CLIMATE CHANGE AND THE EXPANSION OF THERMOPHILIC FISHES IN THE NORTHWESTERN MEDITERRANEAN: THE IMPORTANCE OF STUDYING CONDITION AND REPRODUCTION TO UNDERSTAND THE INCREASE IN THEIR ABUNDANCE

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Universitat de Girona

DOCTORAL THESIS

Climate change and the expansion of thermophilic fishes in the northwestern Mediterranean: the importance of studying condition and reproduction to understand the increase in their abundance

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Departament de Ciències Ambientals

El Dr. Josep Lloret Romañach i la Dra. Marta Muñoz Frigola, del Departament de Ciències Ambientals de la Universitat de Girona,

DECLAREM:

Que el treball, titulat "Climate change and the expansion of thermophilic fishes in the northwestern Mediterranean: the importance of studying condition and reproduction to understand the increase in their abundance", que presenta Harold O. Villegas Hernández per l'obtenció del títol de doctor, ha estat realitzat sota la nostra direcció.

I, perquè així consti i tingui els efectes oportuns, signem aquest document,

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“As human beings, we are vulnerable to confusing the unprecedented with the improbable. In our everyday experience, if something has never happened before, we are generally safe in assuming it is not going to happen in the future, but the exceptions can kill you and climate change is one of those exceptions”

Albert Arnold "Al" Gore Jr.

STRUCTURE OF THE THESIS

This PhD thesis has a format of compendium of scientific articles by chapters and thus the manuscript derived from this thesis dissertation has been structured into seven chapters. The first one (Chp. I) describes the frame in which this research lay and includes a brief description of the study area where the field work was conducted, the study species, the hypothesis, objectives and methodologies of the dissertation. Next, results are presented in five chapters (II-VI), each of them with its own introduction, methodology, results and discussions. It follows a general discussion and conclusions (Chp. VII) considering all the topics that have been tackled in this thesis. Finally, the reference list and appendixes are shown at the end of this manuscript.

It is worth to mention that four chapters (III-VI) corresponded to the exact transcripts of the articles that have been either accepted or still under review for publication in journals indexed by the Journal Citation Reports of the ISI Web of Knowledge. Below is detailed in which editorial process each of one of these articles are at present, along with the complete reference, impact factors (IF) and journal rankings (JR) (last update of 2013) that justify that these studies have the quality required for the submission of the thesis in this format.

1. Villegas-Hernández H., Muñoz M., Lloret J. (**2014**) Life-history traits of temperate and thermophilic barracudas (Teleostei: Sphyraenidae) in the context of sea warming in the Mediterranean. *Journal of Fish Biology*, 84 (6): 1940-1957. DOI: 10.1111/jfb.12411. IF = 1.734; JR = Fisheries (Q2: 16/50).

2. Villegas-Hernández H., Lloret J., Muñoz M. (**2015**) Climate-driven changes in life-history traits of the bastard grunt *Pomadasys incisus* (Teleostei: Haemulidae) in the North-western Mediterranean. *Mediterranean Marine Science* 16 (1): 21-30. DOI: 10.12681/mms.951. IF = 1.734; JR = Marine and Freshwater Biology (Q2: 43/102).

3. Villegas-Hernández H., Lloret J., Muñoz M. (**2015**) Reproduction, condition and abundance of the Mediterranean bluefish (*Pomatomus saltatrix*) in the context of sea warming. *Fisheries Oceanography* 24(1), 42-56. DOI: 10.1111/fog.12091. IF = 2.542; JR = Fisheries (Q1: 4/50).

4. Villegas-Hernández H., Muñoz M, Lloret J. (**in peer reviewing process of submission**) Reproductive traits of the pompano *Trachinotus ovatus* (Linnaeus, 1758) in the north-western Mediterranean. *Journal of the Marine Biological Association of the United Kingdom*. IF = 1.129; JR = Marine and Freshwater Biology (Q3: 61/103).

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LIST OF ABBREVIATIONS

This section details the abbreviations and acronyms used in this thesis. It should also be noticed that all names appearing in this thesis (cities, countries or regions) are written according to the language of their territory.

SST: sea surface temperature (in °C)
CO_2: carbon dioxide
ICOADS: International Comprehensive Ocean-Atmosphere Data Set
ANOVA: analysis of variance
ANCOVA: analysis of covariance
EDEV: early developing stage (gonad development stage)
DEV: developing stage (gonad development stage)
SC: spawning capable stage (gonad development stage)
AS: actively spawning stage (gonad development stage)
RGS: regressing stage (gonad development stage)
RGN: regenerating stage (gonad development stage)
GSI (or I_{G}): gonadosomatic index
HSI (or I_{H}): hepatosomatic index
TL (or L_{T}): total length (in cm)
L_{50}: length at which 50% of specimens sampled were already mature
SW (or M_{E}): somatic or eviscerate weight (in g)
BF (or F_{B}): batch fecundity (eggs per spawning batch)
RBF (or F_{RB}): relative batch fecundity (oocytes g^{-1} of body mass eggs)
CA: cortical alveolar (oocyte developmental stage)
Vtg-1: early vitellogenesis (oocyte developmental stage)
Vtg-2: mid vitellogenesis (oocyte developmental stage)
Vtg-3: advanced vitellogenesis (oocyte developmental stage)
GVM: vesicle migration (oocyte developmental stage)
H: hydration (oocyte developmental stage
IPCC: Intergovernmental Panel on Climate Change
NPP: net primary production

SUMMARIES

ENGLISH

A direct consequence of sea warming in the Mediterranean is a simultaneous increase in the abundance of thermo-tolerant species and the decline or disappearance of cold stenothermal species, which may cause cascade effects on food webs and changes in the local fish supply. Moreover, the decoupling temperature patterns caused by sea warming could lead to reproductive and recruitment declines in certain temperate and cold-water species, meanwhile for warm-water species it could lead to changes in seasonal phasing of reproduction and increases in species range. In this regard, coupled with the sea temperature increasing trends over the last decades, several warm-water fish species such as the yellow-mouth barracuda (*Sphyraena viridensis*), the bastard grunt (*Pomadasys incisus*), the bluefish (*Pomatomus saltatrix*) and the pompano (*Trachinotus ovatus*), are expanding northwards within the Mediterranean.

Here in this thesis, the spatio-temporal variations of the sea surface temperatures (SST) as well as the condition and reproductive-based life-history traits of these fish species were analysed. First of all, SSTs were retrieved and used to describe and compare the anomalies, trends, seasonalities and spatio-temporal variations of two areas with different thermal regimes along the latitudinal gradient of the northwestern Mediterranean Sea: the more northerly (colder) Gulf of Roses and the more southerly (warmer) Ebre River Delta. Next, within these two study areas sampling of specimens was carried out in order to evaluate the spatio-temporal variation and the influence of SSTs on the condition, reproduction and abundance of the study species.

Firstly, the results showed that the annual increasing monotonic trends in the SSTs were found similar in both study areas with alike annual rates of change (0.024-0.027°C yr^{-1}) but with significant monotonic trends only observed at spring and summer. Secondly, with regard of the studied species several interesting findings were observed. For example in *P. saltatrix*, although sea water temperature clearly influences its abundances and spawning phenology, its northward expansion may have been facilitated not only by the physical conditions (currently favourable water temperatures) but also by the higher productivity in the northernmost area, as evidenced by increasing fish condition in these waters. On the other hand in the study of *P. incisus*, the population inhabiting the colder waters was found to be in significantly poorer condition with some deviance in their life-history traits compared to the populations in warmer environments indicating that the plasticity of its life-history traits may contribute to its successful establishment into new habitats. The study of the barracudas showed that the life-history traits of the temperate *S. sphyraena* are, at present, better suited to the environmental conditions of the northern area compared to the more physically restricted life-history traits of *S. viridensis*; however, the thermophilic *S. viridensis* has a considerably higher reproductive potential which may favour its successful establishment within the northern area, especially if the present-day sea warming continues in which case it is likely that changes in spawning phenology would give *S. viridensis* an advantage. Finally, in the study of *T.*

ovatus there were noticeable inter-annual variations in its reproductive traits, all of which might correspond to changes in SST which in turn might indicate an important influence of the water temperature on its reproduction.

The overall results of this thesis indicated that different thermal-related biological responses may exist depending on the species, which in turn strengthens the claim that temperature plays a key role in regulating the physiology of fishes, especially in those warm-water species spreading northwards. Moreover, these results support the theory that climate change is at least partly responsible for the northward spread and increasing abundance of warm-water species in the Mediterranean Sea, and their physiological adaptations to the rising sea temperatures might indeed be playing an important role in the establishment into areas these thermophilic fauna did not previously occupy. Such physiological adaptations, including the changes in size-at-maturity, fecundity, spawning phenology and condition, might improve their colonization capabilities in the coldermost areas coupled with the sea warming trends. Notwithstanding, the biological response of fish to climate change might varies pretty much from one species to another depending if they are able to tolerate environmental changes through phenotypic plasticity by adapting their reproductive traits to the unusual temperate temperatures in those new habitats, and to the food supply available in the new habitats where the species is expanding, which could lead to gain in the energy reserves of the population in the new habitats.

This PhD thesis highlights the importance that, beyond studying the increases in abundance and biomass of warm-water species worldwide due to climate change, is actually necessary to carry out also studies on life-history traits (including the condition and reproduction) of thermophilic species. This later would help us to improve our understanding of the biological mechanisms of the observed changes in the marine communities that models based on fish abundance and biomass alone often fail to reveal.

Keywords: north-western Mediterranean, climate change, sea temperature, *Pomatomus saltatrix*, *Pomadasys incisus*, *Sphyraena viridensis*, *Trachinotus ovatus*, fish condition, reproductive biology.

CATALÀ

Una conseqüència directa de l'escalfament del mar Mediterrani és un augment simultani de l'abundància d'espècies termotolerantes i la disminució o desaparició d'espècies estenotérmicas fredes, el que pot causar efectes en cascada sobre les xarxes tròfiques i canvis en la subministrament local de peixos. D'altra banda, els patrons desacoblats de temperatura causats per l'escalfament del mar podrien conduir a disminucions reproductius i de reclutament de certes espècies d'aigües temperades i fredes, mentres que per espècies d'aigües càlides podria conduir a canvis en l'estacionalitat de la temporada de reproducció i augments en la distribució de l'espècie. En aquest sentit, conjuntament amb les tendències creixents de la temperatura del mar en les últimes dècades, diverses espècies de peixos d'aigües càlides com la barracuda de boca groga (*Sphyraena viridensis*), el roncador (*Pomadasys incisus*), el tallahams (*Pomatomus saltatrix*) i el sorell de penya (*Trachinotus ovatus*), s'estan expandint cap al nord del Mediterrani.

En aquesta tesi, es van analitzar les variacions espacio-temporals de les temperatures de la superfície del mar (SST), així com la condició i els trets d'història de vida basats en la reproducció d'aquestes espècies de peixos. En primer lloc, les SSTS van ser recuperades i utilitzades per descriure i comparar les anomalies, tendències, estacionalitats i variacions espacio-temporals de dues zones amb diferents règims tèrmics al llarg del gradient latitudinal del nord-oest de la Mediterrània: la més al nord (més freda) el golf de Roses i la més al sud (més càlida) el delta del riu Ebre. A continuació, dins d'aquestes dues àrees d'estudi la col·lecció de les mostres es va dur a terme per tal d'avaluar la variació espai-temporal i la influència de la SST en la condició, la reproducció i l'abundància de les espècies d'estudi.

En primer lloc, els resultats van mostrar que les tendències monòtones creixents anuals en les SST van ser similars en ambdues àrees d'estudi amb taxes anuals de canvi (0.024-0.027°C per any) però amb tendències monòtones significatives només observades a la primavera i a l’estiu. En segon lloc, pel que fa a les espècies d'estudi, diverses troballes interessants van ser observades. Per exemple, en l'estudi de *P. saltatrix*, es va observar que encara que la temperatura de l'aigua de mar influeix clarament en les seves abundàncies i la fenologia de la posta, la seva expansió cap al nord pot haver estat facilitada no només per les condicions físiques (les temperatures de l'aigua favorables actualment), sinó també per l'augment de la productivitat a la zona més al nord, com ho demostra l'augment de condició dels peixos en aquestes aigües. D'altra banda en l'estudi de *P. incisus*, la població que habita en les aigües més fredes es va trobar en condicions significativament més pobres mostrant una mica de desviació en els seus trets d'història de vida en comparació amb les poblacions d'ambients més càlids indicant que aquest tipus de plasticitat dels seus trets d'història de vida poden contribuir al seu establiment amb èxit a nous hàbitats. L'estudi de les barracudes va mostrar que els trets d'història de vida de l'espècie temperada *S. sphyraena* estan, actualment, més adequats a les condicions ambientals de la zona nord en comparació amb els trets d'història de vida més restringits físicament de *S. viridensis*; però, l'espècie termòfila *S. viridensis* mostra un potencial reproductiu considerablement més alt la qual cosa pot afavorir el seu establiment amb èxit dins de la zona nord,

especialment si l'escalfament del mar actual continua en aquest cas és probable que els canvis en la fenologia de la posta donarien un avantatge a *S. viridensis*. Finalment, en l'estudi de *T. ovatus* es va observar que hi havia variacions interanuals notables en les seves característiques reproductives, les quals podrien correspondre als canvis en la SST el que indicaria una influència important de la temperatura de l'aigua en la seva reproducció.

Els resultats generals d'aquesta tesi indiquen que poden existir diferents respostes biològiques relacionades amb la temperatura depenent de l'espècie, el que al seu torn reforça la idea que la temperatura juga un paper clau en la regulació de la fisiologia dels peixos, especialment en aquelles espècies d'aigua càlides que s'estan expandint cap al nord. D'altra banda, aquests resultats recolzen la teoria que el canvi climàtic és almenys en part responsable de la propagació cap al nord i l'augment de l'abundància d'espècies d'aigües càlides al Mar Mediterrani, i que les seves adaptacions fisiològiques a l'increment de la temperatura del mar podrien de fet estar jugant un paper important en l'establiment d'aquesta fauna termòfila en zones que no ocupen prèviament. Aquestes adaptacions fisiològiques, incloent els canvis en la talla de maduresa, fecunditat, fenologia de la posta i condició, poden millorar les seves capacitats de colonització en les zones més fredes. No obstant això, la resposta biològica dels peixos deguda a el canvi climàtic podria variar bastant d'una espècie a una altre, depenent si són capaços de tolerar els canvis ambientals a través de la plasticitat fenotípica adaptant les seves característiques reproductives a les temperatures temperades inusuals d'aquells hàbitats nous, i a la disponibilitat d'aliment on l'espècie s'està expandint, el que podria conduir a una millora en les reserves energètiques de la població en el nou hàbitat.

En aquesta tesi es destaca la importància que, més enllà d'estudiar els augments en l'abundància i biomassa de les espècies d'aigües càlides a tot el món a causa del canvi climàtic, és realment necessari dur a terme també estudis de les trets d'història de vida (com la condició i la reproducció) d'espècies termòfiles. Tot això ajudaria a millorar la nostra comprensió dels mecanismes biològics dels els canvis observats en les comunitats marines que els models basats en abundàncies i biomasses sovint no revelen per si sols.

Paraules clau: Mediterrània nord-occidental, canvi climàtic, temperatura del mar, *Pomatomus saltatrix*, *Pomadasys incisus*, *Sphyraena viridensis*, *Trachinotus ovatus*, condició dels peixos, biologia reproductiva.

CASTELLANO

Una consecuencia directa del calentamiento del mar Mediterráneo es un aumento simultáneo de la abundancia de especies termotolerantes y la disminución o desaparición de especies estenotérmicas frías, lo que puede causar efectos en cascada sobre las redes tróficas y cambios en la suministro local de pescados. Por otra parte, los patrones desacoplados de temperatura causados por el calentamiento del mar podrían conducir a disminuciones reproductivas y de reclutamiento de ciertas especies de aguas templadas y frías, mientras que para especies de aguas cálidas podría conducir a cambios en la estacionalidad de la temporada de reproducción y aumentos en la distribución de la especie. En este sentido, junto con las tendencias crecientes de la temperatura del mar en las últimas décadas, varias especies de peces de aguas cálidas como la barracuda de boca amarilla (*Sphyraena viridensis*), el roncador (*Pomadasys incisus*), el pez azul (*Pomatomus saltatrix*) y el pámpano (*Trachinotus ovatus*), se están expandiendo hacia el norte del Mediterráneo.

En ésta tesis, se analizaron las variaciones espacio-temporales de las temperaturas de la superficie del mar (SST), así como la condición y los rasgos de historia de vida basados en la reproducción de estas especies de peces. En primer lugar, las SSTs fueron recuperadas y utilizadas para describir y comparar las anomalías, tendencias, estacionalidades y variaciones espacio-temporales de dos zonas con diferentes regímenes térmicos a lo largo del gradiente latitudinal del noroeste del Mediterráneo: la más al norte (más fría) en el Golfo de Rosas y la más al sur (más cálida) en el delta del río Ebro. A continuación, dentro de estas dos áreas de estudio la colección de las muestras se llevó a cabo con el fin de evaluar la variación espacio-temporal y la influencia de la SST en la condición, la reproducción y la abundancia de la especies de estudio.

En primer lugar, los resultados mostraron que las crecientes tendencias monótonas anuales en las SST fueron similares en ambas áreas de estudio con tasas anuales de cambio (0.024 -0.027°C por año) pero con tendencias monotónicas significativas sólo observadas en la primavera y el verano. En segundo lugar, con respecto a las especies de estudio varios hallazgos interesantes fueron observados. Por ejemplo, en el estudio de *P. saltatrix*, se observó que aunque la temperatura del agua de mar influye claramente en sus abundancias y la fenología del desove, su expansión hacia el norte puede haber sido facilitado no sólo por las condiciones físicas (las temperaturas del agua favorables actualmente), sino también por el aumento de la productividad en la zona más al norte, como lo demuestra el aumento de condición de los peces en estas aguas. Por otra parte en el estudio de *P. incisus*, la población que habita en las aguas más frías se encontró en condiciones significativamente más pobres mostrando algo de desviación en sus rasgos de historia de vida en comparación con las poblaciones de ambientes más cálidos indicando que este tipo de plasticidad de sus rasgos de historia de vida pueden contribuir a su establecimiento con éxito en nuevos. El estudio de las barracudas mostró que los rasgos de historia de vida de la especie templada *S. sphyraena* están, en la actualidad, más adecuados a las condiciones ambientales de la zona norte en comparación con los rasgos de historia de vida más restringidos físicamente de *S. viridensis*; sin embargo, la especie termófila *S. viridensis* muestra un potencial reproductivo considerablemente más alto lo cual puede

favorecer su establecimiento con éxito dentro de la zona norte, especialmente si el calentamiento del mar actual continúa en cuyo caso es probable que los cambios en la fenología del desove darían una ventaja a *S. viridensis*. Por último, en el estudio de *T. ovatus* se observó que había variaciones interanuales notables en sus características reproductivas, los cuales podrían corresponder a los cambios en la SST lo que indicaría una influencia importante en su reproducción.

Los resultados generales de esta tesis indican que pueden existir diferentes respuestas biológicas relacionadas con la temperatura dependiendo de la especie, lo que a su vez refuerza la idea de que la temperatura juega un papel clave en la regulación de la fisiología de los peces, especialmente en aquellas especies de agua cálidas que se están expandiendo hacia el norte. Por otra parte, estos resultados apoyan la teoría de que el cambio climático es al menos en parte responsable de la propagación hacia el norte y el aumento de la abundancia de especies de aguas cálidas en el Mar Mediterráneo, y que sus adaptaciones fisiológicas al incremento de la temperatura del mar podrían de hecho estar jugando un papel importante en el establecimiento de ésta fauna termófila en zonas que no ocupan previamente. Tales adaptaciones fisiológicas, incluyendo los cambios en la talla de madurez, fecundidad, fenología del desove y condición, pueden mejorar sus capacidades de colonización en las zonas más frías. No obstante, la respuesta biológica de los peces a el cambio climático podría variar de una especie a otra, dependiendo si son capaces de tolerar los cambios ambientales a través de la plasticidad fenotípica adaptando sus características reproductivas a las temperaturas templadas inusuales de aquellos hábitats nuevos, y a la disponibilidad de alimento donde la especie se está expandiendo, lo que podría conducir a una mejora en las reservas energéticas de la población en el nuevo hábitat.

En ésta tesis se destaca la importancia de que, más allá de estudiar los aumentos en la abundancia y biomasa de las especies de aguas cálidas en todo el mundo debido al cambio climático, es realmente necesario llevar a cabo también estudios de los rasgos de historia de vida (como la condición y la reproducción) de especies termófilas. Todo esto ayudaría a mejorar nuestra comprensión de los mecanismos biológicos de los cambios observados en las comunidades marinas que los modelos basados en abundancias y biomasas a menudo no revelan por sí solos.

Palabras clave: Mediterráneo noroccidental, cambio climático, temperatura del mar, *Pomatomus saltatrix*, *Pomadasys incisus*, *Sphyraena viridensis*, *Trachinotus ovatus*, condición de los peces, biología reproductiva.

CHAPTER I: General Introduction

The general introduction provides the overall approach of the investigation project developed in this PhD, presenting the scope of the study and describing the main objectives and purposes that have been pursed.

CHAPTER I

General Introduction

1.1. Sea warming context

During the last three decades, sea water temperatures have changed at unprecedented rates worldwide as a result of global warming. This sea water temperature rise has triggered serious events such as the rapid disappearance of sea ice cover in the Arctic, the reduction in volume of Antarctic ice sheets, a rise in sea levels, increases in storm frequency and rainfall, an increase in number and intensity of storms, and early onset of spring (Solomon *et al.* 2007; Hoegh-Guldberg & Bruno 2010; Philippart *et al.* 2011; IPCC 2013). Although a primary concern is the rapid global rate of change currently observed, regional changes are often more relevant than global averages (Walther *et al.* 2002; Root *et al.* 2003; Belkin 2009) because warming trends are thought to be more pronounced at the poles than at the equator (Macdonald *et al.* 2005). For example, European seas are disproportionately affected by climate change, and some of them may experience changes from fast (0.030–0.049°C year^{-1}) to super-fast (≥0.050°C year^{-1}) warming trends (Table 1.1). The observed and predicted temperature increases due to climate change are generally higher in northern than in southern European seas and higher in enclosed than in open systems (Belkin 2009; Philippart *et al.* 2011). Noticeably, enclosed seas appear to have undergone far more dramatic changes than more open seas during recent decades (Table 1.1).

The semi-enclosed Mediterranean basin is a miniature ocean where sea warming is likely to become apparent earlier and to be more pronounced than in other, more open oceans (Astraldi *et al.* 1995; Bethoux *et al.* 1999; Walther *et al.* 2002; Coll *et al.* 2010). The region has been identified as a ‘‘hotspot’’ for climate change and is expected to experience environmental impacts that are considerably greater than those in many other places around the world (Nykjaer 2009; Durrieu de Madron *et al.* 2011); climatic models predict that the Mediterranean basin will be one of the regions most affected by the ongoing warming trend and by an increase in extreme events (Parry 2000). In fact, it has been suggested that the Mediterranean is already one of the most impacted seas in the world, since climate change interacts synergistically with many other disturbances (Lejeusne *et al.* 2010).

Nykjaer (2009) observed warming trends in the Mediterranean Sea, inferred from satellite observations between 1985 and 2006: in the last 2 decades, the temperature in the upper layer of the Mediterranean Sea has been increasing at an average rate of 0.03°C (std. dev. ± 0.008) year^{-1} for the western Mediterranean basin and 0.05±0.009 °C year^{-1} for eastern Mediterranean basin (Table 1.1). Diaz-Almela *et al.* (2007) have observed a rapid warming of surface water masses 0.04±0.01 °C year^{-1}

in NW Mediterranean in recent decades. In the same area, Salat & Pascual (2002) also observed a rise in water temperatures: since 1970, the average annual temperature has increased by 1.1°C (0.04°C year^{-1}) at sea surface and 0.7°C (0.025°C year^{-1}) at 80 meters depth. Similar data was observed by Calvo *et al.* (2011) on the same northern Catalan coast: over 35 years, from 1974–2009, the temperature increased in the upper-most waters (0–50 m) by around 1.1°C and at depths of 80 m by around 0.7°C .

Table 1.1 Observed and predicted changes in sea surface temperatures (SST) of European Seas. Modified from Philippart et al. (2011).

European Sea	ΔSST observation/prediction	Reference
Arctic Ocean		
ΔSST observed	ca.+0.2 °C per decade (1965–'95)	(Steele *et al.* 2008)
ΔSST predicted	+4 to 7 °C (1990s–2090s)	(ACIA 2005; IPCC 2013)
Barents Sea		
ΔSST observed	+0.12 °C (1982–2006)	(Belkin 2009)
ΔSST predicted	+1 to 2 °C (1990s–2080s)	(Furevik *et al.* 2002)
Nordic Seas		
ΔSST observed	+0.85 °C (1982–2006)	(Belkin 2009)
ΔSST predicted	+1 to 2 °C (1990s–2080s)	(Furevik *et al.* 2002)
NE Atlantic		
ΔSST observed	+1 °C (1975–2005)	(Philippart *et al.* 2007)
ΔSST predicted	+2 °C (1990s–2090s)	(Philippart *et al.* 2011)
North Sea		
ΔSST observed	+1.31 °C (1982–2006)	(Belkin 2009)
ΔSST predicted	+0.8 °C (1990s–2040s)	(Clark *et al.* 2003)
Baltic Sea		
ΔSST observed	+1.35 °C (1982–2006)	(Belkin 2009)
ΔSST predicted	+2 to 4 °C (1990s–2090s)	(Graham *et al.* 2008)
Celtic-Biscay Shelf		
ΔSST observed	+0.72 °C (1982–2006)	(Belkin 2009)
ΔSST predicted	+1.5 to 5 °C (1990s–2090s)	(Philippart *et al.* 2011)
Iberian upwelling		
ΔSST observed	+0.68 °C (1982–2006)	(Belkin 2009)
ΔSST predicted	+1.4 to 2.4 °C (1960/1990–2070/2100)	(Philippart *et al.* 2011)
Mediterranean		
ΔSST observed	+0.71 °C (1982–2006)	(Belkin 2009)
	+1.1 °C (1974-2001)	(Salat & Pascual 2002)
	+1.1 °C (1974-2009)	(Calvo *et al.* 2011)
	+0.88 °C (1968-2005)	(Diaz-Almela *et al.* 2007)
ΔSST predicted	+2.6 °C (1961/1990–2070/2099)	(Somot *et al.* 2008)
Black Sea		
ΔSST observed	+0.96 °C (1982–2006)	(Belkin 2009)
ΔSST predicted		

1.2. Mediterranean warming impacts on its living marine resources

Evidence has shown that climate variation and changes in ecosystem properties are related and that global warming may affect many marine species worldwide (Bombace 2001; Roessig *et al.* 2004; Perry *et al.* 2005; Dulvy *et al.* 2008; Brander 2010; Philippart *et al.* 2011; Wernberg *et al.* 2011). Global warming-induced alterations, such as precipitation, temperature, CO$_2$ concentration and wind patterns will result in a cascade of physical changes (e.g. vertical stability of the water column, upwelling regimes, water mass formation and circulation, current patterns) and chemical changes (e.g. seawater pH, salinity, nutrient ratios) in the marine environment, which in turn may impact on the marine ecosystems, either directly (on physiology, behavior, growth, reproductive capacity, mortality and distribution) or indirectly (on productivity, structure and composition of marine ecosystems in the which fish depend for food). Subsequently, the living marine resources shall be affected (Fig. 1.1).

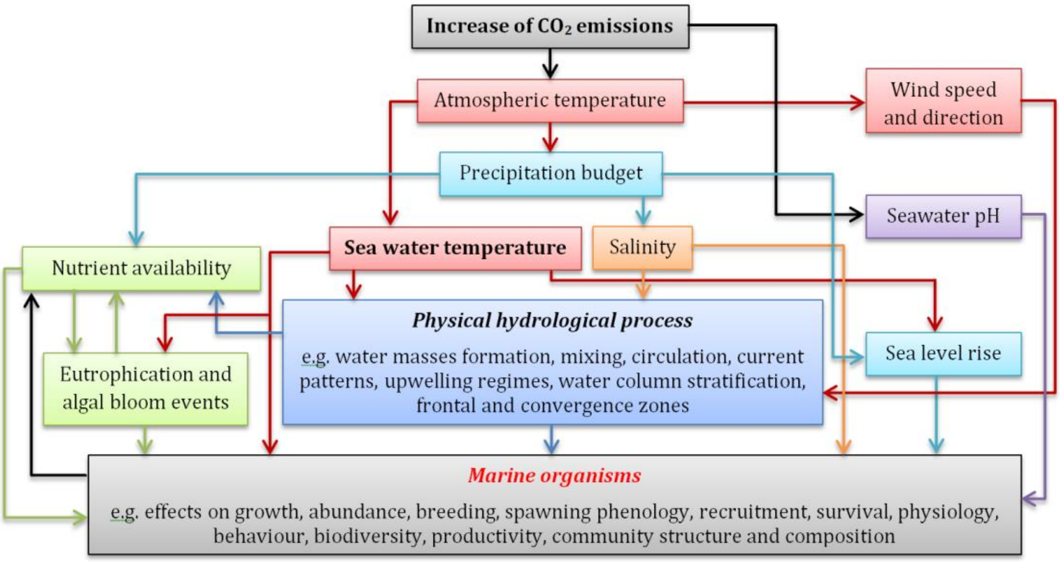

Fig. 1.1 Flux diagram of the main global climate change-driven related factors influencing marine organisms (→: affects). Diagram modified from Gambaiani *et al.* (2009).

It is known that climate variability affects abundance and biogeography of marine fish due to the thermal threshold of their physiological tolerance (Genner *et al.* 2009). In other words, the thermal structure of sea water masses determines the extent of the habitat of certain species since each species has adapted to certain ranges of temperature distribution (Murawski 1993). Therefore, the most notable ecological impact of global warming is the changes in distribution of fish, with some species heading to higher latitudes according to their thermal preferences (Walther *et al.* 2002; Parmesan & Yohe 2003; Daufresne *et al.* 2009; Pörtner & Peck 2010). In regions that have experienced a temperature increase, there may be patterns that appear to be "positive", e.g. increased abundance of warm-water species in colder regions, while there may also be "negative" patterns e.g., decreased numbers of cold-water species (Walther *et al.* 2002). Thus, a direct consequence of warming is a simultaneous increase in the abundance of thermo-tolerant species and the disappearance or rarefaction of 'cold' stenothermal species (Lejeusne *et al.* 2010).

The Mediterranean Sea is characterized by a latitudinal gradient with well-defined seasonality, with relatively cold winters in the north and long hot summers in the south (Lejeusne *et al.* 2010;

Calvo *et al.* 2011; Durrieu de Madron *et al.* 2011). This determines the species distribution in this semi-enclosed sea where subtropical species are mainly found in the warmer eastern and southern basins, meanwhile cold-temperate species inhabit the colder northern areas (Salat 1996; Bianchi & Morri 2000; Coll *et al.* 2010). These features make the Mediterranean Sea a very sensitive area to climate change (Bethoux *et al.* 1999). Over the past three decades, sea warming in the Mediterranean has led warm-water species to shift their ranges northwards and settle in the more northern waters where they were formerly rare or absent (Francour *et al.* 1994; Astraldi *et al.* 1995; Morri & Bianchi 2001; Bodilis *et al.* 2013). An increase in alien species can cause endemic species to decline in abundance and be displaced, which in turn can also alter the infra-littoral communities and induce ecological impacts such as local population decline and extirpation; reduction of genetic diversity in native species; food-web alterations; loss of habitat functions, processes and structure; increase in the risk of extinction and biotic homogenization (Ricciardi 2004; Galil 2007a; b).

Thermophilic species, like the grey triggerfish (*Balistes carolinensis*), Mediterranean parrotfish (*Sparisoma cretense*), round sardine (*Sardinella aurita*), bluefish (*Pomatomus saltatrix*), Senegalese sole (*Solea senegalensis*), dusky grouper (*Epinephelus marginatus*), bastard grunt (*Pomadasys incisus*), ornate wrasse (*Thalassoma pavo*), slackskin blaasop (*Sphoeroides pachygaster*), yellow-mouth barracuda (*Sphyraena viridensis*), white grouper (*Epinephelus aeneus*), and dusky grouper (*Epinephelus marginatus*) have been recorded in various studies amongst the 'cold biota' of the northern Mediterranean in sufficient numbers to suggest a northward expansion of these warm-water species that correlates to the warming of Mediterranean waters (Bianchi & Morri 1994; Francour *et al.* 1994; Relini & Orsi-Relini 1997; Dulčić & Grbec 2000; Bombace 2001; Morri & Bianchi 2001; Galil & Zenetos 2002; Golani *et al.* 2002, 2007; Psomadakis *et al.* 2006; Dulčić *et al.* 2009; Lloret *et al.* 2015b). The northward migration of these warm-water species will induce species competition for the existing niches of cold-water species (IPCC 2001; Hiscock *et al.* 2004; Galil 2007a). In addition to northward migration, evidence suggests that bathymetric displacements are occurring among populations of invasive and endemic species such as in the case of the indigenous red mullet (*Mullus barbatus*) and hake (*Merluccius merluccius*) with both moving into deeper and cooler waters due to their respective warm-water competitors, the gold band goatfish (*Upeneus moluccensis*) and brush-tooth lizardfish (*Saurida undosquamis*) (Galil & Zenetos 2002; Gambaiani *et al.* 2009). Similarly, sea warming can also modify species' migration periods, such as in the case for the amberjack (*Seriola dumerilii*) and bluefin tuna (*Thunnnus thynnus*) which in the last few decades appear to stay longer (until mid-winter instead of autumn) in the northern and central Mediterranean before migrating toward their winter territories (Bombace 2001).

As stated before, one of the major ecological threats of the northward migrations of warm-water species in the Mediterranean is that several of these thermophilic species are top carnivores and among the bigger coastal fish species, so their successful colonization is likely to affect the endemic species and influence local, traditional fisheries. Thus, not only would marine biodiversity be seriously affected by climate changes, but fisheries may also be affect directly by alterations to fish stocks and the overall supply of fish for consumption, or indirectly by influencing fish prices or the cost of goods and services required by fishers (Mieszkowska *et al.* 2009). This would then impact commercial fishing, causing instability in the overall value of fish catches due to changes in the abundance of the species caught, since future climate change impacts on fisheries are likely to be greater for temperate endemics than for tropical species and damage coastal and demersal fisheries more than pelagic and deep-sea fisheries (IPCC 2001). Moreover the replacing traditional, cold-water fauna with unfamiliar warm-water species can be unpopular with consumers of the thermophilic species, despite the fact that some of these alien marine species may constitute a good food source (Lloret *et al.* 2015a).

1.3. Climate-driven alterations of the life-history traits of fish

As well as the impacts on abundances of marine populations, the physiology of individual organisms may also be severely affected. In certain areas, some organisms survive under specific temperature conditions and cannot adapt or move away when the environmental conditions change; these dispersal limitations in some marine animals, such as benthic organisms, are unable to successfully migrate (due to distance or strong currents, for example) toward more suitable environments (Hiscock *et al.* 2004). In addition, by affecting the physiology of marine organisms, sea warming can impact the performance and survival of those organisms that live close to the limits of their thermal tolerance, for example, at the northern or southernmost limit of their distribution (Somero 2002; Poulard & Blanchard 2005). In this sense, sea warming also affects the fish *condition*, a measure of energy reserves and a particularly important attribute in fish population dynamics as it has great influence on growth and reproduction. Individuals in good condition are usually found in environments where optimal physiological conditions prevail, whereas those in poor condition are found in adverse environments and where food is scarce. Specimens in poor condition have low available energy reserves which can have important consequences on population such as reduced reproductive success as well as reduced chances of survival (Lambert & Dutil 1997; Shulman & Love 1999; Lloret *et al.* 2002; Rätz & Lloret 2003).

It is also known that water temperature is one of the main environmental factors that influence the reproductive system of fish and even small changes in temperature (1-2°C) may affect gonadal function (Bromage *et al.* 2001; Pankhurst & Porter 2003), and because of this fish hatcheries are usually linked to particular times of year in order to maximize the reproductive capability, growth and survival of the offspring (Munday *et al.* 2008). In this sense, the uncoupling of temperature patterns caused by sea warming and associated asymmetric thermal fluctuations could lead to spawning taking place in seasons or at temperatures that are probably unsuitable for development and growth of larvae (Soria *et al.* 2008). Indeed, the length of the spawning season (affecting the number of successive spawnings in multiple batch spawners) - and consequently the total annual fecundity of females - has recently been observed to be linked with the duration of favorable environmental conditions (Strüssmann *et al.* 2010).

Although sea warming may have major consequences for the reproduction of fish populations it is likely that any such consequences will mainly depend on various synergic factors such as specific physiological tolerances, capacity for acclimation and adaptation, scope for behavioural avoidance, capacity to extend or shift ranges, and the timing of thermal challenges with respect to the reproductive cycle (Pankhurst & Munday 2011). For certain temperate water species, climate change could lead to complete reproductive and recruitment failure; on the other hand, for warm-water species, it could lead to changes in seasonal phasing of reproduction and possible increases in species range (Munday *et al.* 2008; Pankhurst & Munday 2011). In this sense it is likely that the present-day sea warming trends and the associated changes in spawning phenology would give the thermophilic fish species an advantage and favour their successful establishment into new habitats in the northernmost areas of the Mediterranean Sea. On the other hand, for native temperate fish species, small increases in sea temperature during spawning seasons can dramatically increase egg mortality and decrease survivorship to hatching since the egg stage is one of the most thermally sensitive life stages in fish (Rombough 1997; Gagliano *et al.* 2007). Therefore, small increases in temperature might tend to favour recruitment of some species (especially at higher latitudes) but larger temperature increases could lead to recruitment failures (especially at low latitudes) and at times or places where food supply is limited (Munday *et al.* 2008; Pankhurst & Munday 2011).

1.4. Condition and reproduction of fish in the context of climate change

To our knowledge most of the studies which have investigated the impact of climate change on fish have focused mainly on the changes in abundance and biomass of the fish communities and their ecological assemblages based on complex models (Brander 2003, 2007; Perry *et al.* 2005; Lehodey *et al.* 2006; Collie *et al.* 2008; Dulvy *et al.* 2008; Graham & Harrod 2009; Jennings & Brander 2010; Cheung *et al.* 2013; Hollowed *et al.* 2013; Gamito *et al.* 2015). However, there is a growing need to summarize the ecological complexity of climate impacts not only by comparing the climate-driven changes in species distributions and abundances over long time series but also by investigating the physiology and bioenergetics of these warm-water species in order to get a more detailed view of the biological and physiological mechanisms and processes which are making possible their northward expansion and successful establishment within the northernmost areas of the Mediterranean Sea.

Besides the work presented in this PhD thesis, the relationship between fish biology and climate change has also been investigated in a recently published study by Lloret *et al.* (2015b). These authors used a multidisciplinary approach based on fishery and reproductive data (histological gonad analyses and ichthyoplankton surveys) as well as the local fishermen's traditional ecological knowledge, and found that in the NW Mediterranean, changes in the abundance of fish have followed a particular spatio-temporal sequence, with three different phases of colonization in the case of warm-water species (occasional occurrence, common presence and establishment), and three phases of regression (abundance reduction, range contraction and disappearance from the catch) in the case of cold-water species. This later study has proved that this kind of research approach, focused on fish biology as well as abundances analyses, is very useful in enhancing our understanding on how fish are adapting to rising sea temperatures. It also provides new insight into the observed changes in fish diversity and abundance in relation to climate change in the NW Mediterranean.

It is worth mentioning that other parameters related to fish biology - such as growth (Nunn *et al.* 2010; Baudron *et al.* 2011, 2014), mortality (Stige *et al.* 2006), behaviour (Rijnsdorp *et al.* 2009) and physiological thermotolerance (Elliott & Elliott 1995; Sorte *et al.* 2011) - might also be affected by climate change. However, the study presented here in this thesis will focus on *condition* and *reproduction* because they represent the two key factors in the population viability of a species; and both factors can explain the changes in abundance and biomass within a certain area (Engelhard & Heino 2006; Pankhurst & Munday 2011; Petitgas *et al.* 2013).

1.5. Case studies

Several authors have suggested that changes in biodiversity patterns in the Mediterranean are related to this increasing trend in water temperature, and that those species from warmer waters south of the Mediterranean are extending their range into northern colder regions of the Mediterranean (Francour *et al.* 1994; Astraldi *et al.* 1995; Bianchi & Morri 2000). This could well be true in the case of the following fish species: the bluefish (*Pomatomus saltatrix*), the yellow-mouth barracuda (*Sphyraena viridensis*), the bastard grunt (*Pomadasys incisus*) or the pompano (*Trachinotus ovatus*), all of which are increasing in abundance particularly in the NW Mediterranean Sea, including the waters off the Gulf of Roses. These species could be considered biological indicators of the sea warming in Mediterranean Sea since their origin is tropical and their actual regional proliferation is within the NW Mediterranean Sea. In fact, Lloret *et al.* (2015b) have documented that all four (*P. saltatrix*, *P. incisus*, *S. viridensis* and *T. ovatus*) are warm-water species that are currently in the 'establishment' phase of colonization within the NW Mediterranean according to their spatio-temporal sequence patterns of occupation in relation to sea warming. These phases are 'occasional occurrence' (with unusual, vagrant specimens that are sporadically recorded), then 'common presence' (specimens have become more frequent, but no reproduction is observed in the populations, which can only be restored by immigration), and finally 'establishment' (with indications of reproductive success in the area) (Lloret *et al.* 2015b).

1.5.1. Bluefish (Pomatomus saltatrix)

Bluefish (*Pomatomus saltatrix*, Linnaeus 1766), the only living representative of its genus and family (Pomatomidae), is an oblong, laterally compressed and streamlined predatory species that grows to a maximum total length (TL) of 130 cm (commonly 60 cm) and to a maximum weight of

14.4 kg (Kendall & Walford 1979) (Fig. 1.2). The head is large and compressed with the mouth set obliquely. The maxilla extends to the rear of the eye. The lower jaw projects from the mouth and has a row of long, unequal teeth on each side. Body color is bluish to greenish dorsally, fading to silver ventrally. Ctenoid scales cover the opercule, cheek, and body, but not the top of the head or a ridge that runs above the cheeks. Ninety-five scales run along the lateral line. Two dorsal fins, the first short and low with 7 or 8 relatively weak spines connected by a membrane, the second long, with 1 spine and 23 to 28 soft rays; anal fin a little shorter than soft dorsal fin, with 2 spines and 23 to 27 soft rays; caudal fin moderately forked; pectoral fins short, not reaching origin of soft dorsal fin (Collette 2002).

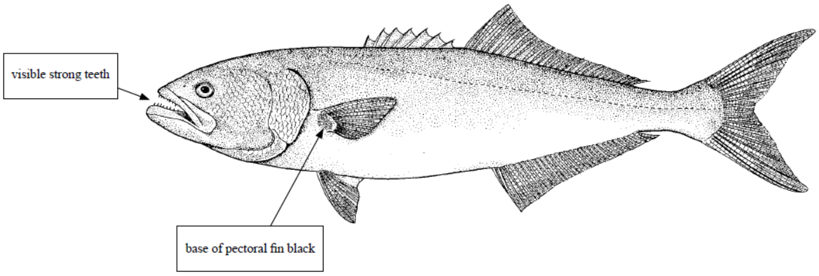

Fig. 1.2 The bluefish, *Pomatomus saltatrix*. Illustration modified from Bariche (2012).

Bluefish are coastal migratory pelagic predators that tend to segregate into schools of similarly sized individuals (Wilk 1977) and are distributed over continental shelves and in estuaries of temperate waters throughout most of the world, with the exception of the northern and mid-Pacific Ocean (Juanes *et al.* 1996). Its distribution in the Indian Ocean includes the east coast of southern Africa, Madagascar, the Malay Peninsula, Tasmania, and the southern and western coasts of Australia. In the eastern Atlantic Ocean, distribution ranges from Portugal to Senegal, including the Azores, the Mediterranean and Black seas, and from Angola to South Africa. In the Western Atlantic, its known range includes the Gulf of Mexico and the eastern coasts of North and South America, encompassing regularly the region northward from Florida to Cape Cod and occasionally to Nova Scotia, and southward to Brazil and Argentina (Briggs 1960; Juanes *et al.* 1996; Salerno *et al.* 2001). Particularly in the Mediterranean, although bluefish are more abundant in the southern and eastern warm waters (Tortonese 1986), unusual records of this species have been reported in the northern Adriatic Sea (Dulčić *et al.* 2005) and increasing abundances have been reported in the NW Mediterranean (Sabatés *et al.* 2012).

The life cycle, distribution, seasonal migration, and spawning of *P. saltatrix* are closely regulated by water temperature. The species is usually found at temperatures from 14–16 to 30°C (Fahay *et al.* 1999). Specific temperature ranges have been reported for seasonal migration linked to reproduction depending on the geographic area, and 20–26°C has been found to be the preferential surface temperature range for spawning (Wilk 1977; Kendall & Walford 1979; Ditty & Shaw 1995;

Juanes *et al.* 1996). The migration patterns along its distributions range share common characteristics: bluefish spends the colder months in warm-water areas and, when the surface temperature reaches a certain value, migrates towards colder waters where the species spawns once a threshold temperature has been attained (Juanes *et al.* 1996). Within the Mediterranean, reproduction-related migrations have been described to take place in the eastern basin, from the Aegean Sea to the Black Sea in spring where spawning takes place, returning in autumn (Gordina & Klimova 1996).

During annual migrations along continental shelves, adults spawn large numbers of small eggs, once as larvae they are typically advected along-shore to juvenile nursery habitats; while juveniles recruit to inshore habitats at a similar size, and there they grow rapidly and are mainly piscivorous, feeding primarily on atherinids and engraulids (Juanes *et al.* 1996). Larvae transform into pelagic juveniles at about 18 to 25 days and 10-12 mm stantard length (Hare & Cowen 1993, 1994), then juveniles remain oceanic for an additional 15 to 45 days before recruiting to nearshore habitats at 40-80 mm fork length (Hare & Cowen 1996). Furthermore, bluefish usually live approximately 9-11 years and males and females grow at approximately the same rates (Richards 1976), and mature sexually during the second year upon reaching approximately 35-45 cm fork length (FL) (Wilk 1977). In the Northeast coast of the U.S., the von Bertalanffy growth parameters for both sexes of this species were $L_\infty = 87.2 \pm 1.6$ cm, $k = 0.26 \pm 0.01$ and $t_0 = -0.93 \pm 0.03$ ($r^2 = 0.985$); the size (FL) at maturity (L_{50}) was 33.9 cm for males and 33.4 cm for females and the age at maturity (A_{50}) was 1.2 and 1.1 years for males and females, respectively (Salerno *et al.* 2001).

1.5.2. Bastard grunt (Pomadasys incisus)

The bastard grunt (*Pomadasys incisus*, Bowdich 1825) has a compressed oblong body and with a small head and mouth. Its dorsal fin has a soft notch between hard and soft rays, which are 12 and 16 in number respectively, and the anal fin has 3 soft rays and 12-13 hard rays. It is gray on the back, with a bright golden and silvery white belly, yellow fins, and a black spot on the opercule (Fig. 1.3).

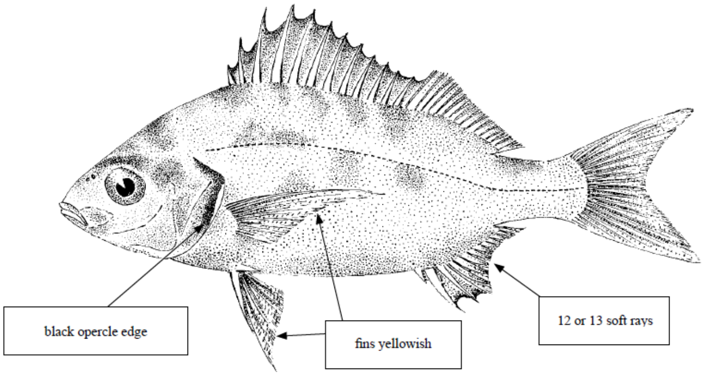

Fig. 1.3 The bastard grunt, *Pomadasys incisus*. Illustration modified from Bariche (2012).

This species is a coastal demersal fish species inhabiting marine and brackish waters, usually near sandy/muddy substrate or in rocky habitats and seagrass meadows, at depths from 10 to 100 m, but usually not deeper than 50 m (Golani *et al.* 2006; Kapiris *et al.* 2008). This species is frequently found along the eastern central Atlantic coasts from the Straits of Gibraltar to Angola, and also in the Canaries, Azores, and Cape Verde Islands (Pajuelo *et al.* 2003a; b). Several references have recorded this species in the Mediterranean Sea, in Greece (Kaspiris 1970) and recently in the Ligurian, Tyrrhenian and Egyptian Seas (Gavagnin *et al.* 1994; Serena & Silvestri 1996; El Mor *et al.* 2002), in the Gulf of Tunis (Fehri-bedoui & Gharbi 2008) and on the French-Catalan coast (Pastor *et al.* 2008).

Information on the biological aspects of this species is very scarce along its distribution range and virtually non-existent in the Mediterranean. Its life-history traits, such as age, growth and reproduction, have been investigated in the Canarian archipelago waters (Northwest Africa) (Pajuelo *et al.* 2003a; b) indicating that *P. incisus* is a fast growing and moderately short-lived species (ages up to seven years) as well as being a gonochoric species with no evidence of sexual dimorphism, which reaches first maturity at the end of the second year of life when the median size at maturity (L_{50}) is 18.3 cm TL and whose spawning takes place throughout the year. Regarding the Mediterranean Sea, the only available information on the reproductive biology of the bastard grunt relates to specimens inhabiting the coastal waters off the Gulf of Tunis (Chakroun-Marzouk & Ktari 2006; Fehri-bedoui & Gharbi 2008) where sexual activity extended from June to September and L_{50} was estimated at 15.33-16.13 cm TL.

1.5.3. European barracuda (Sphyraena sphyraena) and yellow-mouth barracuda (S. viridensis)

Like all barracudas, the yellow-mouth barracuda (*Sphyraena viridensis,* Cuvier 1829), like the European barracuda (*Sphyraena sphyraena,* Linnaeus 1758), have a slender fusiform body with a conical, hydrodynamical snout and their mouth, which is long, has low protractile capacity and a prognatic lower jaw, with two rows of long canine-like teeth (Barreiros *et al.* 2002) (Fig. 1.4). The body of both species is darkish grey to bluish dorsally and silvery ventrally and the upper half of the body has numerous vertical dark bands that extend below the lateral line in the anterior part of the flanks, although juveniles are usually more greenish to dark yellow. Size (total length, TL) is remarkably different between these barracuda species as adults, with *S. viridensis* being considerably larger (commonly from 100 to 120 cm TL but sometimes it can reach 150 to 160 cm TL) than *S. sphyraena,* whose average size is usually between 30 and 50 cm TL (Golani *et al.* 2006; Bariche 2012; Kalogirou *et al.* 2012a). Three main morphological characteristics have been suggested to avoid misidentification between these two barracuda species (Relini & Orsi-Relini 1997; Kožul *et al.* 2005): preoperculum scale pattern (entirely scaled in *S. sphyraena* but not in *S. viridensis*), pectoral fin rays (13 in *S. sphyraena*, 15 in S. *viridensis*) and scales above the lateral line (15-17 in *S. sphyraena,* 21-22 in *S. viridensis*) (Fig. 1.4).

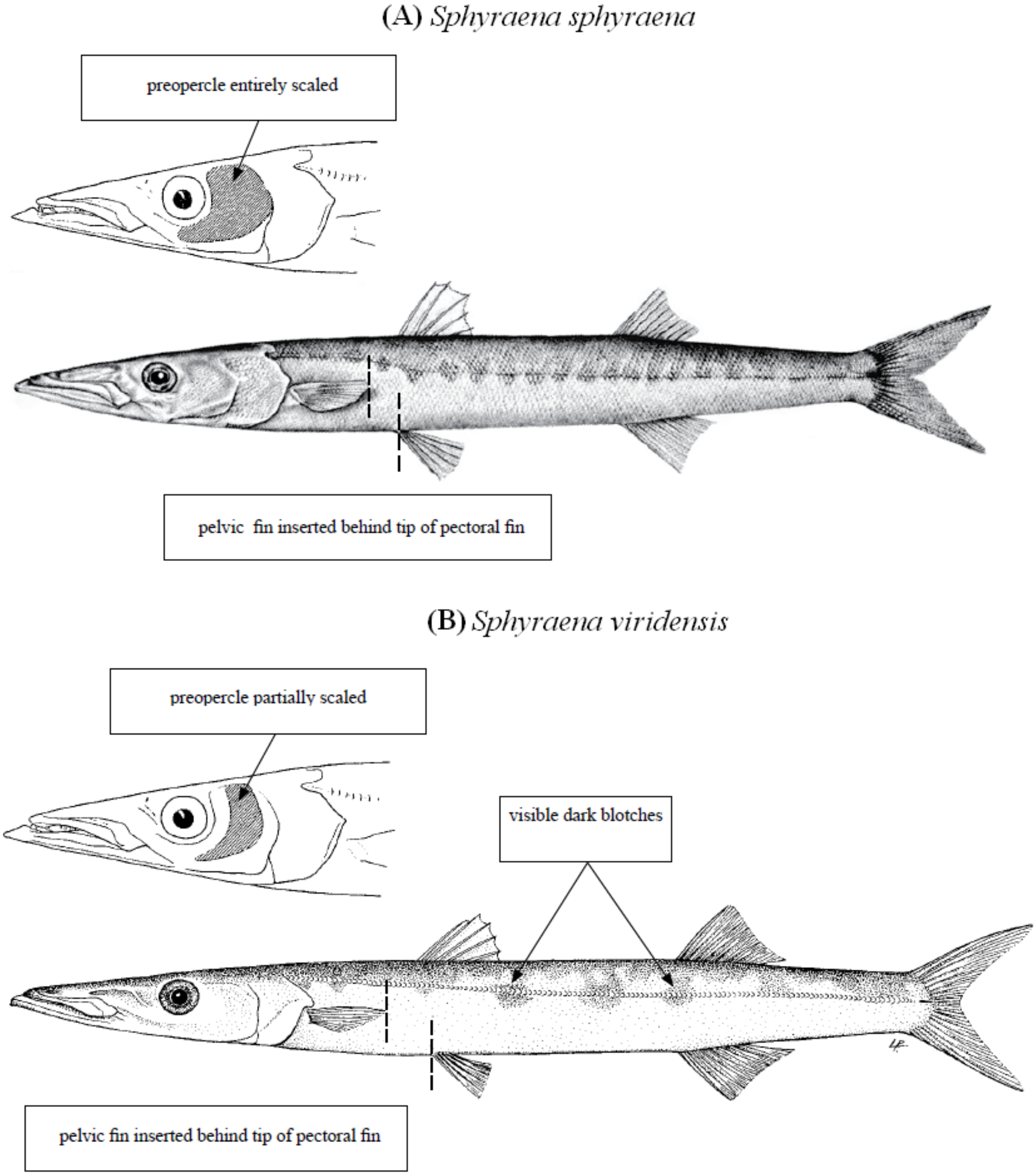

Fig. 1.4 The European barracuda, *Sphyraena sphyraena* (A), and the yellow-mouth barracuda, *Sphyraena viridensis* (B). Illustrations modified from Bariche (2012).

Sphyraena viridensis usually inhabits the pelagic zone of the water column, with smaller individuals in shallow waters, and occurs in Eastern Central Atlantic at Madeira, Cape Verde and Canaries Islands, and in the Mediterranean along the Italian shores as well as in the Balearic and Sardinian waters (Ben-Tuvia 1986; Relini & Orsi-Relini 1997) and the Azores Archipelago (Santos *et al.* 1997; Barreiros *et al.* 2002). However, its geographical range is probably wider because this species is often confused with *S. sphyraena* which has a wider distribution in the Eastern Atlantic: Bay of Biscay to Mossamedes (Angola), including the Mediterranean and Black Sea, Canary Islands, and Azores. However, recently unusual *Sphyraena viridensis* records have been reported in the northern Adriatic Sea (Dulčić & Soldo 2004; Kožul *et al.* 2005; Dulčić *et al.* 2009), in the Balearic Islands (Massutí *et al.* 2001) and French Mediterranean (Seytre & Francour 2009).

The biology of both barracuda species has been treated in only a few scientific publications. The growth (Allam *et al.* 2004a) and reproduction (Allam *et al.* 2004b) of both species have been investigated in the Egyptian Mediterranean waters. The feeding ecology of both species have been also analyzed in the Eastern Mediterranean (Rhodes Island) (Kalogirou *et al.* 2012a); and the food habits, schooling and predatory behaviour of *S. viridensis* in the Azores Archipelago has been also reported (Barreiros *et al.* 2002). However, the information regarding this two barracuda species in the NW Mediterranean has not yet been described in any detail.

1.5.4. Pompano (Trachinotus ovatus)

The pompano (*Trachinotus ovatus*, Linnaeus 1758) is a slender-bodied compressed fish, characterized by 3-5 lateral oval blotches and two black spots on the dorsal and anal fins (Fig. 1.5). The pompano is a pelagic coastal and schooling species, member of the family Carangidae, that occurs primarily in brackish environments (especially young) and as adults are moderately common in shallow waters in areas of surge, over sand or mud bottoms where they are commonly caught commercially with trawls, purse seines, traps, and hook-and-lines (Smith-Vaniz 1986; Schneider 1990).

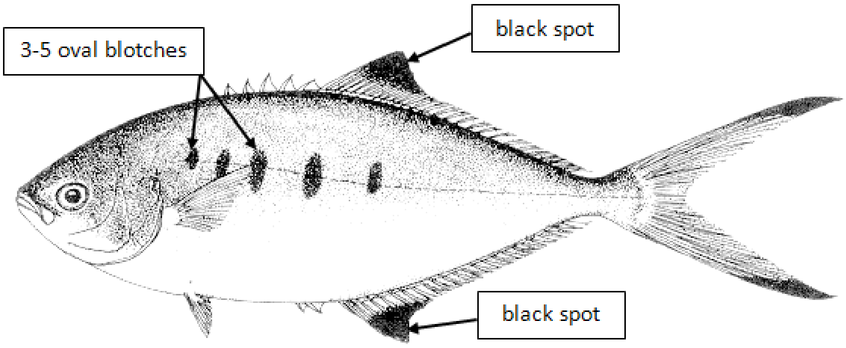

Fig. 1.5 The pompano, *Trachinotus ovatus*. Illustration modified from Schneider (1990).

It is distributed in the Mediterranean (except the Black Sea), the eastern Atlantic northward to the Gulf of Biscay and is a rare vagrant in British and Scandinavian waters (Schneider 1990; Tutman *et al.* 2004). It is also common along the African coast, including the offshore islands, southwards to southern Angola (Smith-Vaniz 1986). Apparently it has become more frequent in the Gulf of Roses and adjacent waters (southern Gulf of Lyon) (Lloret *et al.* 2015b). Unfortunately, records of the abundance of this species within the area are virtually non-existent because, to date, the pompano is caught unintentionally while targeting other species, and thus considered as a bycatch species among the fisheries of the NW Mediterranean Sea. For this reason, the commercial value of the pompano is minor.

The scientific information regarding its biology is considerably sparse, but include the biochemical aspects of the reproduction in female pompano in Egyptian waters (Assem *et al.* 2005); the diet and diel feeding activity of juvenile pompanos from the southern Adriatic Sea (Batistić *et al.* 2005); the feeding and growth of wild-caught pompano reared under captivity in Croatia coastal waters (Tutman *et al.* 2004) and the length-weight relationships for specimens cultured in floating sea cages in South China Sea (Guo *et al.* 2014) as well as for wild populations from the Azores Islands (Morato *et al.* 2001) and from the western Mediterranean (Morey *et al.* 2003). Meanwhile, other reproductive traits that may indicate the breeding season, sexual maturation and spawning in both sexes of this species is virtually non-existent in the NW Mediterranean and elsewhere along its distribution range.

1.6. Hypothesis

I have hypothesized that the sea water temperature would influence the abundance of thermophilic fish in the NW Mediterranean by exerting an effect on different aspects of their condition and reproduction, including life-history traits such as condition, maturity, spawning phenology, fecundity and egg quality. For this reason, I have assessed whether our understanding of the observed changes in the spatio-temporal abundance of these four warm-water species –the yellow-mouth barracuda (*Sphyraena viridensis*), the bastard grunt (*Pomadasys incisus*), the bluefish (*Pomatomus saltatrix*) or the pompano (*Trachinotus ovatus*) – can be enhanced with a research approach focused on the climate-driven spatio-temporal variations of their life-history traits. My aim is to shed light on their physiological adaptations to the rising sea temperatures of the Mediterranean.

1.7. Objectives

The general objective of this PhD thesis was to provide critical knowledge on the spatio-temporal variations of the condition and reproductive-based life-history traits of these four warm-water species, which are expanding northwards within the Catalan Sea (NW Mediterranean) in line with the trends of increasing sea water temperatures over the last decades. The specific objectives were:

- to analyse and describe the temporal and spatial variations (anomalies, trends and seasonalities) of the sea surface temperatures (SST) within the NW Mediterranean Sea over the last three decades using data retrieved from two areas with different thermal regimes: the more northerly Gulf of Roses and the more southerly Ebre Delta (Chapter II).

- to evaluate the influence of SSTs on three important aspects of population dynamics of bluefish (*Pomatomus saltatrix*) in the NW Mediterranean: condition, reproduction and abundance (as reflected in catch per unit effort), by collecting specimens from two areas with different thermal regimes and analyzing the spatial variability of the average parameters (Chapter III).

- to compare two key life-history traits, condition and reproduction, of the bastard grunt (*Pomadasys incisus*) from two separate areas of the north-western Mediterranean with different thermal regimes in order to assess whether or not the particular life history traits of this thermophilic species may contribute to its expansion in the area (Chapter IV).

- to explore and compare the most relevant life-history traits, condition and reproduction of the temperate and thermophilic barracudas in order to investigate whether the recent *S. viridensis* catches in the study area coupled to increased SSTs in the north-west Mediterranean Sea could be explained (Chapter V).

- to explore the reproductive traits of the pompano (*T. ovatus)* and discuss the results in light of the expansion and establishment of this species in the colder waters of the NW Mediterranean along with the temporal variations of the SSTs in order to investigate whether we could explain if its seasonal arrival and/or reproductive traits are triggered by the physical conditions of the study area (Chapter VI).

1.8. Study area

This study was conducted in the north-western (NW) Mediterranean Sea which is located between the Ebre River Delta and the area of Marseille, Toulon, and occupies approximately a sea area of 108,000 km^2, including the Catalan Sea which is 400 km long (from the Ebre Delta to the Cap de Creus) and the Gulf of Lions which is located between the north of Cap de Creus and the islands of Hyères (France) (Salat 1996; Salat & Pascual 2002). Within the NW Mediterranean, two particular study areas were selected as case studies: the more northerly Gulf of Roses and the more southerly Ebre Delta which are known to have different thermal regimes (Fig. 1.6).

The main characteristic of the marine circulation of the study area (Fig 1.6) is the presence of an intense current, known as the Northern Current, which runs through the continental slope of the Northwestern Mediterranean between isobars 1000 and 2000 m depth from northeast to the southwest (Millot 1990). In the Gulf of Lion zone, the Northern Current is reinforced by the presence of the continental slope front that separates the waters of the continental shelf. Therefore, when the Northern Current passes through the Gulf of Lion and goes on to the Catalan Sea, it transports colder and less salty surface water masses than those in the Gulf of Lion (Millot 1990). To the south, this marine current flows following the continental slope in a southwesterly direction to the north of the

Eivissa Channel, where it divides into two branches, one that goes on to the SW and another that turns in cyclonic direction and returns to the NE as the Balearic Current.

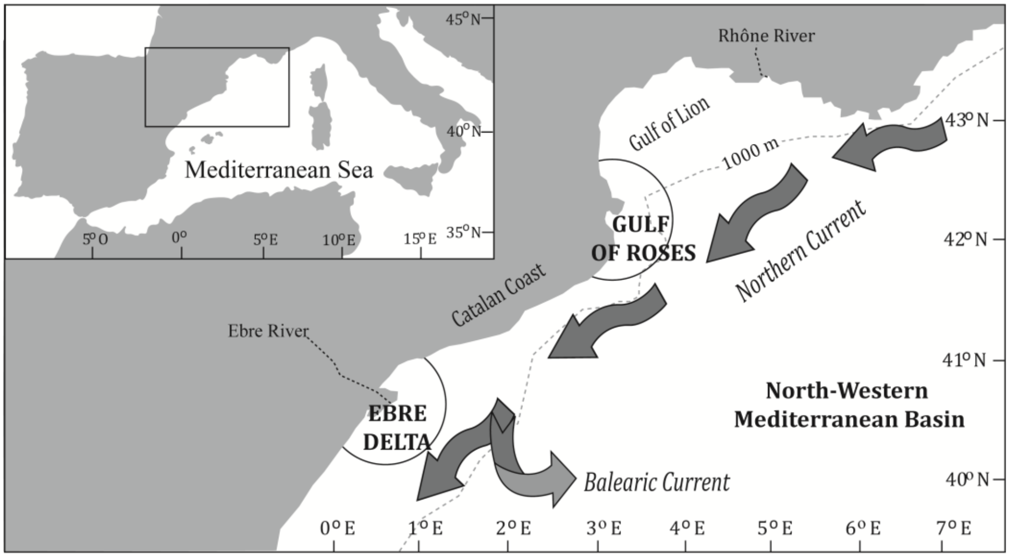

Fig. 1.6 Map of the north-western Mediterranean basin showing both study areas, the more northerly Gulf of Roses and the more southerly Ebre Delta, along the Catalan coast. Principal characteristics of the circulation of the region and 1000 m isobaths are also shown.

The continental shelf of the study area is very thin (less than 6 km width), except the zones of the Gulf of Lion and the Ebre Delta where the continental shelf is 75 and 80 km wide (Fig 1.6), respectively (Rodríguez 1982). The continental shelf width and the limited depth in those areas allows the establishment of upwelling mechanisms linked with the wind action (Rodríguez 1982; Salat *et al.* 2002). In both areas, there are also important hydrographic inputs, such as the Rhone River and the Ebre River, which supply an important quantity of sediments, nutrients and organic matter to the continental shelf in the Gulf of Lion and the Ebre Delta area, respectively (Margalef 1989; Salat 1996; Salat *et al.* 2002). All these meteorological, hydrographical and oceanographic singularities make both the Gulf of Lion and the Ebre Delta highly productive areas compared to the rest of the Mediterranean Sea. In fact, these areas have been considered as Essential Fish Habitats for feeding, spawning and recruitment for a number of marine species of commercial interest (NMFS 1997).

In the NW Mediterranean Sea, several seasonal meteorological variations occur throughout the year. During the winter, the dominant winds are mainly from a northeasterly direction, whereas in summer, Eastern winds dominate in the area. Particularly, Northern and Northeastern dominant winds, known in North Catalonia as the “tramuntana”, occur in the Cap de Creus zone and the Gulf of Lion. The temperature seasonality is characterized by dry and hot summers with the development of a well-defined thermocline that reaches 120 m depth and limits the vertical interchanges in the water column, and by the presence, in late winter (January-March), of other weaker winds, resulting in temperate weather with moderate and rainy winters and dry and hot summers. Although the water temperature is known to vary along the latitudinal gradient within the NW Mediterranean, with significantly colder sea water temperatures in the northern zones compared to more southern zones (Salat *et al.* 2002), in general, the water temperature usually has its maximum values during August (mean 23-24°C) and minimum in January (mean 9-10°C) (Millot 1990; Salat 1996).

1.9. Materials and methods

As stated previously, the data for this study was retrieved from two areas with different thermal regimes in the NW Mediterranean Sea: the more northerly Gulf of Roses and the more southerly Ebre Delta. It is worth mentioning that, although the methodologies used in this thesis are summarized in the following paragraphs, the specific materials and methods are presented for each study case (see the Materials and Methods sections from Chapters II to VI for more details).

1.9.1. Sea temperature data

The data on sea surface temperature (SST, in °C) from both sampling areas was retrieved from the International Comprehensive Ocean-Atmosphere Data Set (ICOADS) (ds540.0-Release 2.5) (Woodruff *et al.* 2011). This data comprised individual daily mean SST observations for 1° latitude x 1° longitude units, in which case the SSTs time series were set from two 1° squares: the Gulf of Roses (42.0 to 43.0°N and 3.0 to 4.0° E) and the Ebre Delta (40.0 to 41.0°N and 0.0 to 1.0° E). The mean monthly and seasonal values of SSTs were calculated by averaging daily temperatures and, once averaged, these data time series were used to estimate the annual SST anomalies per season, the seasonality and the monotonic trends of the annual, as well as seasonal, long-term variations in the SSTs. Subsequently, in order to evaluate whether sea warming variations and trends in both study areas were significantly different or not from each other, all these parameters were compared to test the spatial variation of the SSTs.

1.9.2. Biological data

1.9.2.1. Abundance-sea water temperature relationships

Firstly, it is worth mentioning that the method described in this section was only used for the case study of the bluefish (*P. saltatrix*) since it is currently the only species of our study whose total catches (landings in kg) have actually been recorded on a monthly basis at the fishing ports along the Catalan coast over a long and regular temporal scale. Therefore, the bluefish data - on total monthly landings (recorded in kg) and nominal fishing effort (number of vessels) - was retrieved from the fishery statistics of the Department of Agriculture and Fisheries of the Government of Catalonia (www20.gencat.cat/portal/site/DAR) using information available at two fishing ports from the Gulf of Roses and three from the Ebre Delta area. It should be noticed that the monthly number of active vessels at each port was used as a proxy of fishing effort at each port, in order to estimate the time series of the monthly catches per unit effort (CPUE), expressed as kg per vessels. Then, the analyses focused on determining and quantifying the possible relationships between the monthly time series of bluefish catch per unit effort (CPUE) and SST using bivariate ARIMA (autoregressive-integrated-moving-average) transfer functions (Box & Jenkins 1976).

1.9.2.2. Fish condition and reproduction evaluation

Specimens for each study species were collected monthly from the commercial catch landed at the port of Roses (Gulf of Roses) and at the port of Sant Carles de la Ràpita (Ebre Delta) from 2010 up to 2012, shortly after the small-scale and bottom-trawl fishing vessels had landed their catches. It should be noticed that fishermen were asked for the approximate location and depth where the specimens were caught in order to be sure that the origin of the samples was within the coastal waters of each study area.

The sampling strategy was devised to collect specimens of each species across years, months, seasons and sizes, always subject to availability during the sampling period (Table 1.2). However, this biological information was organized, grouped and then compared in different ways; hence, different biological data-sets were used to cope with the objectives of the study approaches applied in each study case. The first study approach (namely thermal-related spatiotemporal variations) was investigated in *P. saltatrix* (Chp. III) and *P. incisus* (Chp. IV) by selecting specimens from two areas with different thermal regimes and analyzing the spatial variability of the biological parameters between the more northerly Gulf of Roses and the more southerly Ebre Delta. The second study approach (namely temperate vs thermophilic traits comparison) was considered in the case of the barracudas (Chp. V), in which specimens of *S. sphyraena* and *S. viridensis* were retrieved only from the Gulf of Roses and then their biological information was compared to each other. Finally, in the third study approach (namely thermal-related reproductive traits) used in *T. ovatus* (Chp. VI), the dataset was organized inter-annually in order to evaluate whether the temporal variation of its reproductive traits were related to the temporal variations of the SSTs observed in the Gulf of Roses. More details of the organization of the biological datasets and the way in which variables were analysed can be found in in each specific chapter.

Table 1.2 Summary of the general sampling protocol showing the monthly sampling effort (*n*) of specimens collected in each study case per species and sex. Size range (in cm total body length) is also shown in parenthesis. All years pooled.

Month	**Total number of samples (*n*) and size range (in cm TL) per species**									
	P. saltatrix (Chp. III)		*P. incisus* (Chp. IV)		*S. sphyraena* (Chp. V)		*S. viridensis* (Chp. V)		*T. ovatus* (Chp. VI)	
	Females	Males	Females	Males	Females	Males	Females	Males	Females	Males
Jan	1 (30.0)	1 (30.0)	0	0	2 (38.5 - 43.5)	2 (30.0 - 40.5)	0	0	0	0
Feb	0	0	0	0	1 (37.5)	1 (40.5)	0	0	0	0
Mar	0	0	4 (20.5 - 24.0)	3 (22.0 - 24.0)	2 (31.0 - 31.5)	3 (39.0 - 42.0)	2 (69.0 - 71.5)	2 (81.0 - 87.5)	0	0
Apr	0	2 (30.0 - 49.5)	4 (21.5 - 23.5)	3 (22.0 - 23.0)	2 (41.0 - 43.5)	1 (38.5)	2 (67.5 - 74.5)	2 (77.5 - 84.5)	0	0
May	24 (29.0 - 91.0)	28 (29.0 - 62.0)	59 (16.0 - 28.5)	21 (19.5 - 25.5)	29 (33.0 – 49.0)	17 (28.5 - 43.5)	5 (53.5 - 94.5)	3 (53.0 - 67.5)	1 (37.5)	5 (31.0 - 40.0)
Jun	40 (26.0 - 76.5)	33 (26.0 - 66.5)	33 (17.5 - 26.0)	29 (18.0 - 25.0)	30 (30.5 - 48.0)	12 (28.5 - 43.0)	11 (53.0 - 97.0)	16 (52.5 - 85.0)	6 (32.0 - 39.5)	11 (31.0 - 38.0)
Jul	13 (46.0 - 85.0)	4 (49.0 - 66.0)	58 (18.0 - 28.5)	39 (17.5 - 26.5)	42 (29.0 - 49.0)	25 (27.5 - 41.0)	37 (54.5 - 91.0)	55 (54.0 - 83.0)	18 (30.5 - 39.0)	15 (31.0 - 39.0)
Aug	73 (34.0 - 72.5)	61 (32.5 - 79.0)	118 (15.5 - 29.0)	122 (13.0 - 26.0)	42 (32.0 - 46.0)	20 (29.0 - 49.0)	17 (46.0 - 99.5)	28 (44.0 - 94.0)	66 (30.0 - 44.0)	49 (30.0 - 41.0)
Sep	7 (48.5 - 55.0)	7 (44.0 - 50.0)	47 (13.5 - 27.0)	39 (13.5 - 24.5)	24 (35.5 - 45.5)	15 (33.5 - 42.5)	6 (54.0 - 76.5)	8 (41.0 - 67.0)	27 (25.5 - 42.5)	28 (25.5 - 40.0)
Oct	7 (29.5 - 53.0)	4 (49.0 - 52.5)	2 (17.5 - 20.0)	2 (18.5 - 22.0)	8 (37.0 - 42.0)	5 (29.5 - 38.5)	2 (81.5 - 84.0)	2 (28.5 - 75.5)	0	0
Nov	6 (49.0 - 62.0)	6 (47.0 - 53.5)	3 (20.5 - 21.5)	3 (20.5 - 25.0)	17 (28.0 - 47.5)	9 (27.0 - 40.0)	4 (77.5 - 100.0)	2 (30.0 - 60.5)	0	0
Dec	4 (45.0 - 51.5)	4 (48.5 - 50.0)	4 (21.0 - 26.0)	3 (22.0 - 24.0)	4 (27.0 - 41.0)	3 (23.5 - 35.0)	0	0	0	0
Total	**175** **(26.0 - 91.0)**	**150** **(26.0 - 79.0)**	**332** **(13.5 - 29.0)**	**264** **(13.0 - 26.5)**	**203** **(27.0 - 49.0)**	**113** **(23.5 - 43.5)**	**86** **(46.0 - 100.0)**	**118** **(28.5 - 94.0)**	**118** **(25.5 - 44.0)**	**108** **(25.5 - 41.0)**

Once in the laboratory, we recorded the total length to the nearest 0.5 cm and total weight to the nearest 1 mg. Subsequently, the specimens were dissected and eviscerated, and the somatic or eviscerated body weight, the liver and the gonad weights were obtained to the nearest 1 mg. Finally, the gonads were fixed in buffered formalin (4%) for further histological processing and fecundity estimation. The annual reproductive cycle of each study species was also estimated by determining sex and reproductive phase of each specimen using a histological analysis of the gonads to determine the stages of development of their germ cells. The assignment of both female and male reproductive gonadal phases was based on the histological maturity classification criteria from Brown-Peterson *et al.* (2011), in which the developmental phases of the gonads are defined as immature (IMM), developing (DEV), spawning capable (SC) and the corresponding sub-phases: actively spawning (AS), regressing (RGS), and regenerating (RGN). In females, during all these phases of gonadal development, the oocytes develop through two major stages, (1) primary growth (including the chromatin nucleolar and the perinucleolar phases, where oocyte development is gonadotropin-independent) and (2) secondary growth (including cortical alveoli, vitellogenesis and oocyte maturation, where oocyte development is gonadotropin-dependent). Throughout secondary growth, several important and visible changes occur within the oocyte and it is commonly subdivided into the following stages: pre-vitellogenic (cortical alveolar CA), vitellogenic (early Vtg-1, mid Vtg-2, and advanced vitellogenesis Vtg-3), maturation (germinal vesicle migration GVM, and hydration H). It should be noticed that despite the fact that CA oocytes are not vitellogenic, the growth of CA and vitellogenic oocytes are both gonadotropin-dependent and hence part of the secondary growth stage, thus in line with Brown-Peterson *et al.* (2011), the presence of CA necessarily indicated that the female has matured. On the other hand immature individuals were exclusively classified as immature when they presented only oogonia and primary growth oocytes. Meanwhile, male specimens were classified as immature by the presence of only primary spermatogonia (Sg 1) and no lumen in the lobules of their testis. This maturity staging system was adopted for all study cases in this thesis. More detailed information regarding the histological descriptions of the phases of gonadal development can be found in Brown-Peterson *et al.* (2011).

For the fish condition and reproduction evaluation, the following parameters were used: the length-weight relationships (LWR), the hepatosomatic index (HSI), the gonadosomatic index (GSI), size at 50% maturity (body length at which 50% of the individuals were mature), the fecundity (batch fecundity BF and relative batch fecundity RBF), the mean diameter of the oocytes at each oocyte developmental stage, the oocyte size-frequency distribution, the egg quality (dry weight) and atresia (prevalence and relative intensity). The number of samples made available for these analyses (per study case and source of variation examined, i.e., area, species and year) are shown in Table 1.3.

Table 1.3 Summary of the number of samples (*n*) available for the different analyses used in this thesis for each source of variation examined in each study case: (a) the area (GR: Gulf of Roses or ED: Ebre Delta) for the studies of *P. saltatrix* (Chp. III) and *P. incisus* (Chp. IV), (b) the species (*S. sphyraena* or *S. viridensis*) for study of the barracudas (Chp. V), and (c) the year (2010, 2011 or 2012) of the study of *T. ovatus* (Chp. VI).

Analysis/Variation Sources	**Total number of samples (*n*) per study case**								
	P. saltatrix		*P. incisus*		Barracudas		*T. ovatus*		
	GR	ED	GR	ED	*S. sphy*	*S. vir*	2010	2011	2012
Hepatosomatic index	138	187	267	329	316	204	NA	NA	NA
Gonadosomatic index	138	187	267	329	316	204	55	58	113
Histology of the gonads	138	187	267	329	316	204	55	58	113
Length at 50% maturity	138	187	267	329	316	204	55	58	113
Fecundity	5	8	41	57	74	34	8	8	8
Oocyte diameter	200	200	200	200	200	200	150	150	150
Egg quality	20	20	20	20	20	20	20	20	20

CHAPTER II: Spatio-temporal analyses of the sea water temperature of the study area

In this section the 1970-2011 sea surface temperatures of the study areas were retrieved and then used to describe their anomalies, trends, seasonalities and spatio-temporal variations.

CHAPTER II

Spatio-temporal analyses of the sea water temperature of the study area

2.1. Abstract

In this study the sea surface temperatures (SST), over the 1970-2011 period, were retrieved from the International Comprehensive Ocean-Atmosphere Data Set (ICOADS) and used to describe and compare the anomalies, trends, seasonalities and the spatio-temporal variations of two areas with different thermal regimes along the latitudinal gradient of the northwestern Mediterranean Sea: the more northerly Gulf of Roses and the more southerly Ebre Delta. The annual anomalies indicated two SST regimes at each season: the period 1970-1984 mostly characterized by negative SST anomalies, and the period 1985-2011 when positive SST anomalies were more frequently observed. Significant annual increasing monotonic trends were observed in the SSTs either for the Ebre Delta (0.027°C yr^{-1}) and the Gulf of Roses (0.023°C yr^{-1}). Although the SSTs in both study areas showed similar sea warming seasonal trends significant monotonic trends were only observed in spring and summer and not so during autumn and winter. Any significant difference was observed when SST increasing trends were compared between study areas at each season indicating that the sea warming trends are similar between these two areas. However, average SSTs were found significant different between the Gulf of Roses and the Ebre Delta at each season indicating thus that the SSTs have been significantly higher in the south than in the north. The SSTs in showed similar and clear seasonality patterns in both areas: SSTs from June through October were warmer than the annual average when seasonal values were up to 36% above the annual means. A slightly and progressive change in the seasonality variation was observed from 1970 through 2011 in the seasonal values in the spring and summer months might indicate that sea water in the NW Mediterranean nowadays is warming up earlier in the year than 30 years ago.

Keywords: sea surface temperatures; sea warming; trends; anomalies; seasonalities; spatio-temporal variations; north-west Mediterranean; Gulf of Roses; Ebre Delta

2.2. Introduction

Although sea temperature variations are mainly controlled by variations in the air–sea heat flux as well as in the vertical mixing and the horizontal advection of heat (Skliris *et al.* 2011), several studies have shown that the temperature of the Mediterranean Sea surface water has increased during the last decades. Nykjaer (2009) observed between 1985 and 2006 that the temperature in the upper layer of the Mediterranean Sea has been increasing at an average rate of 0.03 ± 0.008 °C year^{-1} for the western Mediterranean basin, and 0.05 ± 0.009 °C year^{-1} for eastern basin. In NW Mediterranean, Diaz-Almela *et al.* (2007) observed over 24 years period a rapid warming of surface water masses (0.04 ± 0.01 °C year^{-1}). In the same area, Salat & Pascual (2002) observed that since 1970 the average annual temperature has increased by 1.1°C (0.04 °C year^{-1}) at surface and 0.7 °C (0.025 °C year^{-1}) at 80 meters depth. Similarly, Calvo *et al.* (2011) observed that the sea temperature has increased around 1.1 °C in the upper-most waters (0–50 m) and around 0.7 °C at 80 m over the 1974–2009 period.

Lelieveld *et al.* (2002), in a study covering the period 1930–2000, noticed that sea surface temperature (SST) variability remained low for several decades after 1930 but cooling took place during the early 1970s followed by an extensive warming period that began in approximately 1980. A similar pattern was observed by Rixen *et al.* (2005) who noticed that cooling took place in the upper 150 m layer of the Western Mediterranean until the mid-1980s, when warming started, while the Eastern Mediterranean cooled between mid-1970 and the mid-1980s, then warmed slowly. Both Lelieveld *et al.* (2002) and Rixen *et al.* (2005) reported an increase in temperature between 1980–2000 to the order of 0.5 °C. A 30-year data set (1974–2005) from the Spanish Catalan coast first demonstrated the warming of the littoral zone at four different depths from the surface to 80m showing a clear trend at all depths, with an impressive warming of 1.4 °C at 20 m (Vargas-Yáñez *et al.* 2008; Coma *et al.* 2009).

The main objective of this study was to explore, analyse and describe the temporal and spatial variations (anomalies, trends and seasonalities) of the SST within the northwestern Mediterranean Sea over last three decades using data retrieved from two areas with different thermal regimes along the latitudinal gradient: the more northerly Gulf of Roses and the more southerly Ebre Delta. It should be noticed that in those very same study areas it was carried out the sampling of specimens of *Pomatomus saltatrix*, *Pomadasys incisus*, *Sphyraena sphyraena* and *Sphyraena viridensis* that were used in the other researches described in the following chapters.

2.3. Materials and methods

2.3.1. Data collection

Sea surface temperature (SST, °C) data from both areas (the Gulf of Roses and the Ebre Delta) was retrieved from the International Comprehensive Ocean-Atmosphere Data Set (ICOADS) for the period 1970-2011 (ds540.0-Release 2.5) (Woodruff *et al.* 2011). These data comprise individual daily mean sea surface temperature observations for 1° latitude x 1° longitude units. In this study we used time series from two 1° squares along the northwestern Mediterranean: the Gulf of Roses (42.0-43.0°N, 3.0-4.0° E) and the Ebre Delta (40.0-41.0°N, 1.0-2.0° E). Mean seasonal and monthly values of SSTs in both areas were calculated by averaging measured several daily temperatures per seasons and per month. Seasons were defined as follows: winter (January, February, and March), spring (April, May, and June), summer (July, August, and September) and autumn (October, November, and December).

2.3.2. SST anomalies and trends in the NW Mediterranean Sea

In order to evaluate the season in which the sea warming was most pronounced, its corresponding SST anomalies and trends were calculated at each season per study area. First, annual SST anomalies per season were computed as deviations from the corresponding overall annual mean per season. Then annual and seasonal long-term variations of mean SST were investigated separately in the Gulf of Roses and the Ebre Delta, as well as the mean rate of change and the long-term linear trends looking for significant existence of monotonic trends with the nonparametric Mann–Kendall trend test (Mann 1945) using the Excel template application MAKESENS (Salmi *et al.* 2002). Subsequently, an overall Seasonal Kendall (SK) test, which combines the individual mean monthly SST into one overall test whether the SST changes in are still in a monotonic trend over time even with seasonal trend in the data, was also carried out using the software developed by Helsel *et al.* (2006). Finally, the slopes of linear regression models (SST increasing trends) of each area were compared to each other using an ANOVA regression lines comparison test in order to evaluate whether sea warming trends in both areas were significant different or not from each other. Spatial variation of SSTs at each season was evaluated using ANOVAs to examine differences between the Gulf of Roses and the Ebre Delta.

2.3.3. ARIMA approach to model seasonality of SSTs

The time series of SSTs were described by calculating the seasonal component using the decomposition method 'tramo-seats' to build univariate ARIMA (autoregressive-integrated-moving-average) models (Box & Jenkins 1976) with the statistical package ForeTESS developed by the Polytechnic University of Catalonia (Prat *et al.* 2000). The SSTs were modelled on a monthly basis as linear functions of past values of the series and/or previous random shocks (or errors) to estimate the seasonal component that shows the spectral peaks at seasonal frequencies (the seasonal value for a given month is the percentage above/below the annual mean).

2.4. Results

2.4.1. Anomalies and trends of the SSTs

The long-term anomalies showed in general two SST regimes at each season either in the Gulf of Roses and the Ebre Delta: the period 1970-1984 mostly characterized by negative SST anomalies, and the period 1985-2011 when positive anomalies were more frequently observed (Fig. 2.1).

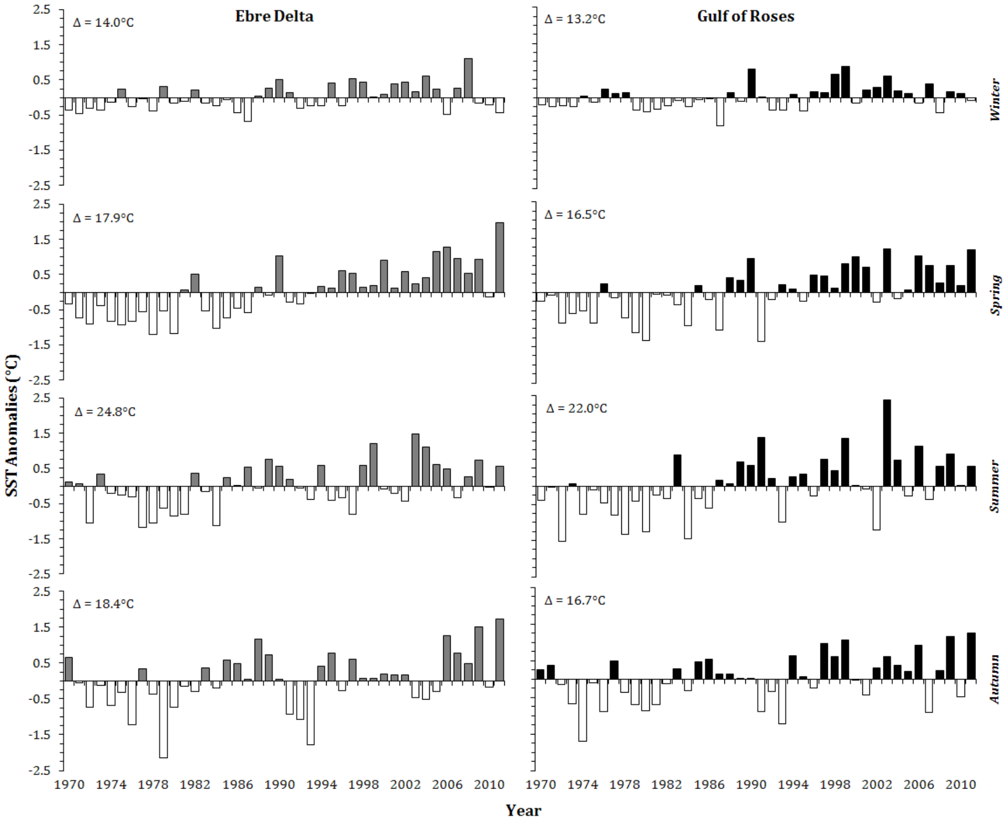

Fig. 2.1 Annual SST anomalies per season (from January 1970 to December 2011) estimated separately for the Gulf of Roses and the Ebre Delta. The overall mean SST for each season is shown as Δ.

The results obtained by applying the Seasonal Kendall (SK) test showed a significant increasing monotonic trend throughout the entire period 1970-2011 in the SSTs (Fig. 2.2) either for the Ebre Delta (0.027 ± 0.016 °C yr^{-1}, Z = 5.78, $p < 0.01$) and the Gulf of Roses (0.024 ± 0.013 °C yr^{-1}, Z = 5.62, $p < 0.01$). Both SK tests showed similar Kendall's tau correlation coefficient, Gulf of Roses ($\tau = 0.301$) and Ebre Delta ($\tau = 0.309$), indicating increasing relationships of SST values over time.

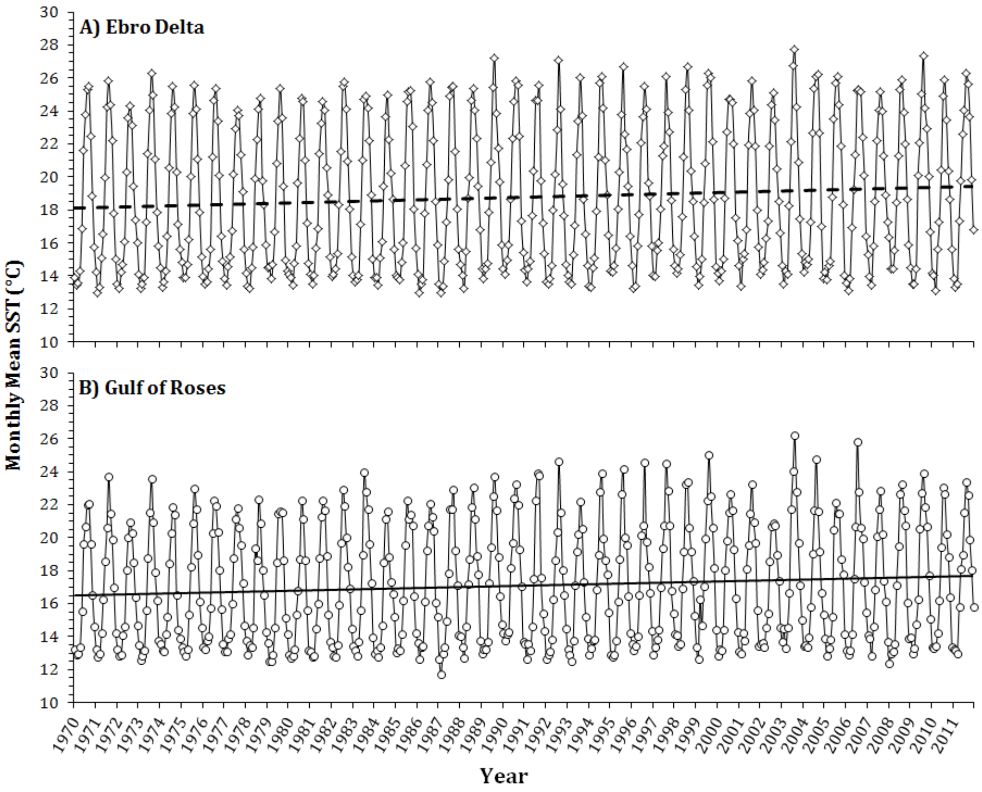

Fig. 2.2 Long-term variations of monthly mean SSTs (since January 1970 to December 2011) in the Ebre Delta (A) and the Gulf of Roses (B). The Seasonal Kendall tests indicated significant a monotonic trend for the Ebre Delta (0.027 ± 0.016 °C yr-1, Z = 5.78, $p < 0.01$) as well for the Gulf of Roses (0.024 ± 0.013 °C yr-1, Z = 5.62, $p < 0.01$). The trends in the Gulf of Roses and the Ebre Delta are illustrated as continuous and dashed lines, respectively.

Although the SSTs in both study areas showed similar sea warming seasonal trends significant monotonic trends were only observed in spring and summer in both study areas and not so during autumn and winter when none significant monotonic trend was observed (Fig. 2.3). The spring mean rate of change was slightly higher in the Ebre Delta (0.047 °C yr^{-1}) than in the Gulf of Roses (0.035 °C yr^{-1}), while the summer mean rate of change was slightly higher in the Gulf of Roses (0.033 °C yr^{-1}) than in the Ebre Delta (0.024 °C yr^{-1}) (Fig. 2.3). Even though, the SST has been always higher at the Ebre Delta area any significant difference was observed when trends were compared between study areas at each season: winter (ANOVA, $F_{1,3} = 0.03$, $p = 0.769$), spring (ANOVA, $F_{1,3} = 1.89$, $p = 0.174$), summer (ANOVA, $F_{1,3} = 0.67$, $p = 0.415$), autumn (ANOVA, $F_{1,3} = 0.09$, $p = 0.759$), which in turn suggests that the sea warming trends are similar between these two areas of the northwestern Mediterranean sea.

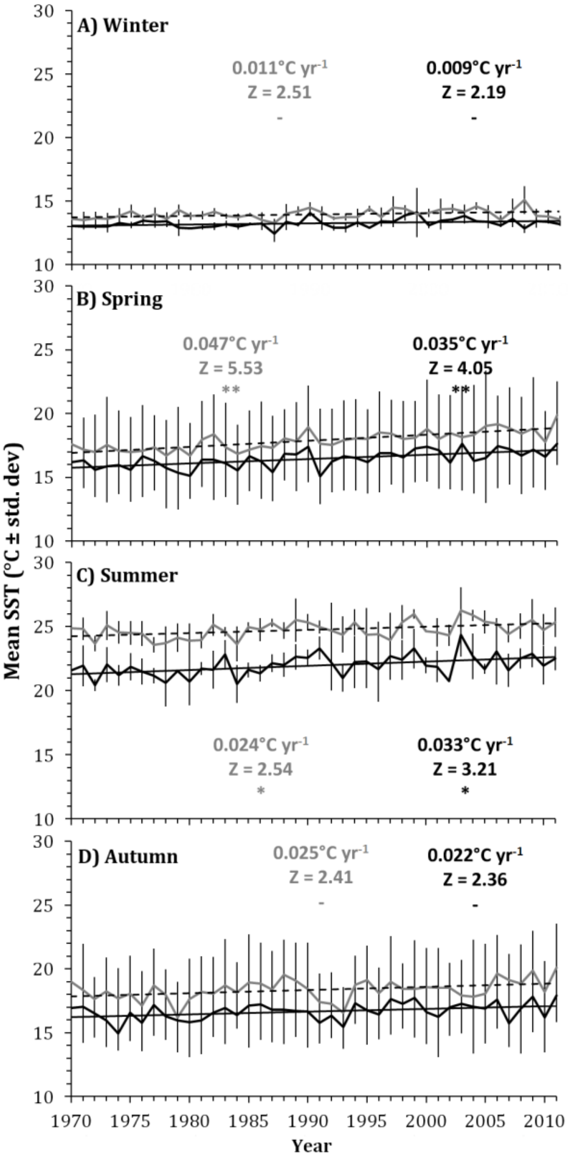

Fig. 2.3 Long-term variations of the mean SSTs per season in the Gulf of Roses (dark lines) and in the Ebre Delta (grey lines). The mean rate of change of each season at the Gulf of Roses (dark) and the Ebre Delta (grey) are given, and the trends in the Gulf of Roses (continuous lines) and in the Ebre Delta (dashed lines) are illustrated. For each season, the Z-statistic of the Mann–Kendall test and the significance level for the existence of a monotonic trend is indicated by one or two asterisks ($p< 0.05$ and $p< 0.01$, respectively) or a dash (no monotonic trend at the $p< 0.05$ level).

Average SSTs were found significant different between the Gulf of Roses and the Ebre Delta at each season (Table 2.1) indicating thus that the SSTs have been significantly higher in the south (Ebre Delta) than in the north (Gulf of Roses) even though only approximately 300 km exists between these two areas.

Table 2.1 SST comparisons between the Gulf of Roses and the Ebre Delta. The mean ± std. dev. (°C) and the coefficient of variation (CV %) are given for each season. The ANOVA significance for each comparison is given with the resulting F-ratio (degrees of freedom) and the p-value.

Source	**Mean ± std. dev. °C (CV %)**		**ANOVA significance**
	Gulf of Roses	*Ebre Delta*	
Winter	13.2 ± 0.3 °C (2.67 %)	14.0 ± 0.4 °C (2.51 %)	$F_{1,82}$ = 88.38; p<0.0001
Spring	16.5 ± 0.7 °C (4.13 %)	17.9 ± 0.7 °C (4.11 %)	$F_{1,82}$ = 87.78; p<0.0001
Summer	22.0 ± 0.8 °C (3.77 %)	24.8 ± 0.6 °C (2.57 %)	$F_{1,82}$ = 299.28; p<0.0001
Autumn	16.7 ± 0.7 °C (3.93 %)	18.4 ± 0.8 °C (4.34 %)	$F_{1,82}$ = 112.31; p<0.0001

2.4.2. Seasonality of the SSTs

The monthly average SSTs in both the Gulf of Roses and the Ebre Delta showed similar and clear seasonality patterns (Fig. 2.4). In both areas, SSTs from June through October were warmer than the annual average when seasonal values were up to 36% above the annual means.

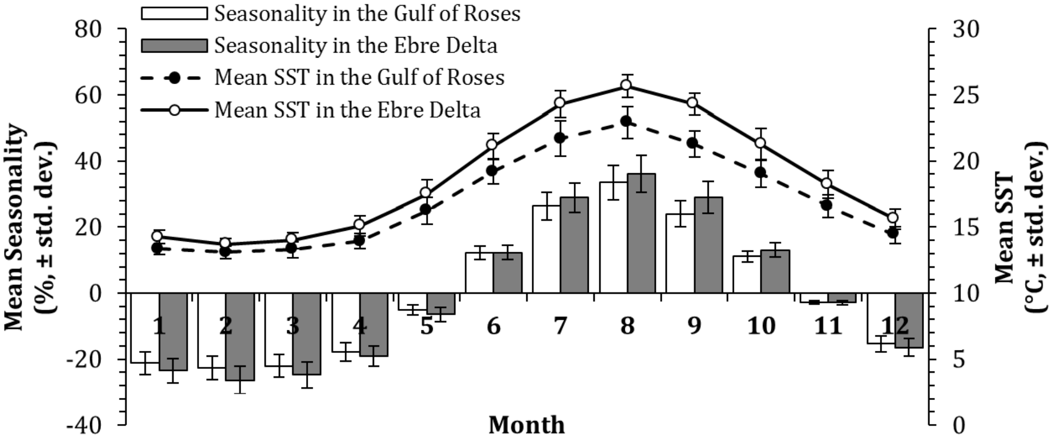

Fig. 2.4 Mean seasonal patterns (% above/below the annual mean) of the SST time series and the actual SST variations per month in the Gulf of Roses and the Ebre Delta, over the period 1970-2011.

A slightly and progressive change in the seasonality variation is noticeable for example when May seasonality values evolution was analyzed (Fig. 2.5). SST seasonal values at the beginning of the time series (May 1970) were about 7.0% and 9.6% below the annual mean in the Gulf of Roses and the Ebre Delta, respectively. And at the end of the time series (May 2011) were about 3.7% and 3.6% below the annual mean in the Gulf of Roses and the Ebre Delta, respectively (Fig. 2.5). This slightly increase from 1970 through 2011 in the seasonal values in this month (May) might indicate a progressive change in the SST seasonality due to the sea warming progressive trend over time. This kind of seasonality change pattern is also observed in the other spring and summer months and could indicate that sea water in the NW Mediterranean nowadays is warming up earlier in the year than 30 years ago.

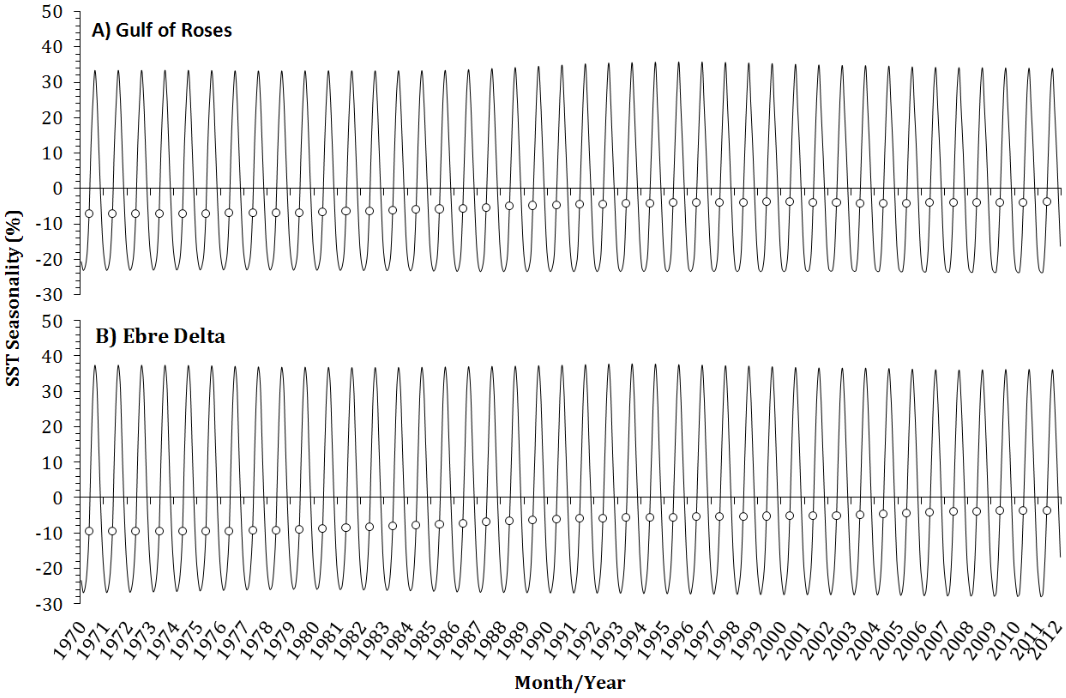

Fig. 2.5 Monthly time series (1970-2011) of SST seasonalities in the (A) Gulf of Roses and (B) the Ebre Delta; ○ indicate the evolution of the May SST seasonality data at their respective seasonal pattern.

2.5. Discussion

The present study has described the anomalies, trends, seasonalities and the spatio-temporal variations of the SST from January 1970 to December 2011 in two areas with different thermal regimes along the latitudinal gradient of the northwestern Mediterranean Sea, the Gulf of Roses and the Ebre Delta.

The annual anomalies indicated two SST regimes at each season: the period 1970-1984 mostly characterized by negative SST anomalies, and the period 1985-2011 when positive SST anomalies were more frequently observed. In contrast with the results presented in this study, Sabatés *et al.* (2012) found analyzing the monthly SST time series (1974-2010) from the L'Estartit meteorological station (located near the Gulf of Roses) three main periods: 1974-1981, characterized by a decreasing trend with monthly values lower than the corresponding monthly means, followed by a transition period from 1982 to 1996, and a period of increasing trend over 1997-2009. Moreover, these authors also detected two remarkable shifts in the sea water temperature: the first one in the early 1980s and the second around 1997.

In this study significant annual increasing monotonic trends in the SSTs were found similar in the Ebre Delta and the Gulf of Roses with alike annual rates of change (0.024-0.027°C yr^{-1}). Similar results have been found by Salat & Pascual, (2002) at the L'Estartit meteorological station, where the linear tendency of the sea water temperatures at surface shows an increase of 1.1°C in 27 years (0.04°C yr^{-1}) and at 80 m depth the tendency shows an increase of 0.7°C in 27 years (0.025°C yr^{-1}). Furthermore, this kind of sea warming trends with around 0.02 °C yr^{-1} order of magnitude have been recorded in other coastal areas of the Mediterranean (Vargas-Yáñez *et al.* 2002, 2005, 2008). These increase trends has not only been observed in the Mediterranean, but also in the nearby North Atlantic (Vargas-Yáñez *et al.* 2004), in the Cantabric Sea (González-Pola *et al.* 2005) and on a global scale (Cabanes *et al.* 2001). In fact, the Working Group of the Intergovernmental on Climate Change (IPCC) shows that, according to different scenarios, the average warming of the planet will be between 1.8 and 4.0°C by 2100 (IPCC 2013).

It has also been suggested that sea warming trends are not a linear or constant processes, and several-years lasting cycles can produce accelerations of the warming rates, as is the case of the 90s decade, or a reduction of them, as was the case from 2001 to 2005, but in both cases these cycles account for a fraction of the mean trend (Vargas-Yáñez *et al.* 2008, 2010). As stated previously in the results section this SST increase is not constant throughout the year. In this study, significant monotonic trends in both study areas were only observed at spring and summer, ranging from 0.024 to 0.047°C yr^{-1}. This large seasonal variability in sea warming has been documented previously in the western basin of the Mediterranean, in which spring display the highest warming rate (Sabatés *et al.* 2006; Nykjaer 2009; Skliris *et al.* 2011). Moreover, in this study it is actually in the spring and summer months that the slightly but progressive change in the annual seasonality variation has been detected from 1970 through 2011 which in turn might indicate that sea water in the NW Mediterranean nowadays is warming up earlier in the year than 30 years ago.

Most numerical models show that the effect of global warming in the Mediterranean Sea during the 21st century will be more pronounced in the upper layers (Marcos & Tsimplis 2008). It has been argued that the observed rapid surface warming in the enclosed and semi-enclosed European Seas such as the Mediterranean, surrounded by major industrial/population agglomerations, may have resulted from the observed large terrestrial warming directly affecting the adjacent coastal seas, whilst regions of freshwater influence seem to play a special role in modulating and exacerbating global warming effects on the regional scale (Belkin 2009). The discussion about an anthropogenic-induced climate change is still open but there is now a wide scientific consensus in favor of this possibility with a growing number of facts supporting the hypothesis (González-Pola *et al.* 2005;

IPCC 2013). A strong correlation has been demonstrated along with other supporting evidence and it is now generally accepted that greenhouse gas emissions are responsible for global warming (Tett *et al.* 2002; IPCC 2013). Regardless the causes, the ocean as a whole also seems to be immersed in a warming process, thus it is very important to continue the monitoring the physical properties of the water masses within the study area in order to improve our knowledge about the processes and changes undergoing in the NW Mediterranean Sea.

CHAPTER III: Reproduction, condition and abundance of the Mediterranean bluefish (*Pomatomus saltatrix*) in the context of sea warming

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CHAPTER III

Reproduction, condition and abundance of the Mediterranean bluefish (*Pomatomus saltatrix*) in the context of sea warming

3.1. Abstract

This study evaluates the link between sea warming and three important aspects of the population dynamics of bluefish, *Pomatomus saltatrix*, in the NW Mediterranean: condition (health measures), reproduction and abundance (as reflected in catch per unit effort, CPUE). We compared the bluefish populations from two areas with different thermal regimes: the Gulf of Roses and the Ebre Delta. First, in order to compare the condition and reproduction parameters of the two populations, specimens were collected from the commercial catch landed in two ports located in these areas. Several indicators of fish condition and reproduction such as hepatosomatic index, gonadosomatic index, maturation timing, length-at-first maturity, fecundity, egg quality and atresia (ovarian follicle resorption) were analysed and compared between study areas. Secondly, time series analyses of sea surface temperatures (SST) and monthly bluefish CPUEs in the two study areas were assessed using Box-Jenkins transfer function models. Our results indicate that bluefish benefit from sea warming in the NW Mediterranean, particularly in the northernmost zone, as evidenced by increasing fish condition in these waters. Sea warming may favour the changes in spawning phenology and the northward expansion of this species. This study provides evidence that a marine fish species that is able to expand or it is forced to shift its distribution due to sea warming, may take advantage of other environmental conditions of new habitats, contributing to the enhancement of the population's productivity in these areas.

Keywords: NW Mediterranean, sea surface temperature, *Pomatomus saltatrix*, fish condition, reproductive biology, predator.

3.2. Introduction

The Mediterranean Sea is a semi-enclosed basin where sea warming is likely to be more pronounced and to become apparent sooner than in other more open oceans (Astraldi *et al.* 1995; Bethoux *et al.* 1999; Walther *et al.* 2002; Coll *et al.* 2010). Climate models predict that the Mediterranean basin will be one of the regions that is most affected by the ongoing warming trend and by an increase in extreme events (Parry 2000; Lejeusne *et al.* 2010; Calvo *et al.* 2011; Durrieu de Madron *et al.* 2011). Subtropical species are found mainly in the eastern basin and southern Mediterranean, where water temperatures are higher, whereas cold-temperate species inhabit the cooler northern areas (Salat 1996; Bianchi & Morri 2000; Coll *et al.* 2010).

A direct consequence of sea warming is a simultaneous increase in the abundance of thermo-tolerant species and the decline or disappearance of 'cold' stenothermal species (Lejeusne *et al.* 2010). In a semi-closed system such as the Mediterranean basin these changes may cause the progressive homogenization of the marine biota, the dislocation of other species, the loss of endemic species coupled with invasion by non-indigenous species and/or cascade effects on food webs (Molinero *et al.* 2005).

Not only could marine biodiversity be seriously affected, but climate change may also affect fisheries directly by influencing fish stocks and the global supply of fish for consumption. Commercial fishing would also be affected by changes to the overall value of fish catches due to changes in the abundance of the species caught. The value of the total catch may decrease as warm-water species - which can be of lower commercial value - increase at the expense of other species of greater commercial value, e.g. the increase of the thermophilic, low value *Sardinella aurita* (Sabatés *et al.* 2006) vs. the decrease of the temperate, high value *Engraulis encrasicolus* and *Sardina pilchardus* (Martín *et al.* 2011).

The bluefish, *Pomatomus saltatrix*, (Linnaeus 1766), is distributed over continental shelves and in estuaries of temperate waters throughout most of the world, with the exception of the northern and mid-Pacific Ocean (Juanes *et al.* 1996). Relatively little is known about the biology of this species in the Mediterranean. Sabatés & Martín (1993) provided a number of observations regarding its presence in certain areas, and its relative importance in terms of fishing activity as well as the duration of spawning. They proposed the southern Catalan as the northernmost boundary of bluefish distribution in the western Mediterranean Basin. However, more recently, Sabatés *et al.* (2012) found that the bluefish distribution range was expanding northwards due to the increasing water temperatures allowing reproduction to take place in more northern areas, as revealed by the presence of bluefish larvae in plankton. Furthermore, it has been suggested that shifts in the bluefish distribution range could be the result of current climate change and that correct management of fish communities required this issue to be assessed (Goodbred & Graves 1996; Juanes *et al.* 1996;

Pardiñas *et al.* 2010). This warm-water species appears to be a good candidate for investigating the effects of sea warming.

The aim of this study was to evaluate the influence of sea temperature on three important aspects of population dynamics of bluefish in the NW Mediterranean: condition, reproduction and abundance (as reflected in catch per unit effort). The hypothesis behind this study is that the abundance, condition and reproduction of bluefish in coastal waters off the north-western Mediterranean Sea are all being influenced by sea warming, manifested through changes in fish condition and spawning characteristics, which may have resulted in increased catches over time.

3.3. Materials and methods

3.3.1. Sampling locations

Samples were collected from two areas with different thermal regimes in the Northwest Mediterranean Sea: the more northerly Gulf of Roses and the more southerly Ebre Delta (Fig. 3.1). The Gulf of Roses and surrounding waters have lower mean water temperatures than the Ebre Delta (Salat *et al.* 2002).

3.3.2. Fish condition and reproduction evaluation

In order to compare the condition and reproduction parameters of the bluefish between the two study areas, samples of bluefish were collected monthly from the commercial catch landed at the port of Roses (Gulf of Roses) from July 2010 to August 2012 and at the port of Sant Carles de la Ràpita (Ebre Delta) from May to August 2012, shortly after the small-scale and bottom-trawl fishing vessels had landed their catches. In the laboratory, we recorded the total length (TL) to the nearest 0.5 cm and total weight (TW) to the nearest 1 mg. Subsequently, the bluefish specimens were dissected and eviscerated, and the somatic or eviscerated body weight (SW), the liver weight (LW) and the gonad weight (GW) were obtained to the nearest 1 mg. Finally, the gonads were fixed in buffered formalin (4%) for further histological processing and fecundity estimation.

The hepatosomatic (HSI) and gonadosomatic (GSI) indices were calculated for each individual. All indices were calculated based on SW in order to avoid possible variations arising from differences in the contents of the digestive tract. The hepatosomatic index (HSI) was calculated as $HSI = 100 (LW/SW)$, where LW and SW represent liver and somatic wet weights, respectively. The liver is the main energy store of many fishes and therefore the HSI is expected to provide the best estimate of bluefish condition. Finally, the gonadosomatic index (GSI) was estimated using the formula $GSI = 100(GW/SW)$, where GW and SW represent gonad and somatic wet weights, respectively.

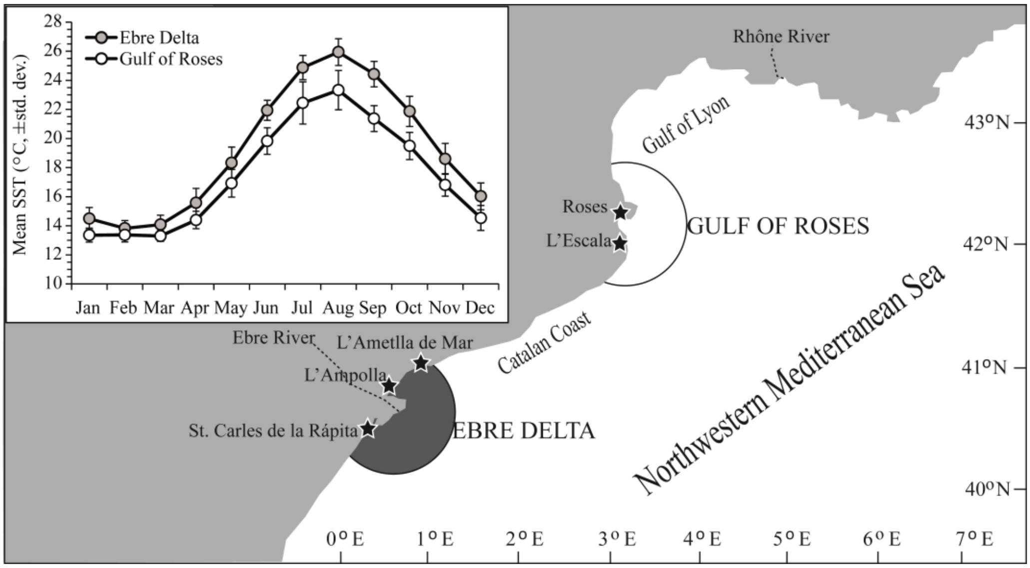

Fig. 3.1 Map of the north-western Mediterranean basin showing the two study areas (Gulf of Roses and Ebre Delta) and the location of fishing ports along the Catalan coast where sampling of *Pomatomus saltatrix* was carried out during the 2010-2011-2012 period. The upper panel shows the mean (± std. dev.) monthly variation of sea surface temperatures (SST, °C) during the study period (2010-2012) at the Gulf of Roses and the Ebre Delta.

Although the sex and reproductive status of specimens were first macroscopically determined, a histological analysis was also performed in order to provide a more accurate analysis of the reproductive characteristics and the annual reproductive cycle of bluefish. Thus, a histological study of the gonads of every single individual was carried out in order to determine the stages of development of their germ cells. Central portions (transverse sections) of the fixed gonads were dehydrated and embedded in paraffin, sectioned at between 3-8 µm, depending of their state of maturity, and stained with haematoxylin-eosin and Mallory's trichrome. The latter staining method highlights the *zona radiata* and its continuity and facilitates the detection of atretic oocytes (Muñoz *et al.* 2010). Maturation stages of the gonads were classified in line with Brown-Peterson *et al.* (2011).

In order to define sexual maturation as a function of body length, the L_{50} (body length at which 50% of the individuals were mature) was estimated separately for samples taken from the Gulf of Roses and from the Ebre Delta. To predict the probability that an individual was mature based on its length, binary maturity observations (0=immature, 1=mature) and length (TL; cm) were fitted to binary logistic models to construct maturity ogives based on logistic equations based on 1 cm length-classes. Size at maturity was estimated from 75 and 103 females (length 26-91 cm TL) and from 63 and 84 males (length 26-79 cm TL) sampled at the Gulf of Roses and the Ebre Delta, respectively.

The presence of hydrated oocytes and postovulatory follicles (POF) was determined to select suitable specimens for the analysis of fecundity. The oocyte size-frequency distribution for each spawning female was analysed in order to detect the batches of oocytes, since this may demonstrate different maturation patterns and associated fecundities (Kjesbu *et al.* 1998). Thus, fecundity was estimated for each specimen in 'Spawning Capable' (SC) or 'Actively Spawning' (AS) phases using the Gravimetric Method combined with Image Analysis as explained by Murua *et al.* (2003). With this aim, subsamples of about 150 mg were taken from the central area of the ovary; oocytes were separated from connective tissue using a washing process (Lowerre-Barbieri & Barbieri 1993) and sorted by size through several sieves (from 1000 to 100 µm), which facilitated the next steps of counting and measuring oocytes using a computer-aided image analysis system (Image-Pro Plus 5.1; www.mediacy.com). In order to explore the size distribution for each oocyte developmental stage, the mean diameter of 200 oocytes from each stage were measured from the histological sections as the average of major and minor axes. Due to their irregular shape the mean diameter of the hydrated oocytes was estimated separately after adding glycerine, which facilitates their differentiation.

Estimations of fecundity were based on Batch Fecundity (BF) defined as the number of eggs spawned per batch (Murua & Motos 2006; Domínguez-Petit & Saborido-Rey 2010). This was estimated as BF = GW*(O/Sw), where GW is the gonad weight after fixation, O is the number of hydrated oocytes in a weighted subsample of ovarian tissue, Sw is the subsample weight. The Relative Batch Fecundity (RBF) was also calculated, as the value of batch fecundity per gram of somatic weight of the fish.

The dry mass and diameter of hydrated oocytes were used to estimate the quality of the oocytes, hence an approximation of the reproductive success (Brooks *et al.* 1997). Thus, mean dry weights were estimated by drying (for 24 h at 110°C) two replicates per sample of the oocytes.

The prevalence of atresia, P_a (percentage of sexually mature females that have α-atretic vitellogenic oocytes) and the relative intensity of atresia, R_{Ia} (percentage of α-atretic vitellogenic oocytes in relation to the total number of vitellogenic oocytes) was estimated from observations at three different focal planes of different histological slides of each specimen (Kurita *et al.* 2003).

3.3.3. Statistical analyses

Generalized linear models (GLMs) (McCullagh & Nelder 1989) were used to investigate the variation of fish condition with sex, stage of maturity and size. GLMs were fitted to HSI and GSI as response variables and using as categorical predictor variables the sex (females and males) and maturity (immature, developing, spawning capable, regressing, regenerating) and as continuous predictor variables the size (total length). All predictors and their first order interactions were initially included in the GLM. Analysis of deviance to evaluate the significance (F-test) of the factors in the model was performed by a stepwise procedure, and the most appropriate error models were chosen on the basis of residual plots. GLMs incorporating the sex and maturity as predictor variables accounted significantly for 36.4% of the deviance of HSI and 43.4% of the variability in GSI (Table 3.1). Size did not significantly accounted for the deviance neither of HSI nor of GSI ($p>0.05$). Thus, we used the GLM approach to standardize HSI and GSI data only for the effects of sex and maturity by estimating the adjusted means of HSI and GSI as the means after adjusting for the variation of the covariables (sex and maturity).

Table 3.1 Analysis of deviance tables for generalized linear models fitted to HSI and GSI using as categorical predictors the stage of maturity and sex. Significance are shown as *** for $p<0.001$ and ** for $p<0.05$; d.f. = degrees of freedom.

Variable	Source	d.f.	Residual deviance	Explained deviance (%)	p-value
HSI	Null		94.088		
	Sex	1	4.334	6.9	***
	Maturity	4	7.162	11.0	***
	Sex*Maturity	4	10.539	15.3	***
	Model	324		**36.4**	
GSI	Null		2005.451		
	Sex	1	73.046	6.2	***
	Maturity	4	771.885	41.2	***
	Sex*Maturity	4	36.573	3.2	**
	Model	324		**43.4**	

In order to carry out the comparative analyses between sampling areas, a sub-dataset of the Gulf of Roses samples was created which matched the temporal scale of the Ebre Delta sampling period (from May to August 2012) so that the spatial variation could be evaluated. This analysis indicated that, even at this reduced temporal scale (2012), there were significant differences between sampling areas in the condition and reproduction variables such as, for example, in GSI (ANOVA, $F_{1,238}=4.67$, $p=0.032$) or HSI (ANOVA, $F_{1,238}=4.91$, $p=0.028$). In contrast, there was an insignificant interannual difference (2010, 2011 and 2012) in the Gulf of Roses, e.g. GSI (ANOVA, $F_{2,137}=2.05$, $p=0.133$) or HSI (ANOVA, $F_{2,137}=2.37$, $p=0.097$). These results support the decision to group of all three reproductive annual cycles in the Gulf of Roses in order to compare each variable with those of the Ebre Delta.

Subsequently, for all aforementioned variables the Shapiro-Wilk test was used to test the assumptions of normality and Levene's test was used to test the homogeneity of variances (Zar 1996). Once assumptions were checked and met, ANOVA models were used to compare all indices between sampling areas. A p-value of $\alpha=0.05$ or less was considered to be statistically significant. Moreover, if the ANOVA indicated significant differences Bonferroni's multiple tests were applied for post hoc comparisons of significant effects (Sokal & Rohlf 1995). Conversely, if the assumptions were not met, the data were analysed with a non-parametric Mann-Whitney U test (Sokal & Rohlf 1995). A p-value of $\alpha = 0.05$ or less was considered to be statistically significant.

Finally, the relationship between batch fecundity (BF) and the total length (TL) was estimated by fitting power functions. Then, ANOVAs (for relative batch fecundity), ANCOVAs (for batch fecundity using TL as covariate) and paired Student's tests (for oocyte quality and relative intensity of atresia) were also used to find out whether, on average, differences between sampling areas in the aforementioned variables were statistically significant (Zar 1996).

3.3.4. Transfer functions between CPUE and SST

Trends in sea surface temperatures (SSTs) and bluefish landings in Catalan waters have already been explored by Sabatés *et al.* (2012), who found that both parameters showed a tendency to increase from 1997 to 2010 (particularly during spring months). They also explored the seasonality of bluefish landings and observed a seasonal pattern, closely matching that of the SSTs, in the monthly landings over the year in which landings were almost nil during the colder months but began increasing at the time SSTs also began to increase; subsequently, landings decreased as SSTs decreased. Thus, our analyses focuses on determining and quantifying the possible relationships between the monthly time series of bluefish catch per unit effort (CPUE) and SST using bivariate ARIMA (autoregressive-integrated-moving-average) transfer functions (Box & Jenkins 1976).

First, the data on sea surface temperature (SST, in °C) from both areas (the Gulf of Roses and the Ebre Delta) was retrieved from the International Comprehensive Ocean-Atmosphere Data Set (ICOADS) for the period 2000-2011 (ds540.0-Release 2.5) (Woodruff *et al.* 2011). The data comprised individual daily mean sea surface temperature observations for 1° latitude x 1° longitude units. In this study, we used the time series from two 1° squares in the north-western Mediterranean: the Gulf of Roses (42.0 to 43.0°N and 3.0 to 4.0° E) and the Ebre Delta (40.0 to 41.0°N and 0.0 to 1.0° E). The mean monthly and seasonal values of SST in both areas were calculated by averaging daily temperatures retrieved from the ICOADS data. The seasons were defined as follows: winter (January, February, and March), spring (April, May, and June), summer (July, August, and September) and autumn (October, November, and December).

Secondly, data was collected - on total monthly bluefish landings (recorded in kg) and nominal fishing effort (number of vessels), from the fishing ports along the Catalan coast (Fig. 3.1) - from the fishery statistics of the Department of Agriculture and Fisheries of the Government of Catalonia (2000-2011) (www20.gencat.cat/portal/site/DAR). It should be noticed that bluefish landings included only those catches landed by the small-scale fleets (devoted to artisanal fishing and whose fishing grounds are located in the vicinity of the base port) because it is the more prevalent vessel type that catches most of the bluefish landings (from 90 to 95%) in all ports. The occasional landings recorded by the bottom trawler and purse-seine fleets were not included, which have been suggested previously and used by Sabatés *et al.* (2012). Since there has been a considerable reduction in the fishing effort in Catalan waters in recent years (Martín *et al.* 2011; Catalonia Fisheries Statistics 2012; Sabatés *et al.* 2012), the monthly number of active vessels at each port was used as a proxy of fishing effort at each port. In this way, the time series of the monthly catches per unit effort (CPUE), expressed as kg per vessels, were estimated for different periods (2000-2011) at two fishing ports from the Gulf of Roses (Roses and L'Escala) and three from the Ebre Delta area (L'Ametlla de Mar, L'Ampolla, and Sant Carles de la Ràpita).

Finally, in order to determine and quantify the possible relationships between the time series of bluefish CPUEs and SST, bivariate ARIMA transfer function models were constructed using the statistical package ForeTESS (Prat *et al.* 2000). These models describe the time-lagged relationship between the dependent (CPUE) and the independent (SST) variables while taking into account the autocorrelation of the disturbance of the data (Box & Jenkins 1976).

In order to look at the temperature thresholds related to the timing of the arrival of bluefish in both study areas as environmental conditions become favourable to this species, we repeated the transfer function models but this time using only the values of those months when SST increased by a factor of 1°C, from 13°C (minimum SST observed) to 27°C (maximum SST observed): $SST_{13} + SST_{14} + ... + SST_{27}$, and only physical values from months when SST was higher than 13°C were included in the transfer function models and the rest of the months when temperature was lower than 13°C were replaced by zeroes, which meant 'no influence on CPUE' in our models. In this way, several transfer function models were explored and applied to the 13-27°C SST range so that a minimum SST threshold could be found for each time series. Models were compared using Akaike's information criterion (AIC) to determine which model offered the best fit for SST thresholds at each time series.

3.4. Results

A total of 138 bluefish (75 females and 63 males) were sampled in the Gulf of Roses, and 187 (103 females and 84 males) in the Ebre Delta. The fish length ranged from 26.0 to 91.0 cm TL.

3.4.1. Fish condition and reproductive biology

Since bluefish specimens were not significantly different between sampling areas in size (ANOVA, $F_{1,324}$=2.86, p=0.092) or sexes (ANOVA, $F_{1,324}$=3.24, p=0.073), data were pooled (grouped into a single dataset per sampling area).

HSI (standardized based on GLMs for sex and maturity) were significantly (ANOVA, $F_{1,324}$=4.56, p=0.034) higher in the Gulf of Roses (1.56±0.48) than in the Ebre Delta (1.26±0.31) indicating better fish conditioning in the northern population (Fig. 3.2). Significant differences were also found in GSI (ANOVA, $F_{1,324}$=5.97, p=0.015), in which case specimens sampled at the Gulf of Roses showed higher GSI (3.64±2.54) compared to specimens from the Ebre Delta (1.86±1.39) indicating that the reproductive investment was much higher in the northern population (Fig. 3.2). In terms of the time of the year, in both sampling areas, the GSI was low during spring and then increased sharply, peaking in the summer before declining again in autumn (Fig. 3.3).

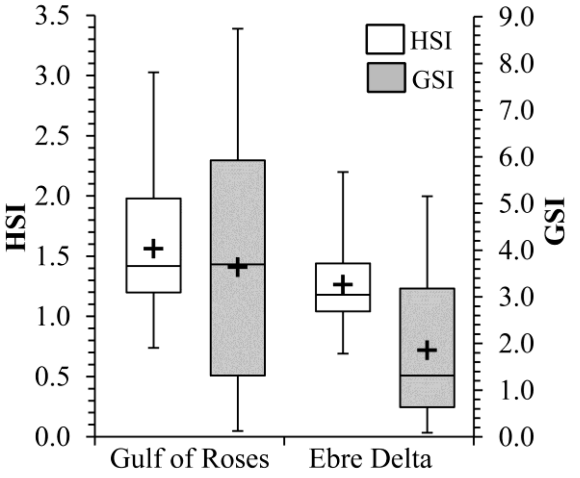

Fig. 3.2 Box-whisker plots of the adjusted means of HSI and GSI (standardized based on GLMs for sex and maturity) per sampling area. Interquartile box range (25-75%), mean (+), median (⊟), whiskers (represented as Q1 and Q3 deviations from the smallest and largest observation, respectively) are also given.

Differences in the timing of gonadal development were also observed between sampling areas (Fig. 3.3). In females from the Gulf of Roses, the early stages of development were observed mainly during the spring (April to June); then, during the summer (July to September) spawning activity occurred; and subsequently, the rate of spawning activity declined in late summer (September) and autumn (October to December) when all the females were in the regeneration stage (Fig. 3.3a). Similarly, the spawning season of females from the Ebre Delta is mainly during the summer, although 'Spawning Capable' females were also observed earlier during the spring (which was not the case in the Gulf of Roses) (Fig. 3.3b). In addition, later on in the summer, the proportion of 'Regressing' females from the Ebre Delta (28.9%) was higher than it was in the Gulf of Roses in the same season (4.4%), indicating that not only did spawning activity begin earlier in the Ebre Delta but also that the rate of spawning activity there declined earlier than it did in the Gulf of Roses. Similar differences between the two sampling areas were observed in the timing of gonadal development of bluefish males (Fig. 3.3). In the Gulf of Roses the early stages of development and 'Spawning Capable' males were observed in the spring, but spawning activity did not peak until the summer, as revealed by the presence of specimens in the samples that were in 'Actively Spawning' and 'Regressing' stages. However, in the Ebre Delta, although the spawning season of males also takes place mainly in summer, some 'Actively Spawning' males were already observed in spring (Fig. 3.3d), suggesting that the spawning activity of males, as was the case with females, began earlier in the Ebre Delta than it did in the Gulf of Roses.

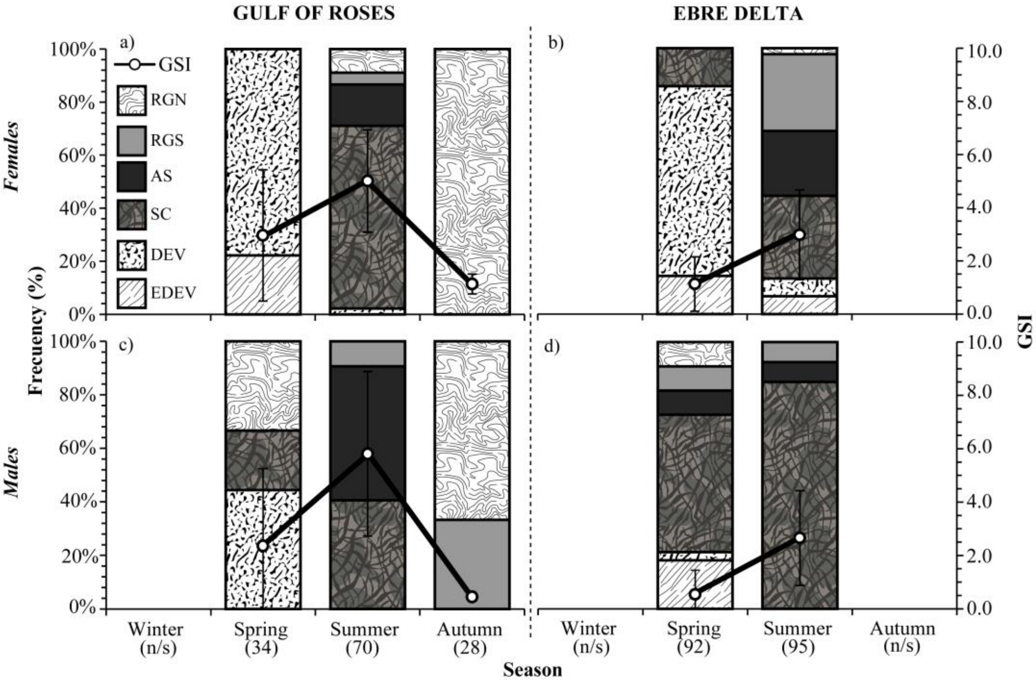

Fig. 3.3 Seasonal ovarian and testis development stages frequency (percent abundance) and mean (± std. dev.) seasonal variation in the GSI of bluefish during the 2010-2012 reproductive cycles in the Gulf of Roses (all years pooled) and the Ebre Delta (2012). Development stages: early developing (EDEV), developing (DEV), spawning capable (SC), actively spawning (AS), regressing (RGS) and regenerating (RGN). Sample number per season (n) is also given in parentheses, n/s denotes periods in which none sample was caught.

The mean length at which 50% specimens were mature (L_{50}) was, for females, 37.5 cm TL in the Gulf of Roses and 37.7 cm TL in the Ebre Delta. For males, the L_{50} in the Gulf of Roses was 36.5 cm TL while in the Ebre Delta it was 36.2 cm TL. In both sampling areas all females and males were mature at about 40 cm TL.

The oocyte size-frequency distribution in bluefish females showed a continuous size-frequency development of oocytes except for ovaries in the ‘Actively Spawning’ phase, which had a separate mode of very large (>600 μm) hydrated oocytes (Fig. 3.4). Only when hydration occurred just before ovulation, did hydrating oocytes outgrow the standing stock of vitellogenic oocytes and a separate mode of mature hydrated oocytes developed. The presence of hydrated oocytes alongside the standing stock of developing oocytes in individual ovaries, as well as the presence of post-ovulatory follicles (POFs) in ovaries with advanced vitellogenic oocytes, indicates that asynchronic multiple batch spawning occurs in this species.

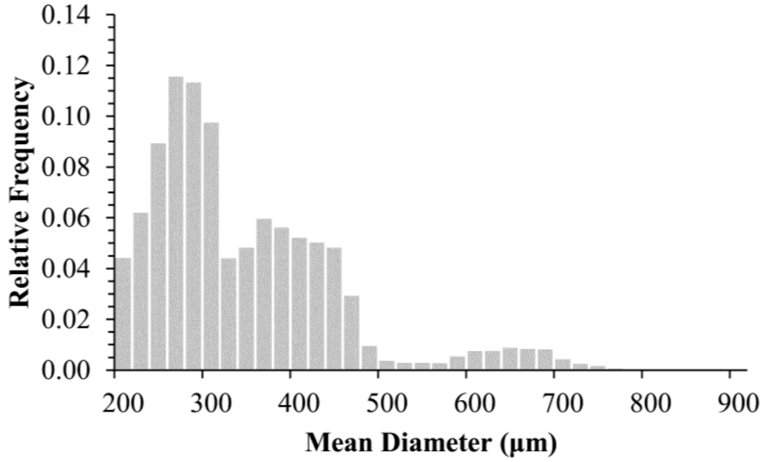

Fig. 3.4 Oocyte size-frequency distribution (per cent abundance per 20 µm diameter classes) in an actively spawning bluefish female (with hydrated oocytes).

The specific size ranges for each stage of secondary oocyte development are shown in Table 3.2. Significant differences (Mann-Whitney U test) in the median diameter of oocytes from the two sampling areas were found at nearly all stages of development: at CA ($U=4331.5$, $p<0.05$), at Vtg-1 ($U=8459.5$, $p<0.05$), at Vtg-2 ($U=4488.5$, $p<0.05$), at Vtg-3 ($U=4224.5$, $p<0.05$), and at GVM ($U=4738.0$, $p<0.05$), with Gulf of Roses oocytes being always slightly larger than Ebre Delta oocytes. However no significant differences were observed in the median diameters of hydrated oocytes ($U=808.5$, $p=0.48$).

Table 3.2 Summary of oocyte size distributions for each developmental stage in bluefish ovaries. Size ranges are given for each stage. For CA, Vgt-1, Vgt-2, Vgt-3 and GVM oocyte developmental stages, measurements were obtained directly from histological sections, and for hydrated oocytes, previously selected by applying glycerin, image analysis was used.

Oocyte Development Stage	Samples (n)	Sampling Area	Mean Diameter (µm ± Std. Dev.)	Diameter Range (µm)
Pre-vitellogenic				
Cortical alveolar (CA)	200	Ebre Delta	144.1 (±25.3)	100 - 200
	200	Gulf of Roses	152.9 (±20.8)	
Vitellogenic (yolked)				
Early Vitellogenesis (Vtg-1)	200	Ebre Delta	228.9 (±24.2)	200 - 300
	200	Gulf of Roses	248.6 (±25.8)	
Mid Vitellogenesis (Vtg-2)	200	Ebre Delta	334.5 (±27.6)	300 - 400
	200	Gulf of Roses	345.6 (±29.2)	
Advanced Vitellogenesis (Vtg-3)	200	Ebre Delta	427.9 (±30.3)	400 - 500
	200	Gulf of Roses	438.6 (±24.0)	
Maturation				
Germinal Vesicle Migration (GVM)	200	Ebre Delta	529.2 (±24.4)	500-600
	200	Gulf of Roses	539.9 (±26.7)	
Hydration	200	Ebre Delta	757.1 (±56.9)	600-1000
	200	Gulf of Roses	763.5 (±50.7)	

Only 13 females (5 from the Gulf of Roses and 8 from the Ebre Delta) met the histological criteria (actively spawning with hydrated oocytes and without POFs) for fecundity analysis. The batch fecundity (BF) of bluefish ranged from 84009 to 259636 eggs per spawning batch in fish ranging from 41.0 to 76.5 cm TL. The relationship between BF and TL was fitted to the following exponential regression model: $BF=832.45 \bullet TL^{1.275}$ ($r^2=0.652$, $n=13$). Among sampling areas, the mean batch fecundities were estimated at 166559(±62062) and 153653(±42613) eggs per spawning batch for the Gulf of Roses and the Ebre Delta, respectively; and the mean relative batch fecundities (RBF) were estimated at 102.1(±32.5) and 92.6(±37.7) oocytes per gram of body mass for each area, respectively. No significant differences were found between the Gulf of Roses and the Ebre Delta either in BF (ANCOVA, $F_{1,12}=0.86$, $p=0.377$) or in RBF (ANOVA, $F_{1,12}=0.22$, $p=0.649$).

As a measure of egg quality, the mean dry mass of hydrated oocytes was estimated at 0.032(±0.011) and 0.036(±0.014) mg per egg for the Gulf of Roses and the Ebre Delta, respectively, which meant there was no significant difference between the two areas ($t=-0.8089$, $p=0.426$, $n=40$).

The prevalence of atresia (P_a) increased in both areas from the 'Spawning Capable' phase to the 'Regressing' phase of the ovaries. No sign of α-atresia was observed in other development stages, such as the 'Developing' or 'Regenerating' phases (Table 3.3). The P_a also varied and differed seasonally between sampling areas, i.e. from spring to summer in the Ebre Delta, the P_a decreased while in the Gulf of Roses it increased. On the other hand, the mean relative intensity of atresia (R_{Ia}) increased in relation to the season and the stage of ovarian development as the spawning period advanced.

Table 3.3 Prevalence of atresia (P_a) and mean relative intensity of atresia (R_{Ia}) for each stage of ovarian development for each season at each study area (NA denotes that no sign of α-atresia was observed).

Variation source	**P_a (%)**		**Mean R_{Ia} (% ± std. dev.)**	
	Gulf of Roses	Ebre Delta	Gulf of Roses	Ebre Delta
Maturity stage				
Developing	NA	NA	NA	NA
Spawning Capable	23.7	17.2	9.9(±5.9)	4.4(±1.1)
Regressing	100.0	23.1	96.3(±2.0)	29.9(±10.3)
Regenerating	NA	NA	NA	NA
Season				
Spring	14.3	50.0	14.3(±0.1)	4.8(±0.1)
Summer	27.0	15.4	26.7(±37.1)	17.0(±15.5)
Autumn	NA	NA	NA	NA
Winter	NA	NA	NA	NA

3.4.2. Relationship between SST and bluefish CPUE

The transfer function models fitted to the CPUEs with SSTs as an independent variable explained a considerable amount of the variability in CPUEs (Table 3.4). The amount of variability explained by these models ranged from 71% for the time series of Sant Carles de la Ràpita to 81% for the time series from Roses. Fig. 3.5 compares the expected CPUE values (from the transfer function models) with the observed (actual) bluefish CPUE for each time series.

Table 3.4 Results of the ARIMA transfer functions between CPUE and SST. Arithmetic mean and standard deviations of the CPUE are given; RSEU is the residual standard error of each transfer function; RSE is the residual standard error of each coefficient; R^2 is the variance explained. Significant coefficients at a t-value >|2| (p<0.05) are shown in bold.

Port	**CPUE (kg vessel^{-1})**		**RSEU (kg vessel^{-1})**	**R^2**	**Time lag (months)**	**Coeff. (kg vessel^{-1})**	**RSE (kg vessel^{-1})**	**t-value**
	Mean	**Std. Dev.**						
Roses	1.21	2.15	0.94	0.81	**0**	**0.42**	0.06	**2.31**
					1	**0.34**	0.08	**3.65**
					2	0.03	0.06	0.59
L'Escala	1.79	2.74	1.21	0.80	**0**	**0.38**	0.08	**2.34**
					1	**0.41**	0.08	**3.80**
					2	0.05	0.08	0.60
L'Ametlla de Mar	28.92	34.76	15.68	0.80	**0**	**1.93**	0.97	**2.36**
					1	**2.27**	0.96	**2.19**
					2	0.16	0.94	0.17
L'Ampolla	3.29	4.20	1.93	0.79	**0**	**2.23**	0.19	**2.32**
					1	**3.42**	0.23	**3.54**
					2	0.02	0.14	0.02
St. Carles de la Ràpita	63.71	53.05	28.62	0.71	**0**	**7.97**	1.85	**2.30**
					1	**3.84**	1.95	**2.85**
					2	1.16	1.48	0.78

The transfer functions models showed that CPUE correlated positively with SSTs with a time lag of between 0 and 1 months (significant at t-value>|2|=p<0.05) in almost all time series (Table 3.4). For example, the transfer function model fitted to bluefish CPUE in Roses (Y_t; output; kg vessel^{-1}) and the corresponding SST (X_t; input; °C) at lags of 0 and 1 month (time lag 0: t-value=2.31, time lag 1: t-value=3.65) is represented by the equation $Y_t=f(X_t)=0.42 \cdot X_{t-0}+0.34 \cdot X_{t-1}+a_t$. Thus, the model estimates that an additional 1°C of SST leads to 0.42(± 0.06) kg vessel^{-1} added to CPUE of this species during the same month, and 0.34(±0.08) kg vessel^{-1} added to CPUE during the following month, giving a total gain of 0.76 kg vessel^{-1} for both months. The R^2 value of the transfer function model was 0.81 (residual standard error of 0.94 kg vessel $^{-1}$). Similar patterns were found in the transfer functions of L'Escala, L'Ametlla de Mar, L'Ampolla and St. Carles de la Ràpita (Table 3.4).

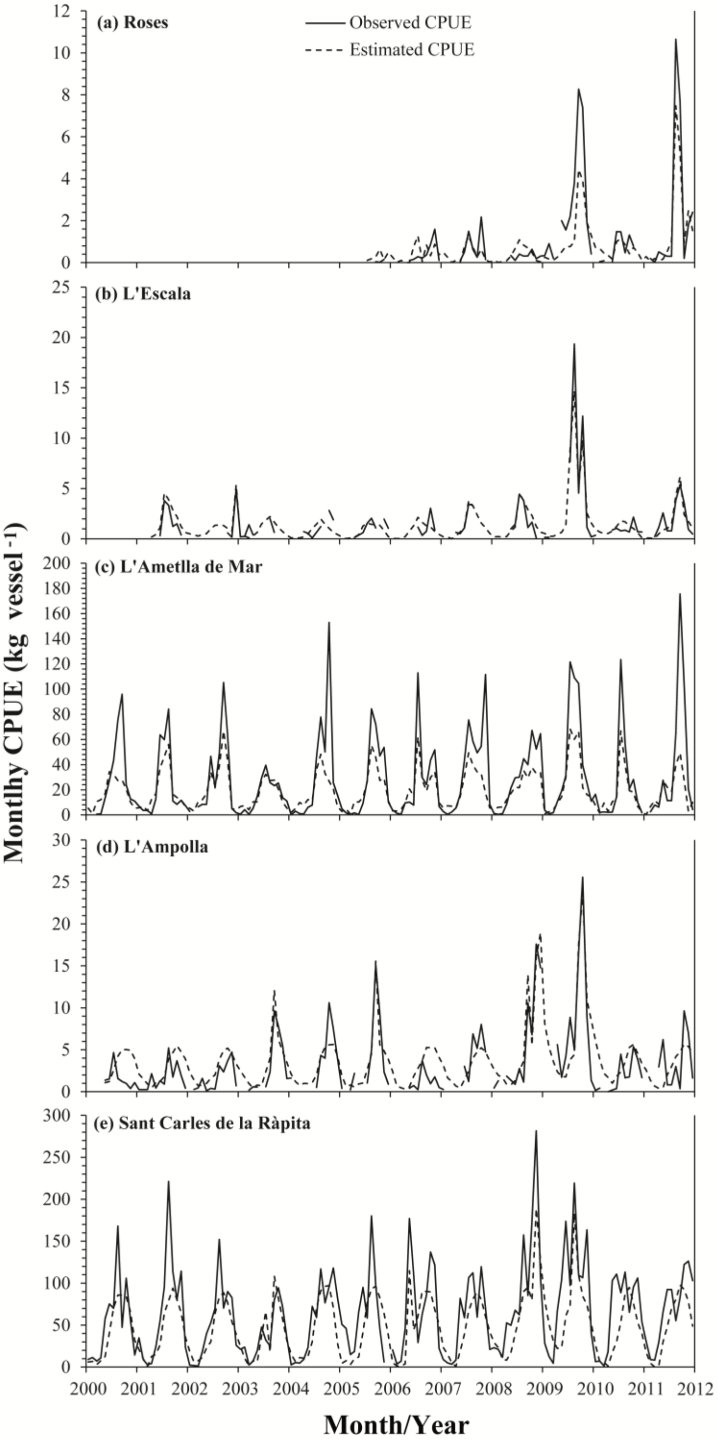

Fig. 3.5 Comparisons between the observed (actual) and the expected bluefish CPUE in two fishing ports in the Gulf of Roses: (a) Roses and (b) L'Escala, and three fishing ports in the Ebre Delta: (c) L'Ametlla de Mar, (d) L'Ampolla and (e) Sant Carles de la Ràpita. The expected CPUE values represent the contribution of the sea surface temperature (SST) to the bluefish CPUE (kg vessel^{-1}).

Finally, the temperature thresholds analysis applied to the transfer function models indicated that the minimum SST that needs to be reached within each study area in order to enhance bluefish CPUE significantly was around 17-18°C since significant t-values (>|2|, $p<0.05$) were only observed from this threshold to higher SSTs at each fishing port (Table 3.5). The AIC value (for each time series) decreased as the SST threshold increased, thereby indicating that the most parsimonious models were those obtained at higher SSTs (Table 3.5), which in turn supports the idea that bluefish CPUE have been closely linked to the sea surface temperatures.

Table 3.5 Results of the SST threshold analyses using the ARIMA transfer functions between bluefish CPUEs and SSTs at different thresholds (SST_{13} + … + SST_{27}). Significant coefficients from the time lag of '0 months' at a t-value > |2| ($p < 0.05$) are shown in bold. The Akaike's Information Criterion (AIC) is also shown in parentheses.

Threshold			**Port**		
	Roses	L'Escala	L'Ametlla de Mar	L'Ampolla	St. Carles de la Ràpita
T_{13}	0.28 (2492)	0.78 (2580)	0.52 (2635)	0.85 (2503)	0.61 (2751)
T_{14}	0.39 (1971)	1.01 (1543)	0.68 (1321)	0.91 (1450)	1.64 (2630)
T_{15}	0.68 (1053)	1.13 (1413)	1.08 (1310)	0.87 (1398)	1.58 (1497)
T_{16}	1.21 (845)	1.14 (1424)	1.32 (1003)	1.69 (928)	1.36 (1399)
T_{17}	**2.45** (721)	**2.09** (1387)	1.95 (991)	1.83 (812)	**2.09** (967)
T_{18}	**2.68** (760)	**2.21** (1326)	**2.13** (945)	**3.56** (820)	**2.07** (841)
T_{19}	**2.97** (612)	**2.62** (955)	**2.31** (819)	**4.45** (736)	**2.16** (804)
T_{20}	**3.34** (694)	**2.54** (838)	**3.33** (809)	**4.84** (735)	**3.91** (629)
T_{21}	**3.28** (657)	**2.93** (705)	**2.41** (795)	**3.96** (601)	**3.93** (612)
T_{22}	**3.56** (535)	**3.12** (645)	**3.01** (663)	**3.01** (647)	**3.75** (506)
T_{23}	**3.68** (501)	**3.55** (537)	**3.93** (661)	**3.23** (473)	**3.83** (494)
T_{24}	**3.34** (589)	**3.11** (525)	**3.84** (607)	**3.72** (414)	**3.09** (337)
T_{25}	**4.45** (423)	**3.17** (424)	**3.05** (541)	**3.31** (415)	**3.25** (345)
T_{26}	**4.98** (425)	**4.33** (416)	**3.64** (552)	**3.48** (311)	**3.22** (234)
T_{27}	**4.51** (422)	**4.19** (313)	**3.99** (501)	**3.94** (398)	**3.77** (293)

3.5. Discussion

Our analysis of different reproductive and condition indices shows that it is not only in terms of reproduction that bluefish seem to benefit from actual environmental conditions in the north, but they also appear to be in better condition. Moreover, oocytes of the females from the Gulf of Roses were significantly larger than those of females from the Ebre Delta, suggesting they have higher quality eggs. Apparently, despite the warmer environment that prevails in the Ebre Delta, bluefish were in significantly better condition in the northern study area where the waters are colder. This later may be due to ecological differences between northern and southern areas of the NW Mediterranean. The Gulf of Lions is known to be affected by a permanent cyclonic circulation of surface waters and intense vertical convections which promote intense algal blooms and elevated primary production: Bosc *et al.* (2004) estimated a 4-year average annual primary production for the Gulf of Lions basin (including the Gulf of Roses) of between 180 and 204 gC m^{-2} y^{-1}. This was relatively higher than their estimates for the Balearic basin (including the Ebre Delta area) which ranged from 153 to 175 gC m^{-2} y^{-1}. Regarding the trophic structure and functioning of these two marine ecosystems, the total biomass (excluding detritus) has been estimated for the Gulf of Lions at 68.9 t km^{-2} (Bănaru *et al.* 2013) and for the Ebre Delta at 58.99 t km^{-2} (Coll *et al.* 2006). It is noteworthy that the calculated total net primary production was noticeably different between these two areas, being considerably higher in the Gulf of Lions, at 1042.4 t km^{-2} y^{-1} (Bănaru *et al.* 2013), than for the Ebre Delta, at 386.68 t km^{-2} y^{-1} (Coll *et al.* 2006). Thus, bluefish inhabiting the more northern area appear to be taking advantage of the high productivity found there.

The results concerning the reproductive biology, such as the oocyte size-frequency distribution and the seasonal relative intensity of atresia, provide evidence that bluefish are multiple batch spawners with asynchronous oocyte development and indeterminate fecundity which is in accordance with previous studies (Conand 1975; Robillard *et al.* 2008). Our estimates of batch fecundities for bluefish in the two Mediterranean areas we sampled were very similar to each other, but smaller than those estimated for the bluefish in U.S. East Coast (Robillard *et al.* 2008) or the West African Coast (Conand 1975), which ranged 0.2-1.4 and 0.6-1.6 million oocytes, respectively. To date, this study represents the first published work that estimates not only the fecundity, but also the size at maturity of this species in the Mediterranean Sea. It should be noticed that the L_{50} values we obtained for females 37.6 cm TL are much lower than those reported for areas in the Atlantic: 48.0 cm TL in the East Coast of the U.S (Robillard *et al.* 2008) and 43.0 cm TL in the West African Atlantic Coast (Conand 1975). It is worth to mention that size at maturity was estimated from relatively similar size ranges (TL): 23.0-97.5 cm (Robillard *et al.* 2008) and 26.0-91.1 cm (this study). It has been suggested that maturation in fish populations usually might be closely related to total population abundance over the life of a cohort, with cohorts maturing at an earlier age and smaller size when population size is low (Morgan & Colbourne 1999). Besides the fact that bluefish mature at smaller sizes in the Mediterranean and also that better fish conditioning was observed in the north would somehow facilitate its capacity for expansion since some studies have shown that fish in better condition may have more surplus energy to devote to reproduction (i.e. an increase number and quality of eggs) which can have a direct impact on spawning biomass and growth of a population (Kjesbu *et al.* 1991; Rideout *et al.* 2000; Morgan 2004).

Our results support the idea previously presented by Sabatés *et al.* (2012) that in the northern areas of the NW Mediterranean the temperature conditions are gradually becoming more favourable to the bluefish reproduction. Although, the spawning occurs mainly during the summer season in both of our sampling areas the presence of ‘Spawning Capable’ females and ‘Actively Spawning’ males during spring in the Ebre Delta (but not in the Gulf of Roses) and a higher proportion of ‘Regressing’ females during the summer in the Ebre Delta further supported the thesis that spawning activity starts and declines earlier in the more southern Ebre Delta. In addition, a higher prevalence of atresia was found in females from the Ebre Delta earlier during spring and this was also found to decrease earlier in summer. This indicates that active oocyte resorption takes place earlier in the Ebre Delta than it does in the Gulf of Roses.

Sea temperature may influence the timing of various life processes such as the spawning date (Kjesbu *et al.* 2010b; Morgan *et al.* 2013). Reproductively active fish from the Ebre Delta were caught when SSTs were between 18.2 and 27.3°C from May to August, while in the Gulf of Roses they were caught when SSTs were between 17.7 and 23.8°C from July to September. Spawning activity started earlier in the Ebre Delta as SSTs rose over 18.0°C in May, in contrast to the Gulf of Roses where spawning individuals were not landed until early summer (July) when SSTs attained similar temperatures, in this case over 17.7°C. However, despite this two-month lag (from May to July), spawning activity was found to begin in both areas at similar temperature thresholds (≈18.0°C). This indicates that, for both areas, temperature may trigger the initiation of spawning activity. In contrast, Sabatés *et al.* (2012) reported that the threshold temperature for spawning was 21°C. The discrepancies with our study may be related to differences in the approaches used to estimate the timing of spawning. In our study, the timing of spawning was estimated by means of a histological study of the gonads, whereas Sabatés *et al.* (2012) used larvae sampling surveys. Other studies have reported that spawning of bluefish in the mid-Atlantic region occurs at temperatures between 17-24°C (Norcross *et al.* 1974; Kendall & Walford 1979), while in the Marmara Sea (Turkey) it occurs from early spring until August at SSTs between 20-26°C (Ceyhan *et al.* 2007).

The difference in the timing of spawning activity in the NW Mediterranean coast may be the result of the seasonal migratory behaviour usually exhibited by this species. Although, to date, no information is available regarding the migration of bluefish in the Mediterranean, this species is known to have large distributions and show seasonal migratory behaviour, spending the colder months in warm-water areas and, when the surface temperature reaches a certain value, migrating towards cooler waters where the species spawns once a threshold temperature has been attained (Juanes *et al.* 1996; Shepherd *et al.* 2006). We suspect the bluefish from the north move towards the south, where the waters are warmer, but we do not have any clear evidence of this at present. Sabatés *et al.* (2012) suggest that the actual sea warming trends and the changes in the seasonality of the sea water temperature - particularly during spring months - may be causing changes in spawning phenology and the timing of the seasonal arrival of bluefish into more northern areas favouring the northward temperature-dependent expansion of this species. Similarly, the round sardinella (*Sardinella aurita*) has expanded its northernmost limit of distribution in the NW Mediterranean (Sabatés *et al.* 2006).

The influence of water temperature on bluefish fisheries is revealed in this study using CPUE and transfer functions, and our findings support the results found by Sabatés *et al.* (2012) who used data on landings and sequential *t*-test analysis to detect regime shifts (STARS method). The use of transfer functions in the present study showed that CPUE correlated positively with SST indicating that an increase of temperature in a particular month is followed by an increase of CPUE in that month and in the following month. Therefore, it seems that higher SSTs contribute to increasing bluefish availability in the NW Mediterranean. Fluctuations in fish availability may be related to environmental factors (Smith & Page 1996), i.e. increased or reduced availability may reflect the temperatures that appear to be avoided or preferred by certain fish species (Swain *et al.* 2000; Colbourne & Bowering 2001).

Bluefish show behavioural thermoregulation, that is to say they are able to avoid or select the right environmental temperature (Olla & Studholme 1985). However, within certain thermal limits, their distribution may be based on other ecological factors such as food availability (small pelagic fish) (Juanes & Conover 1994). In this sense, both the Gulf of Roses and the Ebre Delta have been recognized as important spawning grounds for small pelagic fish (García & Palomera 1996; Olivar *et al.* 2001; Palomera *et al.* 2007); however higher densities of anchovy has been observed in the southern Gulf of Lyon than in the Ebre Delta (Bellido *et al.* 2008). Furthermore, bluefish individuals seem to find an optimal foraging habitat around Mediterranean fish farms of the gilthead seabream (*Sparus aurata*) and the European seabass (*Dicentrarchus labrax*) (Sánchez-Jerez *et al.* 2008; Arechavala-Lopez *et al.* 2015). In open-sea fish farms over the south-eastern Spanish coast of the Mediterranean, Arechavala-Lopez *et al.* (2014) found that tagged bluefish stayed close to fish cages during spring and early summer and then disappeared during autumn when the sea water temperature dropped. This interaction has been observed in the Gulf of Roses, where bluefish tend to congregate during spring-summer time around the existing sea-cages or even break into the cages to prey on the cultured seabass (sea-cage farm technician, *pers. comm.*). Although, the existence of seabass cages in the Gulf of Roses and the Ebre Delta area may thus enhance the bluefish's food supply, it is not quite clear if the increase in bluefish is related to the culture of seabass in the Gulf of Roses because the farm has been active since 20 years ago.

On the whole, we hypothesize that although sea water temperature clearly influences bluefish availability as well as its spawning phenology in the NW Mediterranean, the expansion of bluefish in the NW Mediterranean may have been facilitated not only by the physical conditions (currently favourable water temperatures) but also by the higher productivity in the northernmost area, so that this new habitat therefore may have become a more advantageous ecological niche for this species to exploit.

The increasing abundance of bluefish in the northernmost parts of the western Mediterranean may have important consequences for other coastal species that may be ecologically affected by predation or competition. Bluefish is a top predator that feeds on small pelagic species such as, the anchovy, the sardine, the round sardinella, the gilthead seabream or the Mediterranean horse mackerel (Juanes & Conover 1994; Juanes *et al.* 1996; Sánchez-Jerez *et al.* 2008). Therefore, bearing in mind the trophic level of bluefish and the fact that sea warming is impinging favourably on its biology, the status of bluefish populations needs to be studied and monitored.

Sea temperatures can actually act as an oceanic barrier between fish populations by creating temperature boundaries in their geographic ranges (Crow *et al.* 2007). Although the distribution of bluefish coincides with sea surface temperatures of 18–27°C along the subtropical continental shelves of the world (Juanes *et al.* 1996), it has been suggested by Goodbred & Graves (1996) that shifts in the distribution ranges of bluefish and contact between isolated populations have resulted from historical changes in water temperature. However, although no genetic studies have been carried out yet on the bluefish within our study area, Pardiñas *et al.* (2010) did report insignificant genetic differentiation between eastern Atlantic Ocean (Cadiz and Canary Islands) and Mediterranean Sea (Alicante) populations of this species. We can therefore hypothesize that there is a homogenous bluefish population within the NW Mediterranean, where seasonal migrations take place along a latitudinal gradient in response to changes in water temperature and food supply.

In summary, this study provides evidence that a marine fish species such as bluefish, which is able to expand or it is forced to shift its distribution due to sea warming, may take advantage of other environmental conditions - such as better food availability – in new habitats which will contribute to increasing its energy reserves and reproductive potential and therefore contribute to enhancing the population’s productivity in these areas.

CHAPTER IV: Climate-driven changes in life-history traits of the bastard grunt *Pomadasys incisus* (Teleostei: Haemulidae) in the North-western Mediterranean

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CHAPTER IV

Climate-driven changes in life-history traits of the bastard grunt *Pomadasys incisus* (Teleostei: Haemulidae) in the North-western Mediterranean

4.1. Abstract

This study evaluates the influence of sea water temperature on the life-history traits of the thermophilic bastard grunt *Pomadasys incisus* along the Catalan coast. We compared two key traits of this species, condition and reproduction, from populations in two separate areas with different thermal regimes: the Gulf of Roses (cold area) and the Ebre Delta (warm area). Specimens were collected monthly from each area between 2010 and 2012. The results were also compared with those given in the literature from sites where the species is more common, i.e. the southern Mediterranean and eastern Atlantic. Our findings indicate that, compared to the populations in warmer environments, the population inhabiting the colder waters appears to be in significantly poorer condition and there is some deviance in their life-history traits: egg size and quality being traded-off for higher egg numbers; lower lengths at maturity and alterations to spawning phenology. A certain degree of plasticity in life-history traits may favour the process of expansion and establishment of this thermophilic species into newly available but colder habitats of the north-western Mediterranean under a scenario of climate change.

Keywords: *Pomadasys incisus*; bastard grunt; condition; reproduction; sea warming.

4.2. Introduction

Sea warming is allowing northward expansion of thermophilic species in the Mediterranean (Francour *et al.* 1994; Molinero *et al.* 2005; Perry *et al.* 2005; Sabatés *et al.* 2006, 2012; Lloret *et al.* 2014). It has been observed, in this context, that invading species may dis- play deviant life-history traits showing, for example, great plasticity in growth and fecundity - as compared to well-established conspecific populations in other areas - which in periods of rapid population growth may favour the processes of expansion and establishment of these invading species in new habitats (Rosecchi *et al.* 2001; Bøhn *et al.* 2004; Ribeiro & Collares-Pereira 2010). The extent of this plasticity in their life-history traits, which is a response to either fish density or environmental conditions, is dependent on adaptations to environ- mental variation which, in turn, are limited by the inherent physiological and behavioural characteristics of each fish species (Alcaraz & García-Berthou 2007; Ribeiro & Collares-Pereira 2010). In this sense, fish condition and reproduction are two key life-history traits that can help to characterize certain components of the environment in which fish exist and thus reveal changes - such as sea warming - in environmental conditions (Lloret *et al.* 2002, 2012, 2014; Lloret & Planes 2003; Pankhurst & King 2010; Pankhurst & Munday 2011).

The bastard grunt, *Pomadasys incisus* (Bowdich 1825), is a coastal demersal species inhabiting marine and brackish waters (Pajuelo *et al.* 2003a), usually near sandy or muddy substrate, at depths between 10 and 100 m, although it is more commonly found not far from 50 m (Kapiris *et al.* 2008). Its main distribution encompasses the eastern part of the Atlantic Ocean, from Angola to Gibraltar (including the Canary Islands, Madeira and the Cape Verde Islands). However, this subtropical and thermophilic species is currently spreading and establishing itself within the whole Mediterranean Sea (Bodilis *et al.* 2013). This species naturally entered the Mediterranean Sea through the Straits of Gibraltar but the prevailing currents, sea warming and the availability of suitable soft substrate in relatively shallow waters has recently allowed *P. incisus* to establish itself in the north-western Mediterranean basin (Francour *et al.* 1994; Pastor *et al.* 2008; Bodilis *et al.* 2013). *P. incisus* is an example of the latitudinal extensions and/or demographic increase of thermophilic fishes which are taking advantage of the current climate change (Psomadakis *et al.* 2012). In the Gulf of Roses and adjacent waters in particular (southern Gulf of Lyon), the bastard grunt has apparently become more frequent since the 1950s (Lloret *et al.* 2011). However, landings statistics in this area are inexistent.

Information on the biology of *P. incisus* has so far been restricted to the Canarian Archipelago (Pajuelo *et al.* 2003a; b) and the Gulf of Tunis (Chakroun-Marzouk & Ktari 2006; Fehri-bedoui & Gharbi 2008) where its natural subtropical habitats and warmer environmental conditions prevail. Therefore, since the shifts in the bastard grunt distribution appear to be the result of current climate change, this warm-water species appears to be a good candidate for investigating the effects of sea warming (Francour *et al.* 1994; Bodilis *et al.* 2013). The overall aim of this study was to compare two key life-history traits - condition and reproduction - of the bastard grunt from two separate areas of the north-western Mediterranean with different thermal regimes in order to assess whether or not the particular life history traits of this thermophilic species may contribute to its expansion in the area.

4.3. Materials and methods

4.3.1. Sampling locations

Samples were collected from two different areas with non-identical thermal regimes along the Catalan coast: the northern-most Gulf of Roses and the southern-most Ebre Delta (Fig. 4.1). The Gulf of Roses and surrounding waters have lower mean water temperatures than the Ebre Delta (Salat *et al.* 2002). Therefore, the data on sea surface temperature (SST, in °C) from both sampling areas (the Gulf of Roses and the Ebre Delta) was retrieved from the International Comprehensive Ocean-Atmosphere Data Set (ICOADS) for the period 2010-2012 (ds540.0-Release 2.5) (Woodruff *et al.* 2011). The data comprised individual daily mean SST observations for 1° latitude x 1° longitude units. In this study, we used the time series from two 1° squares in the north-western Mediterranean: the Gulf of Roses (42.0 to 43.0°N and 3.0 to 4.0° E) and the Ebre Delta (40.0 to 41.0°N and 0.0 to 1.0° E). The mean monthly values of SST were calculated by averaging daily temperatures. Monthly SSTs were indeed higher in Ebre Delta than in the Gulf of Roses significantly (ANOVAs, $p < 0.001$). In both areas the monthly SSTs began to increase from April to May, peaked in August, and then decreased during the coldest months from January to March (Fig. 4.2).

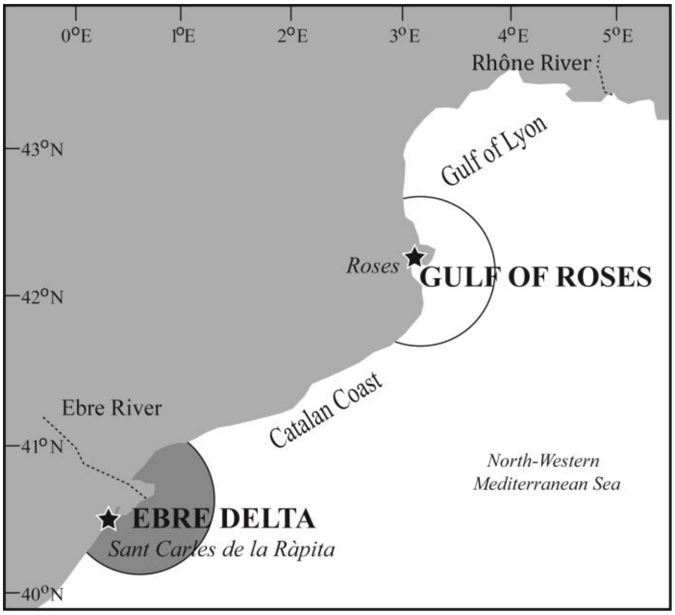

Fig. 4.1 Map of the Catalan coast showing the two study areas (the Gulf of Roses and the Ebre Delta), and the location of the fishing ports (Roses and Sant Carles de la Ràpita) where specimens of *Pomadasys incisus* were sampled.

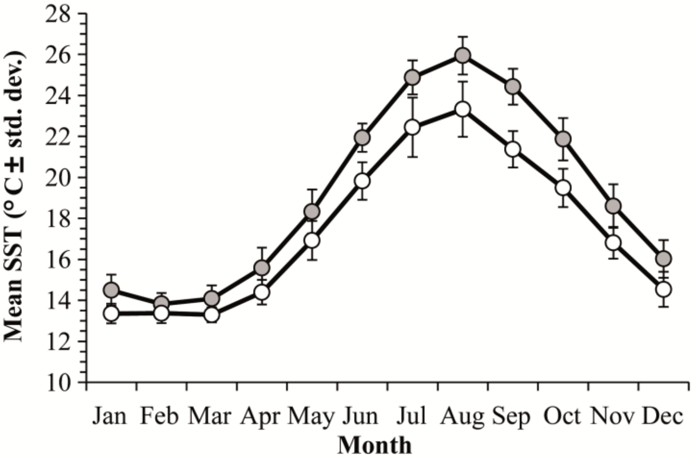

Fig. 4.2 Mean (± std. dev.) monthly variation of the sea surface temperatures (SSTs) in the Gulf of Roses (white circles) and the Ebre Delta (grey circles) during the study period (2010-2012).

In order to compare the growth, condition and reproduction parameters of *P. incisus* between the two studied areas, samples were collected monthly from fishermen (coastal purse seiners) at Roses (Gulf of Roses) from July 2010 to September 2012 and at the port of Sant Carles de la Ràpita (Ebre Delta) from May to September 2012, shortly after the small-scale and trawl fishing vessels had landed their catches. It should be noticed that fishermen were asked for the approximate location and depth where the specimens were caught in order to be sure that the origin of the samples is within the coastal waters of each study area. In the laboratory, we recorded the total length (TL) to the nearest 0.5 cm and total weight (TW) to the nearest 1 mg. All samples were dissected and eviscerated, and the somatic or eviscerated body weight (SW), the liver weight (LW) and the gonad weight (GW) were obtained to the nearest 1 mg. The gonads were fixed in 4% buffered formalin for further histological processing and fecundity estimation.

4.3.2. Fish Condition and Reproductive Biology

The hepatosomatic (HSI) was calculated for each individual as a function of somatic wet weight (SW) in order to avoid possible variations arising from the contents of the digestive tract. Thus, HSI was calculated as HSI = 100*(LW/SW), where LW and SW represent liver and somatic wet weights, respectively.

The gonadosomatic index (GSI) was estimated also for each individual using the formula GSI = 100*(GW/SW), where GW and SW represent gonad and somatic wet weights, respectively. Although the sex and reproductive status of specimens were macroscopically determined initially, a histological analysis was also performed in order to provide a more accurate analysis of the reproductive characteristics and the annual reproductive cycle of *P. incisus*. Thus, a histological study of the gonads of each individual was carried out in order to determine the stages of development of their germ cells. Central portions (transverse sections) of the fixed gonads were dehydrated and embedded in paraffin, sectioned at between 3-8 μm, depending on their state of maturity, and stained with haematoxylin-eosin and Mallory's trichrome. The latter staining method highlights the zona radiata and its continuity, and facilitates the detection of atretic oocytes (Muñoz *et al.* 2010). The maturation stages of the gonads were classified in line with Brown-Peterson *et al.* (2011) in order of developmental appearance as regenerating (RGN), early developing (EDEV), developing (DEV), spawning capable (SC), actively spawning (AS), and regressing (RGS).

In order to define sexual maturation as a function of body length, the L_{50} (body length at which 50% of the individuals were mature) was estimated separately for samples from both sampling areas. To predict the probability that an individual was mature based on its length, binary maturity observations (0 = immature, 1 = mature) and length (TL) were fitted to binary logistic models in order to construct maturity ogives (maturity-at-length probability plots) based on logistic equations using 1 cm length classes. Size at maturity was estimated initially for females and males.

The presence of hydrated oocytes and post-ovulatory follicles (POFs) was histologically determined in order to select suitable specimens for the analysis of fecundity. The oocyte size-frequency distribution for each spawning female was analysed in order to detect the batches of oocytes, since this may demonstrate different maturation patterns and associated fecundities (Kjesbu *et al.* 1998). Thus, fecundity was estimated for each specimen found to be in either spawning capable (SC) or actively spawning (AS) phase - and without post-ovulatory follicles (POFs) - using the gravimetric method combined with image analysis as explained by Murua *et al*. (2003). With this aim, subsamples of about 150 mg were taken from the ovary; oocytes were separated from connective tissue using a washing process (Lowerre-Barbieri & Barbieri 1993) and sorted by size through several sieves (from 1000 to 100 μm), which facilitated the subsequent work of counting and measuring oocytes using a computer-aided image analysis system (Image-Pro Plus 5.1). Subsamples were taken from sections of the middle part of the ovary since there were no significant differences in the number of most advanced oocytes per gram among the anterior, middle and posterior parts of the ovary of 10 specimens that were in the latest developmental stages (ANOVA, $F_{2,29}$ = 2.24, p = 0.125). Thus, estimates of fecundity were based on batch fecundity (BF) - defined as the number of eggs spawned per batch - which was estimated according to Hunter *et al.* (1985) as $BF = GW*(Y/Sw)$, where GW is the gonad weight after fixation, Y is the number of hydrated oocytes in a weighted subsample of ovarian tissue and Sw is the subsample weight. The relative batch fecundity (RBF) was also calculated, as batch fecundity per gram of somatic weight of the fish. Only 98 females (41 from the Gulf of Roses and 57 from the Ebre Delta) met the histological criteria (actively spawning with hydrated oocytes and without POFs) for fecundity analysis.

In order to explore the size range for each oocyte developmental stage, the mean diameter of 200 oocytes from each stage was measured from the histological sections as the average of major and minor axes. Due to their irregular shape, the mean diameter of the hydrated oocytes was estimated separately after adding glycerine, which facilitates their differentiation.

The dry weight and diameter of hydrated oocytes were used to estimate the quality of the eggs, hence an approximation of the potential reproductive success (Brooks *et al.* 1997). Thus, mean dry weights in mg per egg, were estimated by drying (for 24 h at 110°C) two replicates per sample of the eggs from a total of 20 actively spawning females per sampling area.

The prevalence of atresia, Pa (percentage of sexually mature females that have α-atretic vitellogenic oocytes) and the relative intensity of atresia, RIa (percentage of α-atretic vitellogenic oocytes in relation to the total number of vitellogenic oocytes) were estimated from observations at three different focal planes of different histological slides for each specimen (Kurita *et al.* 2003).

4.3.3. Statistical Analyses

Firstly, generalized linear models (GLMs) (McCullagh & Nelder 1989) were used to investigate the variation of fish condition with sex, stage of maturity and size. Therefore, GLMs were fitted to HSI and GSI as response variables; sex (females and males) and maturity (immature, developing, spawning capable, regressing, regenerating) were used as categorical predictor variables, while size (total length) was used as the continuous predictor variable. All predictors and their first order interactions were initially included in the GLM. Analysis of deviance to evaluate the significance (F-test) of the factors in the model was performed by a stepwise procedure, and the most appropriate error models were chosen on the basis of residual plots. GLMs incorporating sex and maturity as predictor variables accounted significantly for 42.3% of the deviance of HSI (ANOVA, $F_{9,595} = 49.48$, $p < 0.0.001$) and 65.4% of the variability in GSI (ANOVA, $F_{9,595} = 125.97$, $p < 0.0.001$). Because size did not significantly account for the deviance neither of HSI nor of GSI ($p > 0.05$), we used the GLM approach to standardize HSI and GSI data only for the effects of sex and maturity by estimating the adjusted means of HSI and GSI for the variation of the covariables (sex and maturity).

Taking into account that the temporal scale of the samplings did not match entirely between study areas, i.e. in the Gulf of Roses from 2010 to 2012, while in the Ebre Delta only during 2012, and in order to carry out the comparative analyses between sampling areas, firstly a sub-dataset of the Gulf of Roses samples was created, which matched the temporal scale of the Ebre Delta sampling period (from May to September 2012). This analysis indicated that, even at this reduced temporal scale (2012), there were significant differences between sampling areas in the condition and reproduction variables such as, for example, GSI (ANOVA, $F_{1,407} = 4.56$, $p = 0.033$) or HSI (ANOVA, $F_{1,407} = 4.84$, $p = 0.028$). Secondly, there were insignificant interannual differences (2010, 2011 and 2012) among samples from the Gulf of Roses, e.g. GSI (ANOVA, $F_{2,266} = 2.13$, $p = 0.1209$) or HSI (ANOVA, $F_{2,266} = 2.51$, $p = 0.0832$). Overall, the significant differences between sampling areas, at the reduced temporal scale (2012), as well as the insignificant interannual differences (2010-2012) within the Gulf of Roses, supported the decision to group of three reproductive annual cycles from the Gulf of Roses in order to compare each variable with those of the Ebre Delta.

Subsequently, for all aforementioned variables (HSI, GSI, batch fecundity, oocytes diameter), the Shapiro- Wilk test was used to test the assumptions of normality and Levene's test was used to test the homogeneity of variances (Zar 1996). If assumptions were met, ANOVA models were used to compare all indices between sexes (females vs. males) and sampling areas (Gulf of Roses vs. Ebre Delta). A p-value of α = 0.05 or less was considered to be statistically significant. Moreover, if the ANOVA indicated significant differences, Bonferroni's multiple tests were applied for post hoc comparisons of significant effects (Sokal & Rohlf 1995).

Finally, the relationship between batch fecundity (BF) and total length (TL) was estimated by fitting power functions. Then, ANOVAs (for relative batch fecundity), ANCOVAs (for batch fecundity using TL as covariate) and paired Student's tests (for oocyte quality and relative intensity of atresia) were also used to find out whether, on average, differences between sampling areas, for the aforementioned variables, were statistically different (Zar 1996).

4.4. Results

Of the 596 fish examined, a total of 267 specimens (158 females and 109 males) and 329 specimens (174 females and 155 males) of *P. incisus* were sampled in the Gulf of Roses and the Ebre Delta, respectively. The total length-frequency distributions ranged similarly in the two study areas from 13.0 to 29.0 cm (Fig. 4.3).

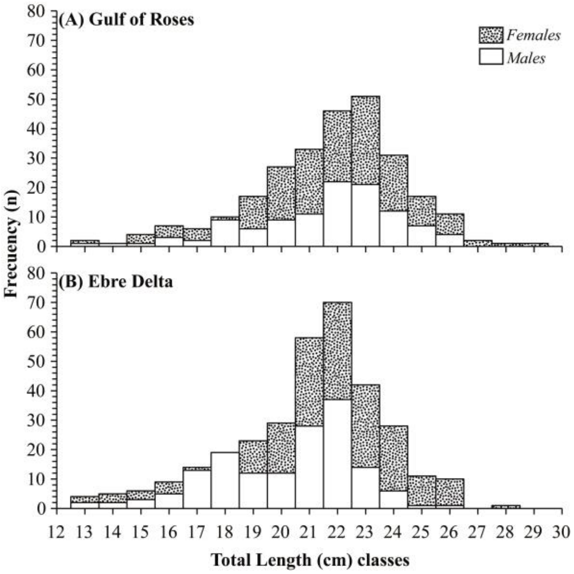

Fig. 4.3 Size-frequency distributions (1 cm TL interval classes) for specimens of *Pomadasys incisus* sampled for this study per sex at each sampling area: (A) Gulf of Roses and (B) Ebre Delta.

The standardized HSI were significantly higher on average in the Ebre Delta than in the Gulf of Roses (ANOVA, $F_{1,595} = 5.95$, p = 0.015), indicating better fish condition in the southern population (Table 1). Ebre Delta specimens also showed significantly higher average GSI compared to those from the Gulf of Roses (ANOVA, $F_{1,595} = 4.90$, p = 0.027), indicating that the reproductive investment was much higher in the southern population (Table 4.1).

Table 4.1 Summary of the mean values (± std. dev.) for specimens of *Pomadasys incisus* and comparison tests evaluating the effect of the sampling area, Ebre Delta (ED) vs. Gulf of Roses (GR), on the following parameters: hepatosomatic index (HSI), gonadosomatic index (GSI), length at maturity (L_{50}, sexes pooled, cm TL), oocyte diameter (µm, for each developmental stage), egg quality (mg per egg), spawning season (months and temperature range), mean intensity of atresia (RIa, % vitellogenic oocytes in α-atretic state), batch fecundity (BF, eggs per spawning batch), relative batch fecundity (RBF, eggs per gram of body mass). P-values indicating significance are also shown where ** indicates p < 0.05; *** indicates p < 0.001, and NS indicates no significant difference.

Variable	**Source**	**Mean (± std. dev.)**		**Outcome**	**n**	**Test**	**Statistic**	**P**
		ED	**GR**					
HSI	Pool	2.02 ± 0.57	1.58 ± 0.45	ED > GR	596	ANOVA	$F_{1,595} = 5.95$	**
GSI	Pool	3.28 ± 1.99	2.56 ± 1.91	ED > GR	596	ANOVA	$F_{1,595} = 4.90$	**
L_{50}	Males	15.3	14.1	ED > GR	264			
	Females	15.6	14.9	ED > GR	332			
Oocyte diameter	CA	154.9 ± 23.5	138.6 ± 19.6	ED > GR	400	ANOVA	$F_{1,399} = 56.20$	***
	Vtg-1	248.8 ± 24.7	228.9 ± 24.1	ED > GR	400	ANOVA	$F_{1,399} = 66.92$	***
	Vtg-2	346.0 ± 25.0	334.5 ± 27.6	ED > GR	400	ANOVA	$F_{1,399} = 18.88$	***
	Vtg-3	457.4 ± 26.7	434.3 ± 23.9	ED > GR	400	ANOVA	$F_{1,399} = 82.71$	***
	GVM	547.4 ± 24.1	529.2 ± 24.4	ED > GR	400	ANOVA	$F_{1,399} = 56.81$	***
	H	728.6 ± 57.1	700.4 ± 60.1	ED > GR	400	ANOVA	$F_{1,399} = 23.14$	***
Egg quality		0.124 ± 0.05	0.116 ± 0.08	ED > GR	40	Student's	t = 2.134	**
Spawning	SSTs	24.0-26.5	19.3-25.0	ED > GR	336			
	Period	Jul to Sep	Jul to Sep	=	336			
Ria		96.1 ± 8.1	95.5 ± 2.1	=	37	Student's	t = 1.788	NS
BF		7971 ± 4371	14033 ± 6912	GR > ED	98	ANCOVA	$F_{1,96} = 42.12$	***
RBF		51.1 ± 19.5	84.2 ± 27.6	GR > ED	98	ANOVA	$F_{1,97} = 48.81$	***

With regard to the time of the year, it was found that the GSI of females and males of P. incisus peaked in July-September in similar fashion in both sampling areas, indicating that this species, in both our study areas, spawns only once per year (Fig. 4.4). This was later confirmed by the similar trends in maturity stages (expressed in frequency of occurrence) throughout the year; no differences between sexes or between sampling areas were observed in the maturation pattern of the gonads of this species (Fig. 4.4). The developing stages were observed mainly from May to June; then, the spawning activity began from July to September; subsequently the spawning activity ceased as the regressing stage became more evident; and finally from late September to April, the proportion of females at the regeneration stage increased. As stated before, similarities in the spawning phenology were observed between sampling areas; however, it was noticeable that spawning specimens began to appear simultaneously in July in both areas even though SSTs were considerably different, i.e. in the Ebre Delta spawning specimens appeared in catches at SSTs ranging from 24.0°C to 26.5°C, whereas in the Gulf of Roses spawning specimens began appearing at SSTs ranging from 19.3°C to 25.0°C.

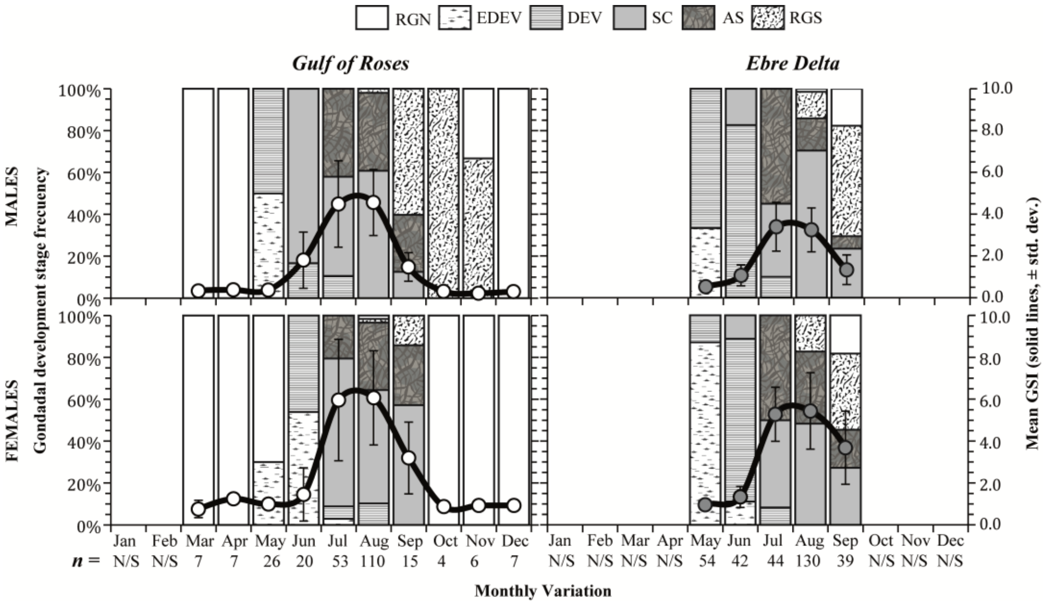

Fig. 4.4 Monthly frequencies (percent abundance) of the ovarian and testis development stages, and mean (± std. dev.) variation in the gonadosomatic index (GSI) for specimens of *Pomadasys incisus* sampled in the Gulf of Roses and the Ebre Delta. Development stages: regenerating (RGN), early developing (EDEV), developing (DEV), spawning capable (SC), actively spawning (AS), and regressing (RGS). Sample number per month (n) is also given. N/S denotes periods in which no samples were caught.

The total lengths (TLs) of immature fish (n = 34) ranged from 13.0 to 18.0 cm, and the mean length at which 50% of females and males were mature (L_{50}) was lower in the Gulf of Roses than in the Ebre Delta (Table 4.1). An overall L_{50} (sexes and areas pooled) was estimated at 14.9 cm TL for the north-western Mediterranean (Gulf of Roses and Ebre Delta together), and no immature individuals were found with TLs greater than 19 cm.

For the two areas combined, the range of oocyte diameter at the different stages of development were as follows: cortical alveolar (CA, 100 – 200 μm), early vitellogenesis (Vtg-1, 200 – 300 μm), mid vitellogenesis (Vtg-2, 300 – 400 μm), advanced vitellogenesis (Vtg-3, 400 – 500 μm), germinal vesicle migration (GVM, 500 – 600 μm) and hydration (H, 600 – 900 μm). However, at each of these stages of development, the mean diameter of oocytes from the warmer Ebre Delta were significantly larger than those captured in the Gulf of Roses ($p < 0.001$) (Table 4.1).

The batch fecundity (BF) ranged from 2738 to 35685 eggs per spawning batch in fish ranging from 18.5 to 29.0 cm TL (Fig. 4.5). The relationship between BF and TL was fitted to the following exponential regression models: in the Gulf of Roses ($BF = 0.0036 \cdot TL^{4.642}$, $r^2 = 0.623$, n = 41) and in the

Ebre Delta (BF = 0.0041·TL$^{4.749}$, r^2 = 0.635, n = 57) (Fig. 4.5). Mean BF for each sampling areas was estimated at 14033(± 6912) and 7971(± 4371) eggs per spawning batch for the Gulf of Roses and the Ebre Delta, respectively. BF was significantly higher in the Gulf of Roses than in the Ebre Delta (ANCOVA with TL, F$_{1,95}$ = 42.12, p < 0.0001). Similarly, the mean relative batch fecundities (RBF) were estimated at 84.2 (± 27.6) and 51.1 (± 19.5) eggs per gram of body mass for the Gulf of Roses and the Ebre Delta (Fig. 4.6 A), respectively. The RBF was significantly higher in the Gulf of Roses than in the Ebre Delta (ANOVA, F$_{1,96}$ = 48.81, p < 0.0001). *P. incisus* in the Gulf of Roses produced on average 40% more eggs per gram of fish (RBF) than fish in the southern Ebre Delta population.

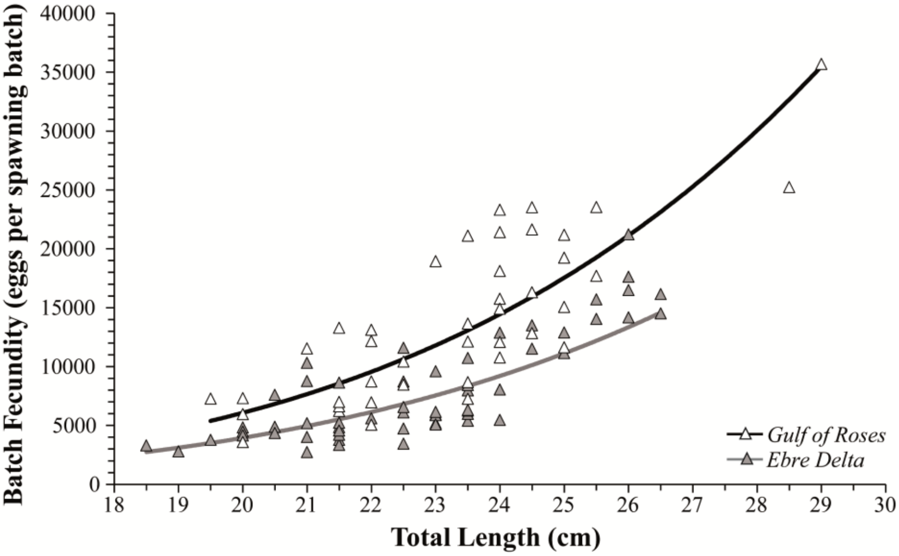

Fig. 4.5 Fitted regression model based on the relationship of the batch fecundity to fish length for specimens of *Pomadasys incisus* sampled in the Gulf of Roses (BF = 0.0036·TL$^{4.642}$, r^2 = 0.623, n = 41) and the Ebre Delta (BF = 0.0041·TL$^{4.749}$, r^2 = 0.635, n = 57).

As a measure of egg quality, the mean dry weight of hydrated oocytes in mg per egg, was estimated for this species at 0.116 (± 0.08) in the Gulf of Roses and 0.124 (± 0.05) in the Ebre Delta (Fig. 4.6 B), that is to say, the hydrated oocytes of *P. incisus* are significantly heavier for specimens from the Ebre Delta than those from the Gulf of Roses (t = 2.134, p = 0.039, n = 40).

Prevalence of atresia (Pa) was estimated at 15.2% of all mature females from the Gulf of Roses (n = 136) and 12.8% of all mature females from the Ebre Delta (n = 125). Signs of α-atresia was observed only during the regressing stage with 95.5 ± 2.1% (Gulf of Roses) and 96.1 ± 8.1% (Ebre Delta) of their vitellogenic oocytes in α-atretic state; that is to say, there was no significant difference in mean intensity of atresia RIa (t = 1.788, p = 0.082, n = 37).

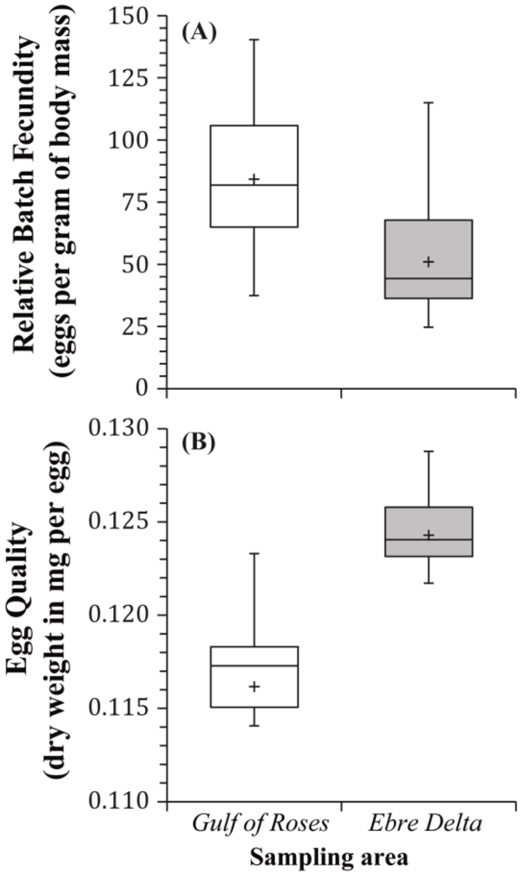

Fig. 4.6 Mean relative batch fecundities (A) and mean dry weights of hydrated oocytes (B) for *Pomadasys incisus* per sampling area are shown as interquartile box range (25-75%), with mean (+) and median (⊟) whiskers (represented as Q1 and Q3 deviations from the smallest and largest observation, respectively).

The oocyte development of *P. incisus* was considered to be asynchronous, since oocytes at different stages of development were simultaneously present in the ovary. Moreover, the variation in the stage-specific oocyte size-frequency distribution of *P. incisus* during the annual reproductive cycle indicated a lack of hiatus separating the yolked oocyte stock from the reservoir of unyolked oocytes (Fig. 4.7 A-C). These oocyte size-frequency distributions showed a continuous size-frequency development of oocytes, except for ovaries in the actively spawning stage which, along with all the secondary growth stages, had a separate mode of the most advanced oocytes (> 500 μm) (Fig. 4.7 D-E). Only when hydration occurred just before ovulation, did most advanced oocytes outgrow the standing stock of vitellogenic oocytes and a separate mode of mature hydrated oocytes developed.

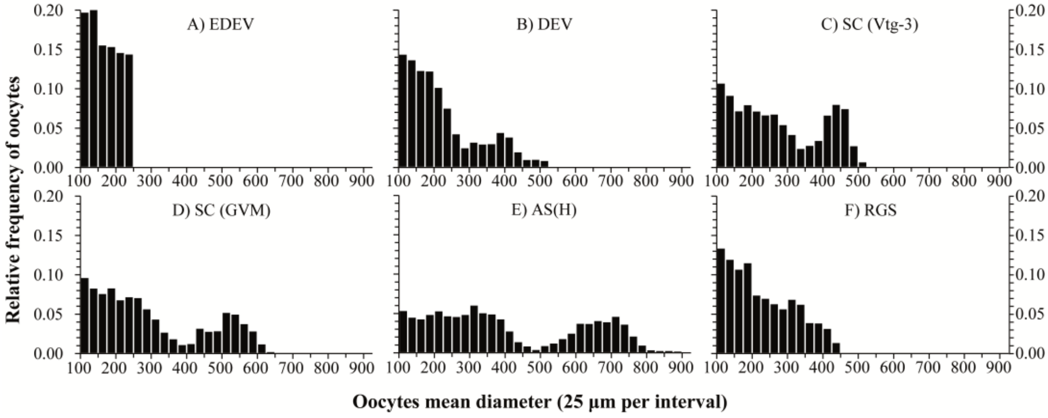

Fig. 4.7 Oocyte size-frequency distributions (per cent abundance per 25 μm diameter class) of a 'standard' 25 cm TL female of *Pomadasys incisus* through subsequent gonadal development stages: (A) early developing (EDEV), (B) developing (DEV), (C) spawning capable (SC-advanced vitellogenic), (D) spawning capable (SC-germinal vesicle migration), (E) actively spawning (AS-hydration), and (F) regressing (RGS). Each distribution corresponds to an individual fish.

4.5. Discussion

The continuous oocyte size frequency distribution, the asynchronous development of oocytes, the lack of hiatus separating the yolked oocyte stock from the reservoir of unyolked oocytes and the fact that massive atresia was observed in post-spawning individuals are evidence of indeterminate fecundity and batch spawning of the bastard grunt (Murua & Saborido-Rey 2003). However, the condition and reproductive traits of the two NW Mediterranean populations of *P. incisus* in this study show that this thermophilic species displays great spatial plasticity in its life-history traits.

Our observations point to different reproductive strategies among populations inhabiting different thermal regimes: in the relatively warmer waters of the Ebre Delta, *P. incisus* develops considerably fewer eggs per batch compared to the population inhabiting the relatively colder waters of the Gulf of Roses. However, in the Ebre Delta, oocytes at all stages of development were significantly larger and also heavier (at hydration) than those of the Gulf of Roses. Thus, the strategy of *P. incisus* in the warmer waters of the Ebre Delta is to spawn better quality eggs at the expense of quantity, while in the colder waters of the Gulf of Roses the strategy is inverted, with a greater number of eggs spawned at the expense of quality. Similar differences in egg quantity and quality among populations inhabiting different temperature regimes have been also reported for the anchoveta *Engraulis ringens* off the Chilean coast. In this case, larger eggs were spawned in the southern population at the cost of a reduction in fecundity, which was attributed to the different temperature conditions in the spawning habitats (Castro *et al.* 2009; Leal *et al.* 2009). Moreover, the significantly higher HSI and GSI levels found in the Ebre Delta compared to the Gulf of Roses indicate that, in warmer waters, *P. incisus* is in better condition and can invest relatively more energy reserves in reproduction than is the case in colder waters. In general terms, better conditioned fish also have a higher reproductive potential, e.g. see Lambert & Dutil (2000) and Lloret *et al.* (2007). This supports the idea that the plasticity of the life history traits of *P. incisus* helps to optimize the survival of its offspring under the environmental conditions that occur in areas inhabited by this species.

This evidence of life-history traits differing between two populations of *P. incisus* inhabiting different water temperature regimes is supported by comparison with the life-history traits observed in populations inhabiting the more southern and warmer waters of the central Mediterranean coast and the eastern Atlantic. For example, the mean length-at- maturity (14.9 cm TL) in our study in the north-western was much lower than those reported for warmer water populations inhabiting the Canarian Archipelago (18.3 cm TL) (Pajuelo *et al.* 2003b); and the Gulf of Tunisia (15.33-16.13 cm TL) (Chakroun-Marzouk & Ktari 2006; Fehri-bedoui & Gharbi 2008). The size-at- maturity of fish is known to vary spatially and temporally and is usually closely related to total population abundance over the life of a cohort, with cohorts maturing at a smaller size when population size is low (Rijnsdorp 1993; Morgan & Bowering 1997; Morgan & Colbourne 1999). Furthermore, water temperature has been assumed to affect only body growth and so the effects of temperature on maturation and reproductive effort appear to be indirect via the optimization of life-history traits in fish populations (Charnov & Gillooly 2004).

The increased fecundity of *P. incisus* in the colder and the northernmost waters of the Mediterranean Sea, along with reduced size-at-maturity compared to warmer populations of the North African coast and the Canarian Archipelago, might be an adaptation aimed at maximizing the reproductive output at an earlier age during the ongoing northward spread of this species in the Mediterranean. This strategy has also been observed and documented during the invasion of the vendace *Coregonus albula* in the subarctic Pasvik watercourse, and has been seen as 'a successful achievement of an effective pioneer strategy' (Bøhn *et al.* 2004). Therefore, the plasticity of its life-history traits probably allows *P. incisus* to respond to the environmental pressures exerted by the new habitats and might play an important role in its successful establishment in northern areas of the Mediterranean Sea.

Our results indicate that spawning of *P. incisus* in the north-western Mediterranean is probably not triggered by a specific temperature since spawning began in both sampling areas simultaneously at the beginning of the warmest season (July) despite a difference in water temperature of approximately 4°C. Nevertheless, in the warmer waters of the eastern Atlantic and the southern central Mediterranean, spawning of *P. incisus* takes places during a more prolonged season from June to November (Chakroun-Marzouk & Ktari 2006; Fehri-bedoui & Gharbi 2008) than in the north-western Catalan Sea (July to September according to our study; Table 1) or even all year round in the

Canarian Archipelago (Pajuelo *et al.* 2003b). In a scenario of sea warming in the Mediterranean, *P. incisus*, as well as other invading warm-water fish species, might take advantage of any increase in sea temperature to change its seasonal phasing of reproduction and hence improve its colonization capabilities.

It has been shown that invading species may display deviant life-history traits as compared to well-established conspecific populations in optimal environmental conditions since adapting to new ecosystems requires bioenergetic trade-offs resulting in variations in fish growth and reproduction (Rosecchi *et al.* 2001; Bøhn *et al.* 2004). Therefore, the plasticity of the life-history traits of *P. incisus* may allow this thermophilic species to response to environmental pressures from the new habitats and might play an important role in the northward spread and successful establishment within the Mediterranean Sea. It has been suggested that the present warming of the Gulf of Lyon and the availability of suitable soft substrate in these shallow waters allowed *P. incisus* to establish itself in the NW Mediterranean Sea recently (Francour *et al.* 1994; Pastor *et al.* 2008; Bodilis *et al.* 2013). Despite the fact that nowadays *P. incisus* can be caught in the Gulf of Roses and the adjacent waters of the southern Gulf of Lyon throughout the year (but considerably in larger abundances during the warmest season), its actual regional proliferation and deviant life-history traits are enhancing its establishment, along with the warmer environmental conditions, within the study area.

Although the distance (about 300 km) between sampling sites is relatively short, the larval transport from the Ebre Delta to the north is unlikely since the dominant current, the Northern Current, flows in opposite direction, from the colder northern waters south-westwards along the continental slope (Millot 1990; Sabatés *et al.* 2004, 2007). It is also doubtful that continuous interchanges of mature individuals occur between the northern and southern areas due to the inshore and demersal nature of *P. incisus* as juvenile/adult and the considerable distance between these two studied areas. However, future molecular studies could clarify the population's connectivity and the dispersal pathway, which has been followed by *P. incisus* during its northward spread in the Mediterranean Sea.

In summary, our results show that the plasticity of two key life-history traits (condition and reproduction) of *P. incisus* in relation to different sea water temperature regimes, may contribute to the successful establishment of this thermophilic species into new, colder habitats in a scenario of climate change, thus facilitating its northward expansion in the Mediterranean Sea. This could also well be the case for other warm-water species that are expanding into the increasingly warmer waters of the Mediterranean Sea. In addition, our results also support the idea that fish condition indices and their reproductive parameters can help to provide indicators of the impacts of environmental factors and habitat characteristics (including the impact of climate change) on the abundance and productivity of marine species (Lloret *et al.* 2014).

CHAPTER V: Life-history traits of temperate and thermophilic barracudas (Teleostei: Sphyraenidae) in the context of sea warming in the Mediterranean

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CHAPTER V

Life-history traits of temperate and thermophilic barracudas (Teleostei: Sphyraenidae) in the context of sea warming in the Mediterranean

5.1. Abstract

This study indicated that the life-history traits of European barracuda *Sphyraena sphyraena* are apparently better suited to their environmental conditions compared to the more physically restricted life-history traits of the yellow-mouth barracuda *Sphyraena viridensis*, which co-habit the north-western Mediterranean Sea. The latter thermophilic species has a considerably higher reproductive potential as it invests its energy reserves in larger numbers of hydrated eggs per spawning batch. This would favour its population growth rates within the study area, especially if sea warming continues, in which case it is likely that the spawning phenology of this species would give it an advantage.

Keywords: condition; north-west Mediterranean; reproduction; sea warming; *Sphyraena sphyraena*; *Sphyraena viridensis.*

5.2. Introduction

When thermophilic species expand into a new habitat, or increase in abundance in response to sea warming, native species may suffer from predation or competition (Golani 1993b). In some cases, these effects may be detected in closely related, confamilial species in which coexistence and competition may occur (Molinero *et al.* 2005). It has been shown that invading species may display deviant life-history traits showing, for example, great plasticity in growth and fecundity as compared to well-established conspecific populations, which in periods of rapid population growth may favour the processes of expansion and establishment of non-native species into new habitats (Bøhn *et al.* 2004; Ribeiro & Collares-Pereira 2010). To understand the characteristics of successful non-native species populations, it is necessary to improve the ability to foresee the potential impacts on native species populations (Rosecchi *et al.* 2001; Bøhn *et al.* 2004). Therefore, comparative life-history studies of strategies between non-native species and closely related native species are necessary (Golani 1993a; Golani *et al.* 2007), mainly for improving understanding and to better manage the rearrangement in species distribution, fish assemblage structure and interspecific competition attributed to climate-driven changes (Kalogirou *et al.* 2012b).

The Mediterranean Sea is characterized by a latitudinal gradient with a well-defined seasonality, with relatively cold winters in the north and long hot summers in the south (Durrieu de Madron *et al.* 2011). This typically determines a species distribution in which subtropical species are found mainly in the eastern basin and southern Mediterranean while temperate species inhabit the colder northern areas (Francour *et al.* 1994; Bianchi & Morri 2000; Coll *et al.* 2010). A direct consequence of sea warming is the meridionalization of the thermophilic biota towards temperate seas (Molinero *et al.* 2005) and the decline of 'cold-temperate' stenothermal species (Lejeusne *et al.* 2010). According to Raitsos *et al.* (2010), the abrupt rising temperature in the Mediterranean Sea since the end of the 1990s has modified the available habitats for warm-water species, facilitating their settlement at an unexpectedly rapid rate. Moreover, an increasing abundance trend and northward expansion of thermophilic fish taxa have been recorded (*i.e.* the Carangidae and Sphyraenidae) meanwhile others (*i.e.* the Scombridae and Clupeidae) have decreased in abundance over time in the Mediterranean Sea (Azzurro *et al.* 2011).

The barracudas, of the family Sphyraenidae, are widely distributed and capable of adapting to diverse ecological conditions ranging from tropical to temperate seas over most of the world, and are found typically in shelf waters up to a depth of *c.* 100 m (Fischer *et al.* 1981; De Sylva 1990; Kadison *et al.* 2010; D'Alessandro *et al.* 2011). Adults are inshore pelagic voracious piscivores (Barreiros *et al.* 2002; Kalogirou *et al.* 2012a). In particular, in the temperate areas within the north-western region of the Mediterranean basin, two barracudas have been recorded so far: the European barracuda *Sphyraena sphyraena* (Linnaeus 1758) and the yellow-mouth barracuda, *Sphyraena viridensis* (Cuvier 1829). *Sphyraena sphyraena* is the usual temperate resident species while the larger, thermophilic barracuda (*S. viridensis*) has apparently become more frequent in the Gulf of Roses and adjacent waters (southern Gulf of Lion) during the last decade; a fact that is possibly attributed to sea warming (Lloret *et al.* 2011).

Both barracuda species are known as inshore pelagics, living close to the surface, usually aggregating to form schools or, in certain circumstances, remaining solitary (Ben-Tuvia 1986). Thus, these barracudas might be using similar habitats within the study area during specific moments of their life cycles. In this sense, it has been acknowledged that a particular habitat can provide different ecological roles for fish species (whether as spawning grounds, nursery areas or feeding grounds), but the invasion and establishment of non-native species could lead to rearrangements of the fish composition and to loss of native biodiversity and alteration of ecosystem functioning (Kalogirou *et al.* 2010). An assessment of the ecological roles of *S. sphyraena* and *S. viridensis* in the Mediterranean will require a better understanding of their life-history traits, as they have received little attention in only a few scientific publications (Barreiros *et al.* 2002; Allam *et al.* 2004a, 2004b; Kalogirou *et al.* 2012a), and none in the north-west Mediterranean Sea; moreover, data on the reproductive biology of *S. viridensis* is virtually non-existent elsewhere, whether in the Mediterranean Sea or in the eastern Atlantic Ocean.

As the thermophilic *S. viridensis* is becoming more frequent in the north-west Mediterranean Sea and share common habitats and resources with the temperate *S. sphyraena* (Kalogirou *et al.* 2012a), the overall aim of this study was to explore and compare the most relevant life-history traits, condition and reproduction of these barracudas in order to investigate whether the recent large *S. viridensis* catches in the study area coupled to increased sea surface temperature (SST) in the north-west Mediterranean Sea could be explained.

5.3. Materials and methods

5.3.1. Fish condition and reproduction evaluation

In order to compare the condition and reproduction variables of *S. viridensis* and *S. sphyraena*, samples of both species were collected monthly from fishermen (coastal purse seiners and trawlers) who landed their catches at the port of Roses (Gulf of Roses) (Fig. 5.1) during the period July 2010 to October 2012. In order to differentiate between *S. sphyraena* and *S. viridensis*, three main characteristics were used for identification (Relini & Orsi-Relini 1997): the preoperculum scale pattern (present only in *S. sphyraena*), the pectoral fin rays (13 in *S. sphyraena* and 15 in S. *viridensis*) and the number of scales above the lateral line (15–17 in *S. sphyraena* and 21–22 in *S. viridensis*). In the laboratory, total length (L_T) to the nearest 0.5 cm and total body mass (M_T) to the nearest 1 mg were recorded. Subsequently, all samples were dissected and eviscerated, and the eviscerated body mass (M_E), the liver mass (M_L) and the gonad mass (M_G) were obtained to the nearest 1 mg. Gonads were fixed in 4% buffered formalin for further histological processing and fecundity estimation.

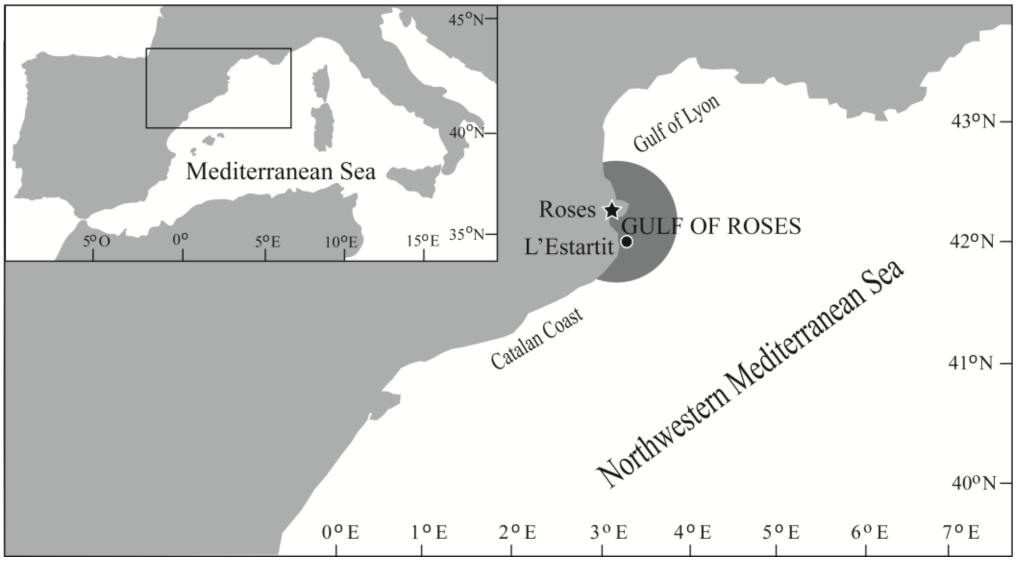

Fig. 5.1 Map of the north-western Mediterranean basin showing the study area (Gulf of Roses and adjacent waters) and the location of the fishing port of Roses (★) and the meteorological station of L'Estartit (●).

The length and mass relationship (LMR) was estimated for each species using the curvilinear formula $M_E = a\, L_T{}^{b}$ (Le Cren 1951), where a is a constant and b is the growth exponent.

The hepatosomatic (I_H) and gonadosomatic (I_G) indices were calculated for each individual. All indices were calculated as a function of M_E in order to avoid possible variations arising from differences in the contents of the gut. I_H was calculated as $I_H = 100\ M_L\ M_E^{-1}$. Similarly, I_G was estimated using the formula $I_G = 100\ M_G\ M_E^{-1}$.

Although the sex and the reproductive status of specimens were as a first step macroscopically determined, histology was also performed to provide a more accurate analysis of the reproductive characteristics and the annual reproductive cycle of both barracuda species. Histology of the gonads of every individual was carried out to determine the stages of development of their germ cells. Central portions (transverse sections) of the fixed gonads were dehydrated and embedded in paraffin, sectioned at 3 to 8 µm, depending on their stage of maturity, and stained with haematoxylin-eosin and Mallory's trichrome. The latter highlights the zona radiata and its continuity and facilitates the detection of atretic oocytes (Muñoz *et al.* 2010). Maturity stages of the gonads were classified according to Brown-Peterson *et al.* (2011) as: early developing (EDEV), developing (DEV), spawning capable (SC), actively spawning (AS), regressing (RGS) and regenerating (RGN).

To assess the average length for each spawning period, logistic regression models were constructed for each species using the proportion of spawning capable females (actively spawning sub-phase included) against the total number of mature females per week (in a calendar year), and developing the models when >50% of the females were in spawning condition in two separate periods to describe the onset and the end of the spawning season. In this way, the extent of the spawning season for each species was estimated from the dates over which 50% of females would be spawning capable between the onset and end of the spawning season (Alonso-Fernández & Saborido-Rey 2011; Lowerre-Barbieri *et al.* 2011).

In order to define sexual maturation as a function of L_T, the L_{50} (the L_T at which 50% of the individuals were mature) was estimated separately for samples of both barracuda species from the Gulf of Roses. To predict the probability that an individual was mature based on its L_T, binary maturity observations (0=immature and 1=mature) and L_T (cm) were fitted to binary logistic models to construct maturity ogives (maturity-at-length probability plots) based on logistic equations using 2 cm L_T classes for both species, and so size at maturity was estimated separately for males and females.

The presence of hydrated oocytes and post-ovulatory follicles (POFs) was determined in order to select suitable specimens for the analysis of fecundity. The oocyte size-frequency distribution for each spawning female was analysed in order to detect the batches of oocytes, as this may demonstrate different maturation patterns and associated fecundities (Kjesbu *et al.* 1998). Thus, fecundity was estimated for each specimen found to be in either spawning capable (SC) or actively spawning (AS) phase, and without POFs, using the gravimetric method combined with image analysis as explained by Murua *et al.* (2003). With this aim, sub-samples of *c.* 150 mg were taken from the central area of the ovary; oocytes were separated from connective tissue using a washing process (Lowerre-Barbieri & Barbieri 1993) and sorted by size through several sieves (from 1000 to 100 μm), which facilitated the subsequent work of counting and measuring oocytes using a computer-aided image analysis system (Image-Pro Plus 5.1; www.mediacy.com). In order to explore the size range for each oocyte developmental stage, the mean diameter of 200 oocytes for each stage was calculated from the histological sections as the average of major and minor axes. Owing to their irregular shape, the mean diameter of the hydrated oocytes was calculated separately after adding glycerine, which facilitates their differentiation.

Estimations of fecundity were based on batch fecundity (F_B), defined as the number of eggs spawned per batch, which was estimated according to Hunter *et al.* (1985) as $F_B = M_G Y M_S^{-1}$, where M_G is the gonad mass after fixation, Y the number of hydrated oocytes in a sub-sample of ovarian tissue and M_S is the sub-sample mass. The relative batch fecundity (F_{RB}) was also calculated as batch fecundity per gram of eviscerated mass of the fish.

The dry mass and diameter of hydrated oocytes were used to estimate the quality of the eggs, hence an approximation of the potential reproductive success (Brooks *et al.* 1997). Thus, mean dry masses were calculated by drying (for 24 h at 110°C) two replicates per sample of the eggs from a total of 20 actively spawning females per barracuda species.

The prevalence of atresia, P_a (per cent of sexually mature females that have α-atretic vitellogenic oocytes), and the relative intensity of atresia, R_{Ia} (percentage of α-atretic vitellogenic oocytes in relation to the total number of vitellogenic oocytes), were estimated from observations at three different focal planes of different histological slides of each specimen (Kurita *et al.* 2003).

5.3.2. Sea temperature and barracuda landings

SST (°C) data for the study period 2010–2012 were obtained from L'Estartit meteorological station (42°3′ N; 3° 13′ 15′′ E; www.meteoestartit.cat) located in the southern part of the Gulf of Roses (Fig. 5.1).

Catch data, total monthly landings (kg) of both species from the fishing port of Roses during the study period (2010–2012), were obtained from the fishery statistics provided by the Department of Agriculture and Fisheries, Government of Catalonia (www20.gencat.cat/portal/site/DAR). Landings were based mainly on small-scale fisheries and trawlers fishing in the Gulf of Roses and adjacent waters.

5.3.3. Statistical analyses

Owing to lack of significant temporal (interannual) variation in the condition variable (I_H) either for *S. sphyraena* (ANOVA, $F_{2,315}$=2.36, P=0.096) or *S. viridensis* (ANOVA, $F_{2,203}$=2.54, P=0.081) as well as in the reproduction variable (I_G) either for *S. sphyraena* (ANOVA, $F_{2,315}$=2.51, P=0.083) or *S. viridensis* (ANOVA, $F_{2,203}$=2.27, P=0.106), the results for all three reproductive annual cycles (2010, 2011 and 2012) for each species were pooled to compare each variable between species.

Pair-wise comparison of analyses of covariance (ANCOVA) was applied between regression coefficients (slopes and intercepts) of the resulting linear regression models of the LMRs of each species (Cone 1989) in order to check for LMR differences between *S. sphyraena* and *S. viridensis* populations.

Pearson's correlations were used to explore the correlation between the indices (I_H and I_G) and L_T in order to test the influence of size as covariate. Since both the I_H and I_G indices analysed were influenced significantly by size (P<0.001), ANCOVA were used to assess whether L_T (as covariate) accounted for any differences in these indices between species. Subsequently, if the ANCOVA test indicated significant differences, Bonferroni's multiple tests were applied for *post hoc* comparisons of significant effects (Sokal & Rohlf 1995). A P-value of α=0.05 or less was considered to be statistically significant.

With regard to size measurements and the aforementioned indices, the Shapiro–Wilk test as used to test the assumptions of normality and Levene's test was used to test the homogeneity of variances (Zar 1996). If assumptions were met, ANOVA models were used to compare between species.

Conversely, if the assumptions were not met, the data were analysed with non-parametric tests, such as the Mann–Whitney Wilcoxon *W*-test for pair-wise comparisons (Sokal & Rohlf 1995).

The relationship between B_F and L_T was estimated by fitting power functions. Paired *t*-tests were also used to find out whether, on average, any differences in F_{RB}, oocyte quality (mean dry mass per oocyte) and R_{Ia} between *S. sphyraena* and *S. viridensis* were statistically different from zero (Zar 1996).

The time series of landings were described by calculating the seasonal component using the decomposition method TRAMO-SEATS by means of multiple moving averages. The time series statistical package ForeTESS (Prat *et al.* 2000) was used to build univariate ARIMA models (autoregressive-integrated-moving-average) (Box & Jenkins 1976) for landings on a monthly basis in order to explore the spectral peaks at seasonal frequencies (*i.e.* the seasonal value of a given month is the percentage above and below the annual mean landings).

5.4. Results

5.4.1. Fish condition and reproductive biology

Three hundred sixteen specimens of *S. sphyraena* (203 females and 113 males) and 204 specimens of *S. viridensis* (86 females and 118 males) were sampled. The L_T of *S. sphyraena* ranged from 23.5 to 49.0 cm, whereas the L_T of *S. viridensis* was considerably larger ranging from 28.5 to 100.0 cm [Fig. 5.2(a)].

LMRs were fitted accurately to curvilinear regression models [Fig. 5.2(a)] but the relative growth in mass was considerably different between these species, for *S. sphyraena* M_E =0.0105 $L_T^{2.688}$ (r^2=0.954, *n*=329) and *S. viridensis* M_E =0.0047 $L_T^{2.913}$ (r^2=0.975, *n*=204). A significant difference, at α=0.01, in LMR was observed between *S. sphyraena* and *S. viridensis* in both regression coefficients: slopes ($F_{1,3}$=23.37, P<0.001) and intercepts ($F_{1,3}$=20.97, P<0.001), which suggests that differences exist between the two species.

The average I_H and I_G values of both females and males in spawning capable phase were significantly (P<0.05) higher in *S. sphyraena* than in *S. viridensis* (Table 5.1). The same pattern also was observed for I_H in both males and females in the regenerating phase, being significantly higher in *S. sphyraena* than in *S. viridensis* (Table 5.1). In terms of time of the year, the I_G of females and males of both species peaked in June. It is noteworthy that in *S. viridensis*, the I_G peak was constrained to a shorter time (from May to July) than was the case with *S. sphyraena*, which showed a more protracted I_G peak (from April to August) (Fig. 5.3). On the other hand, the mean values of I_H also showed different monthly variation between the two species. In both females and males of *S. viridensis*, higher I_H was observed prior to the spawning season; this, then, decreased as the spawning season advanced and began to recover when spawning finished. In contrast, in both females and males of *S. sphyraena*, I_H levels began to increase as the spawning season continued and then decreased once it had finished (Fig. 5.3).

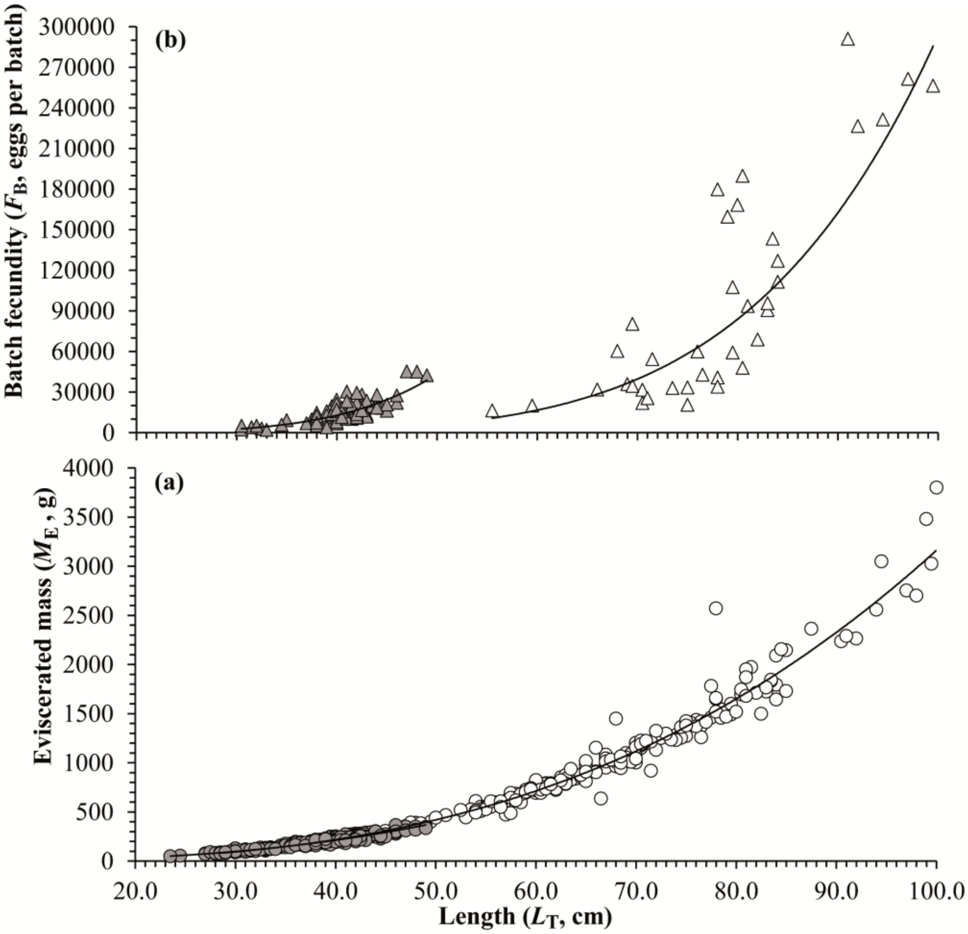

Fig. 5.2 Fitted regression models based on total length (L_T) and (a) eviscerated mass (M_E) relationships for *Sphyraena sphyraena* [●; $M_E = 0.0105\ L_T^{2.688}$ ($r^2 = 0.954$, $n = 316$)] and *Sphyraena viridensis* [○; $M_E = 0.0047\ L_T^{2.913}$ ($r^2 = 0.975$, $n = 204$)] and (b) batch fecundity (F_B) for *S. sphyraena* [▲; $F_B = 0.00003\ L_T^{5.4363}$ ($r^2 = 0.686$, $n = 74$)] and *S. viridensis* [△; $F_B = 0.000002\ L_T^{5.6144}$ ($r^2 = 0.677$, $n = 34$)].

Table 5.1 Summary of the analysis of covariance (ANCOVA) results (using total length L_T, as covariate) and subsequent *post hoc* Bonferroni's multiple comparison test to compare hepato-somatic (I_H) and gonado-somatic (I_G) indices between the two barracuda species [*Sphyraena sphyraena* (*S. sph*) *v. Sphyraena viridensis* (*S. vir*)] for each stage of maturity, per sex. Mean values of I_H and I_G are given for each stage and sex.

Variable	*Variation Source*		**Mean ± S.D.**		*n*	*F-ratio*	*p-value*	*Bonferroni's comparisons*
	Maturity	*Sex*	*S. sph*	*S. vir*				
I_H	Immature	Female	1.59 ± 0.44	1.05 ± 0.20	27	1.29	0.2668	
		Male	1.37 ± 0.50	1.12 ± 0.18	15	1.81	0.2015	
	Developing	Female	1.71 ± 0.50	1.55 ± 0.11	20	0.25	0.6231	
		Male	1.59 ± 0.45	1.46 ± 0.35	31	0.60	0.4448	
	Spawning Capable	Female	2.28 ± 0.78	1.99 ± 0.58	157	10.18	**0.0017**	*S. sph > S. vir*
		Male	1.31 ± 0.46	1.11 ± 0.28	137	10.08	**0.0019**	*S. sph > S. vir*
	Regressing	Female	1.89 ± 0.44	1.25 ± 0.32	42	0.91	0.3458	
		Male	1.53 ± 0.33	1.21 ± 0.27	29	3.69	0.0654	
	Regenerating	Female	1.63 ± 0.48	1.33 ± 0.40	43	11.35	**0.0017**	*S. sph > S. vir*
		Male	1.92 ± 0.42	1.07 ± 0.20	19	7.50	**0.0140**	*S. sph > S. vir*
I_G	Immature	Female	0.63 ± 0.13	0.56 ± 0.20	27	1.34	0.2580	
		Male	0.74 ± 0.69	0.60 ± 0.18	15	2.45	0.1415	
	Developing	Female	2.56 ± 1.61	1.69 ± 0.50	20	0.14	0.7156	
		Male	2.65 ± 1.63	1.40 ± 0.35	31	0.01	0.9538	
	Spawning Capable	Female	6.30 ± 1.81	5.58 ± 0.58	157	13.16	**0.0004**	*S. sph > S. vir*
		Male	4.88 ± 1.56	3.41 ± 0.28	137	12.21	**0.0006**	*S. sph > S. vir*
	Regressing	Female	2.19 ± 1.77	1.71 ± 0.32	42	0.43	0.5176	
		Male	2.15 ± 0.27	1.21 ± 0.88	29	1.23	0.2771	
	Regenerating	Female	1.11 ± 0.21	1.07 ± 0.40	43	2.65	0.1117	
		Male	0.79 ± 0.14	0.62 ± 0.20	19	0.59	0.4522	

Although the average I_G values observed confirmed the maturation pattern of the ovary in both species, there were notable differences in the timing of gonadal development between *S. sphyraena* and *S. viridensis* (Fig. 5.3). In females of *S. sphyraena*, the developing stages were observed from January to early May; then, the spawning activity began from late May to August; in September, the spawning activity ceased as the regressing stage became more evident and finally from late September to December the proportion of females in regeneration stage increased. Unlike *S. sphyraena*, the spawning activity of both female and male specimens of *S. viridensis* was constrained from May to July but peaked in June, as revealed by the considerable presence of specimens in the actively spawning stage. Another noticeable difference was observed especially in July when specimens in the regeneration stage began to appear (the regeneration stage in specimens of *S. sphyraena* was not observed until late September), suggesting that the rate of spawning activity among *S. viridensis* declined earlier than it did among *S. sphyraena*.

On average, a female *S. sphyraena* could spawn for 13 weeks, *i.e. c.* 4 months; whereas a female of *S. viridensis* could spawn for 7 weeks, *i.e. c.* 2 months (Fig. 5.4). The reproductive season of *S. sphyraena* females starts earlier and lasts longer than that of *S. viridensis* females, although spawning peaks in both species at around the same time.

The L_{50} of *S. sphyraena* was 27.16 and 29.5 cm L_T for males and females, respectively. Meanwhile, the L_{50} of *S. viridensis* was 44.45 and 54.84 cm L_T for males and females, respectively.

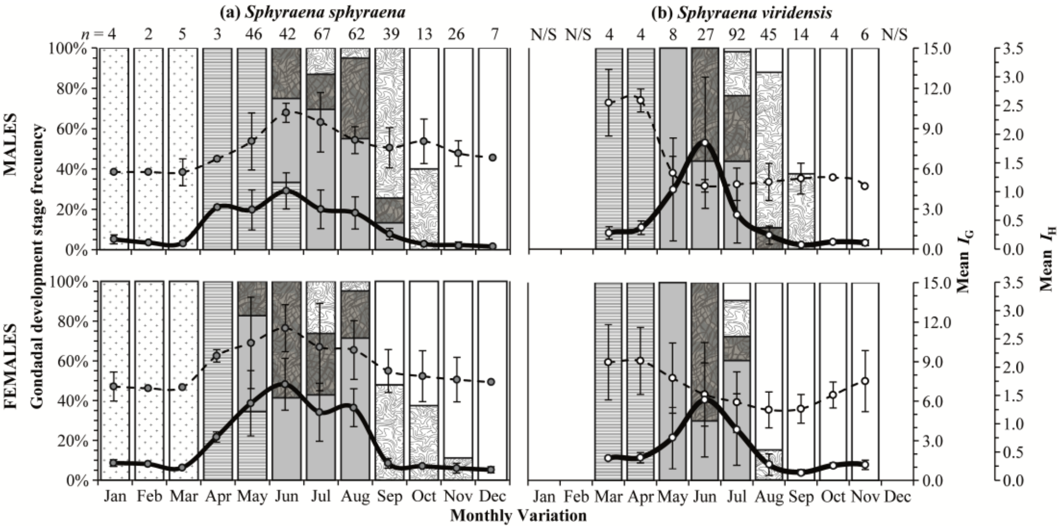

Fig. 5.3 Monthly ovary and testis development stages frequency (per cent abundance) and mean ± S.D. monthly variation in the gonadosomatic index (I_G, ——) and the hepatosomatic index (I_H, – – –) of mature males and females of (a) *S. sphyraena* and (b) *S. viridensis*. Development stages: early developing (□ EDEV), developing (▤ DEV), spawning capable (■ SC), actively spawning (▦ AS), regressing (▒ RGS) and regenerating (□ RGN). Sample number per month (*n*) is also given. N/S, periods in which no samples were caught.

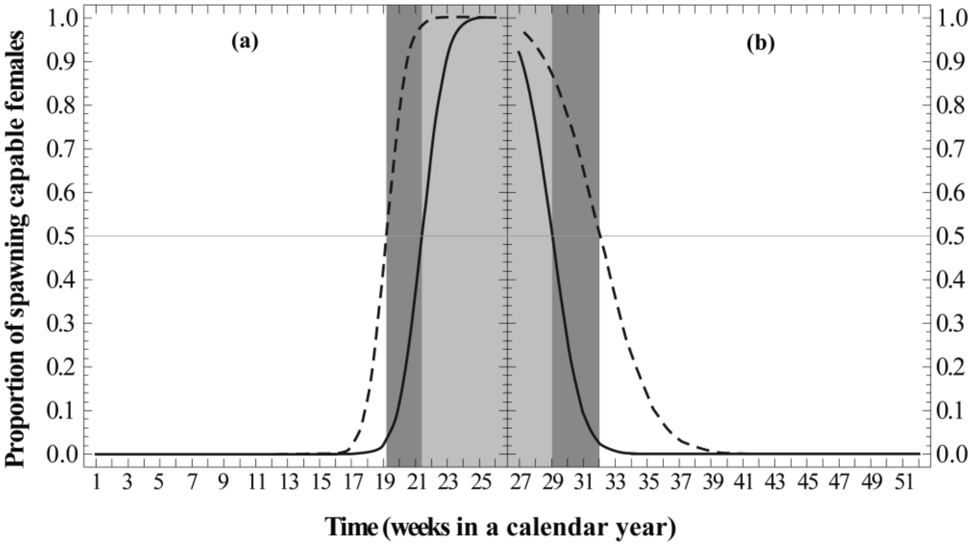

Fig. 5.4 Logistic regression model to estimate the extent of the spawning seasons for females of *Sphyraena sphyraena* (– – –) and *Sphyraena viridensis* (——). Dates in between shaded areas represent the time when >50% of the females were in spawning capable or actively spawning stages at the (a) onset and (b) end of the spawning season. Spawning season extends were estimated for *c.* 13 and 7 week seasons for *S. sphyraena* and *S. viridensis*, respectively.

The oocyte size-frequency distributions in the females of both species showed a continuous size-frequency development of oocytes except for ovaries in the actively spawning stage which, along with all the secondary growth stages of oocytes, had a separate mode of very large hydrated oocytes (>800 µm) [Fig. 5.5(a)]. Only when hydration occurred just before ovulation, did hydrating oocytes outgrow the standing stock of vitellogenic oocytes and a separate mode of mature hydrated oocytes developed.

Significant differences (Mann–Whitney Wilcoxon *W*-test) in the median diameter of oocytes from the two barracuda species were found at all stages of development: at cortical alveolar (CA, 100–250 µm, $W = -6291.0$, $P<0.05$), at early vitellogenesis (Vtg-1, 200–350 µm, $W = -13932.5$, $P<0.05$), at mid vitellogenesis (Vtg-2, 300–450 µm, $W = -15751.0$, $P<0.05$), at advanced vitellogenesis (Vtg-3, 400–600 µm, $W = -1943.5$, $P<0.05$), at germinal vesicle migration (GVM, 550–800 µm, $W = -15217.5$, $P<0.05$) and at hydration (800–1200 µm, $W = -3231.5$, $P<0.05$), with *S. sphyraena* oocytes being always slightly, but significantly, larger than *S. viridensis* oocytes [Fig. 5.5(b)].

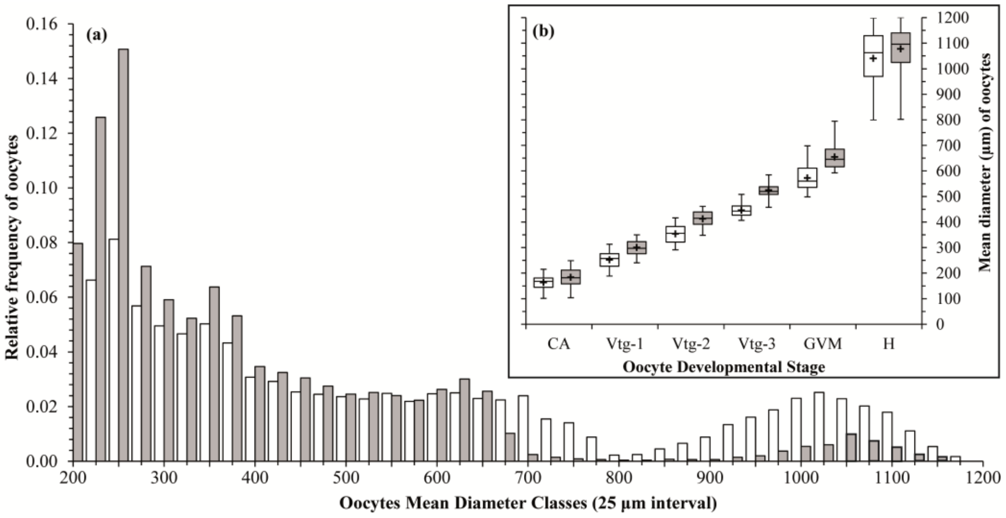

Fig. 5.5 (a) Oocyte size-frequency distributions (per cent abundance per 25 µm diameter classes) and (b) mean diameters of oocytes per development stage in two typical actively spawning females of *S. sphyraena* (▨) and *S. viridensis* (☐). Interquartile box range (25–75%), mean (+), median (⊟) and whiskers (represented as Q1 and Q3 deviations from the smallest and largest observation, respectively) are also given.

One hundred eight female specimens (74 of *S. sphyraena* and 34 of *S. viridensis*) met the histological criteria (actively spawning with hydrated oocytes and without POFs) for fecundity analysis. For *S. sphyraena*, between 2086 and 45164 eggs per spawning batch in fish size ranging from 30.5 to 49.0 cm L_T were recorded, giving an estimated mean ± std. dev. F_B of 15754 ± 8926 eggs per spawning batch. For *S. viridensis*, between 16353 and 291100 eggs per spawning batch in fish size ranging from 55.5 to 99.5 cm were recorded, giving a considerably larger estimated mean batch fecundity of 96915 ± 79199 eggs per spawning batch [Fig. 5.2.(b)]. Mean ± std. dev. relative F_{RB} were estimated at 69.5 ± 28.7 and 56.4 ± 32.8 oocytes g^{-1} of body mass for *S. sphyraena* and *S. viridensis*, respectively, *i.e.* the F_{RB} was significantly higher in *S. sphyraena* than in *S. viridensis* ($t=-2.170$, $P<0.05$, $n=111$).

As a measure of egg quality, the mean ± std. dev. dry mass of hydrated oocytes, in mg per egg, was estimated at 0.167±0.028 for *S. sphyraena* and 0.113±0.012 for *S. viridensis*, *i.e.* the oocytes of *S. sphyraena* are significantly heavier than those of *S. viridensis* ($t = 7.778$, $P<0{\cdot}05$, $n=40$).

Considerable differences between the two species were also found in P_a. Signs of α-atresia were observed in 9.1% of all mature *S. sphyraena* females ($n=110$) and 20.8% of all mature *S. viridensis* females ($n=72$). Although there were no signs of α-atresia in either species during developing or regenerating stages, *S. viridensis* specimens showed α-atresia during the spawning capable stage (P_a =21.1% of SC females), in which, on average, the mean ± std. dev. R_{Ia} was 15.1 ± 7.2% of their vitellogenic oocytes in α-atretic state. It should be pointed out that specimens of *S. viridensis* that presented atresia were captured at the end of their spawning season (July). In contrast, α-atresia was observed in all females of both species (P_a =100%) during the regressing stage with 98.8 ± 3.0% (*S. sphyraena*) and 91.8 ± 8.1% (*S. viridensis*) of their vitellogenic oocytes in α-atretic state; that is to say, there was no significant difference in R_{Ia} ($t=-1.945$, $P=0{\cdot}0631$, $n=27$).

5.4.2. Seasonality of SSTs and barracuda landings

During the study period (2010–2012), the monthly mean ± std. dev. SST began to rise from April to May, peaked in August at 23.0 ± 0.9°C and then decreased during the coldest months from January to March down to a minimum of 12.5 ± 0.3°C (Fig. 5.6). It should be noted that actively spawning *S. sphyraena* were caught when SSTs were between 16.6 and 23.0°C, *i.e.* from May to August, whereas actively spawning *S. viridensis* were caught for a shorter time when SSTs were between 19.3 and 21.6°C, *i.e.* from June to July. Remarkable is the fact that in all three reproductive cycles (2010–2012), actively spawning *S. viridensis* began to appear at a similar SST (*c.* 19·0°C), whereas no clear temperature (15–18°C) for the appearance of actively spawning *S. sphyraena* was identified.

Catches of *Sphyraena* spp. landed in the port of Roses followed a clear seasonal cycle, as reflected in the highly seasonal values compared to annual mean landings (Fig. 5.6). Between June and October, landings were above the annual average peaking in July (at 165% of the annual mean monthly landing). Minimum landings, reduced to at least 50% of the annual average, occurred between November and May. This seasonal pattern of mean monthly *Sphyraena* spp. landings at the port of Roses over the year was closely linked to the pattern of SSTs. *Sphyraena* spp. landings were almost zero during the coldest months and began to increase as SST increased (Fig. 5.6).

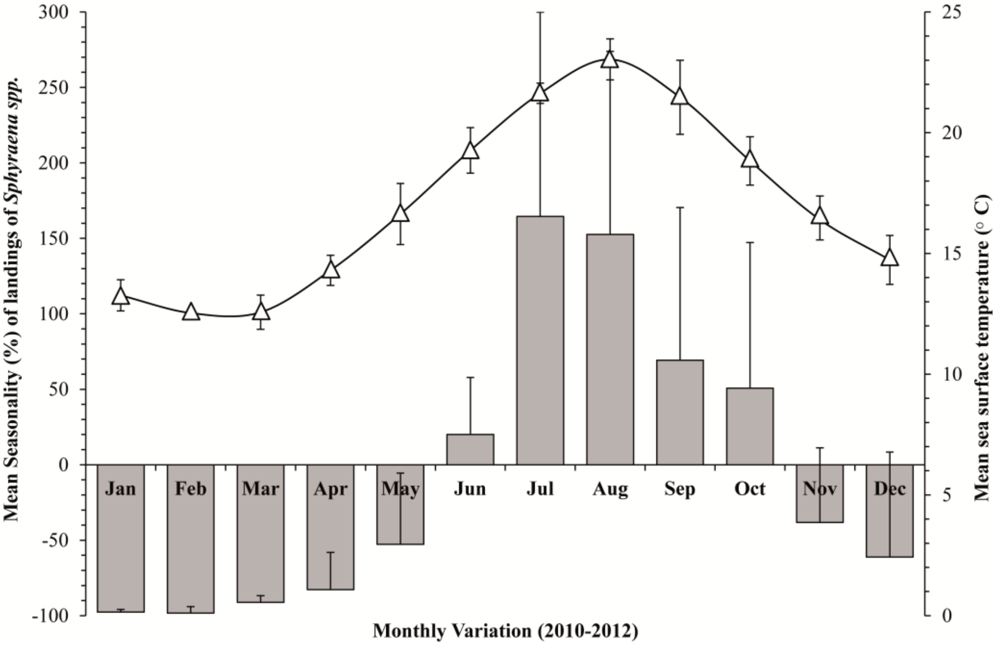

Fig. 5.6 Mean ± std. dev. seasonal patterns (per cent above and below the annual mean) of landings of *Sphyraena* spp. per month at the fishing port of Roses and the mean ± std. dev. monthly sea surface temperatures (Δ; SST) during the study period (2010–2012) at the L'Estartit meteorological station.

5.5. Discussion

On the basis of the general life-history traits and reproductive strategies of these two species, this study has revealed that *S. sphyraena* is apparently better suited than *S. viridensis* to the current temperate environmental conditions of the north-west Mediterranean Sea. *Sphyraena viridensis* has a considerably higher reproductive potential which would favour successful increase in population growth rates for this species within the study area, especially if sea warming continues. Several interesting findings and differences between the temperate *S. sphyraena* and thermophilic *S. viridensis* were found in their basic life-history traits.

The oocyte development of both species was considered to be asynchronous as oocytes at different stages of development were simultaneously present; the oocyte size frequency distribution is continuous and only when hydration occurs there is a clear differentiation stock of larger oocytes (in terms of diameter). This confirms that both species of barracudas are batch spawners, whose oocytes are recruited, hydrated and subsequently ovulated in several batches over the spawning season. Following the criteria established by Murua & Saborido-Rey (2003), asynchronous development of oocytes and massive atresia in post-spawning individuals (*i.e.* in the regressing stage) show indeterminate fecundity in these two barracuda species.

The observation point to different reproductive strategies: *S. sphyraena* develops and releases considerably fewer eggs per batch but does so for a much longer spawning season compared to *S. viridensis* which invests its energy reserves into producing larger numbers of hydrated eggs per spawning batch over a shorter spawning season. Furthermore, the *S. sphyraena* oocytes at all stages of development were found to be significantly larger and heavier (at hydration) than those of *S. viridensis*. Thus, it is apparent that the *S. sphyraena* strategy is larger and better quality eggs at the expense of quantity, while the *S. viridensis* strategy is a greater number of eggs at the expense of size and quality. In addition, significantly higher I_H and I_G levels in the temperate *S. sphyraena* indicate better conditioning and a relatively higher investment of energy reserves (in terms of mass) in reproduction than is the case for *S. viridensis*.

On the basis of life-history theory, the temperate species (*S. sphyraena*) would be considered to have more 'opportunistic' life-history traits (small body size, early maturation, low batch fecundity but high reproductive effort and frequent reproduction) than the thermophilic species (*S. viridensis*), which has a 'periodic' life-history pattern (large body size, late maturation and high batch fecundity) (Winemiller & Rose 1992; King & McFarlane 2003; Fox *et al.* 2007; Mims *et al.* 2010). On the other hand, fishes have developed several strategies between two extremes (capital and income breeders), with regard to energy acquisition and allocation to reproduction, in which the temporal pattern of energy gain depends on reproductive behaviour and spawning (Lowerre-Barbieri *et al.* 2011). Regarding the observed monthly variation of I_H in *S. viridensis*, it can be hypothesized that the reproductive costs are met mainly at the expense of energy reserves stored in the liver prior to the spawning season, in line with a capital breeder strategy. Meanwhile, it appears that *S. sphyraena* might be more of an income, rather than a capital, breeder as energy for reproduction was not stored prior to spawning but financed entirely by means of its concurrent energy income as the spawning season advanced.

It has been hypothesized that reproductive success depends greatly on the match or mismatch between spawning season and the optimal conditions for the survival of the offspring (Kadison *et al.* 2010; D'Alessandro *et al.* 2011; Lowerre-Barbieri *et al.* 2011). Therefore, the short spawning season of *S. viridensis* may indicate that the optimal environmental conditions for this species usually occur in a more restricted seasonal window than those for *S. sphyraena*. The spawning seasonality of fishes is controlled by several synergic factors (*e.g.* inheritance, energy sources and exogenous factors) (Kadison *et al.* 2010; D'Alessandro *et al.* 2011; Lowerre-Barbieri *et al.* 2011). In species with restricted spawning seasons which inhabit cold-temperate climates, however, water temperature has been recognized as the main exogenous cue that ensures that gonadal development occurs at the proper time so that fishes are capable of spawning when conditions favour offspring survival (Wright & Trippel 2009). In this sense, the short duration of the spawning activity of *S. viridensis* began during June (at similar SSTs each year, *c.* 19.0°C), *c.* 2 months before the annual maximum SSTs were reached during August.

Differences in growth and reproductive traits of fishes in response to non-optimal environmental conditions may result in reduced fish condition and reduced reproduction success for any given population at non-optimal locations (Rosecchi *et al.* 2001; Bøhn *et al.* 2004; Alcaraz & García-Berthou 2007). In this sense, back-calculated mass-at-length (estimated from length and mass constants) indicated that both *S. sphyraena* and *S. viridensis* caught in Egyptian Mediterranean waters (Allam *et al.* 2004a) were heavier than those with the same lengths caught in the north-west Mediterranean Sea (this study). These variations in mass-at-length values among regions are mainly attributed to water temperature and food supply in which temperature is thought to be responsible for most of the observed intraspecific differences in their mean growth rates (Brander 1995; Rätz *et al.* 1999; Rätz & Lloret 2003; Brunel & Dickey-Collas 2010). Increased growth rates and greater food conversion efficiency have been observed in fish populations living in warmer waters (Purchase & Brown 2001). This might suggest, in part, that better physiological and feeding conditions for both species of barracuda might prevail at relatively warmer and more eutrophic locations in the Mediterranean Sea.

A northward expansion of thermophilic taxa, including the barracudas (Sphyraenidae), has been previously related with the environmental changes experienced in the Mediterranean Sea over the last decades namely sea warming (Azzurro *et al.* 2011). The climate-driven changes in SSTs, together with the life-history traits of *S. viridensis*, might explain the increase in landings of this thermophilic barracuda in the study area (Lloret *et al.* 2011). Sea warming has been reported in the western Mediterranean Sea throughout the last century (Rixen *et al.* 2005; Vargas-Yáñez *et al.* 2008, 2010), with an increase of 1.1°C in water nearest the surface (0–50 m) over the 1974–2009 period in the northern Catalan coast (Calvo *et al.* 2011). Moreover, considerable seasonal changes have been recorded, especially in the spring season, when the highest sea warming rates occur (Nykjaer 2009). Thus, *S. viridensis* may be taking advantage of sea warming trends to approach its full reproductive potential and success in terms of population growth. The present-day sea temperatures within the study area remain more favourable to *S. sphyraena*. If sea warming continues, however, it is likely that warmer temperatures would lead to changes in the spawning phenology of *S. viridensis*, which in turn would probably lead to a more protracted spawning season. Unfortunately, such an extension of the spawning season of *S. viridensis* is virtually non-existent elsewhere, so there is little indication as to the spawning phenology of this species in warmer environments. If so an increase in the duration of the spawning season of *S. viridensis*, along with its considerably higher fecundity and more rapid growth rates (Allam *et al.* 2004a), would allow the population of this species to grow significantly.

It should be mentioned that during dissection of specimens, 21 of the *S. viridensis* individuals were found with *S. sphyraena* juveniles (*n*=325) in their stomach contents. Each of these *S. viridensis* had ingested a mean ± std. dev. of 17 ± 5 juvenile specimens of *S. sphyraena* with L_T ranging from 8.1 to 10.2 cm (mass 1.34 to 2.93 g). Those specimens of *S. viridensis* whose stomachs contained *S. sphyraena* juveniles had all been captured during the last 2 weeks of June 2012. Thus, the high number of prey among only 21 predators may indicate that these were caught while schooling, a common behaviour of *S. viridensis* (Barreiros *et al.* 2002). The occurrence of small juveniles of *S. sphyraena* within the diet of *S. viridensis* had never been detected previously.

This major presence of *S. sphyraena* juveniles in the diet of *S. viridensis* raises further intriguing questions as to whether the thermophilic barracuda is affecting the population of the temperate species. Such extreme predatory behaviour by *S. viridensis* has been recorded in the Azores archipelago by Barreiros *et al.* (2002) who reported different types of aggregations, small groups and isolated individuals in winter and large schools in summer, and several types of predatory behaviour mainly on pelagic juveniles such as the blue jack mackerel *Trachurus picturatus* (Bowdich 1825). In the eastern Mediterranean Sea, Kalogirou *et al.* (2012a) found that both *S. sphyraena* and *S. viridensis* typically preyed mainly on pelagic and supra-benthic fish species and supplemented their diet with cephalopods, but particularly interesting was the fact that significant diet overlap was found between these species. Although this latter study found no evidence of the two species preying on each other, the authors suggested that interspecific competition might be occurring as both predators were sharing common resources.

In summary, the results of this study showed that the life-history traits of *S. sphyraena* are, at present, better suited to the environmental conditions of the north-west Mediterranean Sea compared to the more physically restricted life-history traits of *S. viridensis*. *Sphyraena viridensis* has a considerably higher reproductive potential which may favour its success and an increase in its population growth within the study area, especially if the present-day sea warming continues in which case it is likely that changes in spawning phenology would give *S. viridensis* an advantage. Previous studies have shown that feeding habits of non-indigenous species can affect some feeding guilds and then cause alterations in the fish assemblages of marine ecosystems (Kalogirou *et al.* 2010; Kalogirou *et al.* 2012b). Similar studies are encouraged within the study area in order to document more information and achieve a more comprehensive understanding of the biological interactions, feeding ecology and space occupation between these two species in the north-west Mediterranean Sea, with particular attention to *S. viridensis*.

CHAPTER VI: Reproductive traits of the pompano, *Trachinotus ovatus* (Linnaeus, 1758), in the north-western Mediterranean

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CHAPTER VI

Reproductive traits of the pompano, *Trachinotus ovatus* (Linnaeus, 1758), in the north-western Mediterranean

6.1. Abstract

This study describes for the first time the reproductive traits of the warm-water pompano, *Trachinotus ovatus*. Specimens were sampled from landings by artisanal fishing vessels in the NW Mediterranean. Monthly collections, from July 2010 through to September 2012, yielded 226 individuals (118 females and 108 males). The size at 50% maturity (L_{50}) was estimated at 30.9 and 29.1 cm TL for females and males, respectively. Specific reproductive traits, such as oocyte size-frequency distributions, presence of recent post-ovulatory follicles along with oocytes in the final phases of gonadal development, and massive atresia in post-spawning individuals, indicated that pompanos are multiple batch spawners with asynchronous oocyte development and indeterminate fecundity. Monthly variations in the gonadosomatic index and in the phases of gonadal development indicated July and August as the spawning season. There were also noticeable inter-annual variations in spawning phenology, mean diameters of the oocytes, relative batch fecundity and eggs quality, all of which corresponded to changes in sea surface temperatures. This study enhances our understanding of the need for research into the reproduction of warm-water species, which are currently expanding into the increasingly warmer waters of the world's more northerly seas and oceans.

Keywords: *Trachinotus ovatus*, pompano, spawning, gonadal development, fecundity, sea temperature.

6.2. Introduction

Since the 1970s, rising temperatures in the Mediterranean have led to an expansion in habitats suitable for warm-water species, facilitating their settlement at an unexpectedly rapid rate (Vargas-Yáñez *et al.* 2008, 2010; Raitsos *et al.* 2010). Trends of increasing abundance and northward expansion have been recorded for warm-water fish taxa, such as the Carangidae and Sphyraenidae families, meanwhile other Mediterranean species, such as the Scombridae and Cupleidae families, have declined in abundance (Azzurro *et al.* 2011). Several species of the Carangidae family presently support a diverse array of economically-important fisheries in tropical and subtropical waters worldwide.

There are several carangid species in the temperate areas within the north-western region of the Mediterranean basin (the Gulf of Lyon and surrounding coastal areas), such as the leer fish *Lichia amia*, the pilot fish *Naucrates ductor*, the greater amberjack *Seriola dumerili*, the Mediterranean horse mackerel *Trachurus mediterraneus*, the blue jack mackerel *Trachurus picturatus*, and the Atlantic horse mackerel *Trachurus trachurus*. However, during the last decade a previously unusual warm-water carangid species, the pompano *Trachinotus ovatus* has become more frequent in the Gulf of Roses and adjacent waters (southern Gulf of Lyon) (Lloret *et al.* 2015b). Unfortunately, accurate records of the abundance of this species within the area are virtually non-existent because up to now the pompano has been caught unintentionally while fishing for other target species, and is considered as a bycatch species among the area's fishing community.

Of the 20 species from the genus Trachinotus described worldwide, only *T. ovatus* inhabits the Mediterranean Sea although its distribution extends north and south of the Eastern Atlantic coasts, from Scandinavian and British waters to the Bay of Biscay and as far south as Angola (Smith-Vaniz 1986; Froese & Pauly 2013). The pompano is a pelagic coastal and schooling species that is found primarily in brackish environments (especially young) and, as adults, are moderately common in shallow water in areas of surge, over sand or muddy bottoms, where they are commonly caught commercially with trawl nets, purse seines, traps, and hook-and-lines (Smith-Vaniz 1986; Schneider 1990). Scientific information on pompano biology is considerably sparse. Its reproductive biology has been investigated in just one scientific publication which explored the biochemical aspects of reproduction in female pompano in Egyptian waters (Assem *et al.* 2005). There is a preliminary study into feeding, growth, food conversion efficiency and feeding behaviour of wild-caught pompano reared in captivity in Croatian coastal waters (Tutman *et al.* 2004). The diet and diel feeding activity of juvenile pompanos from the south-eastern Adriatic Sea has been examined (Batistić *et al.* 2005). The length-weight relationships of this species have also been estimated for specimens reared in floating sea cages in the South China Sea (Guo *et al.* 2014) as well as for wild populations from the Azores Islands (Morato *et al.* 2001) and from the western Mediterranean (Morey *et al.* 2003). However, research into other reproductive traits that may indicate the breeding season, sexual maturity and spawning in both sexes of this species is virtually non-existent for the NW Mediterranean or elsewhere in its distribution range.

Clime-driven changes in the abundance and distribution of fish can lead to readjustments in ecosystems and alterations in the way they function which have been well documented (Francour *et al.* 1994; Perry *et al.* 2005; Coll *et al.* 2010). But it has also been pointed out that we need a better understanding of the physiological and behavioural response of fish to climate change since such impacts might vary across the different stages of the life cycle (Petitgas *et al.* 2013); thus, the more knowledge we have of the life cycles of various species, the better our understanding of the impacts of climate change on fish populations will be. Consequently, the overall aim of this study was to explore the reproductive traits of *Trachinotus ovatus* and our results are discussed in relation to the expansion and establishment of this species in the colder waters of the NW Mediterranean. In addition, temporal variations in sea surface temperatures (SSTs) within the study area were also analyzed in order to investigate whether we could explain if its seasonal arrival and/or reproductive traits are triggered by the physical conditions of the coastal waters off the NW Mediterranean.

6.3. Materials and methods

6.3.1. Study area and sample collection

Pompano specimens were collected monthly from fishermen (coastal purse seiners) at the Port of Roses (Figure 6.1), from July 2010 to September 2012, shortly after landing. It should be noticed that fishermen were asked for the approximate location and depth where the specimens were caught in order to be sure that the origin of the samples was within the coastal waters of the study area. In addition, data on sea surface temperatures (SST, in °C) was retrieved from the International Comprehensive Ocean-Atmosphere Data Set (ICOADS) for the study period 2010-2012 in the north-western Mediterranean (ds540.0-Release 2.5) (Woodruff *et al.* 2011). The data comprised individual daily mean SST observations for 1° latitude x 1° longitude units in surrounding waters off the Gulf of Roses (42.0 to 43.0°N and 3.0 to 4.0° E) (Figure 6.1). Then, the mean monthly values of SSTs were calculated by averaging daily SSTs.

6.3.2. Fish size distribution

Once in the laboratory, all specimens were measured and weighed using the total length (TL) to the nearest 0.5 cm and total weight (TW) to the nearest 1 mg. Then, all samples were dissected and eviscerated, and the somatic or eviscerated body weight (SW) and the gonad weight (GW) were obtained to the nearest 1 mg. The length-weight relationship (LWR) was estimated using the curvilinear formula $SW = a \cdot TL^b$ (Le Cren 1951), where SW is the somatic body weight of the fish and TL is the total length of the fish. The gonads were fixed in 4% buffered formaldehyde for further histological processing and fecundity estimation.

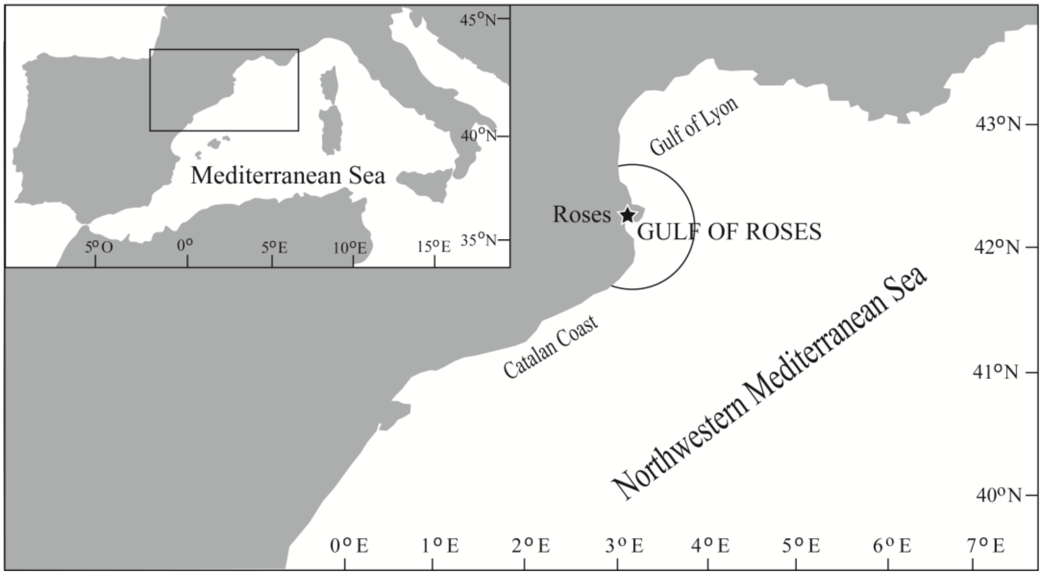


Fig. 6.1 Map of the North-western Mediterranean basin showing the study area (Gulf of Roses and adjacent waters) and the location of the fishing port of Roses.

6.3.3. Gonadal development, spawning season and size at 50% maturity

The gonadosomatic index (GSI) was calculated for each individual based on SW in order to avoid possible variations arising from differences in the contents of the digestive tract with the following formula GSI = 100*(GW/SW), where GW and SW represent gonad and somatic weights, respectively. Although the sex and reproductive status of specimens were first macroscopically determined, a histological analysis was also performed in order to provide a more accurate analysis of the reproductive characteristics of the pompano. Thus, a histological study of the gonads of every single individual was carried out in order to determine the phases of development of their germ cells. Central portions (transverse sections) of the fixed gonads were dehydrated and embedded in paraffin, sectioned at between 3-8 μm, depending on their state of gonadal development because the early phases required thinner sections in order to facilitate the identification of the their germ cells, and then stained with haematoxylin-eosin. The maturity phases of the gonads were classified in line with Brown-Peterson *et al.* (2011) as immature (IMM), developing (DEV), spawning capable (SC), regressing (RGS), and regenerating (RGN). The histological photomicrographs of the gonads of *T. ovatus* are shown in Figure 6.2. It should be noticed that ovarian wall thickness was a key factor in distinguishing between immature and regenerating phases in *T. ovatus*, since a thin ovarian wall was observed in immature specimens whereas a thick ovarian wall (along with atretic oocytes) was observed at specimens in the regenerating phase.

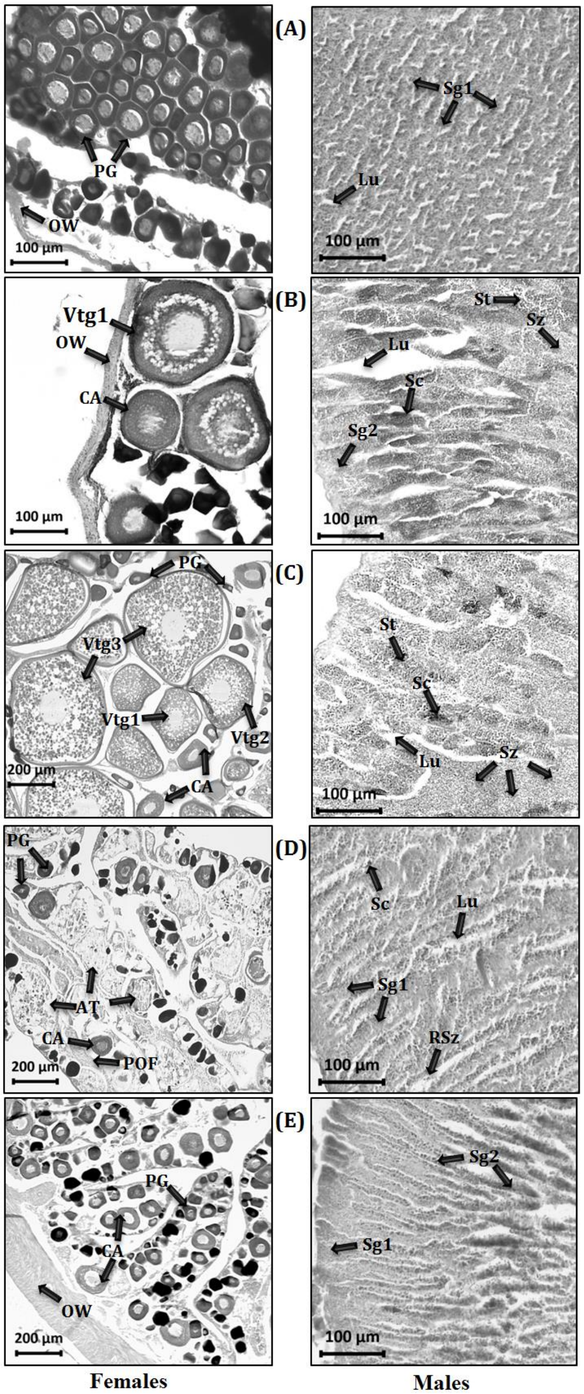


Fig. 6.2 Photomicrographs of ovaries and testis of the pompano (*Trachinotus ovatus*) showing the reproductive phases considered in this study: (a) immature, (b) developing, (c) spawning capable, (d) regressing, and (e) regenerating. Oocyte developmental stages are also shown as PG: primary growth, CA: cortical alveoli, Vtg1: early vitellogenic, Vtg2: mid-vitellogenic, Vtg3: advanced vitellogenic, AT: atretic, POF: post-ovulatory follicles, OW: ovarian wall. Germinal developmental stages are also shown as Sg1: primary spermatogonia, Sg2: secondary spermatogonia, Sc: spermatocyte, St: spermatid, Sz: spermatozoa, Rsz: residual spermatozoa, and Lu: lumen.

Size at 50% maturity (L_{50}) was estimated in order to define sexual maturity as a function of body length (length at which 50% of the individuals were mature) was estimated separately for females and males. To predict the probability that an individual was mature based on its length binary maturity observations (0 = immature, 1 = mature) and length (TL) were fitted to binary logistic models to construct maturity ogives (maturity-at-length probability plots) based on logistic equations.

6.3.4. Oocyte size-frequency distribution and fecundity estimates

The presence of hydrated oocytes and post-ovulatory follicles (POFs) was histologically determined in order to select suitable specimens for the analyses of the oocyte size-frequency distributions and the estimates of the batch fecundity (defined as the number of eggs spawned per batch). Firstly, batch fecundity (BF) was estimated for each specimen in the spawning capable (SC) phase and without POFs - using the gravimetric method combined with image analysis as explained by Murua *et al*. (2003). With this aim, subsamples of about 150 mg were taken from the ovary; oocytes were separated from connective tissue using a washing process (Lowerre-Barbieri & Barbieri 1993) and sorted by size through several sieves (from 1000 to 100 µm), which facilitated the subsequent work of counting and measuring oocytes using a computer-aided image analysis system (Image-Pro Plus 5.1). It is worth to mention that subsamples were taken from sections of the middle part of the ovary since there were no significant differences in the number of most advanced oocytes per gram among the anterior, middle and posterior parts of the ovary of 10 specimens that were in the latest developmental phases (ANOVA, $F_{2,29} = 2.21$, $p = 0.128$). Then, batch fecundity was estimated according to Hunter *et al*. (1985) as $BF = GW*(Y/Sw)$, where GW is the gonad weight after fixation, Y is the number of hydrated oocytes in a weighted subsample of ovarian tissue and Sw is the subsample weight. The relationship between BF and size (TL) was estimated by fitting power functions. The relative batch fecundity (RBF) was also calculated as batch fecundity per gram of somatic weight of the fish.

Secondly, the oocyte size-frequency distributions were analysed by exploring the size range for each oocyte developmental stage in order to define the oocyte recruitment pattern whether synchronous, group-synchronous or asynchronous (Murua & Saborido-Rey 2003). Thus, the mean diameter of 150 oocytes from each gonadal development phase (50 oocytes per sampling year) of 'standard' 35.0 cm TL females (in order to avoid any maternal size effect on estimates) were measured from the histological sections as the average of major and minor axes using the previously mentioned computer-aided image analysis system. Due to their irregular shape in histological transverse sections, the mean diameter of the hydrated oocytes was estimated differently: those largest oocytes previously separated through sieves were separated and then measure them using the computer-aided image analysis system.

6.3.5. Egg quality and follicular atresia estimates

The dry weight of hydrated oocytes were used to estimate the quality of the eggs (hydrated oocytes), hence an approximation of the potential reproductive success (Brooks *et al.* 1997). First, hydrated oocytes were previously separated through sieves and then by adding glycerine which make them translucent under transmitted light they were more easily differentiated and separated from those oocytes not yet hydrated. Once the eggs were selected, the mean dry weights (in mg per egg) were estimated by drying (for 24 h at 110°C) two replicates per sample of the eggs from a total of 20 actively spawning females (with hydrated oocytes) per sampling year.

The numbers of normal and α -stage atretic vitellogenic oocytes (Hunter & Macewicz 1985) were counted at three different focal planes of different histological slides of each specimen in order to estimate the prevalence of follicular atresia, Pa (percentage of sexually mature females that have α-atretic vitellogenic oocytes in relation to total number of females) as well as the relative intensity of atresia, RIa (percentage of α-atretic vitellogenic oocytes in relation to the total number of normal and atretic vitellogenic oocytes in an individual fish) (Kurita *et al.* 2003; Witthames *et al.* 2009; Kjesbu *et al.* 2010a).

6.3.6. Statistical analysis

Pairwise comparison analyses of covariance was applied between regression parameters (slopes and intercepts) of the resulting linear regression models of the length-weight relationships (LWR) of each sex (Cone 1989) in order to look for LWR differences between sexes.

Generalized linear models (GLMs) (McCullagh & Nelder 1989) were used to investigate the variation in GSI with sex, phase of maturity and size. GLMs were fitted to GSI as response variables and using sex and maturity as categorical predictor variables and size as continuous predictor variable. All predictors and their first order interactions were initially included in the GLM. Analysis of deviance to evaluate the significance (F-test) of the factors in the model was performed by a stepwise procedure, and the most appropriate error models were chosen on the basis of residual plots. The GLMs incorporating the sex, maturity and size as predictor variables accounted significantly for 55.8% of the variability in GSI (ANOVA, $F_{10,225} = 24.97$, $p < 0.0.001$). Therefore, the GLM approach was used to standardize GSI data for the effects of sex, maturity and size by estimating the adjusted means of GSI for the variation of the covariables.

Since the mean monthly SSTs recorded during the summer months (July, August, September) in the 2010 sample were significantly lower ($p < 0.05$) than those observed in 2011 or 2012 (Table 6.1), ANOVA models were also used to find out whether, on average, the GSI (adjusted GLM data), the oocyte diameter (per developmental stage), the egg quality (hydrated dry weight), and the relative batch fecundity (RBF) were statistically different among sampling years. Then, if the ANOVA indicated significant differences, Bonferroni's multiple tests were applied for post hoc comparisons of significant effects (Sokal & Rohlf 1995). It should be noticed that a p-value of $\alpha = 0.05$ or less was considered to be statistically significant, and prior to the ANOVAs, for all the aforementioned variables, the Shapiro-Wilk test was used to test the assumptions of normality and Levene's test was used to test the homogeneity of variances (Zar 1996).

6.4. Results

6.4.1. Size distribution and size at 50% maturity

Of the 226 pompano specimens collected during the study, a total of 118 were identified as females and 108 as males. The length-frequency distributions were similar for both sexes, ranging from 25.0 to 44.0 cm, and the length-weight relationships (LWR) were accurately fitted to curvilinear regression models (Figure 6.3 A) separately for males ($SW = 0.0053 \cdot TL^{3.1201}$, $r^2 = 0.919$) as well as for females ($SW = 0.0043 \cdot TL^{3.1805}$, $r^2 = 0.935$), with any significant difference, at $\alpha = 0.01$, between sexes in both regression parameters: slopes (ANOVA, $F_{1,3} = 4.416$, $p = 0.1264$) and intercepts (ANOVA, $F_{1,3} = 3.355$, $p = 0.1644$). On the other hand, the size at 50% maturity (L_{50}) was estimated at 30.9 (± 2.7) cm TL for females and 29.1 (± 1.8) cm TL for males, and no immature individuals were found with TLs greater than 33.0 cm (Figure 6.4).

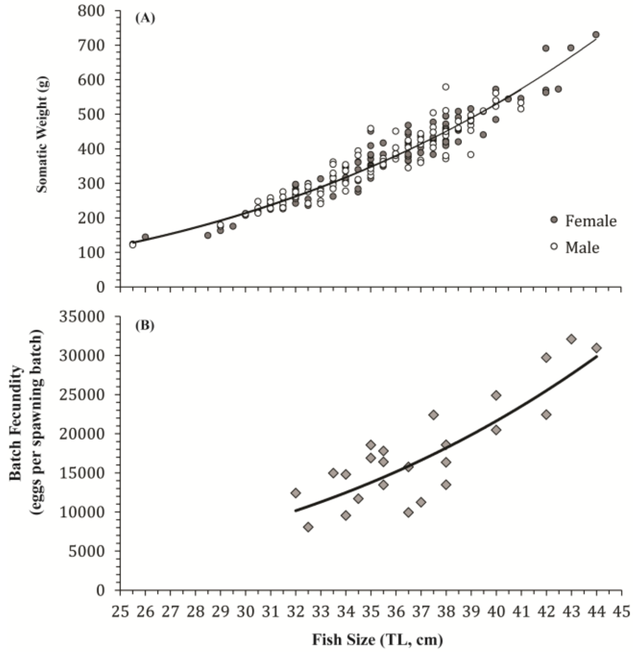


Fig. 6.3 Fitted regression models based on (A) length-weight relationships for males ($SW = 0.0053 \cdot TL^{3.1201}$, $r^2 = 0.919$, $n = 108$) as well as for females ($SW = 0.0043 \cdot TL^{3.1805}$, $r^2 = 0.935$, $n = 118$), and (B) the relationship of the batch fecundity to fish length for females ($BF = 0.0822 \cdot TL^{3.3833}$, $r^2 = 0.6475$, $n = 24$), of *T. ovatus*.

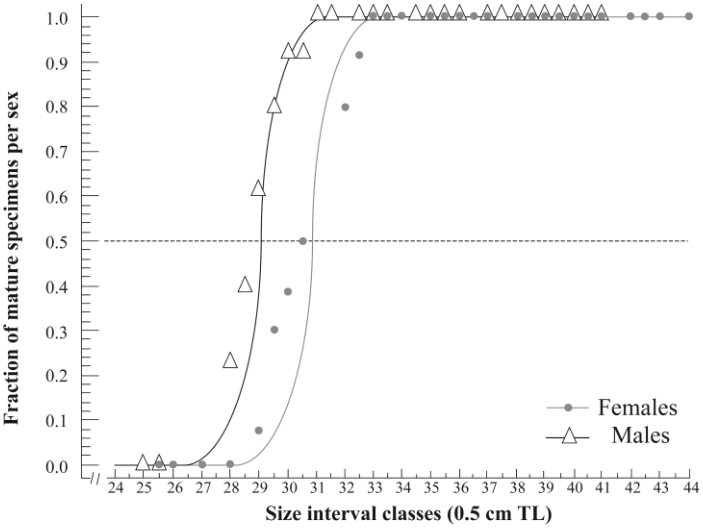


Fig. 6.4 Logistic curves of relative frequency of reproductive females (n = 118) and males (n = 108) of *T. ovatus* as function of size class (total length). The size at 50% maturity (L_{50}) was estimated at 30.5 (± 2.1) cm TL for females and 28.7 (± 1.5) cm TL for males.

6.4.2. Gonadal development and spawning season

Similar gonadal development patterns were observed in both sexes: the developing phases were observed mainly from May to early July followed by spawning activity until September, when subsequently the spawning activity ceased and the regressing and regenerating phases became more evident. With regard to the time of the year, it was found that the GSI of both sexes peaked during the summer months (July and August). This was later confirmed by similar trends in maturity phases (expressed in frequency of occurrence) found throughout the year (Figure 6.5). The inter-annual analysis of the pompano's reproductive investment (GSI) showed statistically lower mean values in specimens sampled in the year 2010 compared to those sampled in 2011 and 2012 (Table 6.1). Moreover, the occurrence of spawning (inferred with both the GSI peaks and the increased frequency of spawning capable specimens) was observed to differ between years: spawning did not start until August in 2010 whereas in 2011 and 2012, spawning started in July (Figure 6.5). Furthermore, it was also noticeable that actively spawning specimens began to appear at similar SSTs: at between 21.3 and 23.3ºC in 2010 and between 21.1 and 23.1ºC in 2011 and 2012. In other words, although spawning activity began a month earlier in 2011 and 2012 compared to 2010, in all three years it began when SSTs had attained similar values (≈21.0°C).

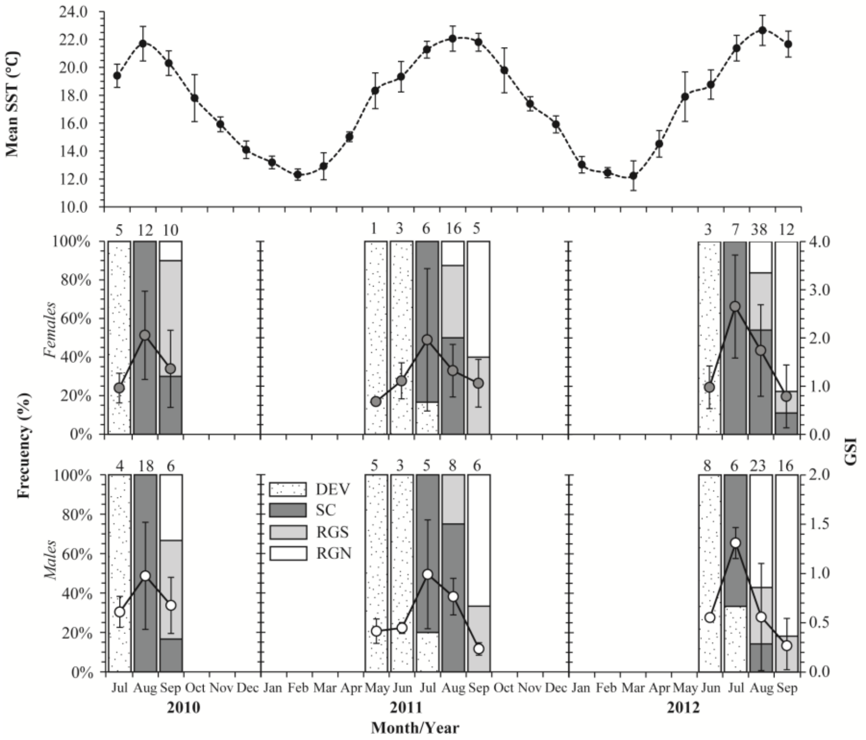


Fig. 6.5 Monthly gonadal development phases frequency (percent abundance), mean (± std. dev.) monthly variation in the gonadosomatic index (GSI) for males and females of *T. ovatus*, and mean (± std. dev.) monthly sea surface temperatures (SSTs) during the study period (2010-2012). Development stages: regenerating (RGN), developing (DEV), spawning capable (SC), and regressing (RGS). Sample number (*n*) per month is also given above bars.

Table 6.1 Summary of the mean values (± std. dev.) for specimens of *T. ovatus* and ANOVA tests evaluating the effect of the inter-annual variation on the following parameters: the monthly sea surface temperatures (SST, in °C), the gonadosomatic index (GSI), the oocyte diameter (µm, for each developmental stage), the egg quality (dry weight of hydrated oocytes in mg per egg), the relative batch fecundity (RBF, eggs per gram of body mass).

Variable	**Source**	**Inter-annual means (± std. dev.)**			**F-ratio (*d.f.*)**	**p-value**	**Bonferroni's outcome**
		2010	*2011*	*2012*			
SST	Jul	19.4 ± 0.83	21.3 ± 0.60	21.4 ± 0.91	$F_{2, 424} = 8.27$	***	2010 < 2011 = 2012
	Aug	21.7 ± 1.24	22.1 ± 0.90	22.7 ± 1.08	$F_{2, 315} = 3.39$	**	2010 < 2011 = 2012
	Sep	20.3 ± 0.88	21.8 ± 0.64	21.7 ± 0.93	$F_{2, 451} = 4.88$	**	2010 < 2011 = 2012
GSI	GLM adj.	1.04 ± 0.57	1.44 ± 0.51	1.51 ± 0.35	$F_{2, 225} = 6.38$	**	2010 < 2011 = 2012
Oocyte diameter	CA	108.5 ± 21.1	112.7 ± 24.6	110.3 ± 21.7	$F_{2, 149} = 2.40$	NS	2010 = 2011 = 2012
	Vtg-1	208.7 ± 23.7	213.5 ± 31.5	205.1 ± 26.2	$F_{2, 149} = 2.68$	NS	2010 = 2011 = 2012
	Vtg-2	304.5 ± 27.6	310.4 ± 30.9	312.4 ± 28.3	$F_{2, 149} = 2.29$	NS	2010 = 2011 = 2012
	Vtg-3	394.3 ± 23.9	425.8 ± 35.6	435.2 ± 29.1	$F_{2, 149} = 4.77$	**	2010 < 2011 = 2012
	GVM	504.3 ± 24.4	521.2 ± 40.5	531.2 ± 30.2	$F_{2, 149} = 5.06$	**	2010 < 2011 = 2012
	H	662.1 ± 39.2	732.6 ± 42.1	745.4 ± 45.9	$F_{2, 149} = 5.18$	**	2010 < 2011 = 2012
Egg quality	Dry weight	0.104 ± 0.08	0.136 ± 0.11	0.141 ± 0.09	$F_{2, 59} = 4.05$	*	2010 < 2011 = 2012
RBF	SC females	36.5 ± 7.77	43.2 ± 8.85	45.2 ± 9.6	$F_{2, 23} = 3.98$	*	2010 < 2011 = 2012

* indicates p<0.05, ** indicates p<0.01; *** indicates p<0.001, and NS indicates no significant difference

6.4.3. Oocyte development and fecundity

The range of oocytes diameters at different stages of development were as follows: cortical alveoli (CA, 75–150 μm), early vitellogenesis (Vtg-1, 150–250 μm), mid vitellogenesis (Vtg-2, 250–350 μm), advanced vitellogenesis (Vtg-3, 350–450 μm), germinal vesicle migration (GVM, 450–550 μm) and hydration (H, 550–800 μm). No significant difference (p > 0.01) was found in the inter-annual variation of oocyte diameters at early stages of development, i.e. CA, Vtg-1 and Vtg-2. However, significantly smaller (p < 0.01) oocyte diameters in the later stages of development (Vtg-3, GVM and H) were observed in specimens sampled in 20110 compared to those sampled in 2011 and 2012 (Table 6.1).

Oocyte development in *T. ovatus* was considered to be asynchronous, since oocytes at different stages of development were simultaneously present in the ovary. Moreover, the variation in the stage-specific oocyte size-frequency distribution during the reproductive cycle indicated a lack of hiatus separating the primary growth oocytes (< 75 μm) from the reservoir of secondary growth oocytes (< 75 μm) (Figure 6.6 A-F). These oocyte size-frequency distributions showed a continuous size-frequency development of oocytes, except for ovaries at the onset of spawning which, as with all the secondary growth stages, had a separate mode of the most advanced oocytes (>350 μm) (Figure 6.6 C-E). That is to say that just before ovulation most advanced oocytes did outgrow the standing stock of vitellogenic oocytes and a separate mode of mature hydrated oocytes developed for ovulation.

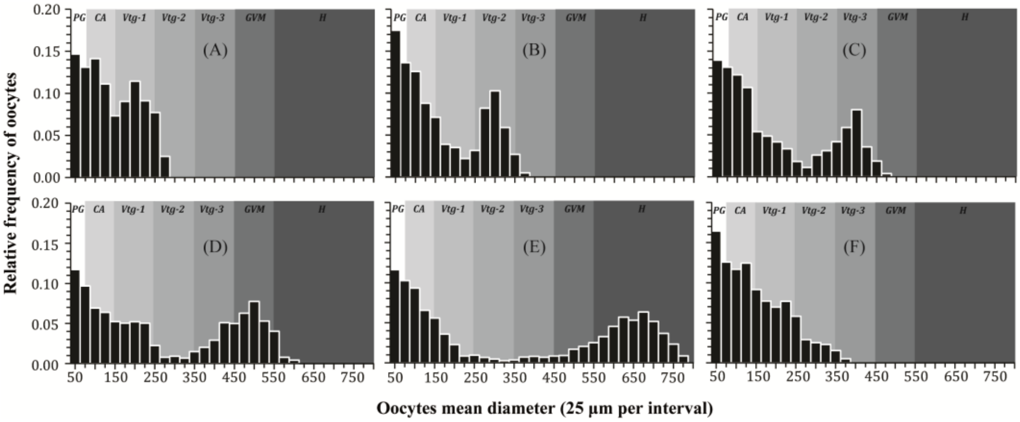


Fig. 6.6 Oocyte size-frequency distributions (per cent abundance per 25 μm diameter class) of 'standard' 35.0 cm TL females of *Trachinotus ovatus* through subsequent gonadal development phases: (A) early developing, (B) developing, (C) advanced developing, (D) spawning capable, (E) actively spawning, and (F) regressing. Each distribution corresponds to an individual fish. The range of oocytes diameters at different stages of development is also illustrated as follows: primary growth (PG, 50-75 μm), cortical alveoli (CA, 75–150 μm), early vitellogenesis (Vtg-1, 150–250 μm), mid vitellogenesis (Vtg-2, 250–350 μm), advanced vitellogenesis (Vtg-3, 350–450 μm), germinal vesicle migration (GVM, 450–550 μm) and hydration (H, 550–800 μm).

24 females met the histological criteria (actively spawning with hydrated oocytes and without POFs) for fecundity analysis. The batch fecundity (BF) ranged from 8070 to 32080 eggs per spawning batch in fish ranging from 32.0 to 44.0 cm TL, and the relationship between BF and TL was fitted to the following exponential regression model $BF = 0.0822 \cdot TL^{3.3833}$ ($r^2 = 0.6475$, $n = 24$) (Figure 6.3 B). The mean BF (± std. dev.) was estimated at 17620 (± 6649) eggs per spawning batch. Meanwhile, the overall mean relative batch fecundity (RBF) was estimated at 40.5 (± 8.9) eggs per gram of body mass for this species, and any size effect was observed between RBF and TL ($p > 0.05$). However, it should be noticed that significant inter-annual differences were found in the RBF (ANOVA, $F_{2,23} = 3.98$, $p = 0.0328$), being significantly lower during 2010 than during 2011 and 2012 (Table 6.1).

6.4.4. Egg quality and follicular atresia

As a measure of egg quality, the mean dry weight of hydrated oocytes (showing also any significant size effect) estimated from specimens caught in 2010 was 0.104 (±0.08) mg per egg which was significantly lighter (ANOVA, $F_{2,\,59} = 4.05$, $p = 0.0225$) than that of specimens collected in 2011 (0.136 ± 0.11) and in 2012 (0.141 ± 0.09) (Table 6.1). Signs of α-atresia were observed only during the regressing gonadal development phase, and the prevalence of atresia (Pa) was estimated at 22.2 % (n = 6) in relation to total number of mature females (n = 27). The mean intensity of atresia (Ria) in these individuals was estimated at 96.8 ± 2.3 % of their vitellogenic oocytes in α-atretic state.

6.5. Discussion

This is the first time that the main reproductive traits of this warm-water species have been described. The oocyte size-frequency distributions indicated an asynchronous oocyte recruitment pattern as oocytes at different stages of development were simultaneously present, whereas accordingly to Murua & Saborido-Rey (2003) the following features suggest multiple batch spawning and an indeterminate nature of the fecundity of this species: (1) continuous size-frequency development of oocytes (in which case only during spawning all the secondary growth stages had a separate mode of the most advanced oocytes), (2) the presence of recent POFs along with oocytes in the final phases of gonadal development, (3) the massive atresia in post-spawning individuals (i.e. in the regressing phase of gonadal development). Moreover, the presence of atresia in the gonads of the females only at the end of spawning season even though not all vitellogenic oocytes are fully developed, indicates that there is a need to eliminate the underdeveloped non-ovulated oocytes, which is done through atresia, as shown by the sudden and marked increase in the relative intensity of atresia detected in the ovaries at the end of the spawning season. On the other hand, the indeterminate fecundity and its batch spawning nature of *T. ovatus*, whose eggs are recruited and ovulated from the population of yolked oocytes in several batches along spawning season, makes quite difficult to estimate more accurately the annual egg production, which in turn is an essential component of the reproductive biology of multiple spawning fishes and can have important implications for the management of fish populations (Ganias *et al.* 2015).

Although specimens of *T. ovatus* were not caught during the whole year due to its absence within the study area during the coldest months, the overall data indicates that this species has a short spawning season (lasting no more than 2 months) restricted to the warmest period of the year (July-August). Other species of carangids also present a short and well-defined spawning period during the spring and summer months, e.g. the giant trevally *Caranx ignobilis* and bluefin trevally *Caranx melampygus* in Hawaii (Sudekum *et al.* 1991); the horse mackerel *Trachurus trachurus* in Greece (Karlou-Riga & Economidis 1997); the permit *Trachinotus falcatus* in Florida (Crabtree *et al.* 2002); the short-fin pompano *Trachinotus teraia* in the Ivory Coast (Sylla *et al.* 2009); and the plata pompano *Trachinotus marginatus* in southern Brazil (Lemos *et al.* 2011). In fact our study indicated that this warm-water species has a narrower spawning season in the northern Catalan Sea (centring on the warmest months of the year) than it has in warmer areas of the Mediterranean such as Egyptian waters where its spawning season ranged from mid-August to mid-October (Assem *et al.* 2005).

As stated previously, inter-annual variations in some reproductive traits, such as the mean diameters of the oocytes, the relative batch fecundity or the mean dry weight of hydrated oocytes, were observed for the pompano in this study. In addition to this, since the maternal size effect on these reproductive traits was disregarded in our data we believe that those sea water temperature inter-annual variations could at least explain those variations in its reproductive features. Similar seasonal or inter-annual variations in batch fecundity and egg-size have been reported for other fish species, e.g. the Atlantic silverside *Menidia menidia* (Conover 1985), the pacific jack mackerel *Trachurus symmetricus* (Lisovenko & Andrianov 1991), the bright-eye darters *Etheostoma lynceum* (Heins *et al.* 2004); and the European hake *Merluccius merluccius* (Murua *et al.* 2006). Furthermore, differences in egg quantity and quality have been attributed to different temperature conditions in the spawning habitats for other species, e.g. the anchoveta *Engraulis ringens* off the Chilean coast (Castro *et al.* 2009; Leal *et al.* 2009). Thus, water temperature appears to be related to different patterns of seasonal, inter-annual or latitudinal changes in egg quantity and quality in fish populations (Conover 1985; Tanasichuk & Ware 1987; Heins *et al.* 2004; Murua *et al.* 2006; Castro *et al.* 2009; Leal *et al.* 2009).

Along with potential temperature effects, food availability for adults may also play a role in determining differences in oocyte number and size, and it might also explain the variability, whether spatial or temporally, in egg traits of a given fish species (Beacham & Murray 1993). In this sense the assessment of the energetic content and relative concentrations of different biochemical components (amount of lipid or protein) in the eggs would provide a complementary insight into the environmental-related variations of the egg quality (Pickova *et al.* 1997; Rainuzzo *et al.* 1997; Riveiro *et al.* 2000, 2004; Castro *et al.* 2009). In fact, Assem *et al.* (2005) have found in females specimens of *T. ovatus* from the Egyptian waters off the Mediterranean that the total protein content in ovaries varied according to different maturity phases recording maximum value at immature ovaries and minimum at spawning and spent (regressing) ovaries; whereas the total lipid contents of ovaries reached their minimal values at immature phase, and their maximum recorded value was at the nearly ripe (late developing) gonad. Unfortunately, here in the present study these later kind of analyses were not carried out to determine if the nutritional content was the same or not across years, however we do recognize that this kind of study is as well very important since differing diets could change the nutritional content and might give us a clue of the temporal changes in egg quality and size.

Several studies has previously shown that sea temperature may influence the timing of various life processes in fish such as, for example, their spawning date (Kjesbu *et al.* 2010b; Morgan *et al.* 2013). In this case, the effects of temperature depend on when, in the annual thermal cycle, spawning normally occurs, with increasing spring temperatures being required to trigger gonadal development in species that spawn in spring and early summer, while falling temperatures stimulate reproduction in autumn-spawning species (Pankhurst & Munday 2011). In our study of the pompano, the inter-annual variation in the spawning phenology could be related to the inter-annual variations in temperature that were also observed within the study area (Table 6.1) since although spawning activity began a month earlier in 2011 and 2012 compared to 2010, in all three years it began when SSTs had attained similar values (≈21.0°C). This indicates that sea temperature may trigger the initiation of spawning activity in this species and the difference in the timing of spawning activity from one year to another may be the result of the seasonal migratory behaviour coupled with the annual seasonality of the sea temperatures in the NW Mediterranean. All of which could indicate that pompano spawning is highly temperature-sensitive and that, in addition, this species is able to adjust the timing of spawning to suit the optimal temperature for embryo development, as is the case with other species of fish (Pankhurst & Munday 2011).

Climate change will have major consequences for fish reproduction, including both temperate and warm-water species, depending on various factors: specific physiological tolerances, capacity for acclimation and adaptation, scope for behavioural avoidance, capacity to extend or shift ranges, and the timing of thermal challenges with respect to the reproductive cycle (Pankhurst & Munday 2011). For certain temperate water species, for example, climate change could lead to reproductive and recruitment failure, whereas for some of the warm-water species, it could lead to changes in seasonal phasing of reproduction and possible increases in species range (Munday *et al.* 2008; Pankhurst & Munday 2011). It appears likely, therefore, that the present-day sea warming trends and the associated changes in spawning phenology would give the pompano (and other warm-water fish species) an advantage and favour their successful establishment into new habitats. Meanwhile, for native fish species, small increases in sea temperature during spawning can dramatically increase egg mortality and decrease survivorship to hatching since the egg stage is one of the most thermally sensitive life stages in fish (Rombough 1997; Gagliano *et al.* 2007). In this sense, small increases in temperature might tend to favour recruitment of some species (especially at higher latitudes) but larger temperature increases could lead to recruitment failures (especially at low latitudes) and at times or places where food supply is limited (Munday *et al.* 2008; Pankhurst & Munday 2011). Therefore, while global warming can benefit warm-water species, allowing their expansion into areas they did not previously occupy (Sabatés *et al.* 2006; Petitgas *et al.* 2013; Lloret *et al.* 2015b), it may threaten cold-water species, leading to local extinctions of certain species (Drinkwater 2005; Perry *et al.* 2005). Changes in the abundance of warm- and cold-water fish species may have far-reaching ecosystem effects, such as trophic cascades driven by the local loss/decrease of cold-water predators or by the appearance/increase of warm-water predators (Lloret *et al.* 2015b).

Although, up to now, no accurate information is available regarding the migration of the pompano in the Mediterranean, we suspect that this species (like other pelagic fish species from the Carangidae family) shows seasonal migratory behaviour, spending the colder months in more southern warm-water areas and, when the sea temperature reaches a certain value, migrating towards cooler waters in the north where the species spawns once a threshold temperature has been attained (Smith-Vaniz 1986). Apparently the pompanos show behavioural thermoregulation, that is to say they are able to avoid or select the right environmental temperature and, within certain thermal limits their distribution may be based on other ecological factors such as food availability. And as far as food availability is concerned, the surrounding coastal waters of the southern Gulf of Lyon (including the Gulf of Roses) are known to be affected by a permanent cyclonic circulation of surface waters and intense vertical convections which promote intense algal blooms and elevated primary production (Bosc *et al.* 2004) which, in turn, enhances the relatively high total biomass present in the area (Bănaru *et al.* 2013). Moreover, this area in the NW Mediterranean has been recognized as an important spawning grounds for similar small pelagic fish such as the European anchovy *Engraulis encrasicolus* or the sardine *Sardina pilchardus* (Olivar *et al.* 2001; Palomera *et al.* 2007; Bellido *et al.* 2008).

It has been suggested previously that present sea warming trends and changes in the seasonality of the sea temperatures may be causing changes in spawning phenology and the timing of the seasonal arrival of other fish species into more northern areas of the Mediterranean, favouring the northward temperature-dependent expansion of warm-water species in the NW Mediterranean (Lloret *et al.* 2015b). Examples of this include the round sardinella *Sardinella aurita* (Sabatés *et al.* 2006); the yellow-mouth barracuda *Sphyraena viridensis* (Villegas-Hernández *et al.* 2014); the bastard grunt *Pomadasys incisus* (Villegas-Hernández *et al.* 2015a); and the bluefish *Pomatomus saltatrix* (Sabatés *et al.* 2012; Villegas-Hernández *et al.* 2015b). This appears to be the case with the pompano: we hypothesize that sea temperature clearly influences its spawning phenology as well as its seasonal arrival which may be facilitated not only by the physical conditions but also by the higher food productivity in the northernmost area. Therefore, bearing in mind that sea temperature seems to influence the pompano reproduction, this study demonstrates a clear need for further researches into the reproductive traits of warm-water species that are currently expanding into the increasingly warmer northern waters.

CHAPTER VII: General Discussion and Conclusions

Even though the results of this PhD thesis are directly applicable to the biological knowledge of the studied species, here in the general discussion the results of the each case study were integrated as a whole in order to make broader ecological interpretations that may apply to other warm-water species which are expanding northwards due to climate change. Finally, the main conclusions of this PhD thesis are presented.

CHAPTER VII

General Discussion and Conclusions

This thesis analyzed the thermal-related spatio-temporal variations of the life-history traits of four warm-water species: the bluefish (*P. saltatrix*), the bastard grunt (*P. incisus*), the yellow-mouth barracuda (*S. viridensis*) and the pompano (*T. ovatus*), whose establishment within the study area has presumably been favoured by the trends of increasing sea temperature in the NW Mediterranean Sea. Several important conclusions emerged from these analyses and, although these apply particularly to each of the study species, some of them are of general interest in the field of fish ecology and fisheries management worldwide as they have implications regarding the increasing abundances of warm-water species in temperate and cold-water environments. For instance, overall, the results support the theory that sea warming is at least partly responsible for the northward spread and increasing abundance of thermophilic species in the Mediterranean Sea, and strongly suggest that their physiological adaptations in terms of physical condition and reproduction to the rising sea temperatures is playing an important role in their establishment into areas they did not previously occupy.

More specifically, regarding reproduction, the changes in size-at-maturity, fecundity and spawning phenology, together with the sea warming trends, appear to improve the colonization capabilities of thermophilic fauna in the northernmost areas of the Mediterranean. In addition, some of these warm-water species are able to show a certain degree of plasticity in their spawning strategies by trading-off egg size and quality for higher egg numbers in areas with colder environmental conditions. This latter reproductive strategy may be an adaptation aimed at maximizing the reproductive output in colder conditions. Secondly, with regard to fish condition, it would seem logical that the condition of a warm-water species would be negatively affected as they expand into colder areas they had not previously occupied; however, this is not always the case. For example, in the case of the bluefish, what we actually found was a marine fish species, which is able to expand its distribution due to sea warming, may take advantage of other environmental conditions - such as better food availability – to improve or maintain their condition in those new habitats.

Overall, I hypothesize that although higher sea water temperatures clearly influences the availability of warm-water species in the NW Mediterranean, the expansion of these species may also be encouraged by the higher productivity in the northernmost areas, so that this new habitat may have become a more advantageous ecological niche for these species to exploit. At the same time, the appearance/increase of warm-water predators (such as *P. saltatrix* and *S. viridensis*) may promote, either by predation or competition, a community reassembly and alter the food web structure by causing shifts in trophic pathways and changes in food availability in these marine ecosystems.

That being said, I recognize that the biological response of fish to climate change can vary substantially from one species to another, as observed in this thesis, depending on whether they have sufficient phenotypic plasticity to be able to tolerate environmental changes, that is to say, whether they are able to adapt their life-history traits to the unusual temperatures that prevail in those habitats (Rosecchi *et al.* 2001). However, this thesis highlights the need to carry out this kind of research into comparative reproductive energetics since it has proved to be a powerful approach to understanding life-history trade-offs among fish populations which, in turn can shed light on the phenotypic plasticity and the adaptation of the reproductive strategies to new environmental conditions (Jørgensen *et al.* 2008; Scarnecchia *et al.* 2011). This is particularly important since, as sea warming continues, it is likely that warmer water temperatures will lead to more protracted spawning seasons among the thermophilic taxa as they approach their full reproductive potential and successful population growth in areas in which they previously had not existed.

7.1. Sea warming effects on life-history traits of thermophilic fish

Significant variations were found in the life-history traits of the species studied in this thesis, indicating a certain degree of plasticity probably related to their physiological sensitivity to the spatio-temporal variations in sea water temperatures in the areas they inhabit (Table 7.1). Thermal-related changes were observed in size-at-maturity, fecundity (egg quality-quantity trade-off), spawning phenology and condition, varying spatially and/or temporally.

Table 7.1 Summary of the main similarities and differences observed in each study case based on the condition and reproductive traits, such as the gonadosomatic index (GSI), the hepatosomatic index (HSI), the oocytes diameter, the egg quality (dry weight of hydrated oocytes), the batch fecundity, the length at first maturity (L_{50}), the spawning season (period and temperature threshold). Sources of variation were compared to each other (within each chapter) and the overall results are presented here in a summarized way using the following symbols: '+' and '–' for *more* and *less* than, respectively; ' ≈ ' stands for *similar*; and NA denotes 'not available'.

Study approach	Study case	Sources of variation	Biological parameters							
			HSI	*GSI*	*Oocytes diameter*	*Egg quality*	*Fecundity*	*Spawning season*	*Spawning threshold*	L_{50}
Thermal-related spatiotemporal variations	*P. saltatrix* (Chp. III)	*Gulf of Roses*	+	+	+	≈	≈	July-Sep	≈ (18°C)	≈
		Ebre Delta	-	-	-			May-Sep		
	P. incisus (Chp. IV)	*Gulf of Roses*	-	-	-	-	+	≈	19°C	-
		Ebre Delta	+	+	+	+	-		24°C	+
Temperate vs thermophilic traits comparison	Barracudas (Chp. V)	*S. sphyraena*	+	+	+	+	-	May-Sep	?	-
		S. viridensis	-	-	-	-	+	May-Jul	19°C	+
Thermal-related reproductive traits	*T. ovatus* (Chp. VI)	*2010*	NA	-	-	-	-	Aug-Sep	≈ (21°C)	≈
		2011	NA	+	+	+	+	Jul-Sep		
		2012	NA	+	+	+	+	Jul-Sep		

7.1.1. Size at maturity

Water temperature has been shown to affect body growth and the effects of temperature on maturation and reproductive effort appear to be indirect via the optimization of life-history traits in fish populations (Charnov & Gillooly 2004; Drinkwater 2005). In this way, an increase in temperature is expected to cause a decrease in the length and age at first maturation, affecting the growth of adults as surplus energy is channelled into reproduction at an earlier age and smaller size (Heino *et al.* 2002; Engelhard & Heino 2006). Size at maturation is known to be a highly plastic parameter that changes under external pressures, such as water temperature or food availability, and the response of fish such pressures is known to vary among species or even among separate populations of the same species (Rose 2005). However, the maturity of fish is also known to be, in some cases, closely related to total population abundance over the life of a cohort, with cohorts maturing at a smaller size when population size is low (Rijnsdorp 1993; Morgan & Bowering 1997; Morgan & Colbourne 1999), which could be also causing the observed lower sizes at maturity within the northernmost populations of *P. saltatrix* and *P. incisus* compared to those reported for their populations inhabiting warmer areas (Conand 1975; Pajuelo *et al.* 2003b; Chakroun-Marzouk & Ktari 2006; Fehri-bedoui & Gharbi 2008; Robillard *et al.* 2008).

7.1.2. Spawning phenology

In species with restricted spawning seasons which inhabit cold-temperate climates, water temperature has been recognized as the main exogenous cue that ensures that gonadal development occurs at the proper time so that fish are capable of spawning when conditions favour offspring survival (Wright & Trippel 2009; Lowerre-Barbieri *et al.* 2011). In this sense, the spawning of both *P. saltatrix* and *P. incisus* takes place during more prolonged seasons in areas where warmer environmental conditions prevails and where they are well established (Norcross *et al.* 1974; Kendall & Walford 1979; Pajuelo *et al.* 2003b; Chakroun-Marzouk & Ktari 2006; Ceyhan *et al.* 2007; Fehri-bedoui & Gharbi 2008), whereas spawning seasons are shorter in the relatively colder areas of the NW Mediterranean. The observed spawning pattern of *P. saltatrix*, which starts earlier in the southern area of the NW Mediterranean and extends progressively northwards, has also been observed in other fish species that reproduce in spring and summer, such as the anchovy (*Engraulis encrasicolus*) or the red band fish (*Cepola rubescens*) (Martín & Sabatés 1991; Palomera 1992). According to Sabatés *et al.* (2007), this spawning pattern of the bluefish is due to the presence of a thermal front at the surface, perpendicular to the coast of the NW Mediterranean Sea, which means that reproduction among the spring-summer spawners is more protracted in the south than in the north. On the other hand, in *P. incisus*, whose spawning began in both sampling areas simultaneously - despite a difference in water temperature of approximately 4°C - we suspect that in the northernmost area, spawning still needs to start at the beginning of the warmest season because otherwise the spawning season would be too short if this species waits to match its spawning to the optimal environmental conditions. In the northernmost area, the SST decreases earlier than in the south (Sabatés *et al.* 2007), hence a more restricted seasonal window might occur in the Gulf of Roses for the spawning of this species. In addition, within the northernmost area of the study area (the Gulf of Roses), the native *S. sphyraena* showed a more prolonged spawning season than *S. viridensis* whose short spawning season may indicate that the optimal environmental conditions for this latter species occur in a more restricted seasonal window.

In our study cases, it was observed that spawning phenology is highly temperature-sensitive, and usually the initiation of spawning activity was shown to be triggered by specific SST thresholds: at 18°C for *P. saltatrix*, at 19°C for *S. viridensis*, and at 21°C for *T. ovatus* (Table 7.1). In addition, especially in the study of *T. ovatus*, a thermal-driven interannual variation was found in its spawning phenology which started one month later in 2010 (a relatively colder year) compared to 2011 and 2012. These kinds of interannual, temperature-driven phenological changes have already been observed in other marine fish species. For example, in the planktonic larval fish assemblages from the Western English Channel (U.K.), the timing of the appearance of the summer-spawning (July-September) group was found to be significantly dependent on sea temperatures in the previous March, with earlier spawning during warmer years (Genner *et al.* 2009). Warmer waters have also been associated with delayed spawning migration in flounder (*Platichthys flesus*) in the English Channel (Sims *et al.* 2004), and are thought to drive earlier spawning of the Pacific herring (*Clupea harengus pallasi*) off British Columbia (Ware & Tanasichuk 1989).

7.1.3. Spawning strategy

Egg development has been recognized as being strongly governed by temperature-dependent rates of vitellogenesis (Miranda *et al.* 1990; Kjesbu 1994; Gillet & Quétin 2006; Mendiola *et al.* 2006; Cunha *et al.* 2008). Therefore, the increased fecundity (at the expense of quality) of warm-water species, such as that observed for *P. incisus* and *S. viridensis* in the colder and northernmost area, might be an adaptation aimed at maximizing the reproductive output in colder conditions. In the warmer Ebre Delta, *P. incisus* spawned better quality eggs at the expense of quantity compared to the colder Gulf of Roses where the opposite pattern was observed (egg size and quality being traded-off for higher egg numbers). Similarly in the case of the barracudas, different reproductive strategies were also revealed when comparing the life-history traits of the temperate *S. sphyraena* to that of the thermophilic *S. viridensis.* Apparently, the *S. sphyraena* spawns larger and better quality eggs at the expense of quantity, while the *S. viridensis* releases a greater number of eggs of minor quality. Similar kinds of temperature-driven changes in egg quantity and quality among populations and/or species, as a result of bioenergetic trade-offs in response to environmental conditions, has been observed in other fish species (Rosecchi *et al.* 2001; Bøhn *et al.* 2004; Castro *et al.* 2009; Leal *et al.* 2009).

It is well known that in response to particular environmental conditions such as temperature or food availability in a specific habitat, species fecundity may vary spatially (Witthames *et al.* 1995) and/or temporally (Kjesbu *et al.* 1998). This was observed spatially in our studies of *P. saltatrix* and *P. incisus* and also temporally in our studies of *T. ovatus*. Thorsen *et al.* (2010) found a latitudinal gradient in fecundity for cod (*Gadus morhua*), suggesting that the major source for those differences lies in the water temperature regime with higher fecundity in warmer waters. There are other good examples where population-specific reproductive strategies are an adaptive response to energetic and environmental conditions (Leggett & Carscadden 1978; Conover 1992; Kinnison *et al.* 2001). For example Kinnison *et al.* (2001) documented a trade-off between upstream migration energetics and the resulting egg size and numbers between populations of Chinook salmon (*Oncorhynchus tshawytscha*) and they hypothesised that migration strongly influences patterns of reproductive allocation, favouring a higher ratio of egg number to egg size with greater migration distance.

There are many other observations that egg size varies inversely with egg number, but it is not always clear whether egg stage or the effects of nutrition or downregulation are controlled for in such field studies (Mcbride *et al.* 2015). However, experiments have proved useful in studying these issues, i.e. it has been observed that spawning rate and batch fecundity declined in response to reduced rations in three-spine stickleback (*Gasterosteus aculeatus*) (Wootton & Fletcher 2009); while in contrast, reduced rations fed to zebrafish (*Danio rerio*) actually increased the numbers of oocytes, although egg size and hatching success declined (Forbes *et al.* 2010). Experiments by Einum & Fleming (2000) examining the effect of Atlantic salmon (*Salmo salar*) egg number and offspring survival demonstrated a stabilizing phenotypic selection for an optimal egg size, which was close to the average size observed in the population, suggesting that adult females appear to prioritize their own maternal fitness rather than immediate offspring survival.

7.1.4. Condition

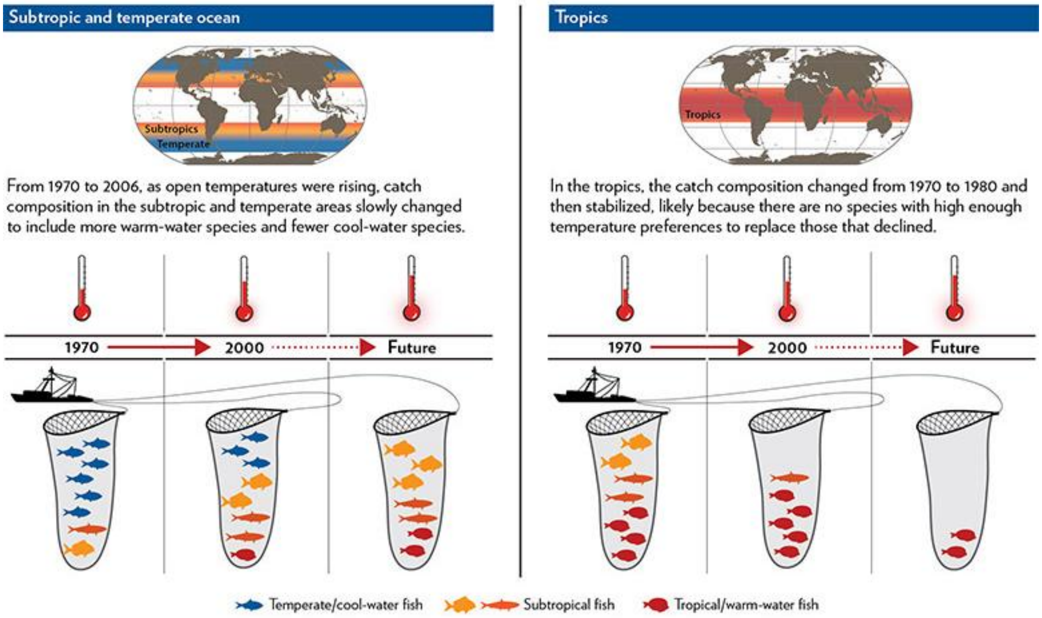
It has been shown that different fish stocks or populations may display different levels of condition according to the environmental characteristics of their habitats (Grecay & Targett 1996; Perry *et al.* 1996; Lloret *et al.* 2002; Rätz & Lloret 2003). Furthermore, it has been assumed that individuals with better condition usually inhabit warmer locations where optimal physiological conditions prevail (Love 1974), as observed in our study case of the bastard grunt (*P. incisus*) (Table 7.1). In this sense, although it might seem that the fish condition of a thermophilic species would be negatively affected during its expansion into colder areas where they were previously absent, this might not always be the case. Here in this thesis, I observed that other environmental effects - such as the feeding conditions (greater food availability at relatively eutrophic locations) - might explain why condition of the bluefish (*P. saltatrix*) is relatively better in the Gulf of Roses in spite of the colder environmental conditions (Table 7.1). In addition to this, differences in total net primary production have been previously documented between northern and southern study areas of the NW Mediterranean, being considerably higher in the Gulf of Lions (including the Gulf of Roses) at 1042.4 t km $^{-2}$ y $^{-1}$ (Bănaru *et al.* 2013) than in the Ebre Delta at 386.68 t km $^{-2}$ y $^{-1}$ (Coll *et al.* 2006).

Therefore, our findings support the theory that a marine fish species, which is able to expand its distribution due to sea warming, may take advantage of other environmental conditions (such as better food availability) in those new habitats, which in turn will contribute to increasing its energy reserves and reproductive potential and thus may also contribute to enhancing the population's productivity in these areas.

7.2. Impacts of sea warming on fish catches

The role of hydro-climatic variations in regulating the abundance of the fish populations is recognized today (IPCC 2014). As stated previously, this study showed that sea water temperature plays an important role in the seasonality of the abundances of thermophilic species within the NW Mediterranean, since the presence of these species within the catches increased considerably when SSTs began to increase. It has been suggested that fluctuations in catchability, defined as the proportion of the population available and captured by a unit effort in a specific space and time, may be related to environmental factors such as water temperature (Arreguín-Sánchez 1996). Smith & Page (1996) suggested that the catchability of certain marine resources could be increased due to higher availability in particular areas of the oceans when they encounter their preferred water mass characteristics, such as sea water temperature. Swain *et al.* (2000) observed that increased or reduced catchability may reflect the temperature conditions that appear to be preferred or avoided by the Atlantic cod (*Gadus morhua*). Similarly, Colbourne & Bowering (2001) showed that the increase in abundance of the yellowtail flounder (*Limanda ferruginea*) was associated with an increase in the sea temperatures and speculated that higher temperatures lead to an increase in catchability. In this sense, our study of the bluefish (*P. saltatrix*) showed that its abundances (CPUE) correlated positively with SSTs and that higher SSTs contribute to the increasing availability of this species in the NW Mediterranean. Although there are no reliable data regarding the abundance of the rest of the thermophilic species considered in this study (*P. incisus*, *S. viridensis* or *T. ovatus*), their abundances are also apparently increasing as noticed by the local fishermen who have highlighted the increasing presence of these species during recent years within the study area (Lloret *et al.* 2015b).

Landings fluctuations of the Mediterranean fisheries have been examined for the most abundant commercial species (59 species) and showed significant year-to-year correlations with temperature for nearly 60% of the cases, and most of them were negatively related, with a reduction of 44% on average (Tzanatos *et al.* 2013). Recently, Gamito *et al.* (2015) have demostrated the existence of a decreasing trend in the catches of fish species in warming large marine ecosystems (LMEs) of the world, where mean catches of polar and temperate species were higher in years of warmer winters in the LMEs located in the northern part of the species range and in years of colder winters in LMEs of the southern regions of their ranges, whereas mean catches of subtropical species were higher in colder years in LMEs of lower latitudes and in warmer years in LMEs of higher latitude regions. Such results obtained for fish catches agree with a poleward shift of fish species as a response to ocean warming. Moreover, Cheung *et al.* (2013) examined the composition of global fisheries catches according to the inferred temperature preferences of the species caught in fisheries, and found that there had been changes in the species composition of marine fisheries catches and that these were significantly related to changes in ocean temperatures. These authors demonstrated that due to sea warming, many marine thermophilic species are gradually moving into cooler waters, and, as a result, species from warmer waters are gradually replacing those traditionally temperate species caught in many fisheries worldwide, especially at higher latitudes (Fig. 7.1).



From 1970 to 2006, as open temperatures were rising, catch composition in the subtropic and temperate areas slowly changed to include more warm-water species and fewer cool-water species.

In the tropics, the catch composition changed from 1970 to 1980 and then stabilized, likely because there are no species with high enough temperature preferences to replace those that declined.

Fig. 7.1 Graphical representation of how warming oceans are reshaping fisheries in which species from warmer waters are replacing those that are traditionally caught in fisheries worldwide. Graphic by The Pew Charitable Trusts' ocean science division presenting the results and concepts from Cheung *et al.* (2013). The thermometers are representative of trends in ocean temperature over time and the fish are representative of trends in catch composition over time. Available at www.pewenvironment.org/research-programs.

By impacting the pattern of marine biodiversity through changes in species' distributions, climate change will most likely affect the abundance, distribution and composition of fisheries catches, which will then lead to large-scale redistribution of global catch potential (Cheung *et al.* 2009; Barange *et al.* 2010), and consequently fishing operations, catch shares and the effectiveness of fisheries management measures (Sumaila *et al.* 2011; Gamito *et al.* 2013). However, these effects might not necessarily be negative, as new fishing opportunities may also arise in some areas of the world, particularly in temperate and polar regions; however, food security in tropical regions may be at risk (Blanchard *et al.* 2005; Cheung *et al.* 2010; Gamito *et al.* 2015).

Cheung *et al.* (2009) suggested that climate change could lead to numerous local extinction events by the year 2050, particularly in subpolar regions, the tropics and semi-enclosed seas (e.g. the Mediterranean Sea), with the distribution of pelagic fish species and demersal species moving pole-wards by an average of 600 and 223 km, respectively. Furthermore, under the climate change scenarios of the IPCC, impacts on fisheries have been projected based on recruitment, growth, mortality, abundance and distribution of fish stocks, as well as changes in ocean net primary production (NPP) and SSTs (Cheung *et al.* 2008; Pörtner *et al.* 2014). In this regard, Polovina *et al.* (2011) suggested that, under the IPCC's scenario (SRES A2) by 2100 relative to 2000, the fish catch in the North Pacific Ocean subtropical biome is projected to increase by 26% through expansion of the biome, while catches in the temperate and equatorial biomes may decrease by 38 and 15%, respectively. Moreover, following the SRES A1B scenario, global climate change is projected to cause a large-scale redistribution of global catch potential, with an average 30 to 70% increase in yield at high latitudes, whereas a 40 to 60% drop will occur in the tropics and in Antarctica by the 2050s relative to the 2000s (Blanchard *et al.* 2005; Cheung *et al.* 2010). Although maximum fisheries catch potential is projected to increase at high latitudes and decrease at low latitudes by 2050 under these climate scenarios, quantifying such projections is constrained by uncertainties in projected primary production rates, biological responses (such as species interactions), and in projected effects of multiple climate drivers and human activities (Pörtner *et al.* 2014).

7.3. Implications and perspectives for management

Although climate change is expected to have a major effect on the distribution and abundance of fish through its influence on recruitment, differences in rates of survival along a latitudinal range will be attributable not only to thermal tolerance, but also to match–mismatch dynamics between the timing of reproduction relative to the production of larval food and predators (Cushing 1990; van der Veer *et al.* 2000; Platt *et al.* 2003; Temming *et al.* 2007) or to the connectivity between spawning sites and required nursery areas of early life stages (Wilderbuer *et al.* 2002). Furthermore, sea warming can alter the growth, survival or reproduction rates of individuals, favouring warm-adapted species and disadvantaging cold-adapted ones, that is to say, it is expected to change the species composition of fish communities in a given region, replacing colder-water species with warmer-water ones (Drinkwater *et al.* 2010). The increasing abundance of warm-water species in the northernmost parts of the western Mediterranean may have important consequences for other coastal species that may be ecologically affected by predation or competition for common resources. Particularly, the predatory behaviour of top predators, such as *P. saltatrix* and *S. viridensis*, which feed on other small fish species, can be threatening the native fauna. This raises further intriguing questions as to whether the thermophilic fauna is affecting the temperate fish populations, as observed by the presence of juveniles of the temperate *S. sphyraena* in the diet of *S. viridensis*. Either by predation or competition, the climate-driven establishment of non-indigenous thermophilic fauna in the NW Mediterranean might be causing a community reassembly that could seriously alter food web structure, for example, causing shifts in trophic pathways and changes in food availability which would then affect fish stocks (Parsons & Lear 2001; Kirby & Beaugrand 2009; Kirby *et al.* 2009; Brown *et al.* 2010).

Furthermore, through species shifts, climate change may also cause overlap of habitats of species targeted by fishing with that of threatened species, potentially increasing the chances of the invading species of being caught as bycatch (Jones *et al.* 2013). This kind of reshaping of the fisheries could have negative effects including the loss of traditional fisheries, decreases in profits and jobs, conflicts over new fisheries that emerge because of distribution shifts, food security concern, and a large decrease in catches in the tropics (Cheung *et al.* 2013). In the latter case, climate change has been thought to impact both fishers' livelihoods (Badjeck *et al.* 2010) and fish production (Barange & Perry 2009), where the consequences of climate change on fishing coastal communities could be determined by (a) their climate change exposure, as some locations will be affected more than others; (b) the sensitivity of climate change in terms of targeted species and the ecosystem on which fishers and communities depend; and (c) on the fishers and their communities' ability to adapt to change (Quentin Grafton 2010). However, it is a fact that fishing communities as well as consumers will need to adapt to new species appearing in fishing nets and the dwindling presence of traditional species.

The evidence available still includes many uncertainties about the future of affected fish species and also their harvesters who may be impacted (negatively or positively) by changes in fish stocks due to climate change. However it is quite clear that the fishing communities which are dependent on local resources of just a few species are likely be the most vulnerable to fluctuations in high-valued fish stocks, whether due to overfishing or climate change or other causes (Brander 2010). Therefore, where climate-driven ecological changes are significant, countries and communities will need to adapt through, for example, changes in fishing practices and operations because the impacts of climate change on the fisheries sector will have implications for availability of the marine resources and food security (Allison *et al.* 2009).

Given the complexity and regional variability of marine ecosystems and their responses to climate change, it is difficult to provide detailed adaptation strategies for fisheries management; however, it is possible to suggest management practices that are likely to be helpful (IPCC 2014). In this sense, the suggested adaptive responses to reduce the vulnerability of fisheries and fishing communities include, among others: management approaches and policies that strengthen the livelihood asset base; improved understanding of the existing response mechanisms to climate variability to assist in adaptation planning; recognizing and responding to the new opportunities brought about by climate change; monitoring biophysical, social, and economic indicators linked to management and policy responses; and adoption of multi-sector adaptive strategies to minimize negative impacts (Allison *et al.* 2009; Daw *et al.* 2009; Badjeck *et al.* 2010).

If we want to counteract the impacts of climate change on marine communities, the best strategy would involve fisheries management, so that native fish stocks could increase their resilience, i.e. by reducing the fishing pressure (Cochrane *et al.* 2009) or preserving their essential fish habitats (EFH) - where fish spawn, breed, feed, or grow to maturity - as marine protected areas (MPAs) (Bellido *et al.* 2008). Maintaining their resilience should prevent a fishery from failing to deliver benefits by nurturing and preserving those ecological features that enable it to renew and reorganize itself, and thus increasing the chances of those fish stocks developing better life-history traits (condition, growth and reproductive potential) in order to tackle the impacts of climate change. In this sense, several studies have recognized that fishing negatively affects the life-history traits of marine populations, which in turn makes them more vulnerable to climate change impacts (Begg *et al.* 1999; Lundberg *et al.* 2000; Lehodey *et al.* 2006; Ottersen *et al.* 2006; Bradford *et al.* 2009; Planque *et al.* 2010). As exploitation can affect the way populations respond to climatic forcing, it is likely that recovery to a given population abundance or biomass will not be sufficient to also restore the patterns of population responses to climate. As fishing mortality increases, these changes in life-histories could in some cases partially compensate for the lost reproductive value. A series of recent studies have found that another key factor in increasing a stock's resilience is the age structure of the spawning populations, since older and larger females are not only more fertile (the number of eggs per gram of body weight is generally rather constant), but they also produce larger eggs, more viable larvae and spawn in a different temporal and spatial window (Marteinsdottir & Thorarinsson 1998; Cardinale & Arrhenius 2000; Berkeley *et al.* 2004a; Birkeland & Dayton 2005). From this point of view, the population's reproductive potential is greater if larger/older individuals are proportionally more abundant, and the presence of older individuals in the spawning stock should increase the viability of the eggs and larvae leading to potentially higher chances of survival and recruitment success under a wider range of environmental conditions (Berkeley *et al.* 2004b).

On the basis of the issues described in the previous paragraph, Lloret *et al.* (2015a) have made several recommendations to minimize the effects of climate change on fish security and safety, including: (a) the reduction in fishing effort, (b) the promotion of environmental-friendly fishing techniques that minimize the discards and that avoid degradation and loss of marine habitats; (c) the promotion of integrated and ecosystem approaches (ecosystem-based fisheries management), (d) the establishment of new marine protected areas to increase not only fish abundance and biomass, but also to enhance fish energetic reserves, and (e) the promotion of sustainable harvesting practices that allow individual replacement associated with the maximum catch in a long term perspective. The latter can be achieved following the three rules summarized by Froese (2004): (1) let fish spawn (the target would be to let all fish spawn at least once before they are caught to rebuild and maintain healthy spawning stocks); (2) let fish grow (the target would be to catch all fish at sizes close to their optimum length; and (3) let the mega-spawners live (no mega-spawners being caught because the quantity and quality of the eggs they spawn are higher than those of smaller spawners).

According to the report entitled *Assessment of Potential Effects and Adaptations for Climate Change in Europe* (ACACIA 2000), the main planning strategy for adaptation or mitigation of future impacts of climate change on regional fisheries is to promote economic incentives to switch target species or use other fishing gears to counteract the climate-driven impacts of fish distribution changes and species composition. However, the decision of fishers on whether to change target species and gear depends on several factors, such as resource abundance, commercial value, information from other fishers, weather conditions, distance to fishing grounds, cultural aspects and fisheries management measures, and thus, any adaptation of fisheries to the changes in the fish communities is unlikely to be as fast or easy as thought (Christensen & Raakjær 2006). On the Portuguese coast, Gamito *et al.* (2013) have observed an increasing relative importance of subtropical species caught mainly by the multi-gear fisheries, and these authors suggested that an easier way to adapt Portuguese fisheries to the effects of climate change on fish distribution would be to promote the use of trammel nets since these can catch a wider variety of species and a wider size range than other multi-gear fisheries (such as gill nets or longlines), with fishers focusing on subtropical species.

On the other hand, there have been some fishing initiatives to eradicate invasive alien species from marine ecosystems such as that for the pufferfish (*Lagocephalus sceleratus*) within the Eastern Mediterranean where this species is considered nowadays as a pest by fisheries and a potential threat to biodiversity and to humans due to its lethal poison effects (Bentur *et al.* 2008; Kalogirou 2013). The Bern Convention on the Conservation of European Wildlife and Natural Habitats has developed a European Strategy on Invasive Alien Species (Genovesi & Shine 2004) in which eradication programmes are encouraged to mitigate the threats. However, in marine environments, eradication is very difficult to carry out, especially if the species is not in the earliest stages of invasion, and thus, for many long-established invasive alien species, eradication will simply not be feasible. Similarly, the Florida Fish and Wildlife Conservation Commission (FWC) encourages people to remove lionfish (*Pterios volitans* and *P. miles*) from Florida waters to help limit negative impacts to native marine life and ecosystems within the Western Atlantic. However, due to the extent of the lionfish invasion, Barbour *et al.* (2011) suggested that complete eradication of this species through fishing is unlikely, and a substantial reduction of adult abundance will require a long-term commitment and may be feasible only in small, localized areas where annual exploitation can be intense over multiple consecutive years. Otherwise control strategies as attempts to eradicate existing lionfish populations would be impractical and probably unsuccessful. However, these targeted removal regimes could indeed lower the densities of lionfish populations, thus reducing detrimental predation of particularly vulnerable fish species (Frazer *et al.* 2012). Regardless of the viability and effectiveness of these interventionist measures on the invasive alien species, these strategies are unlikely to be able to restore the ecosystem balance, but it is hoped it may perhaps slow it down.

At present, none of the thermophilic species studied in this thesis (*P. saltatrix*, *P. incisus*, *S. viridensis* or *T. ovatus*) are considered fishing targets; they are merely bycatch species in the fishing ports of the NW Mediterranean and their landings correspond mainly to the artisanal and coastal small-scale fishing fleets which target a wide range of fish species. Therefore, a good adaptive response to climate-driven changes in species distributions in the NW Mediterranean would probably be to promote the fishing of some thermophilic fish, which in turn may increase the resilience of stocks of native temperate species that are currently under high fishing pressure. Lloret *et al.* (2015a) have suggested that for certain small and medium-sized pelagic fish, the promotion of invasive warm-water (often not exploited or little exploited) and less accepted species among consumers over cold-water (often overexploited) species, might be a feasible management strategy. In the NW Mediterranean, the consumption of warm-water species such as *Sardinella aurita*, *Pomatomus saltatrix*, *Sphyraena viridensis* and *Trachinotus ovatus* could be promoted. However, this recommendation must be considered case-by-case with extreme caution, and will be not desirable in the case of certain warm-water species that have life history traits that render them very vulnerable to fishing such as thermophilic groupers or billfishes, which are also spreading into new areas because of sea warming (see e.g. Lloret *et al.* 2015b).

All the above mentioned operational strategies must be set up on a regional level since it is highly probable that the regional effects of climate change will contribute towards the perturbation of sea activities in the Mediterranean where the pelagic, demersal and benthic species are severely affected by artisanal, semi-industrial and industrial fleets. Moreover, further programmes must contribute to the knowledge on the effects of climate change on the marine and coastal biodiversity and to the knowhow in terms of adaptation and implementation of solutions for the conservation of ecosystems and natural resources. Adopting action plans stemming from holistic concepts, such as integrated management of the ecosystem approach, are urgently needed even if it means having complex governance mechanisms at several spatial levels (local, regional, national, and trans-national).

7.4. Final overview

The results of this thesis highlight the important fact that, beyond studying the increases in abundance and biomass of warm-water species worldwide due to climate change, it is also necessary to study the biology of such thermophilic species because it will help us improve our understanding of the biological mechanisms of these sea warming driven changes in the marine communities. To date, most of the published studies have focused mainly on the study of changes in the abundance and biomass of fish communities and their ecological assemblages based on complex models (Brander 2003, 2007; Perry *et al.* 2005; Lehodey *et al.* 2006; Collie *et al.* 2008; Dulvy *et al.* 2008; Graham & Harrod 2009; Jennings & Brander 2010; Cheung *et al.* 2013; Hollowed *et al.* 2013; Gamito *et al.* 2015), however these models often fail to reveal the biological mechanisms behind the temporal and spatial changes in species abundance. The results presented here in this thesis show that these changes can be addressed more properly by studying the physiology and bioenergetics of those species, so that we can adequately predict and better understand the impact of climate change on the distribution of marine organisms. Moreover, the results of this research introducing biological data of fish - such as reproduction and condition - suggest that the climate-driven changes in fish populations can also be investigated by assembling comparative data from populations inhabiting environments with different temperature regimes. This kind of spatial comparative approach may enable us to study the links between water temperature and life-history traits when long-term series of temporal (inter-annual) data is lacking.

7.5. Recommendations in future researches

In future research, firstly, it is crucial to continue the monitoring of sea water temperatures within the study area in order to improve our knowledge about the processes and changes underway in the NW Mediterranean which may be influencing the observed changes in the marine communities. Secondly, it is highly recommended that proper abundance-based monitoring programmes be implemented with regard to the fish species studied here (as well as for other non-native warm-water species) in order to study the status, growth and establishment of their populations within the NW Mediterranean Sea. Diet ecology and fish assemblages studies are also encouraged in order to achieve a more comprehensive understanding of the biological interactions, feeding ecology and space occupation between native and non-native species.

Finally, it is crucial to continue to undertake studies on the life-history traits of fish in relation to sea warming so that we can understand the biological mechanisms behind the changes in abundance and biomass of fish related to climate change. Such knowledge would provide adequate suitable foundation on which ecosystem-level complexities can be addressed. This conceptual framework needs to be considered for developing further hypotheses which will deepen our integrative understanding of the effects of climate change on fish.

7.6. Conclusions

- Although water temperature clearly influences the presence and spawning phenology of the bluefish (*Pomatomus saltatrix*), its northward expansion may have been facilitated not only by favourable temperatures but also by the higher productivity in the northernmost area, as evidenced by the increased fish condition in these waters.
- The bastard grunt (*Pomadasys incisus*) is taking advantage of its ability to show a certain degree of plasticity in the spawning strategies by trading-off egg size and quality for higher egg numbers in areas with colder environmental conditions.
- The life-history traits of the European barracuda (*Sphyraena sphyraena*) are, at present, better suited to the environmental conditions of the NW Mediterranean compared to the more physically restricted life-history traits of the non-native yellow-mouth barracuda (*S. viridensis*). However, the thermophilic *S. viridensis* has a considerably higher reproductive potential which may favour its population growth within the study area, especially if the present-day sea warming continues.
- Temporal variations in the reproductive traits of the pompano (*Trachinotus ovatus*) were observed inter-annually, all of which might correspond to the changes in water temperatures, indicating an important influence of the water temperature on its reproduction and explaining its seasonal presence within the northernmost areas of the Mediterranean.
- Sea warming plays a role in the northward spread and increasing abundance of warm-water species in the NW Mediterranean Sea, mediated through physiological adaptations - such as the changes in size-at-maturity, fecundity, spawning phenology and condition - to the rising sea temperatures, which appear to be playing an important role in the establishment of this thermophilic fauna into areas they did not previously occupy.
- Overall, the results provided in this PhD show that not only is it necessary to continue studying the increases in abundance and biomass of warm-water species due to climate change, there is also a need for research into their life-history traits, particularly condition and reproduction, in order to improve our understanding of the biological mechanisms behind the changes in marine communities due to sea warming.
- In order to enhance the resilience of local fish stocks to climate change, fishing pressure must be maintained at sustainable levels and the essential fish habitats (EFHs) should be preserved, providing areas for native fish species to enhance their condition, growth and reproductive potential and thus decrease their vulnerability to ecological threats arising from the increasing numbers of non-native thermophilic fish species that threaten the sustainability of temperate/cold water stocks.

REFERENCES

ACACIA. (2000). Assessment of Potential Effects and Adaptations for Climate Change in Europe: The Europe ACACIA Project. Jackson Environment Institute, University of East Anglia. 320 p.

ACIA. (2005). Arctic Climate Impact Assessment. Cambridge University Press. 1042 p.

Alcaraz C. & García-Berthou E. (2007). Life history variation of invasive mosquitofish (*Gambusia holbrooki*) along a salinity gradient. *Biological Conservation*, 139(1-2): 83–92.

Allam S. M., Faltas S. N., & Ragheb E. (2004a). Age and growth of barracudas in the Egyptian Mediterranean waters. *Egyptian Journal of Aquatic Research*, 30(B): 281–289.

Allam S. M., Faltas S. N., & Ragheb E. (2004b). Reproductive biology of Sphyraena species in the Egyptian Mediterranean waters off Alexandria. *Egyptian Journal of Aquatic Research*, 30(B): 255–270.

Allison E. H., Perry A. L., Badjeck M.-C., Neil Adger W., Brown K., Conway D., Halls A. S., Pilling G. M., Reynolds J. D., Andrew N. L., & Dulvy N. K. (2009). Vulnerability of national economies to the impacts of climate change on fisheries. *Fish and Fisheries*, 10(2): 173–196.

Alonso-Fernández A. & Saborido-Rey F. (2011). Maternal influence on the variation of the reproductive cycle of *Trisopterus luscus* (Gadidae). *Ciencias Marinas*, 37(4B): 619–632.

Arechavala-Lopez P., Izquierdo-Gomez D., Uglem I., & Sanchez-Jerez P. (2015). Aggregations of bluefish *Pomatomus saltatrix* (L.) at Mediterranean coastal fish farms: seasonal presence, daily patterns and influence of farming activity. *Environmental Biology of Fishes*, 98(2): 499–510.

Arreguín-Sánchez F. (1996). Catchability: assessment a key parameter for fish stock. *Reviews in Fish Biology and Fisheries*, 6: 221–242.

Assem S. S., El-Serafy S. S., El-Garabawy M. M., El-Absawy M. E. G., & Kaldus S. K. (2005). Some biochemical aspects of reproduction in female *Trachinotus ovatus* (Carangidae). *Egyptian Journal of Aquatic Research*, 31(1): 315–327.

Astraldi M., Bianchi C. N., Gasparini G. P., & Morri C. (1995). Climatic fluctuations, current variability and marine species distribution: a case study in the Ligurian Sea (north-west Mediterranean). *Oceanologica Acta*, 18: 139–149.

Azzurro E., Moschella P., & Maynou F. (2011). Tracking signals of change in Mediterranean fish diversity based on local ecological knowledge. *PloS One*, 6(9): e24885.

Badjeck M.-C., Allison E. H., Halls A. S., & Dulvy N. K. (2010). Impacts of climate variability and change on fishery-based livelihoods. *Marine Policy*, 34(3): 375–383.

Bănaru D., Mellon-Duval C., Roos D., Bigot J.-L., Souplet A., Jadaud A., Beaubrun P., & Fromentin J.-M. (2013). Trophic structure in the Gulf of Lions marine ecosystem (north-western Mediterranean Sea) and fishing impacts. *Journal of Marine Systems*, 111-112: 45–68.

Barange M., Cheung W. W. L., Merino G., & Perry R. I. (2010). Modelling the potential impacts of climate change and human activities on the sustainability of marine resources. *Current Opinion in Environmental Sustainability*, 2(5-6): 326–333.

Barange M. & Perry R. I. (2009). Physical and ecological impacts of climate change relevant to marine and inland capture fisheries and aquaculture. In: Cochrane K., C. De Young, D. Soto, & T. Bahri (Eds.), Climate Change Implications for Fisheries and Aquaculture: Overview of Current Scientific Knowledge. Rome, Italy: Food and Agricultural Organization of the United Nations (FAO). 7–106 pp.

Barbour A. B., Allen M. S., Frazer T. K., & Sherman K. D. (2011). Evaluating the potential efficacy of invasive lionfish (*Pterois volitans*) removals. *PLoS ONE*, 6(5): e19666.

Bariche M. (2012). Field identification guide to the living marine resources of the Eastern and Southern Mediterranean. FAO Species Identification Guide for Fishery Purposes. Rome, Italy: Food and Agricultural Organization of the United Nations (FAO). 610 p.

Barreiros J. P., Santos R. S., & Borba A. E. (2002). Food habits, schooling and predatory behaviour of the yellowmouth barracuda, *Sphyraena viridensis* (Perciformes: Sphyraenidae) in the Azores. *Cybium*, 26(2): 83–88.

Batistić M., Tutman P., Bojanić D., Skaramuca B., Kožul V., Glavić N., & Bartulović V. (2005). Diet and diel feeding activity of juvenile pompano (*Trachinotus ovatus*) (Teleostei: Carangidae) from the southern Adriatic, Croatia. *Journal of the Marine Biological Association of the United Kingdom*, 85(06): 1533–1534.

Baudron A. R., Needle C. L., & Marshall C. T. (2011). Implications of a warming North Sea for the growth of haddock *Melanogrammus aeglefinus*. *Journal of Fish Biology*, 78(7): 1874–89.

Baudron A. R., Needle C. L., Rijnsdorp A. D., & Marshall C. T. (2014). Warming temperatures and smaller body sizes: synchronous changes in growth of North Sea fishes. *Global Change Biology*, 20(4): 1023–31.

Beacham T. & Murray C. (1993). Fecundity and egg size variation in north American Pacific salmon (Oncorhynchus). *Journal of Fish Biology*, 42: 485–508.

Begg G. A., Friedland K. D., & Pearce J. B. (1999). The role of life history parameters as indicators of stock structure. *Fisheries Research*, 43(1): 141–163.

Belkin I. M. (2009). Rapid warming of Large Marine Ecosystems. *Progress in Oceanography*, 81: 207–213.

Bellido J. M., Brown A. M, Valavanis V. D., Giráldez A., Pierce G. J, Iglesias M., & Palialexis A. (2008). Identifying essential fish habitat for small pelagic species in Spanish Mediterranean waters. *Hydrobiologia*, 612(1): 171–184.

Bentur Y., Ashkar J., Lurie Y., Levy Y., Azzam Z. S., Litmanovich M., Golik M., Gurevych B., Golani D., & Eisenmanh A. (2008). Lessepsian migration and tetrodotoxin poisoning due to *Lagocephalus sceleratus* in the eastern Mediterranean. *Toxicon*, 52(8): 964–968.

Ben-Tuvia A. (1986). Sphyraenidae. In: Whitehead P. J. P., M.-L. Bauchot, J.-C. Hureau, J. Nielsen, & E. Tortonese (Eds.), Fishes of the North-east Atlantic and the Mediterranean (FNAM) Vol. III. Paris: UNESCO. 1194–1196 pp.

Berkeley S. A., Chapman C., & Sogard S. M. (2004a). Maternal age as a determinant of larval growth and survival in a marine fish, *Sebastes melanops*. *Ecology*, 85(5): 1258–1264.

Berkeley S. A., Hixon M. A., Larson R. J., & Love M. S. (2004b). Fisheries sustainability via protection of age structure and spatial distribution of fish populations. *Fisheries*, 29: 23–32.

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. *Progress in Oceanography*, 44(1-3): 131–146.

Bianchi C. N. & Morri C. (1994). Southern species in the Ligurian Sea (northern Mediterranean): new records and a review. *Bollettino Dei Musei E Degli Istituti Biologici dell'Universita Di Genova*, 58–59: 181–197.

Bianchi C. N. & Morri C. (2000). Marine biodiversity of the Mediterranean Sea: situation, problems and prospects for future research. *Marine Pollution Bulletin*, 40(5): 367–376.

Birkeland C. & Dayton P. K. (2005). The importance in fishery management of leaving the big ones. *Trends in Ecology and Evolution*, 20(7): 356–358.

Blanchard J. L., Mills C., Jennings S., Fox C. J., Rackham B. D., Eastwood P. D., & O'Brien C. M. (2005). Distribution abundance relationships for North Sea Atlantic cod (*Gadus morhua*):

observation versus theory. *Canadian Journal of Fisheries and Aquatic Sciences*, 62(9): 2001–2009.

Bodilis P., Crocetta F., Langeneck J., & Francour P. (2013). The spread of an Atlantic fish species, *Pomadasys incisus* (Bowdich, 1825) (Osteichthyes: Haemulidae), within the Mediterranean Sea with new additional records from the French Mediterranean coast. *Italian Journal of Zoology*, 80(2): 273–278.

Bøhn T., Sandlund O. T., Amundsen P., & Primicerio R. (2004). Rapidly changing life history during invasion. *Oikos*, 106: 138–150.

Bombace G. (2001). Influence of climatic changes on stocks, fish species and marine ecosystems in the Mediterranean Sea. *Archivio Di Oceanografia E Limnologia*, 22: 67–72.

Bosc E., Bricaoud A., & Antoine D. (2004). Seasonal and interannual variability in algal biomass and primary production in the Mediterranean Sea, as derived from 4 years of SeaWiFS observations. *Global Biogeochemical Cycles*, 18(1): 1–17.

Box G. E. P. & Jenkins G. M. (1976). Time series Analysis: Forecasting and Control. New York: Prentice Hall, Inc. 575 p.

Bradford M., Hidalgo M., Massutí E., Guijarro B., Moranta J., Ciannelli L., Lloret J., Oliver P., & Stenseth N. C. (2009). Population effects and changes in life history traits in relation to phase transitions induced by long-term fishery harvesting: European hake (*Merluccius merluccius*) off the Balearic Islands. *Canadian Journal of Fisheries and Aquatic Sciences*, 66(8): 1355–1370.

Brander K. (1995). The effect of temperature on growth of Atlantic cod (*Gadus morhua*). *ICES Journal of Marine Science*, 52: 1–10.

Brander K. (2003). What kinds of fish stock predictions do we need and what kinds of information will help us to make better predictions? *Scientia Marina*, 67(S1): 21–33.

Brander K. (2010). Impacts of climate change on fisheries. *Journal of Marine Systems*, 79(3-4): 389–402.

Brander K. M. (2007). Global fish production and climate change. *Proceedings of the National Academy of Sciences of the United States of America*, 104(50): 44–46.

Briggs J. C. (1960). Fishes of world-wide (circumtropical) distribution. *Copeia*, 3: 171–180.

Bromage N., Porter M., & Randall C. (2001). The environmental regulation of maturation in farmed finfish with special reference to the role of photoperiod and melatonin. *Aquaculture*, 197(1-4): 63–98.

Brooks S., Tyler C. R., & Sumpter J. P. (1997). Egg quality in fish: what makes a good egg? *Reviews in Fish Biology and Fisheries*, 7: 387–416.

Brown C. J., Fulton E. A., Hobday A. J., Matear R. J., Possingham H. P., Bulman C., Christensen V., Forrest R. E., Gehrke P. C., Gribble N. A., Griffiths S. P., Lozano-Montes H., Martin J. M., Metcalf S., Okey T. A., Watson R., & Richardson A. J. (2010). Effects of climate-driven primary production change on marine food webs: implications for fisheries and conservation. *Global Change Biology*, 16(4): 1194–1212.

Brown-Peterson N. J., Wyanski D. M., Saborido-Rey F., Macewicz B. J., & Lowerre-Barbieri S. K. (2011). A Standardized Terminology for Describing Reproductive Development in Fishes. *Marine and Coastal Fisheries: Dynamics Management and Ecosystem Science*, 3(1): 52–70.

Brunel T. & Dickey-Collas M. (2010). Effects of temperature and population density on von Bertalanffy growth parameters in Atlantic herring: a macro-ecological analysis. *Marine Ecology Progress Series*, 405: 15–28.

Cabanes C., Cazenave A., & Le Provost C. (2001). Sea level rise during past 40 years determined from satellite and in situ observations. *Science*, 294(5543): 840–842.

Calvo E., Simó R., Coma R., Ribes M., Pascual J., Sabatés A., Gili J. M., & Pelejero C. (2011). Effects of climate change on Mediterranean marine ecosystems: the case of the Catalan Sea. *Climate Research*, 50: 1–29.

Cardinale M. & Arrhenius F. (2000). The relationship between stock and recruitment: are the assumptions valid? *Marine Ecology Progress Series*, 196: 305–309.

Castro L. R., Claramunt G., Krautz M. C., Llanos-Rivera A., & Moreno P. (2009). Egg trait variation in anchoveta *Engraulis ringens*: a maternal response to changing environmental conditions in contrasting spawning habitats. *Marine Ecology Progress Series*, 381: 237–248.

Catalonia Fisheries Statistics. (2012). Department of Agriculture and Fisheries of the Government of Catalonia. Generalitat de Catalunya . Available at http://www20.gencat.cat/portal/site/DAR.

Ceyhan T., Akyol O., Ayaz A., & Juanes F. (2007). Age, growth, and reproductive season of bluefish (*Pomatomus saltatrix*) in the Marmara region, Turkey. *ICES Journal of Marine Science*, 64(3): 531–536.

Chakroun-Marzouk N. & Ktari M. H. (2006). Caractéristiques de la reproduction et de la croissance pondérale relative de Pomadasys incisus (Haemulidae) du golfe de Tunis (Reproduction and length-weight relationships of Pomadasys incisus (Haemulidae) from Tunis Gulf. *Cybium*, 30(4): 333–342.

Charnov E. L. & Gillooly J. F. (2004). Size and temperature in the evolution of fish life histories. *Integrative and Comparative Biology*, 44(6): 494–497.

Cheung W. W. L., Close C., Lam V. W. Y., Watson R., & Pauly D. (2008). Application of macroecological theory to predict effects on climate change on global fisheries potential. *Marine Ecology Progress Series*, 365: 187–197.

Cheung W. W. L., Lam V. W. Y., Sarmiento J. L., Kearney K., Watson R., & Pauly D. (2009). Projecting global marine biodiversity impacts under climate change scenarios. *Fish and Fisheries*, 10(3): 235–251.

Cheung W. W. L., Lam V. W. Y., Sarmiento J. L., Kearney K., Watson R., Zeller D., & Pauly D. (2010). Large-scale redistribution of maximum fisheries catch potential in the global ocean under climate change. *Global Change Biology*, 16(1): 24–35.

Cheung W. W. L., Watson R., & Pauly D. (2013). Signature of ocean warming in global fisheries catch. *Nature*, 497(7449): 365–368.

Christensen A.-S. & Raakjær J. (2006). Fishermen's tactical and strategic decisions. *Fisheries Research*, 81(2-3): 258–267.

Clark R. A., Fox C. J., Viner D., & Livermore M. (2003). North Sea cod and climate change–modelling the effects of temperature on population dynamics. *Global Change Biology*, 9(11): 1669–1680.

Cochrane K., De Young C., Soto D., & Bahri T. (2009). Climate change implications for fisheries and aquaculture: Overview of current scientific knowledge. Rome, Italy: FAO Fisheries and Aquaculture Technical Paper No. 530. 221 p.

Colbourne E. B. & Bowering W. R. (2001). Recent trends in bottom temperatures and distribution and abundance of yellowtail flounder (*Limanda ferruginea*) in NAFO Divisions 3LNO during the spring and fall. North Atlantic Fisheries Organization SCR Doc. No. 32. 17 p.

Coll M., Palomera I., Tudela S., & Sardà F. (2006). Trophic flows, ecosystem structure and fishing impacts in the South Catalan Sea, Northwestern Mediterranean. *Journal of Marine Systems*, 59(1-2): 63–96.

Coll M., Piroddi C., Steenbeek J., Kaschner K., Ben Rais Lasram F., Aguzzi J., Ballesteros E., Bianchi C. N., Corbera J., Dailianis T., Danovaro R., Estrada M., Froglia C., Galil B. S., Gasol

J. M., Gertwagen R., Gil J., … Voultsiadou E. (2010). The biodiversity of the Mediterranean Sea: estimates, patterns, and threats. *PLoS ONE*, 5(8): e11842.

Collette B. B. (2002). Volume 3: Bony fishes part 2 (Opistognathidae to Molidae), sea turtles and marine mammals. In: Carpenter K. E. (Ed.), The Living Marine Resources of the Western Central Atlantic. Rome, FAO: FAO Species Identification Guide for Fishery Purposes and American Society of Ichthyologists and Herpetologists Special Publication No. 5. 1412–1413 pp.

Collie J. S., Wood A. D., & Jeffries H. P. (2008). Long-term shifts in the species composition of a coastal fish community. *Canadian Journal of Fisheries and Aquatic Sciences*, 65(7): 1352–1365.

Coma R., Ribes M., Serrano E., Jiménez E., Salat J., & Pascual J. (2009). Global warming-enhanced stratification and mass mortality events in the Mediterranean. *Proceedings of the National Academy of Sciences of the United States of America*, 106(15): 6176–6181.

Conand C. (1975). Maturité sexuelle et fecondité du tassergal (*Pomatomus saltator*) (L., 1766), Poissons: Pomatomidae. *Bulletin de l'Institut Fondamental d'Afrique Noire*, 37(A): 2.

Cone R. S. (1989). The need to reconsider the use of condition indices in fishery science. *Transactions of the American Fisheries Society*, 118: 510–514.

Conover D. O. (1985). Field and laboratory assessment of patterns in fecundity of a multiple spawning fish: the Atlantic silverside *Menidia menidia*. *Fishery Bulletin*, 83(3): 331–341.

Conover D. O. (1992). Seasonality and the scheduling of life history at different latitudes. *Journal of Fish Biology*, 41(B): 161–178.

Crabtree R. E., Hood P. B., & Snodgrass D. (2002). Age, growth, and reproduction of permit (*Trachinotus falcatus*) in Florida waters. *Fishery Bulletin*, 100(1): 26–34.

Crow K. D., Munehara H., Kanamoto Z., Balanov A., Antonenko D., & Bernardi G. (2007). Maintenance of species boundaries despite rampant hybridization between three species of reef fishes (Hexagrammidae): implications for the role of selection. *Biological Journal of the Linnean Society*, 91: 135–147.

Cunha M. E., Vendrell C., & Gonçalves P. (2008). Experimental study of the dependence of embryonic development of *Trachurus trachurus* eggs on temperature. *ICES Journal of Marine Science*, 65: 17–24.

Cushing D. (1990). Plankton production and year-class strength in fish populations: an update of the match/mismatch hypothesis. *Advances in Marine Biology*, 26: 249–293.

D'Alessandro E. K., Sponaugle S., Llopiz J. K., & Cowen R. K. (2011). Larval ecology of the great barracuda, *Sphyraena barracuda*, and other sphyraenids in the Straits of Florida. *Marine Biology*, 158(12): 2625–2638.

Daufresne M., Lengfellner K., & Sommer U. (2009). Global warming benefits the small in aquatic ecosystems. *Proceedings of the National Academy of Sciences of the United States of America*, 106(31): 12788–12793.

Daw T., Adger N., Brown K., & Badjeck M.-C. (2009). Climate change and capture fisheries. *Climate Change Implications for Fisheries and Aquaculture: Overview of Current Scientific Knowledge. Fisheries Technical Paper*, 530: 95–135.

De Sylva D. P. (1990). Sphyraenidae. In: Quero J. C., J. . Hureau, C. Karrer, A. Post, & L. Saldanha (Eds.), Check-list of the fishes of the eastern tropical Atlantic. Vol. 3. (CLOFE- TA). Lisbon: JNICT; Paris: SEI and UNESCO. 860–864 pp.

Diaz-Almela E., Marba N., & Duarte C. M. (2007). Consequences of Mediterranean warming events in seagrass (*Posidonia oceanica*) flowering records. *Global Change Biology*, 13: 224–235.

Ditty J. G. & Shaw R. F. (1995). Seasonal occurrence, distribution, and abundance of larval bluefish, *Pomatomus saltatrix* (Family: Pomatomidae), in the northern Gulf of Mexico. *Bulletin of Marine Science*, 56(2): 592–601.

Domínguez-Petit R. & Saborido-Rey F. (2010). New bioenergetic perspective of European hake (*Merluccius merluccius* L.) reproductive ecology. *Fisheries Research*, 104(1-3): 83–88.

Drinkwater K. F. (2005). The response of Atlantic cod (*Gadus morhua*) to future climate change. *ICES Journal of Marine Science*, 62(7): 1327–1337.

Drinkwater K. F., Beaugrand G., Kaeriyama M., Kim S., Ottersen G., Perry R. I., Pörtner H. O., Polovina J. J., & Takasuka A. (2010). On the processes linking climate to ecosystem changes. *Journal of Marine Systems*, 79(3-4): 374–388.

Dulčić J. & Grbec B. (2000). Climate change and Adriatic ichthyofauna. *Fisheries Oceanography*, 9(2): 187–191.

Dulčić J., Kovačić M., & Dragičević B. (2009). Range extension and additional records of the yellowmouth barracuda, *Sphyraena viridensis* (Actinopterygii: Perciformes: Sphyraenidae) in the eastern Adriatic Sea. *Acta Ichthyologica Et Piscatoria*, 39(1): 59–61.

Dulčić J., Kraljević M., Pallaoro A., & Glamuzina B. (2005). Unusual catch of bluefish *Pomatomus saltatrix* (Pomatomidae) in Tarska cove (northern Adriatic). *Cybium*, 29(2): 207–208.

Dulčić J. & Soldo A. (2004). On the occurrence of the yellowmouth barracuda, *Sphyraena viridensis* Cuvier, 1829 (Pisces: Sphyraenidae), in the Adriatic Sea. *Annales Series Historia Naturalis*, 14(2): 225–228.

Dulvy N. K., Rogers S. I., Jennings S., Stelzenmüller V., Dye S. R., & Skjoldal H. R. (2008). Climate change and deepening of the North Sea fish assemblage: a biotic indicator of warming seas. *Journal of Applied Ecology*, 45(4): 1029–1039.

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., ... Verney R. (2011). Marine ecosystems' responses to climatic and anthropogenic forcings in the Mediterranean. *Progress in Oceanography*, 91(2): 97–166.

Einum S. & Fleming I. A. (2000). Highly fecund mothers sacrifice offspring survival to maximize fitness. *Nature*, 405(1981): 565–567.

El Mor M., El-Etreby S., & Sapota M. R. (2002). Species composition and size structure of beach seine by-catches in Port-Said fishing harbour. *Oceanological Studies*, 31(3-4): 31–43.

Elliott J. M. & Elliott J. A. (1995). The effect of the rate of temperature increase on the critical thermal maximum for parr of Atlantic salmon and brown trout. *Journal of Fish Biology*, 47(5): 917–919.

Engelhard G. H. & Heino M. (2006). Climate change and condition of herring (*Clupea harengus*) explain long-term trends in extent of skipped reproduction. *Oecologia*, 149(4): 593–603.

Fahay M. P., Berrien P. L., Johnson D. L., & Morse W. W. (1999). Bluefish, *Pomatomus saltatrix*, life history and habitat characteristics. NOAA Technical Memorandum, NMFS-NE-144. 68 p.

Fehri-bedoui R. F. & Gharbi H. (2008). Sex-ratio, reproduction and feeding habits of *Pomadasys incisus* (Haemulidae) in the Gulf of Tunis (Tunisia). *Acta Adriatica*, 49(1): 5–19.

Fischer W., Bianchi G., & Scott W. B. (1981). Sphyraenidae. In: Fiches FAO d'Identification des Espèces pour les Besoins de la Pêche. Atlantique Centre-Est. Vol. IV. Ottawa: FAO. 12 p.

Forbes E. L., Craig D. P., & Mark Lokman P. (2010). Zebrafish (*Danio rerio*) and the egg size versus egg number trade off: effects of ration size on fecundity are not mediated by orthologues of the Fec gene. *Reproduction, Fertility and Development*, 22(6): 1015–1021.

Fox M. G., Vila-Gispert A., & Copp G. H. (2007). Life-history traits of introduced Iberian pumpkinseed *Lepomis gibbosus* relative to native populations. Can differences explain colonization success? *Journal of Fish Biology*, 71(D): 56–69.

Francour P., Boudouresque C. F., Harmelin J. G., Harmelin-Vivien M. L., & Quignard J. P. (1994). Are the Mediterranean waters becoming warmer? Information from biological indicators. *Marine Pollution Bulletin*, 28(9): 523–526.

Frazer T. K., Jacoby C. A., Edwards M. A., Barry S. C., & Manfrino C. M. (2012). Coping with the Lionfish Invasion: Can Targeted Removals Yield Beneficial Effects? *Reviews in Fisheries Science*, 20(4): 185–191.

Froese R. (2004). Keep it simple: three indicators to deal with overfishing. *Fish and Fisheries*, 5(1): 86–91.

Froese R. & Pauly D. (2013). Species of Trachinotus. FishBase . Available at www.fishbase.org/identification/SpeciesList.php?genus=Trachinotus.

Furevik T., Drange H., & Sorteberg A. (2002). Anticipated changes in the Nordic Seas marine climate: scenarios for 2020, 2050 and 2080. *Fisken Og Havet 4*, (Section 2): 1–13.

Gagliano M., McCormick M. I., & Meekan M. G. (2007). Temperature-induced shifts in selective pressure at a critical developmental transition. *Oecologia*, 152(2): 219–25.

Galil B. S. (2007a). Loss or gain? Invasive aliens and biodiversity in the Mediterranean Sea. *Marine Pollution Bulletin*, 55(7-9): 314–22.

Galil B. S. (2007b). Seeing Red: Alien species along the Mediterranean coast of Israel. *Aquatic Invasions*, 2(4): 281–312.

Galil B. S. & Zenetos A. (2002). A sea change - exotics in the Eastern Mediterranean. In: Leppakoski E., S. Gollasch, & S. Olenin (Eds.), Invasive aquatic species of Europe. Distribution, impacts and management. Dordrecht: Kluwer Academic Publishers. 325–336 pp.

Gambaiani D. D., Mayol P., Isaac S. J., & Simmonds M. P. (2009). Potential impacts of climate change and greenhouse gas emissions on Mediterranean marine ecosystems and cetaceans. *Journal of the Marine Biological Association of the United Kingdom*, 89(01): 179–201.

Gamito R., Costa M. J., & Cabral H. N. (2015). Fisheries in a warming ocean: trends in fish catches in the large marine ecosystems of the world. *Regional Environmental Change*, 15(1): 57–65.

Gamito R., Teixeira C. M., Costa M. J., & Cabral H. N. (2013). Climate-induced changes in fish landings of different fleet components of Portuguese fisheries. *Regional Environmental Change*, 13(2): 413–421.

Ganias K., Murua H., Claramunt G., Dominguez-Petit R., Gonçalves P., Juanes F., Keneddy J., Klibansky N., Korta M., Kurita Y., Lowerre-Barbieri S. K., Macchi G., Matsuyama M., Medina A., Nunes C., Plaza G., Rideout R. M., … Yoneda M. (2015). Egg Production. In: Domínguez-Petit R., H. Murua, F. Saborido-Rey, & E. A. Trippel (Eds.), Handbook of applied fisheries reproductive biology for stock and management. Vigo, Spain: Digital CSIC. 109 p.

García A. & Palomera I. (1996). Anchovy early life history and its relation to its surrounding environment in the Western Mediterranean basin. *Scientia Marina*, 60(2): 155–166.

Gavagnin P. S., Garibaldi F., & Relini M. (1994). Occurrence of *Pomadasys incisus* (Bowdich) (Osteichthyes: Haemulidae) in Italian waters. *Biologia Marina Mediterranea*, 1(1): 285–286.

Genner M. J., Halliday N. C., Simpson S. D., Southward A. J., Hawkins S. J., & Sims D. W. (2009). Temperature-driven phenological changes within a marine larval fish assemblage. *Journal of Plankton Research*, 32(5): 699–708.

Genovesi P. & Shine C. (2004). European Strategy on Invasive Alien Species. Convention on the Conservation of European Wildlife and Habitats (Bern Convention). Nature and Environment, No. 137. Council of Europe Publishing. 68 p. Available at http://scholar.google.com/scholar?hl=en&btnG=Search&q=intitle:European+strategy+on+invasive+alien+species#0

Gillet C. & Quétin P. (2006). Effect of temperature changes on the reproductive cycle of roach in Lake Geneva from 1983 to 2001. *Journal of Fish Biology*, 69(2): 518–534.

Golani D. (1993a). The biology of the Red Sea migrant, *Saurida undosquamis* in the Mediterranean and comparison with the indigenous confamilial Synodus saurus (Teleostei: Synodontidae). *Hydrobiologia*, 271(2): 109–117.

Golani D. (1993b). Trophic adaptation of Red Sea fishes to the eastern Mediterranean environment - review and new data. *Israel Journal of Zoology*, 39(4): 391–402.

Golani D., Orsi-Relini L., Massutí E., & Quig-Nard J. . (2002). CIESM Atlas of exotic Species in the Mediterranean. Monaco: CIESM publishers. 254 p.

Golani D., Orsi-Relini L., Massutí E., Quignard J. P., & Dulčić J. (2007). Fish invasion of the Mediterranean-retrospective and prospective. *Rapport Commission International Mer Mediterranee*, 38: 2007.

Golani D., Östurk B., & Basusta N. (2006). The Fishes of Eastern Mediterranean. Istanbul: Turkish Marine Research. 260 p.

González-Pola C., Lavín A., & Vargas-Yáñez M. (2005). Intense warming and salinity modification of intermediate water masses in the southeastern corner of the Bay of Biscay for the period 1992–2003. *Journal of Geophysical Research*, 110(C5): C05020.

Goodbred C. O. & Graves J. E. (1996). Genetic relationships among geographically isolated populations of bluefish (*Pomatomus saltatrix*). *Marine and Freshwater Research*, 47: 347–355.

Gordina A. D. & Klimova T. N. (1996). On bluefish (*Pomatomus saltatrix* L.) in the Black Sea. *Marine and Freshwater Research*, 47: 315–318.

Graham C. T. & Harrod C. (2009). Implications of climate change for the fishes of the British Isles. *Journal of Fish Biology*, 74(6): 1143–205.

Graham L. P., Chen D., Christensen O. B., Kjellström E., Krysanova V., Meier H. E. M., Radziewski M., Räisänen J., Rockel B., & Ruosteenoja K. (2008). Projection of future anthropogenic climate change. In: Assessment of Climate Change for the Baltic Sea Basin. The BACC Author Team. Berlin: Springer Verlag. 133–219 pp.

Grecay P. A. & Targett T. E. (1996). Spatial patterns in condition and feeding of juvenile weakfish in Delaware Bay. *Transactions of the American Fisheries Society*, 125: 803–808.

Guo H., Ma Z., Jiang S., Zhang D., Zhang N., & Li Y. (2014). Length-weight relationship of oval pompano, *Trachinotus ovatus* (Linnaeus 1758)(Pisces: Carangidae) cultured in open sea floating sea cages in South. *Indian Journal of Fisheries*, 61(1): 93–95.

Hare J. A. & Cowen R. K. (1993). Ecological and evolutionary implications of the larval transport and reproductive strategy of bluefish *Pomatomus saltatrix*. *Marine Ecology Progress Series*, 98(1-2): 1–16.

Hare J. A. & Cowen R. K. (1994). Ontogeny and otolith microstructure of bluefish *Pomatomus saltatrix* (Pisces: Pomatomidae). *Marine Biology*, 118: 541–550.

Hare J. A. & Cowen R. K. (1996). Transport mechanisms of larval and pelagic juvenile bluefish (*Pomatomus saltatrix*) from South Atlantic Bight spawning grounds to Middle Atlantic Bight nursery habitats. *Limonology and Oceanography*, 41: 1264–1280.

Heino M., Dieckmann U., & Godø O. (2002). Measuring probabilistic reaction norms for age and size at maturation. *Evolution*, 56(4): 669–678.

Heins D. C., Baker J. A., & Guill J. M. (2004). Seasonal and interannual components of intrapopulation variation in clutch size and egg size of a darter. *Ecology of Freshwater Fish*, 13: 258–265.

Helsel D. R., Mueller D. K., & Slack J. R. (2006). Computer program for the Kendall family of trend tests: U.S. Geological Survey Scientific Investigations Report 2005–5275.

Hiscock K., Southward A., Tittley I., & Hawkins S. (2004). Effects of changing temperature on benthic marine life in Britain and Ireland. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 14: 333–362.

Hoegh-Guldberg O. & Bruno J. F. (2010). The impact of climate change on the world's marine ecosystems. *Science*, 328(5985): 1523–8.

Hollowed A. B., Barange M., Beamish R. J., Brander K., Cochrane K., Drinkwater K. F., Foreman M. G. G., Hare J. A., Holt J., Ito S., Kim S., King J. R., Loeng H., MacKenzie B. R., Mueter F. J., Okey T. A., Peck M. A., … Yamanaka Y. (2013). Projected impacts of climate change on marine fish and fisheries. *ICES Journal of Marine Science*, 70(5): 1023–1037.

Hunter J. R., Lo N. C. H., & Leong R. J. H. (1985). Batch fecundity in multiple spawning fishes. *NOAA Technical Report NMFS 36*, : 67–78.

Hunter J. R. & Macewicz B. J. (1985). Rates of atresia in the ovary of captive and wild northern anchovy, *Engraulis mordax*. *Fisheries Bulletin*, 83: 119–136.

IPCC. (2001). Climate Change 2001: The Scientific Basis. Contribution of Working Group I to the Third Assessment Report of the Intergovernmental Panel on Climate Change. (Houghton J. T., Y. Ding, D. J. Griggs, M. Noguer, P. J. van der Linden, X. Dai, K. Maskell, & C. A. Johnson, Eds.). Cambridge, United Kingdom and New York, NY, USA: Cambridge University Press. 881 p.

IPCC. (2013). Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. (Stocker T. F., D. Qin, G.-K. Plattner, M. Tignor, S. K. Allen, J. Boschung, A. Nauels, Y. Xia, V. Bex, & P. M. Midgley, Eds.). Cambridge, United Kingdom and New York, NY, USA: Cambridge University Press. 1535 p. Available at http://www.slvwd.com/agendas/Full/2007/06-07-07/Item 10b.pdf

IPCC. (2014). Climate Change 2014: Impacts, Adaptation, and Vulnerability. Part A: Global and Sectoral Aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. (Field C. B., V. R. Barros, D. J. Dokken, K. J. Mach, M. D. Mastrandrea, T. E. Bilir, M. Chatterjee, K. L. Ebi, Y. O. Estrada, R. C. Genova, B. Girma, E. S. Kissel, A. N. Levy, S. MacCracken, P. R. Mastrandrea, & L. L. White, Eds.). Cambridge, United Kingdom and New York, NY, USA: Cambridge University Press. 1132 p.

Jennings S. & Brander K. (2010). Predicting the effects of climate change on marine communities and the consequences for fisheries. *Journal of Marine Systems*, 79(3-4): 418–426.

Jones M. C., Dye S. R., Fernandes J. A., Frölicher T. L., Pinnegar J. K., Warren R., & Cheung W. W. L. (2013). Predicting the impact of climate change on threatened species in UK waters. *PloS One*, 8(1): e54216.

Jørgensen C., Dunlop E. S., Opdal A. F., & Fiksen Ø. (2008). The evolution of spawning migrations: State dependence and fishing-induced changes. *Ecology*, 89(12): 3436–3448.

Juanes F. & Conover D. O. (1994). Rapid growth, high feeding rates, and early piscivory in young-of-the-year bluefish (*Pomatomus saltatrix*). *Canadian Journal of Fisheries and Aquatic Sciences*, 51(8): 1752–1761.

Juanes F., Hare J. A., & Miskiewicz A. G. (1996). Comparing early life history strategies of Pomatomus saltatrix: a global approach. *Marine and Freshwater Research*, 47(2): 365–379.

Kadison E., D'Alessandro E. K., Davis G. O., & Hood P. B. (2010). Age, growth, and reproductive patterns of the great barracuda, *Sphyraena barracuda*, from the Florida Keys. *Bulletin of Marine Science*, 86(4): 773–784.

Kalogirou S. (2013). Ecological characteristics of the invasive pufferfish *Lagocephalus sceleratus* (Gmelin, 1789) in Rhodes, Eastern Mediterranean Sea. A case study. *Mediterranean Marine Science*, 14(2): 251–260.

Kalogirou S., Corsini-Foka M., Sioulas A., Wennhage H., & Pihl L. (2010). Diversity, structure and function of fish assemblages associated with *Posidonia oceanica* beds in an area of the eastern Mediterranean Sea and the role of non-indigenous species. *Journal of Fish Biology*, 77(10): 2338–2357.

Kalogirou S., Mittermayer F., Pihl L., & Wennhage H. (2012a). Feeding ecology of indigenous and non-indigenous fish species within the family Sphyraenidae. *Journal of Fish Biology*, 80(7): 2528–2548.

Kalogirou S., Wennhage H., & Pihl L. (2012b). Non-indigenous species in Mediterranean fish assemblages: Contrasting feeding guilds of Posidonia oceanica meadows and sandy habitats. *Estuarine, Coastal and Shelf Science*, 96: 209–218.

Kapiris K., Kallias E., & Conides A. (2008). Preliminary biological data on *Pomadasys incisus* (Osteichthyes: Haemulidae) in the Aegean Sea, Greece. *Mediterranean Marine Science*, 9(2): 53–62.

Karlou-Riga C. & Economidis P. (1997). Spawning frequency and batch fecundity of horse mackerel, *Trachurus trachurus* (L.), in the Saronikos Gulf (Greece). *Journal of Applied Ichthyology*, 13: 97–104.

Kaspiris P. (1970). Presenza di *Pomadasys incisus* (Bow.) nelle acque della Grecia (Piscies percoidei) (Presence of Pomadasys incisus (Bow.) in Greek waters (Piscies percoidei). *Annali Del Museo Civico Di Storia Naturale Giacomo Doria*, 4(192): 1–3.

Kendall A. W. & Walford L. A. (1979). Sources and distribution of bluefish, *Pomatomus saltatrix*, larvae and juveniles off the east coast of the United States. *Fishery Bulletin*, 77: 213–227.

King J. R. & McFarlane G. A. (2003). Marine fish life history strategies: applications to fishery management. *Fisheries Management and Ecology*, 10(4): 249–264.

Kinnison M. T., Unwin M. J., Hendry A. P., & Quinn T. P. (2001). Migratory costs and the evolution of egg size and number in introduced and indigenous salmon populations. *Evolution*, 55(8): 1656–1667.

Kirby R. R. & Beaugrand G. (2009). Trophic amplification of climate warming. *Proceedings of the Royal Society B*, 276(1676): 4095–4103.

Kirby R. R., Beaugrand G., & Lindley J. A. (2009). Synergistic Effects of Climate and Fishing in a Marine Ecosystem. *Ecosystems*, 12(4): 548–561.

Kjesbu O. S. (1994). Time of start of spawning in Atlantic cod (*Gadus morhua*) females in relation to vitellogenic oocyte diameter, temperature, fish length and condition. *Journal of Fish Biology*, 45(5): 719–735.

Kjesbu O. S., Fonn M., Gonzáles B. D., & Nilsen T. (2010a). Stereological calibration of the profile method to quickly estimate atresia levels in fish. *Fisheries Research*, 104(1-3): 8–18.

Kjesbu O. S., Klungsoyr J., Kryvi H., Witthames P. R., & Greer-Walker M. (1991). Fecundity, atresia, and egg size of captive Atlantic cod (*Gadus morhua*) in relation to proximate body composition. *Canadian Journal of Fisheries and Aquatic Sciences*, 48: 2333–2343.

Kjesbu O. S., Righton D., Krüger-Johnsen M., Thorsen A., Michalsen K., Fonn M., & Witthames P. R. (2010b). Thermal dynamics of ovarian maturation in Atlantic cod (*Gadus morhua*). *Canadian Journal of Fisheries and Aquatic Sciences*, 67(4): 605–625.

Kjesbu O. S., Witthames P. R., Solemdal P., & Greer-Walker M. (1998). Temporal variations in the fecundity of Arcto-Norwegian cod (*Gadus morhua*) in response to natural changes in food and temperature. *Journal of Sea Research*, 40(3-4): 303–321.

Kožul V., Tutman P., Glavić N., Skaramuca B., & Bolotin J. (2005). First record of the yellowmouth barracuda, *Sphyraena viridensis* (Sphyraenidae) from Adriatic Sea. *Cybium*, 29(2): 201–202.

Kurita Y., Meier S., & Kjesbu O. S. (2003). Oocyte growth and fecundity regulation by atresia of Atlantic herring (*Clupea harengus*) in relation to body condition throughout the maturation cycle. *Journal of Sea Research*, 49(3): 203–219.

Lambert Y. & Dutil J. D. (1997). Can simple condition indices be used to monitor and quantify seasonal changes in the energy reserves of cod (*Gadus morhua*)? *Canadian Journal of Fisheries and Aquatic Sciences*, 54(S1): 104–112.

Lambert Y. & Dutil J. D. (2000). Energetic consequences of reproduction in Atlantic cod (*Gadus morhua*) in relation to spawning level of somatic energy reserves. *Canadian Journal of Fisheries and Aquatic Sciences*, 57(4): 815–825.

Leal E. M., Castro L. R., & Claramunt G. (2009). Variability in oocyte size and batch fecundity in anchoveta (*Engraulis ringens*, Jenyns 1842) from two spawning areas off the Chilean coast. *Scientia Marina*, 73(1): 59–66.

LeCren E. D. (1951). The length-weight relationship and seasonal cycle in gonad weight and condition in the perch (*Perca fluviatilis*). *The Journal of Animal Ecology*, 20(2): 201–219.

Leggett W. C. & Carscadden J. E. (1978). Latitudinal variation in reproductive characteristics of American shad (*Alosa sapidissima*): evidence for population specific life history strategies in fish. *Journal of the Fisheries Research*, 35: 1469–1478.

Lehodey P., Alheit J., Barange M., Baumgartner T., Beaugrand G., Drinkwater K. F., 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. *Journal of Climate*, 19(20): 5009–5030.

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 in Ecology & Evolution*, 25(4): 250–60.

Lelieveld J., Berresheim H., Borrmann S., Crutzen P. J., Dentener F. J., Fischer H., Feichter J., Flatau P. J., Heland J., Holzinger R., Korrmann R., Lawrence M. G., Levin Z., Markowicz K. M., Mihalopoulos N., Minikin A., Ramanathan V., … Ziereis H. (2002). Global air pollution crossroads over the Mediterranean. *Science*, 298: 794–799.

Lemos V. M., Varela Junior A. S., Velasco G., & Vieira J. P. (2011). The reproductive biology of the plata pompano, *Trachinotus marginatus* (Teleostei: Carangidae), in southern Brazil. *Zoologia*, 28(5): 603–609.

Lisovenko L. A. & Andrianov D. P. (1991). Determination of absolute fecundity of intermittently spawning fishes. *Journal of Applied Ichthyology*, 31: 143– 155.

Lloret J., Demestre M., & Sánchez-Pardo J. (2007). Lipid reserves of red mullet (*Mullus barbatus*) during pre-spawning in the northwestern Mediterranean. *Scientia Marina*, 71(2): 269–277.

Lloret J., Faliex E., Shulman G. E., Raga J.-A., Sasal P., Muñoz M., Casadevall M., Ahuir-Baraja A. E., Montero F. E., Repullés-Albelda A., Cardinale M., Rätz H.-J., Vila S., & Ferrer D. (2012). Fish Health and Fisheries, Implications for Stock Assessment and Management: The Mediterranean Example. *Reviews in Fisheries Science*, 20(3): 165–180.

Lloret J., Font T., Muñoz M., Casadevall M., Demestre M., Martín P., Sabatés A., Goméz S., Solé I., & Zaragoza N. (2011). Final report project "Impacte del canvi climàtic sobre les reserves marines: l'exemple del cap de Creus." Fundació Abertis. Girona, Spain. 83 p . Available at http://www.fundacioabertis.org/rcs_est/resum_impacte_del_canvi_climtic_sobre_les_reserves_marines_cap_de_creus.pdf.

Lloret J., Gil de Sola L., Souplet A., & Galzin R. (2002). Effects of large-scale habitat variability on condition of demersal exploited fish in the north-western Mediterranean. *ICES Journal of Marine Science*, 59(6): 1215–1227.

Lloret J. & Planes S. (2003). Condition, feeding and reproductive potential of white seabream *Diplodus sargus* as indicators of habitat quality and the effect of reserve protection in the northwestern Mediterranean. *Marine Ecology Progress Series*, 248(1999): 197–208.

Lloret J., Rätz H. J., Lleonart J., & Demestre M. (2015a). Challenging the links between seafood and human health in the context of global change. *Journal of the Marine Biological Association of the United Kingdom.*

Lloret J., Sabatés A., Muñoz M., Demestre M., Solé I., Font T., Casadevall M., Martín P., & Gómez S. (2015b). How a multidisciplinary approach involving ethnoecology, biology and fisheries can help explain the spatio-temporal changes in marine fish abundance resulting from climate change? *Global Ecology and Biogeography*, 24(4): 448–461.

Lloret J., Shulman G., & Love R. M. (2014). Condition and Health Indicators of Exploited Marine Fishes. West Sussex, UK.: Wiley-Blackwell. 262 p.

Love R. M. (1974). The Chemical Biology of Fishes. Academic Press, London. 547 p.

Lowerre-Barbieri S. K. & Barbieri L. R. (1993). A new method of oocyte separation and preservation for fish reproduction studies. *Fishery Bulletin*, 91(1): 165–170.

Lowerre-Barbieri S. K., Ganias K., Saborido-Rey F., Murua H., & Hunter J. R. (2011). Reproductive Timing in Marine Fishes: Variability, Temporal Scales, and Methods. *Marine and Coastal Fisheries: Dynamics Management and Ecosystem Science*, 3(1): 71–91.

Lundberg P., Ranta E., Ripa J., & Kaïtala V. (2000). Population variability in space and time. *Trends in Ecology and Evolution*, 15: 460–464.

Macdonald R. W., Harnerb T., & Fyfe J. (2005). Recent climate change in the Arctic and its impact on contaminant pathways and interpretation of temporal trend data. *Science of the Total Environment*, 342: 5–86.

Mann H. B. (1945). Non-parametric tests against trend. *Econometrica*, 13: 245–259.

Marcos M. & Tsimplis M. N. (2008). Comparison of results of AOGCMs in the Mediterranean Sea during the 21st century. *Journal of Geophysical Research*, 113(C12): C12028.

Margalef R. (1989). Introducción al Mediterráneo. In: Margalef R. (Ed.), El Mediterráneo Occidental. Barcelona, España: Ediciones Omega. 1–17 pp.

Marteinsdottir G. & Thorarinsson K. (1998). Improving the stock–recruitment relation- ships in Icelandic cod (*Gadus morhua*) by including age diversity of spawners. *Canadian Journal of Fisheries and Aquatic Sciences*, 55: 1372–1377.

Martín P. & Sabatés A. (1991). Spatio-temporal distribution pattern of the red band-fish *Cepola rubescens* Linnaeus at different stages of its life cycle in the northwestern Mediterranean. *Journal of Fish Biology*, 39(4): 549–557.

Martín P., Sabatés A., Lloret J., & Martin-Vide J. (2011). Climate modulation of fish populations: the role of the Western Mediterranean Oscillation (WeMO) in sardine (*Sardina pilchardus*) and anchovy (*Engraulis encrasicolus*) production in the north-western Mediterranean. *Climatic Change*, 110(3-4): 925–939.

Massutí E., Morey G., Moranta J., & Riera F. (2001). Presencia de Sphyraena viridensis (Pisces, Sphyraenidae) a les Illes Balears. *Bolletí de La Societat d'Història Natural de Les Balears*, 44: 97–101.

Mcbride R. S., Somarakis S., Fitzhugh G. R., Albert A., Yaragina N. A., Wuenschel M. J., Alonso-Fernández A., & Basilone G. (2015). Energy acquisition and allocation to egg production in relation to fish reproductive strategies. *Fish and Fisheries*, 16(1): 23–57.

McCullagh P. & Nelder J. A. (1989). Generalized linear models. London: Chapman and Hall. 509 p.

Mendiola D., Alvarez P., Cotano U., Etxebeste E., & Martínez de Murguia A. (2006). Effects of temperature on development and mortality of Atlantic mackerel fish eggs. *Fisheries Research*, 80: 158–168.

Mieszkowska N., Genner M. J., Hawkins S. J., & Sims D. W. (2009). Effects of climate change and commercial fishing on Atlantic Cod *Gadus morhua*. *Advances in Marine Biology*, 56: 213–273.

Millot C. (1990). The Gulf of Lyon hydrodinamics. La Seyne, France: Antenne du Centre d'Océanologie de Marseille.

Mims M. C., Olden J. D., Shattuck Z. R., & Poff N. L. (2010). Life history trait diversity of native freshwater fishes in North America. *Ecology of Freshwater Fish*, 19(3): 390–400.

Miranda A., Cal R. M., & Iglesias J. (1990). Effect of temperature on the development of eggs and larvae of sardine *Sardina pilchardus* Walbaum in captivity. *Journal of Experimental Marine Biology and Ecology*, 140: 69–77.

Molinero J. C., Ibanez F., Nival P., Buecher I., & Souissi S. (2005). North Atlantic climate and northwestern Mediterranean plankton variability. *Limnology and Oceanography*, 50: 1213–1220.

Morato T., Afonso P., Lourinho P., Barreiros J. P., Santos R. S., & Nash R. D. M. (2001). Length-weight relationships for 21 coastal fish species of the Azores, north-eastern Atlantic. *Fisheries Research*, 50(3): 297–302.

Morey G., Moranta J., Massutí E., Grau A., Linde M., Riera F., & Morales-Nin B. (2003). Weight-length relationships of littoral to lower slope fishes from the western Mediterranean. *Fisheries Research*, 62(1): 89–96.

Morgan M. J. (2004). The relationship between fish condition and the probability of being mature in American plaice (*Hippoglossoides platessoides*). *ICES Journal of Marine Science*, 61(1): 64–70.

Morgan M. J. & Bowering W. R. (1997). Temporal and geographic variation in maturity at length and age of Greenland halibut (*Reinhardtius hippoglossoides*) from the Canadian north-west Atlantic with implications for fisheries management. *ICES Journal of Marine Science*, 54: 875–885.

Morgan M. J. & Colbourne E. B. (1999). Variation in maturity-at-age and size in three populations of American plaice. *ICES Journal of Marine Science*, 56: 673–688.

Morgan M. J., Wright P. J., & Rideout R. M. (2013). Effect of age and temperature on spawning time in two gadoid species. *Fisheries Research*, 138: 42–51.

Morri C. & Bianchi C. N. (2001). Recent changes in biodiversity in the Ligurian Sea (NW Mediterranean): is there a climatic forcing. In: Faranda F. M., L. Guglielmo, & G. C. Spezie (Eds.), Mediterranean Ecosystems: Structures and Processes. Springer Milan. 375–384 pp.

Munday P. L., Jones G. P., Pratchett M. S., & Williams A. J. (2008). Climate change and the future for coral reef fishes. *Fish and Fisheries*, 9(3): 261–285.

Muñoz M., Dimitriadis C., Casadevall M., Vila S., Delgado E., Lloret J., & Saborido-Rey F. (2010). Female reproductive biology of the bluemouth *Helicolenus dactylopterus dactylopterus*: spawning and fecundity. *Journal of Fish Biology*, 77(10): 2423–2442.

Murawski S. A. (1993). Climate-Change and Marine Fish Distributions - Forecasting from Historical Analogy. *Transactions of the American Fisheries Society*, 122: 647–658.

Murua H., Kraus G., Saborido-Rey F., Witthames P. R., Thorsen A., & Junquera S. (2003). Procedures to estimate fecundity of marine fish species in relation to their reproductive strategy. *Journal of Northwest Atlantic Fishery Science*, 33: 33–54.

Murua H., Lucio P., Santurtún M., & Motos L. (2006). Seasonal variation in egg production and batch fecundity of European hake *Merluccius merluccius* (L.) in the Bay of Biscay. *Journal of Fish Biology*, 69(5): 1304–1316.

Murua H. & Motos L. (2006). Reproductive strategy and spawning activity of the European hake *Merluccius merluccius* (L.) in the Bay of Biscay. *Journal of Fish Biology*, 69(5): 1288–1303.

Murua H. & Saborido-Rey F. (2003). Female reproductive strategies of marine fish species of the North Atlantic. *Journal of Northwest Atlantic Fishery Science*, 33: 23–31.

NMFS. (1997). Magnuson-Stevens Act Provisions: Essential Fish Habitat (EFH). *Federal Register: The Daily Journal of the United States Goverment*, 62(244): 66531–66559.

Norcross J. J., Richardson S. L., Massmann W. H., & Joseph. E. B. (1974). Development of young bluefish (*Pomatomus saltatrix*) and distribution of eggs and young in Virginia coastal waters. *Transactions of the American Fisheries Society*, 103(3): 477–497.

Nunn A. D., Frear P. A., Lee M., & Cowx I. G. (2010). Is there evidence for a shift in fish growth and recruitment success linked to climate change? *Journal of Fish Biology*, 77(8): 1780–92.

Nykjaer L. (2009). Mediterranean Sea surface warming 1985–2006. *Climate Research*, 39: 11–17.

Olivar M. P., Salat J., & Palomera I. (2001). Comparative study of spatial distribution patterns of the early stages of anchovy and pilchard in the NW Mediterranean Sea. *Marine Ecology Progress Series*, 217: 111–120.

Olla B. L. & Studholme A. L. (1985). Behavior of juvenile bluefish Pomatomus saltatrix in vertical thermal gradients: influence of season, temperature acclimation and food. *Marine Ecology Progress Series*, 23: 165–177.

Ottersen G., Hjermann D. O., & Stenseth N. C. (2006). Changes in spawning stock structure strengthen the link between climate and recruitment in a heavily fished cod (*Gadus morhua*) stock. *Fisheries Oceanography*, 15(3): 230–243.

Pajuelo J. G., Lorenzo J. M., & Gregoire M. (2003a). Age and growth of the bastard grunt (*Pomadasys incisus*) Haemulidae) inhabiting the Canarian archipelago, Northwest Africa. *Fishery Bulletin*, 101(4): 851–859.

Pajuelo J. G., Lorenzo J. M., Gregoire M., & Domínguez-Seoane R. (2003b). Life history of the *Pomadasys incisus* (Osteichthyes: Haemulidae) of the Canarian Archipelago. *Scientia Marina*, 67(2): 241–248.

Palomera I. (1992). Spawning of anchovy *Engraulis encrasicolus*, in the North-Western Mediterranean relative to hydrographic features in the region. *Marine Ecology Progress Series*, 79: 215–223.

Palomera I., Olivar M. P., Salat J., Sabatés A., Coll M., García A., & Morales-Nin B. (2007). Small pelagic fish in the NW Mediterranean Sea: An ecological review. *Progress in Oceanography*, 74(2-3): 377–396.

Pankhurst N. W. & King H. R. (2010). Temperature and salmonid reproduction: implications for aquaculture. *Journal of Fish Biology*, 76(1): 69–85.

Pankhurst N. W. & Munday P. L. (2011). Effects of climate change on fish reproduction and early life history stages. *Marine and Freshwater Research*, 62(9): 1015–1026.

Pankhurst N. W. & Porter M. J. R. (2003). Cold and dark or warm and light: variations on the theme of environmental control of reproduction. *Fish Physiology and Biochemistry*, 28(1-4): 385–389.

Pankratz A. (1983). Forecasting with Univariate Box - Jenkins Models: Concepts and Cases. New York, USA: John Wiley & Sons, Inc. Wiley Series in Probability and Statistics. 576 p.

Pankratz A. (1991). Forecasting with Dynamic Regression Models. New York, USA: John Wiley & Sons, Inc. Wiley Series in Probability and Statistics. 400 p.

Pardiñas A. F., Campo D., Pola I. G., Miralles L., Juanes F., & Garcia-Vazquez E. (2010). Climate change and oceanic barriers: genetic differentiation in *Pomatomus saltatrix* (Pisces: Pomatomidae) in the North Atlantic Ocean and the Mediterranean Sea. *Journal of Fish Biology*, 77(8): 1993–1998.

Parmesan C. & Yohe G. (2003). A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, 421(6918): 37–42.

Parry M. L. (2000). Assessment of Potential Effects and Adaptations for Climate Change in Europe: the Europe ACACIA Project. University of East Anglia, Norwich, UK. 320 p.

Parsons L. . & Lear W. . (2001). Climate variability and marine ecosystem impacts: a North Atlantic perspective. *Progress in Oceanography*, 49(1-4): 167–188.

Pastor J., Astruch P., Prats E., Dalias N., & Lenfant P. (2008). Premières observations en plongée de *Pomadasys incisus* (Haemulidae) sur la côte catalane française. *Cybium*, 32(2): 185–186.

Perry A. L., Low P. J., Ellis J. R., & Reynolds J. D. (2005). Climate change and distribution shifts in marine fishes. *Science (New York, N.Y.)*, 308(5730): 1912–1915.

Perry R. I., Hargreaves N. B., Waddell B. J., & Mackas D. L. (1996). Spatial variations in feeding and condition of juvenile pink and chum salmon off Vancouver Island, British Columbia. *Fisheries Oceanography*, 5(2): 73–88.

Petitgas P., Rijnsdorp A. D., Dickey-Collas M., Engelhard G. H., Peck M. A., Pinnegar J. K., Drinkwater K. F., Huret M., & Nash R. D. M. (2013). Impacts of climate change on the complex life cycles of fish. *Fisheries Oceanography*, 22(2): 121–139.

Philippart C. J. M., Anadón R., & Danovaro R. (2007). Position Paper 9. Impacts of Climate Change on the European Marine and Coastal Environment: Ecosystems Approach. Strasbourg, France: European Science Foundation. 84 p.

Philippart C. J. M., Anadón R., Danovaro R., Dippner J. W., Drinkwater K. F., Hawkins S. J., Oguz T., O'Sullivan G., & Reid P. C. (2011). Impacts of climate change on European marine ecosystems: Observations, expectations and indicators. *Journal of Experimental Marine Biology and Ecology*, 400(1-2): 52–69.

Pickova J., Dutta P. C., Larson P. O., & Kiessling A. (1997). Early embryonic cleavage pattern, hatching success, and egg lipid fatty acid composition: comparison between two cod stocks. *Canadian Journal of Fisheries and Aquatic Sciences*, 54: 2410–2416.

Planque B., Fromentin J.-M., Cury P., Drinkwater K. F., Jennings S., Perry R. I., & Kifani S. (2010). How does fishing alter marine populations and ecosystems sensitivity to climate? *Journal of Marine Systems*, 79(3-4): 403–417.

Platt T., Fuentes-Yaco C., & Frank K. T. (2003). Spring algal bloom and larval fish survival. *Nature*, 423: 398–399.

Polovina J. J., Dunne J. P., Woodworth P. A., & Howell E. a. (2011). Projected expansion of the subtropical biome and contraction of the temperate and equatorial upwelling biomes in the North Pacific under global warming. *ICES Journal of Marine Science*, 68(6): 986–995.

Pörtner H. O., Karl D. M., Boyd P. W., Cheung W. W. L., Lluch-Cota S. E., Nojiri Y., Schmidt D. N., & Zavialov P. O. (2014). Ocean systems. In: Field C. B., V. R. Barros, D. J. Dokken, K. J. Mach, M. D.

Mastrandrea, T. E. Bilir, M. Chatterjee, K. L. Ebi, Y. O. Estrada, R. C. Genova, B. Girma, E. S. Kissel, A. N. Levy, S. MacCracken, P. R. Mastrandrea, & L. L. White (Eds.), Climate Change 2014: Impacts, Adaptation, and Vulnerability. Part A: Global and Sectoral Aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge, United Kingdom and New York, NY, USA: Cambridge University Press. 411–484 pp.

Pörtner H. O. & Peck M. A. (2010). Climate change effects on fishes and fisheries: towards a cause-and-effect understanding. *Journal of Fish Biology*, 77(8): 1745–1779.

Poulard J. & Blanchard F. (2005). The impact of climate change on the fish community structure of the eastern continental shelf of the Bay of Biscay. *ICES Journal of Marine Science*, 62(7): 1436–1443.

Prat A., Gómez V., Solé I., & Catot J. M. (2000). ForeTESS, System for Automatic Seasonal Adjustment and Forecasting of Time Series. In: Proceedings in Computational Statistics. Physica-Verlag. Vol. 29.387–394 pp.

Psomadakis P. N., Giustino S., & Vacchi M. (2012). Mediterranean fish biodiversity: an updated inventory with focus on the Ligurian and Tyrrhenian seas. *Zootaxa*, 3263: 1–46.

Psomadakis P. N., Scacco U., & Vacchi M. (2006). Recent findings of some uncommon fishes from the central Tyrrhenian Sea. *Cybium*, 30(4): 297–304.

Purchase C. F. & Brown J. A. (2001). Stock-specific changes in growth rates, food conversion efficiencies, and energy allocation in response to temperature change in juvenile Atlantic cod. *Journal of Fish Biology*, 58(1): 36–52.

Quentin Grafton R. (2010). Adaptation to climate change in marine capture fisheries. *Marine Policy*, 34(3): 606–615.

Rainuzzo J. R., Reitan K. I., & Olsen Y. (1997). The significance of lipids at early stages of marine fish: a review. *Aquaculture*, 155: 103–105.

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. *Limnology and Oceanography*, 55(4): 1478–1484.

Rätz H. J. & Lloret J. (2003). Variation in fish condition between Atlantic cod (*Gadus morhua*) stocks, the effect on their productivity and management implications. *Fisheries Research*, 60(2-3): 369–380.

Rätz H. J., Stein M., & Lloret J. (1999). Variation in growth and recruitment of Atlantic cod (*Gadus morhua*) off Greenland during the second half of the twentieth century. *Journal of Northwest Atlantic Fishery Science*, 25: 161–170.

Relini M. & Orsi-Relini L. (1997). The two species of barracuda (Sphyraenidae) in the Western Mediterranean. *Cybium*, 21(2): 216–222.

Ribeiro F. & Collares-Pereira M. J. (2010). Life-history variability of non-native centrarchids in regulated river systems of the lower River Guadiana drainage (south-west Iberian Peninsula). *Journal of Fish Biology*, 76(3): 522–537.

Ricciardi A. (2004). Assessing species invasions as a cause of extinction. *Trends in Ecology and Evolution*, 19(12): 619.

Richards S. W. (1976). Age, growth and food of bluefish (*Pomatomus saltatrix*) from east-central Long Island Sound from July through November 1975. *Transactions of the American Fisheries Society*, 105(4): 523–525.

Rideout R. M., Burton M. P. M., & Rose G. A. (2000). Observations on mass atresia and skipped spawning in northern Atlantic cod, from Smith Sound, Newfoundland. *Journal of Fish Biology*, 57(6): 1429–1440.

Rijnsdorp A. D. (1993). Fisheries as a large-scale experiment on life-history evolution: disentangling phenotypic and genetic effects in changes in maturation and reproduction of North Sea plaice, *Pleuronectes platessa* L. *Oecologia*, 96(3): 391–401.

Rijnsdorp A. D., Peck M. A., Engelhard G. H., Möllmann C., & Pinnegar J. K. (2009). Resolving the effect of climate change on fish populations. *ICES Journal of Marine Science*, 66(7): 1570–1583.

Riveiro I., Guisande C., Lloves M., Maneiro I., & Cabanas J. M. (2000). Importance of parental effects on larval survival in *Sardina pilchardus*. *Marine Ecology Progress Series*, 205: 249–258.

Riveiro I., Guisande C., Maneiro I., & Vergara A. R. (2004). Parental effects in the European sardine *Sardine pilchardus*. *Marine Ecology Progress Series*, 274: 225–234.

Rixen M., Beckers J., Levitus S., Antonov J., Boyer T., Maillard C., Fichaut M., Balopoulos E., Iona S., Dooley H., García M. J., Manca B., Giorgetti A., Manzella G., Mikhailov N., Pinardi N., & Zavatarelli M. (2005). The Western Mediterranean Deep Water: A proxy for climate change. *Geophysical Research Letters*, 32(12): 1–10.

Robillard E., Reiss C. S., & Jones C. M. (2008). Reproductive biology of bluefish (*Pomatomus saltatrix*) along the East Coast of the United States. *Fisheries Research*, 90(1-3): 198–208.

Rodríguez J. (1982). Oceanografía del Mar Mediterráneo. Madrid: Ediciones Pirámide. 174 p.

Roessig J. M., Woodley C. M., Cech J. J., & Hansen L. J. (2004). Effects of global climate change on marine and estuarine fishes and fisheries. *Reviews in Fish Biology and Fisheries*, 14(2): 251–275.

Rombough P. J. (1997). The effects of temperature on embryonic and larval development. In: Wood C. M. & D. . McDonald (Eds.), Global Warming: Implications for Freshwater and Marine Fish. Cambridge, U.K.: Cambridge University Press. 177–223 pp.

Root T. L., Price J. T., Hall K. R., Schneider S. H., Rosenzweig C., & Pounds J. A. (2003). Fingerprints of global warming on wild animals and plants. *Nature*, 421: 57–60.

Rose G. A. (2005). On distributional responses of North Atlantic fish to climate change. *ICES Journal of Marine Science*, 62: 1360–1374.

Rosecchi E., Thomas F., & Crivelli A. J. (2001). Can life-history traits predict the fate of introduced species? A case study on two cyprinid fish in southern France. *Freshwater Biology*, 46: 846–853.

Sabatés A. & Martín P. (1993). Spawning and distribution of bluefish *Pomatomus saltatrix* (L.) in the northwestern Mediterranean. *Journal of Fish Biology*, 43: 109–118.

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. *Global Change Biology*, 12(11): 2209–2219.

Sabatés A., Martín P., & Raya V. (2012). Changes in life-history traits in relation to climate change: bluefish (*Pomatomus saltatrix*) in the northwestern Mediterranean. *ICES Journal of Marine Science*, 69(4): 1–10.

Sabatés A., Olivar M. P., Salat J., Palomera I., & Alemany F. (2007). Physical and biological processes controlling the distribution of fish larvae in the NW Mediterranean. *Progress in Oceanography*, 74: 355–376.

Sabatés A., Salat J., & Masó M. (2004). Spatial heterogeneity of fish larvae across a meandering current in the northwestern Mediterranean. *Deep Sea Research Part I: Oceanographic Research Papers*, 51(4): 545–557.

Salat J. (1996). Review of hydrographic environmental factors that may influence anchovy habitats in northwestern Mediterranean. *Scientia Marina*, 60(2): 21–32.

Salat J., Garcia M. A., Cruzado A., Palanques A., Gomis D., Guillén J., de León A., Puigdefàbregas J., Sospedra J., & Velásquez Z. R. (2002). Seasonal changes of water mass structure and shelf slope exchanges at the Ebro Shelf (NW Mediterranean). *Continental Shelf Research*, 22(2): 327–348.

Salat J. & Pascual J. (2002). The oceanographic and meteorological station at L'Estartit (NW Mediterranean). In: CIESM Workshop Series. No. 16. Tracking long-term hydrological change in the Mediterranean Sea. Monaco Vol. 16.29–32 pp.

Salerno D. J., Burnett J., & Ibara R. M. (2001). Age, growth, maturity, and spatial distribution of bluefish, *Pomatomus saltatrix* (Linnaeus), off the northeast coast of the United States, 1985-96. *Journal of Northwest Atlantic Fishery Science*, 29: 31–39.

Salmi T., Määttä A., Anttila P., Ruoho-Airola T., & Amnell T. (2002). Detecting trends of annual values of atmospheric pollutants by the Mann-Kendall test and Sen's slope estimates – the Excel template application MAKESENS. *Publications of Air Quality*, 31: 1–35.

Sánchez-Jerez P., Fernandez-Jover D., Bayle-Sempere J., Valle C., Dempster T., Tuya F., & Juanes F. (2008). Interactions between bluefish *Pomatomus saltatrix* (L.) and coastal sea-cage farms in the Mediterranean Sea. *Aquaculture*, 282(1-4): 61–67.

Santos R. S., Porteiro F. M., & Barreiros J. P. (1997). Marine fishes of the Azores: An annotated checklist and bibliography. *Arquipélago Life Marine Science*, 1: 1–231.

Scarnecchia D. L., Gordon B. D., Schooley J. D., Ryckman L. F., Schmitz B. J., Miller S. E., & Lim Y. (2011). Southern and Northern Great Plains (United States) Paddlefish Stocks Within Frameworks of Acipenseriform Life History and the Metabolic Theory of Ecology. *Reviews in Fisheries Science*, 19(3): 279–298.

Schneider W. (1990). Field guide to the commercial marine resources of the Gulf of Guinea. Rome, Italy: FAO Species Identification Guide for Fishery Purposes. 268 p.

Serena F. & Silvestri R. (1996). First record of *Pomadasys incisus* (Haemulidae) in the Northern Tyrrhenean sea. *Cybium*, 20(4): 409–414.

Seytre C. & Francour P. (2009). The Cap Roux MPA (Saint-Raphaël, French Mediterranean): changes in fish assemblages within four years of protection. *ICES Journal of Marine Science*, 66(1): 180–187.

Shepherd G. R., Moser J., Deuel D., & Carlsen P. (2006). The migration patterns of bluefish (*Pomatomus saltatrix*) along the Atlantic coast determined from tag recoveries. *Fishery Bulletin*, 104(1962): 559–570.

Shulman G. E. & Love R. M. (1999). The biochemical ecology of marine fishes. In: Southward A. J., P. A. Tayler, & C. M. Young (Eds.), Advances in Marine Biology, Vol. 36. San Diego: Academic Press Inc. 351 p.

Sims D. W., Wearmouth V. J., Genner M. J., Southward A. J., & Hawkins S. J. (2004). Low-temperature-driven early spawning migration of a temperate marine fish. *Journal of Animal Ecology*, 73(2): 333–341.

Skliris N., Sofianos S., Gkanasos A., Mantziafou A., Vervatis V., Axaopoulos P., & Lascaratos A. (2011). Decadal scale variability of sea surface temperature in the Mediterranean Sea in relation to atmospheric variability. *Ocean Dynamics*, 62(1): 13–30.

Smith S. J. & Page F. H. (1996). Associations between Atlantic cod (*Gadus morhua*) and hydrographic variables: implications for the management of the 4VsW cod stock. *ICES Journal of Marine Science*, 53: 597–614.

Smith-Vaniz W. F. (1986). Carangidae. In: Whitehead P. J. P., M.-L. Bauchot, J.-C. Hureau, J. Nielsen, & E. Tortonese (Eds.), Fishes of the north-eastern Atlantic and the Mediterranean. Paris: UNESCO. vol. 2.815–844 pp.

Sokal R. R. & Rohlf F. J. (1995). Biometry. New York: W.H. Freeman and Company. 887 p.

Solomon S., Qin D., Manning M., Chen Z., Marquis M., Averyt K. B., Tignor M., & Miller H. L. (2007). Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge. United Kingdom and New York, NY, USA: Cambridge University Press. 996 p.

Somero G. N. (2002). Thermal physiology and vertical zonation of intertidal animals: optima, limits, and costs of living. *Integrative and Comparative Biology*, 42(4): 780–789.

Somot S., Sevault F., Déqué M., & Crépon M. (2008). 21st century climate change scenario for the Mediterranean using a coupled atmosphere-ocean regional climate model. *Global and Planetary Change*, 63: 112–126.

Soria F. N., Strüssmann C. A., & Miranda L. A. (2008). High water temperatures impair the reproductive ability of the pejerrey fish *Odontesthes bonariensis*: effects on the hypophyseal-gonadal axis. *Physiological and Biochemical Zoology*, 81(6): 898–905.

Sorte C. J. B., Jones S. J., & Miller L. P. (2011). Geographic variation in temperature tolerance as an indicator of potential population responses to climate change. *Journal of Experimental Marine Biology and Ecology*, 400(1-2): 209–217.

Steele M., Ermold W., & Zhang J. (2008). Arctic Ocean surface warming trends over the past 100 years. *Geophysical Research Letters*, 35(L02614): 1–6.

Stige L. C., Ottersen G., Brander K., Chan K.-S., & Stenseth N. C. (2006). Cod and climate: effect of the North Atlantic Oscillation on recruitment in the North Atlantic. *Marine Ecology Progress Series*, 325: 227–241.

Strüssmann C. A., Conover D. O., Somoza G. M., & Miranda L. A. (2010). Implications of climate change for the reproductive capacity and survival of New World silversides (family Atherinopsidae). *Journal of Fish Biology*, 77(8): 1818–1834.

Sudekum A. E., Parrish J. D., Radtke R. L., & Ralston S. (1991). Life history and ecology of large jacks in undisturbed, shallow, oceanic communities. *Fisheries Bulletin*, 89: 493–513.

Sumaila U. R., Cheung W. W. L., Lam V. W. Y., Pauly D., & Herrick S. (2011). Climate change impacts on the biophysics and economics of world fisheries. *Nature Climate Change*, 1: 449–456.

Swain D., Poirier G. A., & Sinclair A. F. (2000). Effect of water temperature on catchability of Atlantic cod (*Gadus morhua*) to the bottom-trawl survey in the southern Gulf of St Lawrence. *ICES Journal of Marine Science*, 57(1): 56–68.

Sylla S., Atse B. C., & Kouassi N. J. (2009). Stratégie de Reproduction du Carangidae *Trachinotus teraia* Cuvier, 1832 dans la lagune Ebrié (Côte d'Ivoire). *Sciences & Nature*, 6(1): 83–94.

Tanasichuk R. & Ware D. (1987). Influence of interannual variations in winter sea temperature on fecundity and egg size in Pacific herring (*Clupea herengus pallasi*). *Canadian Journal of Fisheries and Aquatic Sciences*, 44: 1485–1495.

Temming A., Floeter J., & Ehrich S. (2007). Predation hot spots: large scale impact of local aggregations. *Ecosystems*, 10: 865–876.

Tett S. F. B., Jones G. S., Stott P. A., Hill D. C., Mitchell J. F. B., Allen M. R., Ingram W. J., Johns T. C., Johnson C. E., Jones A., Roberts D. L., Sexton D. M. H., & Woodage M. (2002). Estimation of natural and anthropogenic contributions to twentieth century temperature change. *Journal of Geophysical Research*, 107(D16): 1–24.

Thorsen A., Witthames P. R., Marteinsdóttir G., Nash R. D. M., & Kjesbu O. S. (2010). Fecundity and growth of Atlantic cod (*Gadus morhua* L.) along a latitudinal gradient. *Fisheries Research*, 104: 45–55.

Tortonese E. (1986). Pomatomidae. In: Whitehead P. J. P., M. L. Bauchot, J. C. Hureau, J. Nielsen, & E. Tortonese (Eds.), Fishes of the Northeastern Atlantic and Mediterranean. Paris: UNESCO. 812–813 pp.

Tutman P., Glavić N., Kožul V., Skaramuca B., & Glamuzina B. (2004). Preliminary information on feeding and growth of pompano, *Trachinotus ovatus* (Linnaeus, 1758) (Pisces; Carangidae) in captivity. *Aquaculture International*, 12(4/5): 387–393.

Tzanatos E., Raitsos D. E., Triantafyllou G., Somarakis S., & Tsonis A. A. (2013). Indications of a climate effect on Mediterranean fisheries. *Climatic Change*, 122(1-2): 41–54.

Van der Veer H. W., Berghahn R., Miller J. M., & Rijnsdorp A. D. (2000). Recruitment in flatfish, with special emphasis on North Atlantic species: Progress made by the Flatfish Symposia. *ICES Journal of Marine Science*, 57(2): 202–215.

Vargas-Yáñez M., García J. M., Salat J., García-Martínez M. C., Pascual J., & Moya F. (2008). Warming trends and decadal variability in the Western Mediterranean shelf. *Global and Planetary Change*, 63(2-3): 177–184.

Vargas-Yáñez M., Moya F., García-Martínez M. C., Tel E., Zunino P., Plaza F., Salat J., Pascual J., López-Jurado J. L., & Serra M. (2010). Climate change in the Western Mediterranean Sea 1900–2008. *Journal of Marine Systems*, 82(3): 171–176.

Vargas-Yáñez M., Parrilla G., Lavín A., Vélez-Belchí P., & González-Pola C. (2004). Temperature and salinity increase in the eastern North Atlantic along the 24.5°N in the last ten years. *Geophysical Research Letters*, 31(L06210): 1–4.

Vargas-Yáñez M., Ramírez T., Cortés D., & Sebastián M. (2002). Warming trends in the continental shelf of Málaga Bay (ALBORÁN SEA). *Geophysical Research Letters*, 29(22): 1–4.

Vargas-Yáñez M., Salat J., Luz Fernández de Puelles M., López-Jurado J. L., Pascual J., Ramírez T., Cortés D., & Franco I. (2005). Trends and time variability in the northern continental shelf of the western Mediterranean. *Journal of Geophysical Research*, 110(C10019): 1–18.

Villegas-Hernández H., Lloret J., & Muñoz M. (2015a). Climate-driven changes in life-history traits of the bastard grunt *Pomadasys incisus* (Teleostei: Haemulidae) in the North-western Mediterranean. *Mediterranean Marine Science*, 16(1): 21–30.

Villegas-Hernández H., Lloret J., & Muñoz M. (2015b). Reproduction, condition and abundance of the Mediterranean bluefish (*Pomatomus saltatrix*) in the context of sea warming. *Fisheries Oceanography*, 24(1): 42–56.

Villegas-Hernández H., Muñoz M., & Lloret J. (2014). Life-history traits of temperate and thermophilic barracudas (Teleostei: Sphyraenidae) in the context of sea warming in the Mediterranean Sea. *Journal of Fish Biology*, 84(6): 1940–1957.

Walther G. R., Post E., Convey P., Menzel A., Parmesan C., Beebee T. J. C., Fromentin J.-M., Hoegh-Guldberg O., & Bairlein F. (2002). Ecological responses to recent climate change. *Nature*, 416(6879): 389–95.

Ware D. M. & Tanasichuk R. W. (1989). Biological basis of maturation and spawning waves in Pacific herring (*Clupea harengus pallasi*). *Canadian Journal of Fisheries and Aquatic Sciences*, 46: 1776–1784.

Wernberg T., Russell B. D., Moore P. J., Ling S. D., Smale D. A., Campbell A., Coleman M. A., Steinberg P. D., Kendrick G. A., & Connell S. D. (2011). Impacts of climate change in a global hotspot for temperate marine biodiversity and ocean warming. *Journal of Experimental Marine Biology and Ecology*, 400(1-2): 7–16.

Wilderbuer T. K., Hollowed a. B., Ingraham W. J., Spencer P. D., Conners M. E., Bond N. a., & Walters G. E. (2002). Flatfish recruitment response to decadal climatic variability and ocean conditions in the eastern Bering Sea. *Progress in Oceanography*, 55(1-2): 235–247.

Wilk S. J. (1977). Biological and fisheries data on bluefish Pomatomus saltatrix: Technical Series Report 11. Highlands, N. J.: U.S. National Marine Fisheries Service. 56 p.

Winemiller K. O. & Rose K. A. (1992). Patterns of life-history diversification in North American fishes: implications for population regulation. *Canadian Journal of Fisheries and Aquatic Sciences*, 49: 2196–2218.

Witthames P. R., Greer Walker M., Dinis M. T., & Whiting C. L. (1995). The geographical variation in the potential annual fecundity of dover sole *Solea solea* (L.) from European shelf waters during 1991. *Netherlands Journal of Sea Research*, 34(1-3): 45–58.

Witthames P. R., Thorsen A., Murua H., Saborido-Rey F., Greenwood L., Domínguez-Petit R., Korta M., & Kjesbu O. S. (2009). Advances in methods for determining fecundity: application of the new methods to some marine fishes. *Fishery Bulletin*, 107: 148–164.

Woodruff S. D., Worley S. J., Lubker S. J., Ji Z., Eric Freeman J., Berry D. I., Brohan P., Kent E. C., Reynolds R. W., Smith S. R., & Wilkinson C. (2011). ICOADS Release 2.5: extensions and enhancements to the surface marine meteorological archive. *International Journal of Climatology*, 31(7): 951–967.

Wootton R. J. & Fletcher D. A. (2009). Effect of spawning number and ration on reproductive performance of the batch-spawning three-spined stickleback *Gasterosteus aculeatus*. *Journal of Fish Biology*, 75(3): 618–629.

Wright P. J. & Trippel E. A. (2009). Fishery-induced demographic changes in the timing of spawning: consequences for reproductive success. *Fish and Fisheries*, 10(3): 283–304.

Zar J. H. (1996). Biostatistical Analysis. Upper Saddle River, NJ.: Prentice-Hall, Inc. 662 p.

APPENDIXES

Appendix 1: Box and Jenkins modelling strategy

The Box and Jenkins modelling strategy considers three steps: identify the model, estimate the coefficients and verify the model. These procedures apply to stationary series (time series with no systematic change in mean and variance) with data that are normally distributed. First- or second-order differencing (non-seasonal and/or seasonal) remedies non stationary mean, and logarithmic transformation remedies non-stationary variance and non-normal distributions of original data. All the time series were nearly stationary. In the same way that autocorrelation function was used to identify univariate ARIMA models, the data analysis tool employed for the identification of transfer function models is the cross correlation function between the input and output. Identification of the number of terms to be included in the model was based on the examination of the autocorrelation (ACF) and partial autocorrelation (PACF) functions of the differenced, log-transformed time series. The coefficients of the model were estimated by the maximum likelihood method. Verification of the model was done through diagnostic checks of residuals.

Verification of each univariate-ARIMA model was performed through diagnostic checks of the histogram and normal probability plots of residuals and the standardized residuals (which are found by dividing each residual by the residual standard deviation). For the transfer function models, the ACF and the PACF functions of the residuals (noise or disturbance) and the cross correlation functions involving input and residuals were examined. In case of evidence of transfer model inadequacy from the behavior of individual autocorrelations, autoregressive and/or moving-average parameters were fitted to noise and the iterative cycle of identification, estimation and diagnostic checking was repeated until a suitable model was found. A detailed description of the non-seasonal and seasonal ARIMA models and the standardized notation used in this paper is provided in Appendix 2.

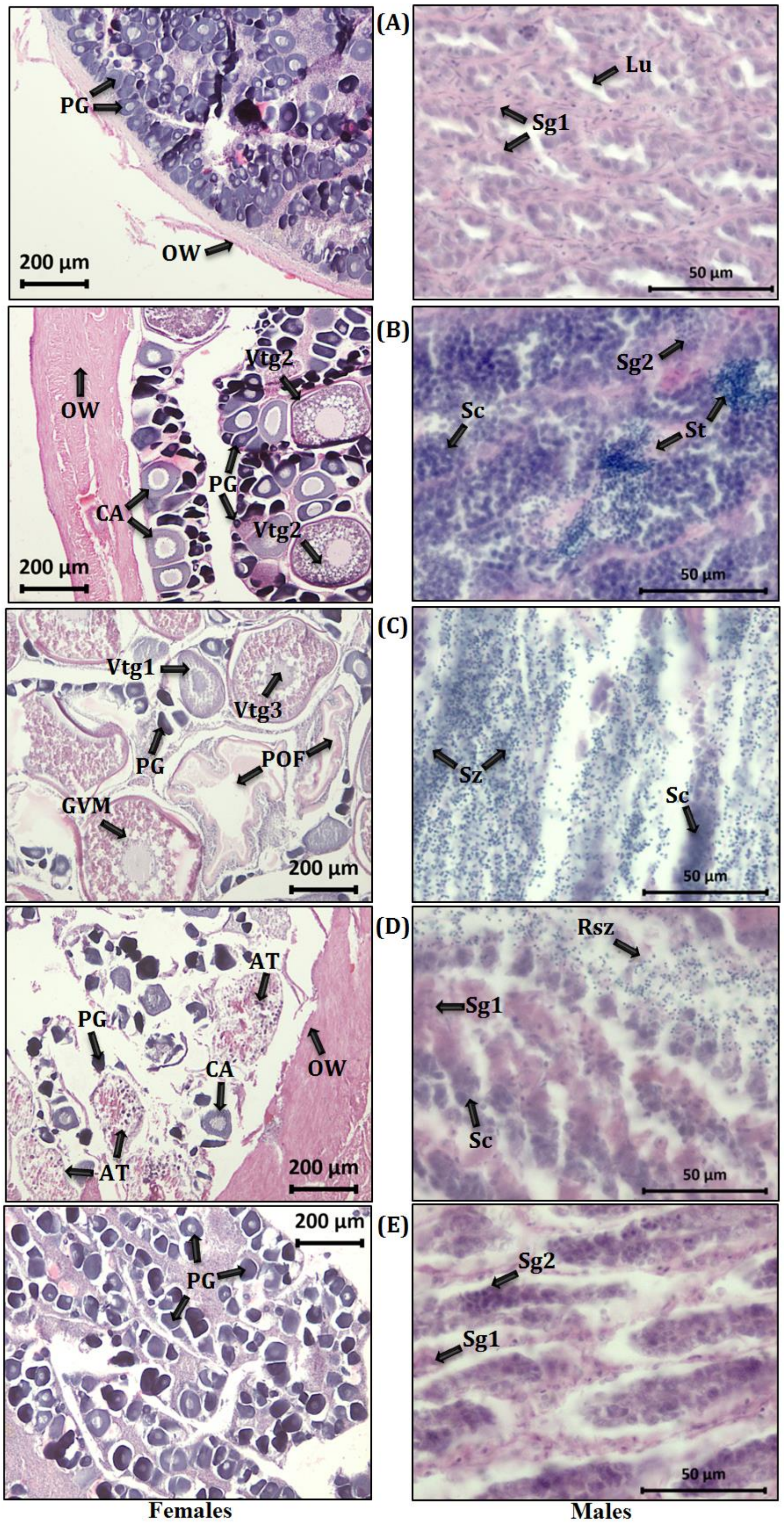
The residual standard error was used to compare the accuracy between the univariate-ARIMA and the transfer models obtained. It is important to notice that we were not interested here in forecasting catch using temperature variable, but only in assessing the role of the input variable (SST) in accounting for the variability of the output variable (catch). Therefore, we simplified the transfer function models as much as we could, neither differencing nor transforming logarithmically the raw data (all time series were nearly stationary), and allowing the random appearance of some outliers in the residuals of the models (diagnostic checking of residuals did not indicate any inadequacy; disturbance series were stationary and did not show any structure).

The bivariate transfer function models are expressed by the following general equation (Pankratz 1983, 1991): $Y_t = f(X_t) = v_0 X_t + v_1 X_{t-1} + v_2 X_{t-2} + \ldots a_t$, where coefficient v_0 is a weight that states how Y_t responds to a change in X_t (current month change in X_t); coefficient v_1 states how Y_t responds to a change in X_{t-1} (one month earlier change in X_t); coefficient v_2 states how Y_t responds to a change in X_{t-2} (two months earlier change in X_t), and so forth. The v weights can be positive or negative. Of course, the larger the absolute value of any weight v_k, the larger the response of Y_t to a change in X_{t-k}. The sum of these weights gives the total gain. Only significant coefficients at a t-value $>|2|$ ($P < 0.05$) were considered. The a_t are random shocks. Before fitting transfer function models, univariate ARIMA models (Box and Jenkins, 1976) were built for the local temperature factor and catch using the monthly data. There are several advantages to performing these preliminary analyses. Firstly, univariate time series models give a baseline model for the output series of the transfer function models. In particular, we can consider the transfer function residual standard errors and compare them with the residual standard errors of the ARIMA models for the output variables. Secondly, in the transfer function model testing stage, residuals from ARIMA models for the input series are needed at the checking stage of transfer function models.

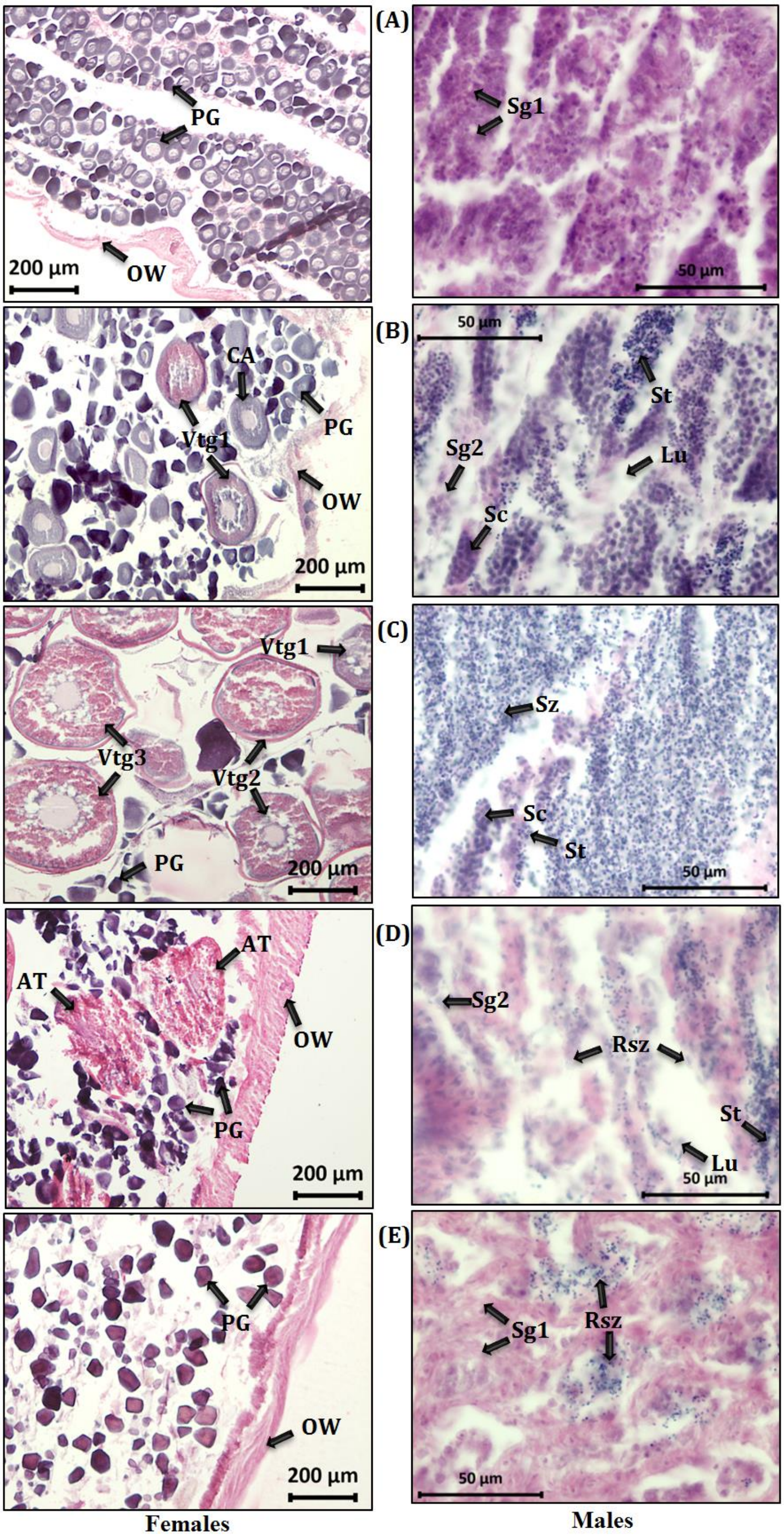
Appendix 2: Gonad photomicrographs

Photomicrographs of ovaries and testis of the studied species *s*howing the following reproductive phases: (A) immature, (B) developing, (C) spawning capable, (D) regressing, and (E) regenerating. Oocyte developmental stages are also shown as PG: primary growth, CA: cortical alveoli, Vtg1: early vitellogenic, Vtg2: mid-vitellogenic, Vtg3: advanced vitellogenic, AT: atretic, POF: post-ovulatory follicles, OW: ovarian wall. Germinal developmental stages are also shown as Sg1: primary spermatogonia, Sg2: secondary spermatogonia, Sc: spermatocyte, St: spermatid, Sz: spermatozoa, Rsz: residual spermatozoa, and Lu: lumen.

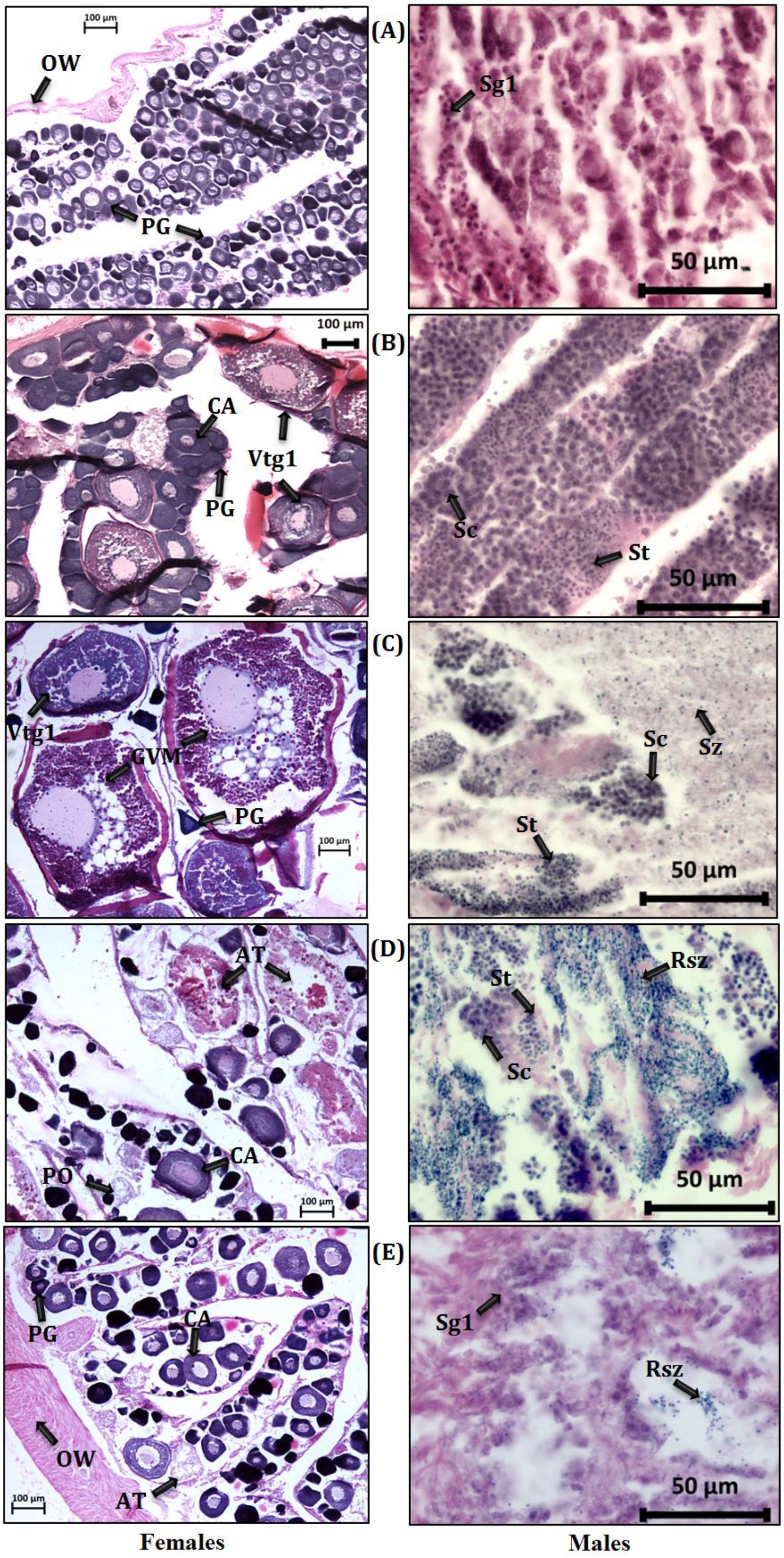
A2.1. Bluefish (*Pomatomus saltatrix*)



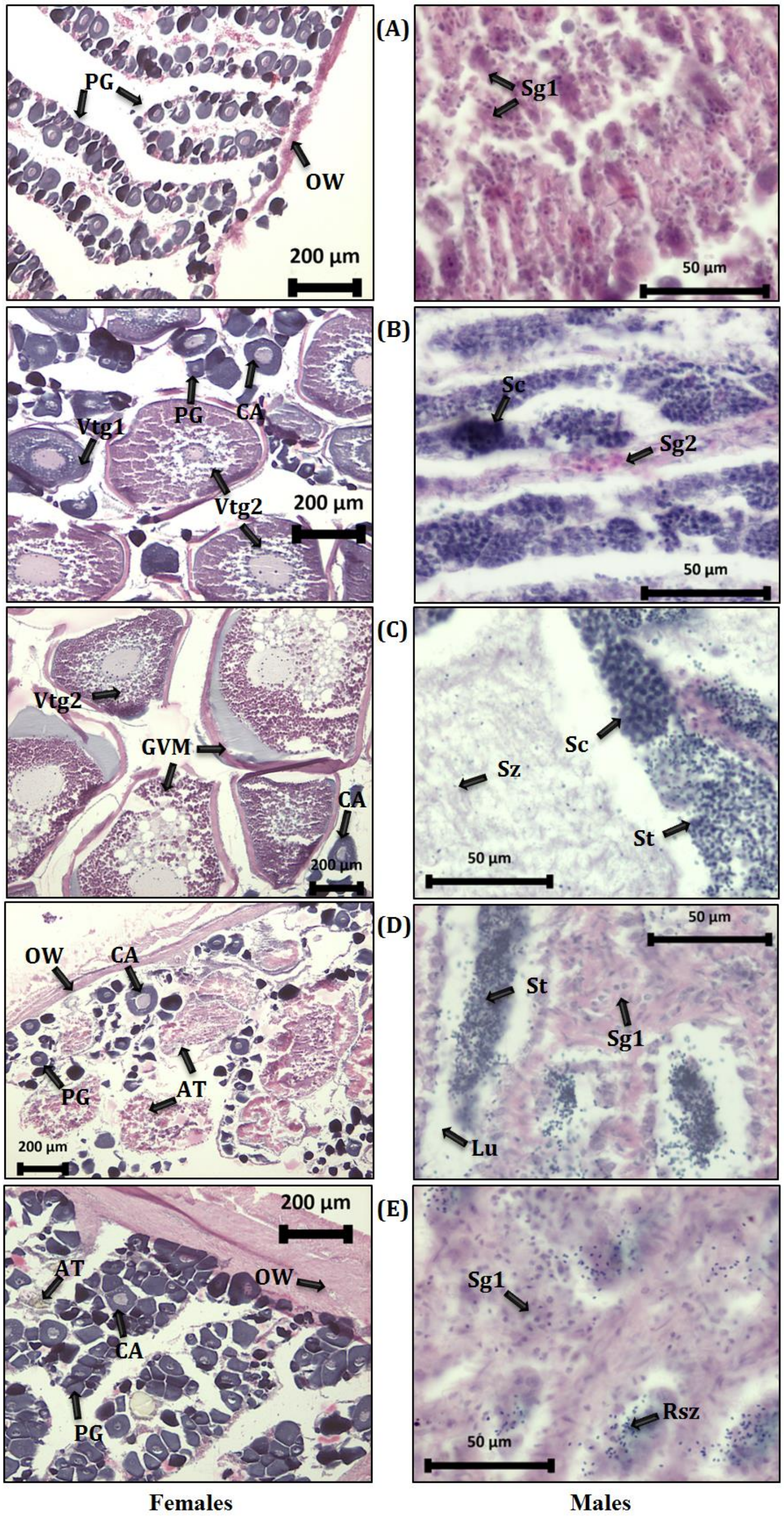
A2.2. Bastard grunt (*Pomadasys incisus*)



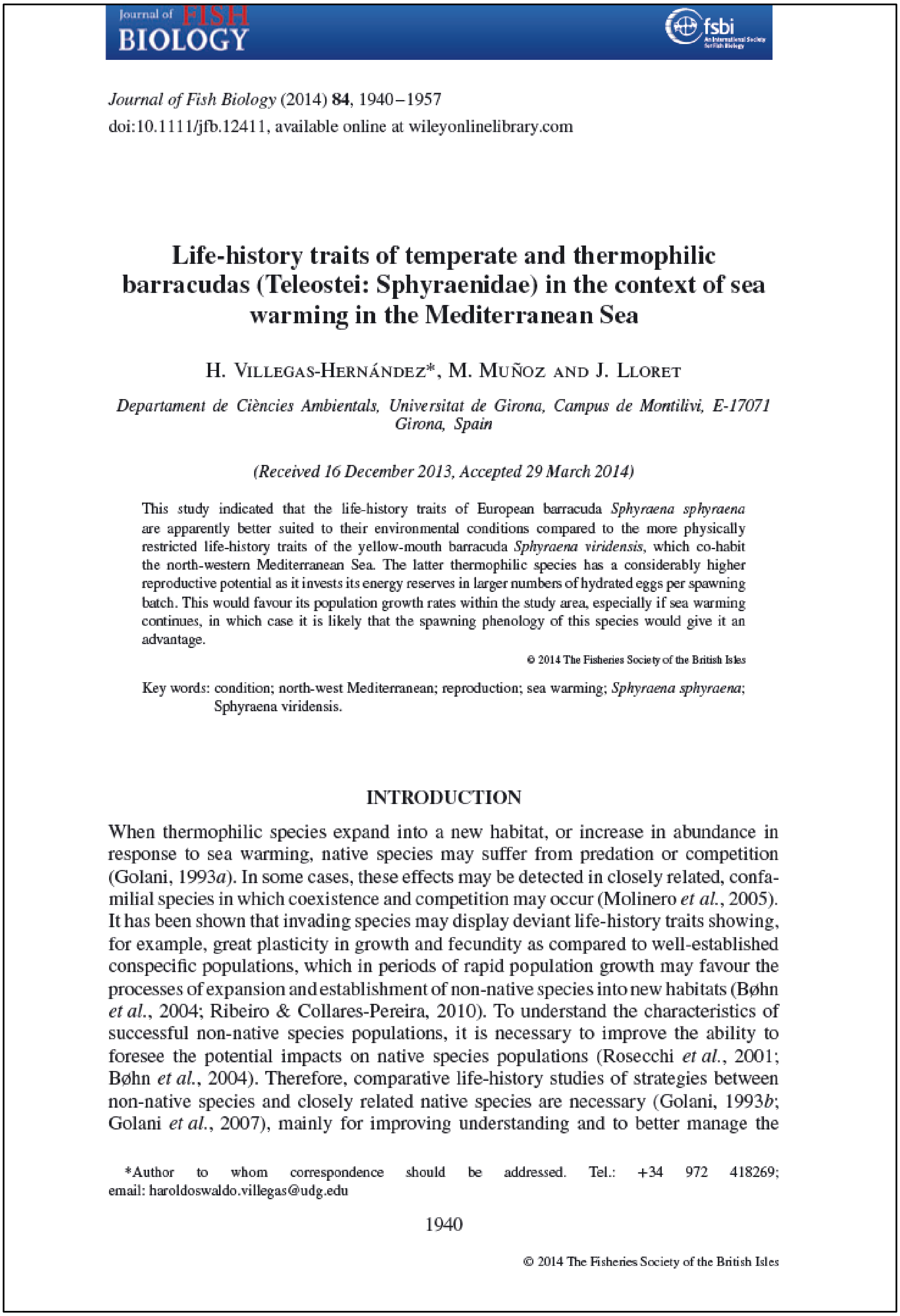
A2.3. European barracuda (*Sphyraena sphyraena*)



A2.4. Yellow-mouth barracuda (*Sphyraena viridensis*)



Appendix 3: Front pages of the articles published for this PhD thesis



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Life-history traits of temperate and thermophilic barracudas (Teleostei: Sphyraenidae) in the context of sea warming in the Mediterranean Sea

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This study indicated that the life-history traits of European barracuda *Sphyraena sphyraena* are apparently better suited to their environmental conditions compared to the more physically restricted life-history traits of the yellow-mouth barracuda *Sphyraena viridensis*, which co-habit the north-western Mediterranean Sea. The latter thermophilic species has a considerably higher reproductive potential as it invests its energy reserves in larger numbers of hydrated eggs per spawning batch. This would favour its population growth rates within the study area, especially if sea warming continues, in which case it is likely that the spawning phenology of this species would give it an advantage.

Key words: condition; north-west Mediterranean; reproduction; sea warming; *Sphyraena sphyraena*; Sphyraena viridensis.

INTRODUCTION

When thermophilic species expand into a new habitat, or increase in abundance in response to sea warming, native species may suffer from predation or competition (Golani, 1993*a*). In some cases, these effects may be detected in closely related, confamilial species in which coexistence and competition may occur (Molinero *et al.*, 2005). It has been shown that invading species may display deviant life-history traits showing, for example, great plasticity in growth and fecundity as compared to well-established conspecific populations, which in periods of rapid population growth may favour the processes of expansion and establishment of non-native species into new habitats (Bøhn *et al.*, 2004; Ribeiro & Collares-Pereira, 2010). To understand the characteristics of successful non-native species populations, it is necessary to improve the ability to foresee the potential impacts on native species populations (Rosecchi *et al.*, 2001; Bøhn *et al.*, 2004). Therefore, comparative life-history studies of strategies between non-native species and closely related native species are necessary (Golani, 1993*b*; Golani *et al.*, 2007), mainly for improving understanding and to better manage the

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Research Article

Climate-driven changes in life-history traits of the bastard grunt *Pomadasys incisus* (Teleostei: Haemulidae) in the north-western Mediterranean

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Abstract

This study evaluates the influence of sea water temperature on the life-history traits of the thermophilic bastard grunt *Pomadasys* incisus along the Catalan coast. We compared two key traits of this species, condition and reproduction, from populations in two separate areas with different thermal regimes: the Gulf of Roses (cold area) and the Ebre Delta (warm area). Specimens were collected monthly from each area between 2010 and 2012. The results were also compared with those given in the literature from sites where the species is more common, i.e. the southern Mediterranean and eastern Atlantic. Our findings indicate that, compared to the populations in warmer environments, the population inhabiting the colder waters appears to be in significantly poorer condition and there is some deviance in their life-history traits: egg size and quality being traded-off for higher egg numbers; lower lengths at maturity and alterations to spawning phenology. A certain degree of plasticity in life-history traits may favour the process of expansion and establishment of this thermophilic species into newly available but colder habitats of the north-western Mediterranean under a scenario of climate change.

Keywords: *Pomadasys incisus*, bastard grunt, condition, reproduction, sea warming.

Introduction

Sea warming is allowing northward expansion of thermophilic species in the Mediterranean (Francour *et al.*, 1994; Molinero *et al.*, 2005; Perry *et al.*, 2005; Sabatés *et al.*, 2006, 2012; Lloret *et al.*, 2014). It has been observed, in this context, that invading species may display deviant life-history traits showing, for example, great plasticity in growth and fecundity - as compared to well-established conspecific populations in other areas - which in periods of rapid population growth may favour the processes of expansion and establishment of these invading species in new habitats (Rosecchi *et al.*, 2001; Bøhn *et al.*, 2004; Ribeiro & Collares-Pereira, 2010). The extent of this plasticity in their life-history traits, which is a response to either fish density or environmental conditions, is dependent on adaptations to environmental variation which, in turn, are limited by the inherent physiological and behavioural characteristics of each fish species (Alcaraz & García-Berthou, 2007; Ribeiro & Collares-Pereira, 2010). In this sense, fish condition and reproduction are two key life-history traits that can help to characterize certain components of the environment in which fish exist and thus reveal changes - such as sea warming - in environmental conditions (Lloret *et al.*, 2002, 2012, 2014; Lloret & Planes, 2003; Pankhurst & King, 2010; Pankhurst & Munday, 2011).

The bastard grunt, *Pomadasys incisus* (Bowdich 1825), is a coastal demersal species inhabiting marine and brackish waters (Pajuelo *et al.*, 2003a), usually near sandy or muddy substrate, at depths between 10 and 100 m, although it is more commonly found not far from 50 m (Kapiris *et al.*, 2008). Its main distribution encompasses the eastern part of the Atlantic Ocean, from Angola to Gibraltar (including the Canary Islands, Madeira and the Cape Verde Islands). However, this subtropical and thermophilic species is currently spreading and establishing itself within the whole Mediterranean Sea (Bodilis *et al.*, 2013). This species naturally entered the Mediterranean Sea through the Strait of Gibraltar but the prevailing currents, sea warming and the availability of suitable soft substrate in relatively shallow waters has recently allowed *P. incisus* to establish itself in the north-western Mediterranean basin (Francour *et al.*, 1994; Pastor *et al.*, 2008; Bodilis *et al.*, 2013). *P. incisus* is an example of the latitudinal extensions and/or demographic increase of thermophilic fishes, which are taking advantage of the current climate change (Psomadakis *et al.*, 2012). In the Gulf of Roses and adjacent waters in particular (southern Gulf of Lyon), the bastard grunt has apparently become more frequent since the 1950s (Lloret *et al.*, 2011). However, landings statistics for this area are inexistent.

Information on the biology of *P. incisus* has so far been restricted to the Canarian Archipelago (Pajuelo *et al.*, 2003a, 2003b) and the Gulf of Tunis (Chakroun-Marzouk

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Reproduction, condition and abundance of the Mediterranean bluefish (*Pomatomus saltatrix*) in the context of sea warming

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ABSTRACT

This study evaluates the link between sea warming and three important aspects of the population dynamics of bluefish, *Pomatomus saltatrix*, in the north-western (NW) Mediterranean: condition (health measures), reproduction and abundance (as reflected in catch per unit effort, CPUE). We compared the bluefish populations from two areas with different thermal regimes: the Gulf of Roses and the Ebre Delta. First, in order to compare the condition and reproduction parameters of the two populations, specimens were collected from the commercial catch landed in two ports located in these areas. Several indicators of fish condition and reproduction such as hepatosomatic index, gonadosomatic index, maturation timing, length-at-first maturity, fecundity, egg quality and atresia (ovarian follicle resorption) were analysed and compared between study areas. Second, time series analyses of sea surface temperatures (SST) and monthly bluefish CPUEs in the two study areas were assessed using Box–Jenkins transfer function models. Our results indicate that bluefish benefit from sea warming in the NW Mediterranean, particularly in the northernmost zone, as evidenced by increasing fish condition in these waters. Sea warming may favour the changes in spawning phenology and the northward expansion of this species. This study provides evidence that a marine fish species that is able to expand or is forced to shift its distribution as a result of sea warming may take advantage of other environmental conditions of new habitats, contributing to the enhancement of the population's productivity in these areas.

Key words: fish condition, NW Mediterranean, *Pomatomus saltatrix*, predator, reproductive biology, sea surface temperature

INTRODUCTION

The Mediterranean Sea is a semi-enclosed basin where sea warming is likely to be more pronounced and to become apparent sooner than in other more open oceans (Astraldi *et al.*, 1995; Bethoux *et al.*, 1999; Walther *et al.*, 2002; Coll *et al.*, 2010). Climate models predict that the Mediterranean basin will be one of the regions that is most affected by the ongoing warming trend and by an increase in extreme events (Parry, 2000; Lejeusne *et al.*, 2010; Calvo *et al.*, 2011; Durrieu de Madron *et al.*, 2011). Subtropical species are found mainly in the eastern basin and southern Mediterranean, where water temperatures are higher, whereas cold-temperate species inhabit the cooler northern areas (Salat, 1996; Bianchi and Morri, 2000; Coll *et al.*, 2010).

A direct consequence of sea warming is a simultaneous increase in the abundance of thermo-tolerant species and the decline or disappearance of 'cold' stenothermal species (Lejeusne *et al.*, 2010). In a semi-closed system such as the Mediterranean basin these changes may cause the progressive homogenization of the marine biota, the dislocation of other species, the loss of endemic species coupled with invasion by non-indigenous species and/or cascade effects on food webs (Molinero *et al.*, 2005).

Not only could marine biodiversity be seriously affected, but climate change may also affect fisheries directly by influencing fish stocks and the global supply of fish for consumption. Commercial fishing would also be affected by changes to the overall value of fish catches owing to changes in the abundance of the species caught. The value of the total catch may decrease as warm water species – which can be of lower commercial value – increase at the expense of other species of greater commercial value, e.g., the increase of the thermophilic, low value *Sardinella aurita* (Sabatés *et al.*, 2006) versus the decrease of the temperate, high value *Engraulis encrasicolus* and *Sardina pilchardus* (Martín *et al.*, 2011).

The bluefish, *Pomatomus saltatrix*, (Linnaeus 1766), is distributed over continental shelves and in estuaries of temperate waters throughout most of the world, with the exception of the northern and mid-Pacific

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