature peak, which may be an adaptive strategy to improve offspring survival in their habitat envelope. This finding has significant implications for the understanding of the species' life history and ecology.
- It was possible to predict juvenile length at catch by developing a growth model that incorporated sea surface temperature and photoperiod at birth. This model can be used to inform management strategies for dolphinfish fisheries.
- The temperature-dependent models developed within this thesis allow us to project the effects of thermal scenarios resulting from climate change on dolphinfish ecological processes, such as growth and spawning phenology. This information is crucial to understand long-term population dynamics and fishery management plans.
- The development of automated data collection methodologies, such as the fish size sampling strategy based on artificial intelligence developed in this thesis, enable the collection of rich datasets at a low cost, which represents a significant advance in the compilation of the basic biological data requested in fisheries science, and hence has significant implications for the study of fisheries dynamics.
- The multiannual five fleets generalized depletion model developed in this thesis allows for the integration of different catch-effort dynamics of every fleet targeting dolphinfish in the Mediterranean, providing for the first-time reference points to assess the stock status.
- The Mediterranean dolphinfish stock shows stability in catch trends and annual recruitment patterns; instantaneous catch rates are moderate, only slightly over 40% during the month of peak captures. This suggests that the stock is not

overfished, but with the precautionary approach that fishing effort should not be increased.

Català

- La revisió bibliogràfica sobre la biologia i ecologia de la llampuga i les seves pesqueries en el Mediterrani mostren que, tot i els avanços durant les dues darreres dècades, existeixen incerteses quant a les relacions entre l'ambient i els trets biològics de l'espècie, així com la necessitat d'una avaluació d'estoc formal.
- La temperatura superficial de la mar és un paràmetre ambiental clau que afecta la fenologia de posta de la llampuga en un ampli rang latitudinal. A partir dels perfils anuals de temperatura és possible predir el patró estacional de posta de l'espècie de forma raonable.
- La distribució de freqüències de naixement observades, inferides a partir de mostrejos de juvenils procedents de la pesqueria poden estar esbiaixats degut als processos de mortalitat i la distribució temporal dels mostrejos. Es poden corregir els biaixos en l'estima de les distribucions de naixements incloent les taxes de mortalitat, tant natural com per pesca, paràmetres derivats de la pesqueria com vedats temporals o la talla de vulnerabilitat a la pesca, juntament amb el creixement depenent de temperatura.
- El període reproductiu de la llampuga ocorre consistentment entre 51 i 63 dies abans del pic anual de temperatura. Aquest fet pot ser uns estratègia adaptativa per afavorir la supervivència de la descendència en les seves condicions ambientals. Aquesta observació podria tenir implicacions significatives per a la comprensió de l'adaptació d'aquest espècie a diferents sistemes.
- És possible predir la talla de captura d'individus juvenils mitjançant el desenvolupament d'un model de creixement incorporant la temperatura superficial i el fotoperíode en el moment del naixement. Aquest model resulta útil per al disseny d'estratègies de gestió per a les pesqueries de llampuga.
- Els models depenents de temperatura desenvolupats en aquesta tesi permeten projectar els efectes d'escenaris tèrmics sobre els processos ecològics de la llampuga, tals com el creixement o la fenologia de posta. Aquesta informació és crucial per a comprendre la dinàmica poblacionals a llarg termini, així com per al disseny de plans de gestió per a la pesqueria.
- El desenvolupament de metodologies de recopilació de dades automatitzades, tal com l'estratègia de mostreig de talles de peixos basada en intel·ligència artificial desenvolupada en aquesta tesi, permet generar grans bases de dades a baix cost, representant un avanç significatiu en la recopilació de dades biològiques bàsiques requerides en ciència pesquera i, per tant, amb implicacions significatives per a l'estudi de les dinàmiques de les pesqueries.
- El model de depleció generalitzat multi-anual adaptat a cinc flotes desenvolupat en aquesta tesi ha permès la integració de diferents dinàmiques de captura i esforç de cada flota que explota la llampuga al Mediterrani, obtenint per primera vegada punts de referència per a l'avaluació de l'estoc.
- L'estoc de llampuga del Mediterrani mostra tendències de captures i reclutament anual estables; les taxes de captura instantànies són moderades, sols superant el 40% durant el mes que dona lloc al pic de captures. Aquestes referències suggereixen que l'estoc no es troba en situació de sobrepesca, encara que amb l'enfocament precautori de no incrementar l'esforç pesquer.

Castellà

- La revisión bibliográfica sobre la biología y ecología de la lampuga y sus pesquerías en el Mediterráneo muestra que, a pesar de los avances durante las últimas dos décadas, existen incertidumbres en cuanto a las relaciones entre el ambiente y los rasgos biológicos de la especie, así como la necesidad de una evaluación formal del stock.
- La temperatura superficial del mar es un parámetro ambiental clave en la influencia sobre la fenología de puesta de la lampuga a lo largo de un amplio rango latitudinal. A partir de perfiles anuales de temperatura es posible predecir razonablemente el patrón estacional de puesta de la especie.
- La distribución de frecuencias de nacimiento observadas, inferidas a partir de muestreos procedentes de la pesquería puede estar sesgada debido a los procesos de mortalidad y la distribución temporal de los muestreos. Al incluir las tasas de mortalidad tanto natural como mortalidad por pesca, parámetros derivados de la pesquería tales como vedas temporales o la talla de vulnerabilidad a la pesca, junto con el crecimiento dependiente de temperatura de la especie, es posible corregir los sesgos en la estima de la distribución de nacimientos.
- El periodo reproductivo de la lampuga se da consistentemente entre 51 y 63 días antes del pico de temperatura anual. Este hecho puede ser una estrategia adaptativa para favorecer la supervivencia de la prole en sus condiciones ambientales. Este resultado tiene implicaciones significativas para la comprensión del desarrollo ontogénico de la especie y su ecología.
- Es posible predecir la talla de captura de individuos juveniles mediante el desarrollo de un modelo de crecimiento incorporando la temperatura superficial y el fotoperíodo en el momento del nacimiento. Este modelo resulta útil para el diseño de estrategias de gestión para las pesquerías de lampuga.
- Los modelos dependientes de temperatura desarrollados en esta tesis permiten proyectar los efectos de futuros escenarios térmicos derivados del cambio climático sobre procesos ecológicos de la llampuga, tales como el crecimiento o la fenología de puesta. Esta información es crucial para comprender la dinámica poblacional a largo plazo, así como para el diseño de planes de gestión para la pesquería.
- El desarrollo de metodologías de recopilación de datos automatizados, como la estrategia de muestreo de las tallas de peces basada en inteligencia artificial desarrollada en esta tesis, permite generar grandes bases de datos a bajo coste, representando un avance significativo en la recopilación de datos biológicos básicos requeridos en ciencias pesqueras y, por tanto, con implicaciones importantes para el estudio de la dinámica de las pesquerías.
- El modelo de depleción generalizado multianual adaptado a cinco flotas desarrollado en esta tesis ha permitido la integración de diferentes dinámicas de captura y esfuerzo de cada flota que explota la lampuga en el Mediterráneo, obteniendo por primera vez puntos de referencia para evaluar el estado del stock.
- El stock de lampuga del Mediterráneo muestra tendencias de capturas y reclutamiento anual estables; las tasas de captura instantánea son moderadas, solo ligeramente superiores al 40% durante el mes en que ocurre el pico de capturas.

Estas referencias sugieren que el stock no se encuentra en situación de sobrepesca, aunque se recomienda un enfoque precautorio de no incrementar el esfuerzo pesquero.

References

Abecasis, D., Steckenreuter, A., Reubens, J., Aarestrup, K., Alós, J., Badalamenti, F., Bajona, L., Boylan, P., Deneudt, K., Greenberg, L., Brevé, N., Hernández, F., Humphries, N., Meyer, C., Sims, D., Thorstad, E.B., Walker, A.M., Whoriskey, F., Afonso, P., 2018. A review of acoustic telemetry in Europe and the need for a regional aquatic telemetry network. Anim. Biotelemetry 6, 1–7. https://doi.org/10.1186/s40317-018-0156-0

Adloff, F., Somot, S., Sevault, F., Jordà, G., Aznar, R., Déqué, M., Herrmann, M., Marcos, M., Dubois, C., Padorno, E., Alvarez-Fanjul, E., Gomis, D., 2015. Mediterranean Sea response to climate change in an ensemble of twenty first century scenarios. Clim. Dyn. 45, 2775–2802. https://doi.org/10.1007/s00382-015-2507-3

Alemany, F., Quintanilla, L., Velez-Belchí, P., García, a., Cortés, D., Rodríguez, J.M., Fernández de Puelles, M.L., González-Pola, C., López-Jurado, J.L., 2010. Characterization of the spawning habitat of Atlantic bluefin tuna and related species in the Balearic Sea (western Mediterranean). Prog. Oceanogr. 86, 21–38. https://doi.org/10.1016/j.pocean.2010.04.014

Alós, J., Aarestrup, K., Abecasis, D., Afonso, P., Alonso-Fernandez, A., Aspillaga, E., Barcelo-Serra, M., Bolland, J., Cabanellas-Reboredo, M., Lennox, R., McGill, R., Özgül, A., Reubens, J., Villegas-Ríos, D., 2022. Toward a decade of ocean science for sustainable development through acoustic animal tracking. Glob. Chang. Biol. 28, 5630–5653. https://doi.org/10.1111/gcb.16343

Asch, R.G., 2015. Climate change and decadal shifts in the phenology of larval fishes in the California Current ecosystem. Proc. Natl. Acad. Sci. U. S. A. 112, E4065–E4074. https://doi.org/10.1073/pnas.1421946112

Asch, R.G., Stock, C.A., Sarmiento, J.L., 2019. Climate change impacts on mismatches between phytoplankton blooms and fish spawning phenology. Glob. Chang. Biol. 25, 2544–2559. https://doi.org/10.1111/gcb.14650

Auth, T.D., Daly, E.A., Brodeur, R.D., Fisher, J.L., 2018. Phenological and distributional shifts in ichthyoplankton associated with recent warming in the northeast Pacific Ocean. Glob. Chang. Biol. 24, 259–272. https://doi.org/10.1111/gcb.13872

Bailey, K.M., Houde, E.D., 1989. Predation on eggs and larvae of marine fishes and the recruitment problem, in: Advances in Marine Biology. Elsevier, pp. 1–83.

Bakun, A., 2006. Fronts and eddies as key structures in the habitat of marine fish larvae: opportunity, adaptive response and competitive advantage. Sci. Mar. 70S2, 105–122. https://doi.org/10.3989/scimar.2006.70s2105

Battaglia, P., Romeo, T., Consoli, P., Scotti, G., Andaloro, F., 2010. Characterization of the artisanal fishery and its socio-economic aspects in the central Mediterranean Sea (Aeolian Islands, Italy). Fish. Res. 102, 87–97. https://doi.org/10.1016/j.fishres.2009.10.013

Beardsley, J.G.L., 1967. Age, Growth, and Reproduction of the Dolphin, *Coryphaena hippurus*, in the Straits of Florida. Copeia 2, 441–451.

Beaugrand, G., Kirby, R.R., 2018. How do marine pelagic species respond to climate change? Theories and observations. Ann. Rev. Mar. Sci. 10, 169–197. https://doi.org/10.1146/annurev-marine-121916-063304

Bellard, C., Bertelsmeier, C., Leadley, P., Thuiller, W., Courchamp, F., 2012. Impacts of climate change on the future of biodiversity. Ecol. Lett. 15, 365–377.

https://doi.org/10.1111/j.1461-0248.2011.01736.x

Benseddik, A.B., Besbes, R., Vitale, S., Ezzeddine-Najai, S., Cannizzaro, L., Mrabet, R., 2011. Determination of age and growth of dolphinfish, *Coryphaena hippurus*, off Tunisia by otolith microstructure analysis. Cybium 35, 173–180.

Besbes Benseddik, A., 2017. Bio-écologie, pêche et évaluation du stock de la coryphène *Coryphaena hippurus* (Linnaeus, 1758) dans la région Est de la Tunisie. Institut Suérieur de Biotechnologie de Monastir.

Besbes Benseddik, A., Besbes, R., Ezzeddine Najaï, S., Jarboui, O., Mrabet, R., 2015. Cycle reproductif et gamétogenèse de la dorade coryphène *Coryphaena hippurus* (Coryphaenidae) des eaux tunisiennes. Cybium 39, 47–58.

Besbes Benseddik, A., Besbes, R., Missaoui, H., Najaï, S.E., Jarboui, O., 2019. Reproductive dynamics and fecundity of *Coryphaena hippurus* (Linnaeus, 1758) in the Eastern Tunisian coast (Central Mediterranean). Curr. Trends Fish. Aquac. 2019.

Bethoux, J.P., Gentili, B., 1999. Functioning of the Mediterranean sea: Past and present changes related to freshwater input and climate changes. J. Mar. Syst. 20, 33–47. https://doi.org/10.1016/S0924-7963(98)00069-4

Bethoux, J.P., Gentili, B., Morin, P., Nicolas, E., Pierre, C., Ruiz-Pino, D., 1999. The Mediterranean Sea: A miniature ocean for climatic and environmental studies and a key for the climatic functioning of the North Atlantic. Prog. Oceanogr. 44, 131–146. https://doi.org/10.1016/S0079-6611(99)00023-3

Bigg, G.R., Bigg, G.R., 2003. The oceans and climate. Cambridge University Press.

Cerrano, C., Bavestrello, G., Bianchi, C.N., Cattaneo-Vietti, R., Bava, S., Morganti, C., Morri, C., Picco, P., Sara, G., Schiaparelli, S., Siccardi, A., Sponga, F., 2000. A catastrophic mass-mortality episode of gorgonians and other organisms in the Ligurian Sea (North-western Mediterranean), summer 1999. Ecol. Lett. 3, 284–293. https://doi.org/10.1046/j.1461-0248.2000.00152.x

Cheng, L., von Schuckmann, K., Abraham, J.P., Trenberth, K.E., Mann, M.E., Zanna, L., England, M.H., Zika, J.D., Fasullo, J.T., Yu, Y., Pan, Y., Zhu, J., Newsom, E.R., Bronselaer, B., Lin, X., 2022. Past and future ocean warming. Nat. Rev. Earth Environ. 3, 776–794. https://doi.org/10.1038/s43017-022-00345-1

Chrysafi, A., Kuparinen, A., 2015. Assessing abundance of populations with limited data: Lessons learned from data-poor fisheries stock assessment. Environ. Rev. 24, 25–38. https://doi.org/10.1139/er-2015-0044

Coll, M., Piroddi, C., Steenbeek, J., Kaschner, K., Lasram, F.B.R., Aguzzi, J., Ballesteros, E., Bianchi, C.N., Corbera, J., Dailianis, T., Danovaro, R., Estrada, M., Froglia, C., Galil, B.S., Gasol, J.M., Gertwage, R., Gil, J., Guilhaumon, F., Kesner-Reyes, K., Kitsos, M.S., Koukouras, A., Lampadariou, N., Laxamana, E., de la Cuadra, C.M.L.F., Lotze, H.K., Martin, D., Mouillot, D., Oro, D., Raicevich, S., Rius-Barile, J., Saiz-Salinas, J.I., Vicente, C.S., Somot, S., Templado, J., Turon, X., Vafidis, D., Villanueva, R., Voultsiadou, E., 2010. The biodiversity of the Mediterranean Sea: Estimates, patterns, and threats. PLoS One 5. https://doi.org/10.1371/journal.pone.0011842

Coma, R., Ribes, M., Serrano, E., Jiménez, E., Salat, J., Pascual, J., 2009. Global warming-enhanced stratification and mass mortality events in the Mediterranean. Proc. Natl. Acad. Sci. U. S. A. 106, 6176–6181.

https://doi.org/10.1073/pnas.0805801106

Crossin, G.T., Heupel, M.R., Holbrook, C.M., Hussey, N.E., Lowerre-Barbieri, S.K., Nguyen, V.M., Raby, G.D., Cooke, S.J., 2017. Acoustic telemetry and fisheries management. Ecol. Appl. 27, 1031–1049. https://doi.org/10.1002/eap.1533

Darmaraki, S., Somot, S., Sevault, F., Nabat, P., Cabos Narvaez, W.D., Cavicchia, L., Djurdjevic, V., Li, L., Sannino, G., Sein, D. V., 2019. Future evolution of Marine Heatwaves in the Mediterranean Sea. Clim. Dyn. 53, 1371–1392. https://doi.org/10.1007/s00382-019-04661-z

Diaz-Barroso, L., Hernandez-Carrasco, I., Orfila, A., Reglero, P., Balbín, R., Hidalgo, M., Tintore, J., Alemany, F., Alvarez-Berastegui, D., 2022. Singularities of surface mixing activity in the Western Mediterranean influence bluefin tuna larval habitats. Mar. Ecol. Prog. Ser. 685, 69–84. https://doi.org/10.3354/meps13979

Doney, S.C., Ruckelshaus, M., Emmett Duffy, J., Barry, J.P., Chan, F., English, C.A., Galindo, H.M., Grebmeier, J.M., Hollowed, A.B., Knowlton, N., Polovina, J., Rabalais, N.N., Sydeman, W.J., Talley, L.D., 2012. Climate change impacts on marine ecosystems. Ann. Rev. Mar. Sci. 4, 11–37. https://doi.org/10.1146/annurev-marine-041911-111611

Durant, J.M., Hjermann, D., Ottersen, G., Stenseth, N.C., 2007. Climate and the match or mismatch between predator requirements and resource availability. Clim. Res. 33, 271–283. https://doi.org/10.3354/cr033271

Durrieu de Madron, X., Guieu, C., Sempéré, R., Conan, P., Cossa, D., D'Ortenzio, F., Estournel, C., Gazeau, F., Rabouille, C., Stemmann, L., Bonnet, S., Diaz, F., Koubbi, P., Radakovitch, O., Babin, M., Baklouti, M., Bancon-Montigny, C., Belviso, S., Bensoussan, N., Bonsang, B., Bouloubassi, I., Brunet, C., Cadiou, J.-F., Carlotti, F., Chami, M., Charmasson, S., Charrière, B., Dachs, J., Doxaran, D., Dutay, J.-C., Elbaz-Poulichet, F., Eléaume, M., Eyrolles, F., Fernandez, C., Fowler, S., Francour, P., Gaertner, J.C., Galzin, R., Gasparini, S., Ghiglione, J.-F., Gonzalez, J.-L., Goyet, C., Guidi, L., Guizien, K., Heimbürger, L.-E., Jacquet, S.H.M., Jeffrey, W.H., Joux, F., Le Hir, P., Leblanc, K., Lefèvre, D., Lejeusne, C., Lemé, R., Loÿe-Pilot, M.-D., Mallet, M., Méjanelle, L., Mélin, F., Mellon, C., Mérigot, B., Merle, P.-L., Migon, C., Miller, W.L., Mortier, L., Mostajir, B., Mousseau, L., Moutin, T., Para, J., Pérez, T., Petrenko, A., Poggiale, J.-C., Prieur, L., Pujo-Pay, M., Pulido-Villena, Raimbault, P., Rees, A.P., Ridame, C., Rontani, J.-F., Ruiz Pino, D., Sicre, M.A., Taillandier, V., Tamburini, C., Tanaka, T., Taupier-Letage, I., Tedetti, M., Testor, P., Thébault, H., Thouvenin, B., Touratier, F., Tronczynski, J., Ulses, C., Van Wambeke, F., Vantrepotte, V., Vaz, S., Verney, R., 2011. Marine ecosystems' responses to climatic and anthropogenic forcings in the Mediterranean. Prog. Oceanogr. 91, 97–166. https://doi.org/10.1016/j.pocean.2011.02.003

Edelist, D., Rilov, G., Golani, D., Carlton, J.T., Spanier, E., 2013. Restructuring the Sea: Profound shifts in the world's most invaded marine ecosystem. Divers. Distrib. 19, 69–77. https://doi.org/10.1111/ddi.12002

Font, T., Lloret, J., 2014. Biological and ecological impacts derived from recreational fishing in Mediterranean coastal areas. Rev. Fish. Sci. Aquac. 22, 73–85. https://doi.org/10.1080/10641262.2013.823907

Free, C.M., Thorson, J.T., Pinsky, M.L., Oken, K.L., Wiedenmann, J., Jensen, O.P., 2019. Impacts of historical warming on marine fisheries production. Science (80-.). 363,

979–983. https://doi.org/10.1126/science.aau1758

Fujita, R., 2021. The assessment and management of data limited fisheries: Future directions. Mar. Policy 133, 104730. https://doi.org/10.1016/j.marpol.2021.104730

Garrabou, J., Coma, R., Bensoussan, N., Bally, M., Chevaldonné, P., Cigliano, M., Diaz, D., Harmelin, J.G., Gambi, M.C., Kersting, D.K., Ledoux, J.B., Lejeusne, C., Linares, C., Marschal, C., Pérez, T., Ribes, M., Romano, J.C., Serrano, E., Teixido, N., Torrents, O., Zabala, M., Zuberer, F., Cerrano, C., 2009. Mass mortality in Northwestern Mediterranean rocky benthic communities: Effects of the 2003 heat wave. Glob. Chang. Biol. 15, 1090–1103. https://doi.org/10.1111/j.1365-2486.2008.01823.x

Garrabou, J., Perez, T., Sartoretto, S., Harmelin, J.G., 2001. Mass mortality event in red coral *Corallium rubrum* populations in the Provence region (France, NW Mediterranean). Mar. Ecol. Prog. Ser. 217, 263–272. https://doi.org/10.3354/meps217263

Gatt, M., Dimech, M., Schembri, P.J., 2015. Age, Growth and Reproduction of *Coryphaena hippurus* (Linnaeus, 1758) in Maltese Waters, Central Mediterranean. Mediterr. Mar. Sci. 16, 334–345. https://doi.org/10.12681/mms.706

Genner, M.J., Halliday, N.C., Simpson, S.D., Southward, A.J., Hawkins, S.J., Sims, D.W., 2010. Temperature-driven phenological changes within a marine larval fish assemblage. J. Plankton Res. 32, 699–708. https://doi.org/10.1093/plankt/fbp082

Giorgi, F., 2006. Climate change hot-spots. Geophys. Res. Lett. 33, L08707. https://doi.org/10.1029/2006GL025734

Hewitt, H.T., Roberts, M., Mathiot, P., Biastoch, A., Blockley, E., Chassignet, E.P., Fox-Kemper, B., Hyder, P., Marshall, D.P., Popova, E., Treguier, A.M., Zanna, L., Yool, A., Yu, Y., Beadling, R., Bell, M., Kuhlbrodt, T., Arsouze, T., Bellucci, A., Castruccio, F., Gan, B., Putrasahan, D., Roberts, C.D., Van Roekel, L., Zhang, Q., 2020. Resolving and Parameterising the Ocean Mesoscale in Earth System Models. Curr. Clim. Chang. Reports 6, 137–152. https://doi.org/10.1007/s40641-020-00164-w

Hoegh-Guldberg, O., Bruno, J.F., 2010. The impact of climate change on the world's marine ecosystems. Science 328, 1523–1528. https://doi.org/10.1126/science.1189930

Hunter, J.R., 1981. Feeding Ecology and predation of marine fish larvae. R. Lasker ed. 1, 34–77.

Kitchens, L.L., Rooker, J.R., 2014. Habitat associations of dolphinfish larvae in the Gulf of Mexico. Fish. Oceanogr. 23, 460–471. https://doi.org/10.1111/fog.12081

Kooijman, S.A.L.M., 2010. Summary of concepts of Dynamic Energy Budget theory. https://doi.org/10.1098/rstb.2010.0167

Kraul, S., 1989. Review and current status of the aquaculture potential for the Mahimahi, *Coryphaena hippurus*. Adv. Trop. Aquac. 445–459.

Lazzari, P., Mattia, G., Solidoro, C., Salon, S., Crise, A., Zavatarelli, M., Oddo, P., Vichi, M., 2014. The impacts of climate change and environmental management policies on the trophic regimes in the Mediterranean Sea: Scenario analyses. J. Mar. Syst. 135, 137–149. https://doi.org/10.1016/j.jmarsys.2013.06.005

Lehodey, P., Alheit, J., Barange, M., Baumgartner, T., Beaugrand, G., Drinkwater, K., Fromentin, J.M., Hare, S.R., Ottersen, G., Perry, R.I., Roy, C., van der Lingen, C.D., Werner, F., 2006. Climate variability, fish, and fisheries. J. Clim. 19, 5009–5030. https://doi.org/10.1175/JCLI3898.1

Lejeusne, C., Chevaldonné, P., Pergent-Martini, C., Boudouresque, C.F., Pérez, T., 2010. Climate change effects on a miniature ocean: the highly diverse, highly impacted Mediterranean Sea. Trends Ecol. Evol. 25, 250–260. https://doi.org/10.1016/j.tree.2009.10.009

Lett, C., Ayata, S.D., Huret, M., Irisson, J.O., 2010. Biophysical modelling to investigate the effects of climate change on marine population dispersal and connectivity. Prog. Oceanogr. 87, 106–113. https://doi.org/10.1016/j.pocean.2010.09.005

Levitus, S., Antonov, J., Boyer, T., 2005. Warming of the world ocean, 1955-2003. Geophys. Res. Lett. 32, 1–4. https://doi.org/10.1029/2004GL021592

Marbà, N., Duarte, C.M., 2010. Mediterranean warming triggers seagrass (*Posidonia oceanica*) shoot mortality. Glob. Chang. Biol. 16, 2366–2375. https://doi.org/10.1111/j.1365-2486.2009.02130.x

Massutí, E., 1997. Biology of *Coryphaena hippurus* Linnaeus, 1758 (Pisces: Coryphaenidae) in the Western Mediterranean. Universitat de les Illes Balears.

Massutí, E., Morales-Nin, B., 1997. Reproductive biology of dolphin-fish (*Coryphaena hippurus* L.) off the island of Majorca (western Mediterranean). Fish. Res. 30, 57–65. https://doi.org/10.1016/S0165-7836(96)00562-0

Massutí, E., Morales-Nin, B., 1995. Seasonality and reproduction of dolphin-fish (*Coryphaena hippurus*) in the Western Mediterranean*. Sci. Mar. 59, 357–364.

Massutí, E., Morales-Nin, B., Moranta, J., 1999. Otolith microstructure, age, and growth patterns of dolphin, *Coryphaena hippurus*, in the western Mediterranean. Fish. Bull. 97, 891–899.

Massuti, E., Valls, M., Ordines, F., 2010. Changes in the western Mediterranean ichthyofauna: signs of tropicalization and meridianization. Golani, D. Appelbaum-Golani, B.(Eds) 293–312.

Matley, J.K., Klinard, N. V., Barbosa Martins, A.P., Aarestrup, K., Aspillaga, E., Cooke, S.J., Cowley, P.D., Heupel, M.R., Lowe, C.G., Lowerre-Barbieri, S.K., Mitamura, H., Moore, J.S., Simpfendorfer, C.A., Stokesbury, M.J.W., Taylor, M.D., Thorstad, E.B., Vandergoot, C.S., Fisk, A.T., 2022. Global trends in aquatic animal tracking with acoustic telemetry. Trends Ecol. Evol. 37, 79–94. https://doi.org/10.1016/j.tree.2021.09.001

Merten, W., Appeldoorn, R., Hammond, D., 2016. Movement dynamics of dolphinfish (*Coryphaena hippurus*) in the northeastern Caribbean Sea: Evidence of seasonal re-entry into domestic and international fisheries throughout the western central Atlantic. Fish. Res. 175, 24–34. https://doi.org/10.1016/j.fishres.2015.10.021

Merten, W., Appeldoorn, R., Hammond, D., 2014a. Movements of dolphinfish (*Coryphaena hippurus*) along the U.S. east coast as determined through mark and recapture data. Fish. Res. 151, 114–121. https://doi.org/10.1016/j.fishres.2013.10.021

Merten, W., Appeldoorn, R., Hammond, D., 2014b. Spatial differentiation of dolphinfish

(*Coryphaena hippurus*) movements relative to the Bahamian archipielago. Bull. Mar. Sci. 90, 849–864. https://doi.org/10.5343/bms.2013.1078

Morales-Nin, B., Cannizzaro, L., Massuti, E., Potoschi, A., Andaloro, F., 2000. An overview of the FADs fishery in the Mediterranean Sea. Proc. Tuna Fish. Fish Aggregating Devices Symp. 184–207.

Morales-Nin, B., di Stefano, M., Potoschi, A., Massutí, E., Rizzo, P., Gancitano, S., 1999. Differences between the sagitta, lapillus and vertebra in estimating age and growth in juvenile Mediterranean dolphinfish (*Coryphaena hippurus*)*. Sci. Mar. 63, 327–336.

Morales-Nin, B., Grau, A.M., Palmer, M., 2010. Managing coastal zone fisheries: A Mediterranean case study. Ocean Coast. Manag. 53, 99–106. https://doi.org/10.1016/j.ocecoaman.2010.01.003

Morales-Nin, B., Moranta, J., García, C., Tugores, M.P., Grau, A.M., Riera, F., Cerdà, M., 2005. The recreational fishery off Majorca Island (western Mediterranean): Some implications for coastal resource management. ICES J. Mar. Sci. 62, 727–739. https://doi.org/10.1016/j.icesjms.2005.01.022

Morrongiello, J.R., Thresher, R.E., Smith, D.C., 2012. Aquatic biochronologies and climate change. Nat. Clim. Chang. 2, 849–857. https://doi.org/10.1038/nclimate1616

Moullec, F., Barrier, N., Drira, S., Guilhaumon, F., Marsaleix, P., Somot, S., Ulses, C., Velez, L., Shin, Y.J., 2019. An end-to-end model reveals losers and winners in a warming Mediterranean Sea. Front. Mar. Sci. 6, 1–19. https://doi.org/10.3389/fmars.2019.00345

Myers, R.A., 1998. When do environment-recruitment correlations work? Rev. Fish Biol. Fish. 8, 285–305. https://doi.org/10.1023/A:1008828730759

Newman, D., Berkson, J., Suatoni, L., 2015. Current methods for setting catch limits for data-limited fish stocks in the United States. Fish. Res. 164, 86–93. https://doi.org/10.1016/j.fishres.2014.10.018

Nisbet, R.M., Jusup, M., Klanjscek, T., Pecquerie, L., 2012. Integrating dynamic energy budget (DEB) theory with traditional bioenergetic models. J. Exp. Biol. 215, 892–902. https://doi.org/10.1242/jeb.059675

Norton, J.G., 1999. Apparent habitat extensions of dolphinfish (*Coryphaena hippurus*) in response to climate transients in the California Current*. Sci. Mar. 63, 239–260. https://doi.org/10.3989/scimar.1999.63n3-4261

Nykjaer, L., 2009. Mediterranean Sea surface warming 1985-2006. Clim. Res. 39, 11–17. https://doi.org/10.3354/cr00794

Oxenford, H.A., 1999. Biology of the dolphinfish (*Coryphaena hippurus*) in the western central Atlantic: a review. Sci. Mar. 63, 277–301. https://doi.org/10.3989/scimar.1999.63n3-4303

Palko, B.J., Beardsley, G.L., Richards, W.J., 1982. Synopsis of the Biological Data on Dolphin-Fishes, *Coryphaena hippurus* Linnaeus and *Coryphaena equiselis* Linnaeus. NOAA Tech. Rep. NMFS Circ. 443, 1–28.

Palmer, M., Tolosa, B., Grau, A.M., Gil, M. del M., Obregón, C., Morales-Nin, B., 2017. Combining sale records of landings and fishers knowledge for predicting métiers in

a small-scale, multi-gear, multispecies fishery. Fish. Res. 195, 59–70. https://doi.org/10.1016/j.fishres.2017.07.001

Perrichon, P., Stieglitz, J.D., Xu, E.G., Magnuson, J.T., Pasparakis, C., Mager, E.M., Wang, Y., Schlenk, D., Benetti, D.D., Roberts, A.P., Grosell, M., Burggren, W.W., 2019. Mahi-mahi (*Coryphaena hippurus*) life development: morphological, physiological, behavioral and molecular phenotypes. Dev. Dyn. 248, 337–350. https://doi.org/10.1002/dvdy.27

Poloczanska, E.S., Brown, C.J., Sydeman, W.J., Kiessling, W., Schoeman, D.S., Moore, P.J., Brander, K., Bruno, J.F., Buckley, L.B., Burrows, M.T., Duarte, C.M., Halpern, B.S., Holding, J., Kappel, C. V., O'Connor, M.I., Pandolfi, J.M., Parmesan, C., Schwing, F., Thompson, S.A., Richardson, A.J., 2013. Global imprint of climate change on marine life. Nat. Clim. Chang. 3, 919–925. https://doi.org/10.1038/nclimate1958

Potoschi, A., Cannizzaro, L., Milazzo, A., Scalisi, M., Bono, G., 1999a. Sicilian dolphinfish (*Coryphaena hippurus*) fishery*. Sci. Mar. 63, 439–445.

Potoschi, A., Reñones, O., Cannizzaro, L., 1999b. Sexual development, maturity and reproduction of dolphinfish (*Coryphaena hippurus*) in the western and central Mediterranean*. Sci. Mar. 63, 367–372. https://doi.org/10.3989/scimar.1999.63n3-4367

Putman, N., 2018. Marine migrations. Curr. Biol. 28, 972–976. https://doi.org/10.1016/j.cub.2018.07.036

Quetglas, A., Merino, G., Ordines, F., Guijarro, B., Garau, A., Grau, A.M., Oliver, P., Massutí, E., 2016. Assessment and management of western Mediterranean small-scale fisheries. Ocean Coast. Manag. 133, 95–104. https://doi.org/10.1016/j.ocecoaman.2016.09.013

Raitsos, D.E., Beaugrand, G., Georgopoulos, D., Zenetos, A., Pancucci-Papadopoulou, A.M., Theocharis, A., Papathanassiou, E., 2010. Global climate change amplifies the entry of tropical species into the eastern Mediterranean Sea. Limnol. Oceanogr. 55, 1478–1484. https://doi.org/10.4319/lo.2010.55.4.1478

Reglero, P., Balbín, R., Abascal, F.J., Medina, A., Alvarez-Berastegui, D., Rasmuson, L., Mourre, B., Saber, S., Ortega, A., Blanco, E., De La Gándara, F., Alemany, F.J., Ingram, G.W., Hidalgo, M., 2019. Pelagic habitat and offspring survival in the eastern stock of Atlantic bluefin tuna. ICES J. Mar. Sci. 76, 549–558. https://doi.org/10.1093/icesjms/fsy135

Richards, K.J., Whitt, D.B., Brett, G., Bryan, F.O., Feloy, K., Long, M.C., 2021. The Impact of Climate Change on Ocean Submesoscale Activity. J. Geophys. Res. Ocean. 126, 1–15. https://doi.org/10.1029/2020JC016750

Rooker, J.R., Simms, J.R., David Wells, R.J., Holt, S.A., Holt, G.J., Graves, J.E., Furey, N.B., 2012. Distribution and habitat associations of billfish and swordfish larvae across mesoscale features in the gulf of Mexico. PLoS One 7. https://doi.org/10.1371/journal.pone.0034180

Sabatés, A., Martín, P., Lloret, J., Raya, V., 2006. Sea warming and fish distribution: the case of the small pelagic fish, Sardinella aurita, in the western Mediterranean. Glob. Chang. Biol. 12, 2209–2219. https://doi.org/10.1111/j.1365-2486.2006.01246.x

Salvadeo, C., Auliz-Ortiz, D.M., Petatán-Ramírez, D., Reyes-Bonilla, H., Ivanova-

Bonchera, A., Juárez-León, E., 2020. Potential poleward distribution shift of dolphinfish (*Coryphaena hippurus*) along the southern California Current System. Environ. Biol. Fishes 103, 973–984.

Schroeder, K., Chiggiato, J., Bryden, H.L., Borghini, M., Ben Ismail, S., 2016. Abrupt climate shift in the Western Mediterranean Sea. Sci. Rep. 6, 1–7. https://doi.org/10.1038/srep23009

Shaltout, M., Omstedt, A., 2014. Recent sea surface temperature trends and future scenarios for the Mediterranean Sea. Oceanologia 56, 411–443. https://doi.org/10.5697/oc.56-3.411

Stieglitz, J.D., Hoenig, R.H., Kloeblen, S., Tudela, C.E., Grosell, M., Benetti, D.D., 2017. Capture, transport, prophylaxis, acclimation, and continuous spawning of Mahi-mahi (*Coryphaena hippurus*) in captivity. Aquaculture 479, 1–6. https://doi.org/10.1016/j.aquaculture.2017.05.006

Thaxton, W.C., Taylor, J.C., Asch, R.G., 2020. Climate-associated trends and variability in ichthyoplankton phenology from the longest continuous larval fish time series on the east coast of the United States. Mar. Ecol. Prog. Ser. 650, 269–287. https://doi.org/10.3354/meps13404

van Gennip, S.J., Popova, E.E., Yool, A., Pecl, G.T., Hobday, A.J., Sorte, C.J.B., 2017. Going with the flow: the role of ocean circulation in global marine ecosystems under a changing climate. Glob. Chang. Biol. 23, 2602–2617. https://doi.org/10.1111/gcb.13586

Vargas-Yáñez, M., Jesús García, M., Salat, J., García-Martínez, M.C., Pascual, J., Moya, F., 2008. Warming trends and decadal variability in the Western Mediterranean shelf. Glob. Planet. Change 63, 177–184. https://doi.org/10.1016/j.gloplacha.2007.09.001

Vella, A., 1999. Dolphinfish fishery around the Maltese Islands *. Sci. Mar. 63, 465–467.

Venturini, S., Campodonico, P., Cappanera, V., Fanciulli, G., Cattaneo Vietti, R., 2017. Recreational fisheries in Portofino Marine Protected Area, Italy: Some implications for the management. Fish. Manag. Ecol. 24, 382–391. https://doi.org/10.1111/fme.12241

Vezzulli, L., Previati, M., Pruzzo, C., Marchese, A., Bourne, D.G., Cerrano, C., 2010. Vibrio infections triggering mass mortality events in a warming Mediterranean Sea. Environ. Microbiol. 12, 2007–2019. https://doi.org/10.1111/j.1462-2920.2010.02209.x

Walther, G., Post, E., Convey, P., Menzel, A., Parmesank, C., Beebee, T.J.C., Fromentin, J., I, O.H., Bairlein, F., 2002. Ecological response to recent climate change. Nature 416, 389–395.

Weigel, B., Mäkinen, J., Kallasvuo, M., Vanhatalo, J., 2021. Exposing changing phenology of fish larvae by modeling climate effects on temporal early life-stage shifts. Mar. Ecol. Prog. Ser. 666, 135–148. https://doi.org/10.3354/meps13676

Wilson, L.J., Fulton, C.J., Hogg, A.M., Joyce, K.E., Radford, B.T.M., Fraser, C.I., 2016. Climate-driven changes to ocean circulation and their inferred impacts on marine dispersal patterns. Glob. Ecol. Biogeogr. 25, 923–939. https://doi.org/10.1111/geb.12456

Zaouali, J., Missaoui, H., 1999. Small-scale Tunisian fishery for dolphinfish*. Sci. Mar. 63, 469–472. https://doi.org/10.3989/scimar.1999.63n3-4469