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Published online: 10 Jun 2020.

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REVIEW

A Global Review on the Biology of the Dolphinfish (*Coryphaena hippurus*) and Its Fishery in the Mediterranean Sea: Advances in the Last Two Decades

Vicenç Moltó[a,b] , Pilar Hernández[c], Mauro Sinopoli[d], Amina Besbes-Benseddik[e], Raouf Besbes[e], Adriano Mariani[f], Miriam Gambin[g], Francisco Alemany[h,b], Beatriz Morales-Nin[a], Antoni María Grau[i], Juan Antonio Camiñas[j], José Carlos Báez[j,k], Marcelo Vasconcellos[l], Luca Ceriola[l], and Ignacio A. Catalán[a]

[a]IMEDEA, CSIC/UIB, Esporles, Illes Balears, Spain; [b]Instituto Español de Oceanografía, Centre Oceanogràfic de Balears, Moll de Ponent s/n, Mallorca, Spain; [c]Marine and Inland Fisheries Branch (FIAF). Fisheries and Aquaculture Department, Food and Agriculture Organization of the United Nations (FAO), Málaga, Spain; [d]Stazione Zoologica Anton Dohrn (SZN), Centro Interdipartimentale Della Sicilia, Integrative Marine Ecology Department, Palermo, Italy; [e]Institut National des Sciences et Technologie de la Mer (INSTM), Centre of Monastir, Tunisia; [f]Unimar, Roma, Italy; [g]Department of Fisheries and Aquaculture, Ministry for Agriculture, Fisheries and Animal Rights. Marsa, Malta; [h]International Commission for the Conservation of Atlantic Tunas, Madrid, Spain; [i]Marine Resources Service, Govern de Les Illes Balears, Palma, Mallorca, Spain; [j]Instituto Español de Oceanográfico, Centro Oceanogràfico de Málaga, Puerto Pesquero s/n, Fuengirola, Spain; [k]Facultad de Ciencias de la Salud, Universidad Autónoma de Chile, Providencia, Chile; [l]Marine and Inland Fisheries Branch (FIAF), Fisheries and Aquaculture Department, Food and Agriculture Organization of the United Nations (FAO), Viale delle Terme di Caracalla, Rome, Italy

ABSTRACT

The common dolphinfish (*Coryphaena hippurus*) is an epipelagic thermophilic species with a worldwide distribution in tropical and subtropical regions that is characterized by its migratory behavior and fast growth rates. This species is targeted by artisanal small-scale and recreational fisheries in most regions where it is found. This paper updates and analyzes the global scientific knowledge on the biology and ecology of this species, which was last revised at a regional level 20 years ago. This review showed an increase in knowledge about the population structure and regional differences in biological traits, in parallel with a notable lack of mechanistic and even empirical knowledge about the ecology of this species, which hampers a good understanding of the population dynamics and the potential impacts of environmental change. This paper also updates the information about the Mediterranean dolphinfish fishery, where the main four countries that exploit this species deploy 30% of fish aggregation devices (FAD) worldwide. The results suggest, among other effects, some temporal synchronicity in landings across countries, potential interannual stock movement affecting inter-country catches, diverging trends in prices and insufficient quality in the estimates of fishing effort. The authors propose a suite of specific measures to ameliorate this lack of knowledge and to better manage this complex living resource.

Introduction

The Coryphaenidae family is composed of two congeneric species, the common dolphinfish (*Coryphaena hippurus*, Linneaus 1758) and pompano dolphinfish (*Coryphaena equiselis*, Linnaeus 1758). Commonly called dolphinfish, they are highly migratory pelagic species, distributed circumglobally between the latitudes of 38°S and 46°N (Shcherbachev 1973). Their distribution and abundance are highly influenced by hydroclimatic conditions, especially temperature, with the 20 °C isotherm roughly marking their distribution limit (Gibbs and Collette 1959; Ditty et al. 1994), but they are more common in water temperatures between 21 and 30 °C (Maguire et al. 2006; FAO

2019). Pompano dolphinfish present oceanic behavior but may enter coastal waters, being mostly present over 24 °C, whereas the common dolphinfish is common in coastal waters in its juvenile life stage. Juvenile individuals of these species are difficult to differentiate, making it necessary to define the population identity in areas where they coexist. The overwhelming majority of fisheries of *Coryphaena* spp. worldwide target *C. hippurus*, thus this review focuses only on this species.

Commercial global captures of dolphinfish have increased over time, from less than 10k in the 1950s to approximately 100k metric tons from 2008 onwards (FAO 2019). Additionally, recreational fisheries on

this species are important and increasing in some areas (SAFMC 2003). Although no regular assessments exist for this species, there are no identified threats that could endanger the stability of the populations, and, thus, the IUCN Red List of Threatened Species has classified it as "least concern" (Collette et al. 2011). Furthermore, recent evidence shows that this globally distributed species has greater genetic structure than previously thought (Díaz-Jaimes et al. 2010), which calls for better information on biological traits and exploitation patterns at the relevant managerial scales. The last reviews on the biology of dolphinfish at the global scale date back approximately 30 years (Palko et al. 1982), and there is only one regional review for the western-central Atlantic, which was published 20 years ago (Oxenford 1999). In the case of the Mediterranean, most research on biology and fisheries was carried out throughout the 1990s and in the 2000s within two European projects (EU projects N° 95/073, 94/031 (DG XIV Fisheries)) and in the framework of a working group of experts from western and central Mediterranean called CORY-WG, which is driven by the FAO regional project "Coordination to Support Fisheries Management in the western and central Mediterranean" (CopeMed), initially funded by Spanish government. These early funding impulses enabled the description of the fisheries and the age and growth patterns as well as their reproductive characteristics. These initial works, together with other relevant studies around the world were compiled as a monograph 20 years ago (Massutí and Morales-Nin 1999).

The need to update biological knowledge, and compile and regionally compare key parameters for modeling the potential effects of fisheries and the environment on highly mobile and data-poor species such as *C. hippurus* is clear, and this review aims to contribute to meeting this need. The updating of the biological and ecological information of a widely distributed species, if it is to be useful in the context of sustainable management of the resource, should inform analytical tools that incorporate environmental and fisheries data at relevant regional scales where the technical peculiarities of exploitation of the resource are well known. Dolphinfish fishing exhibits large regional variation and is subject to multiple laws. Reviewing all fisheries is beyond the scope of this work. Most reviews on this topic are country- or sub-region-based, with few addressing basins/oceans (e.g., Arocha et al. 1999; Kojima 1964), and there are no reviews of the biology of the species in the Mediterranean, for which the last published updates

about the fishery are 20 years old (Morales-Nin et al. 2000).

Since that last review of Mediterranean fisheries, the CopeMed CORY-WG has been producing new information to assist the Scientific Advisory Committee (SAC) of the General Fisheries Commission for the Mediterranean (GFCM). Several reports were produced between 2000 and 2005 (http://www.faocopemed.org) and later (Camiñas and Fernández 2011), but no formal quantitative assessment has been possible with the available data. In 2006, the GFCM adopted a binding recommendation "on the establishment of a closed season for the dolphinfish fisheries based on fishing aggregation devices (FAD) from 1 January to 14 August of each year." This recommendation included a request to the SAC to analyze the impact of this measure on the stocks and to recommend any changes that may be necessary to improve its effectiveness following its implementation in 2010. In line with this work, in 2016, the Mediterranean experts on dolphinfish, including managers and scientists, gathered under the framework of phase II of the FAO-CopeMed project, and agreed to compile the existing information on Mediterranean dolphinfish to set the stage for the future assessment of this stock (Copemed II 2016). Furthermore, the GFCM has recently adopted a new recommendation (GFCM/43/2019/1) with a set of transitional management measures consistent with the precautionary approach to maintain the fishing effort and minimize the impact of FAD in the ecosystem. A research program will be launched at the Mediterranean regional level to provide the necessary scientific advice to the commission for the preparation of a regional management plan.

The abovementioned regional efforts inspired this review, which, in light of the mounting evidence that the Mediterranean populations may constitute a coherent management unit (Díaz-Jaimes et al. 2010; Sacco et al. 2017; Maggio et al. 2018), make the present work even more timely and useful. This review has been structured in two general parts. The first updates and reviews the biological and ecological characteristics of dolphinfish around the world. This section also describes and analyzes the environmental preferences, larval biology, ecology and recruitment, diet, age and growth, and reproductive processes. The second part, which is centered on Mediterranean dolphinfish fisheries, updates and compares the main fishing mechanisms and drivers of dolphinfish harvesting, based on exploitation statistics (captures and CPUE) and socioeconomic indicators, as well as stock assessment measures. In all cases, data and particularly detailed

additional information are presented in the form of tables or appendix to facilitate future investigations. Finally, a series of identified gaps and recommendations for future research are discussed.

Methodological approach

The review contains six formal sections covering the main aspects of the biology of the species, and the fisheries in the Mediterranean. Each section analyzes the existing or newly compiled information, with emphasis on new findings and identified knowledge gaps in the last 20 years. To compile information on dolphinfish biology around the world and its Mediterranean fisheries, both indexed citation journals and gray literature were used. For the indexed journals, the keywords *dolphinfish*, *Coryphaena hippurus*, and/or *larvae*, *age and growth*, *reproduction*, *diet* and *fisheries* were introduced in the search engines SCOPUS and ISI Web of Knowledge. Gray literature that included all ICCAT and FAO reports, as well as regional governmental studies, was also consulted.

Temperature-related habitat ranges for different life stages were analyzed using presence/absence data, which were mostly obtained from the Global Biodiversity Information Facility (GBIF.org 2018) and complemented with bibliographic data, yielding 7717 validated records that included information on geographical coordinates, year and month. Sea surface temperature (SST) data (1° resolution), downloaded from Met Office Hadley Center (Dataset ID: erdHadISST) were assigned to these records. The gonadosomatic index values used to explore reproductive patterns were extracted from the literature and related to the average SST obtained from NASA (https://giovanni.gsfc.nasa.gov/giovanni), using monthly averages at 4 km resolution over areas specified in the corresponding works. In the case of old literature, that lack satellite products, a 10 year (2002–2012) monthly average of SST was used as a proxy. The trophic levels of different-sized dolphinfish were calculated through TrophLab (Pauly et al. 2000) using diet data from the literature. For the fisheries analysis in the Mediterranean, the information on fleet characteristics was aggregated in different strata considering the geographical and fleet characteristics, following the criteria in FAO-CopeMed (2003). The time series of captures or total annual production data were obtained from the CORY project (Morales-Nin 2003) or provided by the official statistics of the different Mediterranean countries. Where available, the relevant administration of each country provided data

on the catch per unit effort (CPUE, kg/trip). The R statistical software (R Core Team 2019) was used for data visualization.

Distribution and environmental preferences of the species

The dolphinfish is an oceanic epipelagic species inhabiting the surface waters of coastal areas above continental shelves, where it is relatively abundant, but it is also well adapted to the open ocean, where it is frequently observed in surface waters of the abyssal plain (Gibbs and Collette 1959; Kojima 1964; Potthoff 1971; Shcherbachev 1973; Palko et al. 1982). SST is a dominant factor for adult and juvenile presence, with most records in all seas ranging from 17 to 30 °C, with median values of approximately 28 °C and some occasional observations below 15 °C or over 30 °C (Figure 1). Larvae have a more restricted thermal range from approximately 19–30 °C (see the corresponding section), and the described preferred global temperatures range between 23 °C and 29 °C (Norton 1999; Martínez-Rincón et al. 2009; Marín-Enríquez and Muhlia-Melo 2017; Marín-Enríquez et al. 2018). The Mediterranean data fit into this general description, with the lowest temperature for dolphinfish presence at 16 °C (Massutí and Morales-Nin 1995), although the median values are lower than in other areas, at approximately 25 °C (Figure 1). At the regional scale, other environmental factors are known to affect their distribution. These factors include food availability, water column stability, current flow, wind regime, bottom topography, and configuration of the coasts (Belvèze and Bravo de Laguna 1980). Nevertheless, the few existing species distribution models depict temperature as the main forcing variable, followed by surface chlorophyll (Farrell et al. 2014).

Dolphinfish are typically associated with floating objects. For instance, the occurrence of dolphinfish in the central Atlantic Ocean depends on the presence of sargassum (*Sargassum natans* and *Sargassum fluitans*) (Dooley, 1972). This suggests the use of floating algae both as a shelter against predators (such as tuna, sharks, marlins, swordfish, etc.) and as a source of food, as some of the prey species are associated with floating algae (Rose and Hassler 1974; Oxenford and Hunte 1999). Dolphinfish associated with floating objects spend more than 95% of their time in the first ten meters below the sea surface, while specimens not associated with floating objects have more diverse vertical behavior, displaying sporadic excursions to depths down to 160 meters, but staying at
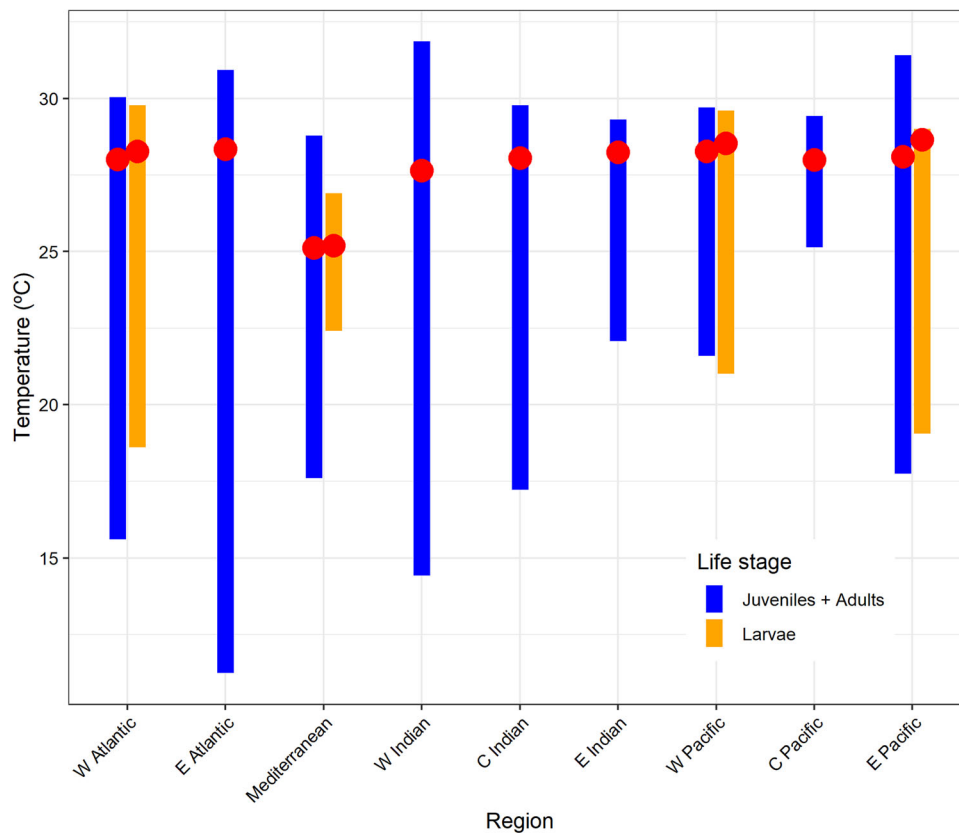
Figure 1. Field-derived temperature ranges (bars) and median values (dots) for dolphinfish (*Coryphaena hippurus*) larvae and juvenile + adult stages. Most data were obtained from the Global Biodiversity Information Facility (GBIF.org 2018). Data from the Mediterranean were obtained from Alemany et al. (2006); Koched et al. (2011) and unpublished data from the authors. Data were sorted by oceans and regions where dolphinfish subpopulations have been recorded (Díaz-Jaimes et al. 2010).

temperatures not beyond 3 °C than the uniform-temperature surface layer (Whitney et al. 2016).

Migration patterns and drivers

Temperature is a major trigger for dolphinfish movements; temperatures below 20 °C limit metabolism and growth (Martínez-Rincón et al. 2009), whereas temperatures over 28 °C tend to be suboptimal and promote migration (Norton 1999). Nikolsky (1963) and Harden Jones (1968) suggested that factors including physical variables, nutrition and reproduction could drive migration movements. Palko et al. (1982) reported that the movements of floating objects in the open sea could partly explain the migration and movements of dolphinfish. Other hypotheses consider pre-spawning and trophic needs to partly explain these spatial dynamics (Benetti et al. 1995). Several recent works have demonstrated the existence of defined sub-regional migration patterns, including the eastern Pacific off of Mexico and the Baja California Peninsula (Zúñiga-Flores et al. 2011; Marín-Enríquez et al. 2018) and in the western-central Atlantic (Merten et al. 2014a, 2014b, 2016). These studies used satellite tags and mark-recapture data to show the

linear distance migrations of up to approximately 2000 km (e.g., Merten et al. 2016) and showed how cyclical annual movements can occur among largely distant areas spanning several jurisdictions. Despite these studies, the data on movement for this species are restricted to few areas.

At the extremes of its latitudinal distribution, such as the Mediterranean, the migration patterns of the dolphinfish are particularly relevant, as they may explain the seasonality of catches and among-country catch dynamics. The officially reported captures and fisheries-independent observations are mainly centered around the Balearic Islands in the western sub-basin (Iglesias et al. 1994; Massutí and Morales-Nin 1995), Sicily (Potoschi et al. 1999), Malta (Galea 1961; Vella 1999) and Tunisia (Besbes Benseddik et al. 1999; Zaouali and Missaoui, 1999) in the central Mediterranean; and Libya (Ben-Abdallah et al. 2005) in the eastern sub-basin. A key knowledge gap exists in the identification of other Mediterranean areas where the species may occur. Massutí and Morales-Nin (1995) reported adult dolphinfish in the Mediterranean between May and December when the surface water temperature exceeds 16–18 °C. These

authors suggested genetic migration occurs from the Atlantic to the Mediterranean through the Strait of Gibraltar, in a similar manner to that of bluefin tuna (*Thunnus thynnus*); adults penetrate into the Mediterranean Sea following the Atlantic surface current (Millot 1987; López-Jurado et al. 2008), which coincides with the spawning season of these species. This hypothesis has not yet been confirmed. In the Mediterranean, adults are observed in the open sea, where they are captured as bycatch by longlines between spring and autumn (Massutí and Morales-Nin 1995; Macías et al. 2012). In contrast, age-0 specimens are frequently found between July and December, when the temperature exceeds 24–25 °C, which is associated with the occurrence of natural and anthropogenic floating objects, especially in coastal regions (Massutí and Morales-Nin 1995; Besbes Benseddik et al. 1999; Deudero et al. 1999; Massutí et al. 1999; Andaloro et al. 2007; Sinopoli et al. 2012). Therefore, several authors consider these coastal areas nursery habitats for a few months until December, when fish leave the region, as the water temperatures decrease below 18 °C (Galea 1961; Iglesias et al. 1994; Massutí and Morales-Nin 1995; Besbes Benseddik et al. 1999; Vella 1999; Andaloro et al. 2007). It is during the juvenile phases, at the end of summer and autumn, when coastal artisanal vessels intensively exploit the species.

Early stage biology, ecology and recruitment

Biomass fluctuations in short-lived species such as dolphinfish are highly dependent on recruitment (Fréon et al. 2005; Ruiz et al. 2013). The meristic characteristics and morphology of the different stages of the eggs and larvae have been exhaustively described (Mito 1960; Ditty et al. 1994; Moser 1996; Alemany and Massuti 1998; Ditty 2001; Alemany et al. 2010; Rodríguez et al. 2017; Perrichon et al. 2019). This species has been the object of aquaculture interest since the 1970s, which has allowed the generation of the first laboratory-derived data about the early life stages (Kraul 1989). The recent oil spill in the Gulf of Mexico has boosted the experimental research on the direct and interactive effects of oil on several aspects of the physiology and development of this species, including effects on cardiac muscle, sensory development, oxygen consumption or mortality of larvae and juveniles. This led to the compilation of a life table that condenses much of the experimental knowledge on the morphology, physiology, behavior and molecular biology of dolphinfish throughout its development (Perrichon et al. 2019). Further studies have analyzed the effects of climate

change on the early life stages. Pimentel et al. (2014) showed that the increased acidification projected by the end of the century would reduce the oxygen consumption rate by up to 17%, swimming duration by 50% and orientation frequency by 62.5%. The mass specific respiration (nmol O_2 µg M^{-1} h^{-1}, where Md is µg of fresh mass) based on this paper shows values of 0.1015 (Peck and Moyano 2016). Bignami et al. (2014) showed significant positive temperature-dependent effects of the projected acidification on growth and otolith at size, and negative effects on swimming velocity. All these data may be biased because they refer to particular stocks or derive from single-factor experiments. As recognized in Catalán et al. (2019), it is necessary to compare data from populations in different areas to account for phenotypic or genetic adaptation, and to analyze interactions between experimental drivers.

The compiled field data show that larvae are present in a narrower thermal range than adults and juveniles. The temperature records are concentrated between 18 °C and 30 °C (Figure 1), which is clearly linked with the reproductive data (see reproduction section). Previously published data show that individuals are present throughout the warm season regardless of the region of origin (see Table 1), varying in each ocean to adapt to approximately these ranges. The seasonal pattern of larval occurrence has been described for the western Atlantic (Ditty et al. 1994; Kitchens and Rooker 2014), coinciding with further records by other authors (Wells and Rooker 2009; Habtes et al. 2014). These patterns have also been described in non-tropical areas of the western Pacific (Ozawa and Tsukahara 1971; Yoo et al. 1999; Huh et al. 2013; Park et al. 2017), the central Pacific (Hyde et al. 2005), the eastern Pacific (Norton 1999; Sánchez 2008) and E-SW Australia (Kingsford and Defries 1999). The few published larval records in the Mediterranean Sea come from the NW and central Mediterranean and were captured in spring and early summer. Most records correspond to recently hatched larvae (3.25–4.95 mm standard length (SL)), which have been captured at very low densities in the Balearic Islands (Alemany and Massuti 1998; Alemany et al. 2006; García and Alemany 2011), in the Adriatic Sea (Dulčić, 1999) and on the eastern coast of Tunisia (Koched et al. 2011). There were additional larval records used in Figure 1, all of which were collected in the NW Mediterranean (Alemany, unpublished).

Despite the rapid increase in the available molecular and toxicological information of this species, there is a need to increase the amount of data on physiology, behavior and field-derived information (other

Table 1. Published dolphinfish larvae records including environmental ranges, if available.

Region	Year	Sampling gears	Sampling methodology	Larvae length range (mm SL)	Quantitative info	Season	Temperature range (°C)	Salinity range	References
Mediterranean	1985-1995	Bongo, WP2 and Juday Bogoroff nets	Oblique, vertical and horizontal tows	3.25-4.80	4 larvae	June			Alemany and Massutí (1998)
Mediterranean	2006	Bongo 40; 333 µm mesh size	Oblique tows from 100 m depth to surface		19 larvae; 0.98±3.55 larvae/1000m³		22.4-24.2	37.5-37.94	Alemany et al. (2006)
Mediterranean	2001-2005	Squared Bongo 90; 500 µm mesh size	Surface tows		16 larvae	June-July			García and Alemany (2011)
Mediterranean	1998	Hensen biconical net; 73 cm mouth diameter; 0.333 µm mesh size		4.75-4.95	2 larvae	August			Dulcic (1999)
Western Atlantic	1982-1986	unmetered neustonic net; 1 × 2 m mouth; 0.947 mm mesh size and Bongo 60 0.333 µm mesh size	Surface 10 min tows for neuston net and oblique tows from 200m depth to surface	3.5-15	25 larvae	April-November	>=24 (90% larvae)	>=33ppt (>=75% larvae)	Ditty et al. (1994)
Western Atlantic	2009-2011	Bongo 61; 0.335mm mesh size; Neuston 1 × 2 m mouth; 0.950 mm mesh size; S10 1 × 2 m mouth; 0.505 mesh size. Occasionally MOCNESS 1 m mouth, 9 500 µm mesh size nets		Between 4 and 8mm body length	607 with S10 net; 84 with bongo net; 82 with neuston net. <0.01 larvae/ m³ in each case	Late April-May, some years extended to July			Habtes et al. (2014)
Western Atlantic	2007-2010	Paired neuston nets 2 × 1 m mouth; 500 and 1200 µm mesh sizes		Mean: 7.8	1145 dolphinfish larvae; Densities: 0.4-1.6larvae/ 1000m3; mean 0.73larvae/1000m³	summer season		Associated with high salinities	Kitchens and Rooker (2014)
Western Atlantic	1993-2007	Bongo 61; 333 µm mesh size			9% presence across 1632 stations across the northern Gulf of Mexico				Lindo-Atichati et al. (2012)
Western Atlantic	2003-2004	MOCNESS 4m² mouth; 1000 µm mesh size and 1m² mouth; 150um mesh size simultaneously samplers. Combined neuston nets 1x2m² mouth;			1.28 larvae/1000m³				Richardson et al. (2010)

(Continued)

Table 1. Continued.

Region	Year	Sampling gears	Sampling methodology	Quantitative info	Larvae length range (mm SL)	Season	Temperature range (°C)	Salinity range	References
Western Atlantic	2007-2008	1000 μm mesh size attached with 0.5 × 1 m mouth; 150 μm mesh size 2 neuston nets 2 × 1 m mouth; 500 and 1200 μm mesh sizes				June and July			Wells and Rooker (2009)
Western Pacific	2001-2012	RN 80 net					23.7 in July 2011		Huh et al. (2013)
Western Pacific	1981-1983	net with 0.5 m^2 mouth; 500 μm mesh size		7 larvae	Larvae from preflexion under 5mm notochord to 20mm	From summer to autumn			Kingsford and Defries (1999)
Western Pacific	1983/1989	net with 0.39 m^2 mouth; 500 μm mesh size		24 larvae in 1983 and 14 larvae in 1989	Larvae from preflexion under 5mm notochord to 20mm	Austral summer and autumn			Kingsford and Defries (1999)
Western Pacific	1990	net with 0.39 m^2 mouth; 500 μm mesh size	Depth stratified tows from 30m to surface	5 larvae	Larvae from preflexion under 5mm notochord to 20mm				Kingsford and Defries (1999)
Eastern Pacific	1956-1984			<1000 larvae in 29 yr.					Norton (1999)
Western Pacific	1968	net with 1.6 m diameter; 500 μm mesh size	2kn 10min	Between 5 and 10		May - June			Ozawa and Tsukahara (1971)
Western Pacific	1996-1997			1 larva		Sept. 96, Nov. 96, Feb. 97, May 97			Yoo et al. (1999)
Western Atlantic	2011	Neuston net 1 × 2 m mouth; 0.947 mm mesh size; S10 1x2m mouth 0.505 μm mesh size	2kn 10min		eggs	20 - 22 April			Leyva-Cruz et al. (2016)
Central Pacific	2003	1.8 Isaacs-Kidd Trawl (0.505 μm mesh size) or a 1.5 m diameter ring net fitted with PVC cod-end 0.505 μm mesh size		8 eggs	eggs	May			Hyde et al. (2005)
Central Pacific	2004	1.8 Isaacs-Kidd Trawl (0.505 μm mesh size) and 1.5 m diameter ring net fitted with PVC cod-end 0.505 μm mesh size			eggs	July			Hyde et al. (2005)

Location	Year	Gear	Sampling method	Sample	Developmental stage (size)	Season	Temperature	Reference
Eastern Pacific	1990-1996	Bongo 1000 and 500 μm mesh size; cylindroconical net 500 μm mesh size	Surface tows at 3.5 kn 15 min	167 larvae	108 preflex (2.8-4.2), 15 flex (4.4-5.7); 20 postflex (5.9-8), 12 transformation (8.3-13.3), 4 juveniles (14-48)	Spring - Autumn	27-29	Sánchez (2008)
Western Atlantic	1974	2 × 1 m mouth net with 505 and 707 μm mesh size		Aquaculture experiment: 280 eggs fished from the field		From March to September	24-29; mean: 27 ± 1	Hassler and Rainville (1975)
Eastern Pacific 1987-1990; 1998-2000		Neustonic MANTA type net 15 × 86 cm mouth; 333 μm mesh size	Surface tows at 0.77 m/s 15 min	298 larvae		July - December. Warm season		Ortiz (2013)
Western Pacific	1953-1954			8 eggs	eggs		22	Mito (1960)
Western Pacific	1953-1954			5 eggs	eggs		29.6	Mito (1960)
Western Pacific	1953-1954			3 eggs	eggs		21	Mito (1960)
Indian				1 larva			22.2 - 25.3	Scherbachev (1973)
Western Pacific	2011	RN 80 net; 80 cm mouth; 0.33 mm mesh size	Surface tows during day at 2 - 3 kn during 10 min	42 larvae	3.5 notochord length - 14.7 Total length	July and September	31.2 - 33.4	Park et al. (2017)
Mediterranean	2008	Bongo 60,335 μm and 505 μm mesh sizes		2 larvae		June - July	mean = 37.35 ± 0.2	Koched et al. (2011)
Western Atlantic		Long handled dipnets of 5 mm mesh size, fish attracted with 200W light				Year round		Lao (1989) in Oxenford (1999)
Western Atlantic	1955					April-May		Oxenford et al. 1995
Western Atlantic	1988	Neuston sampler. 1 × 0.5 m mouth; 1.27 mm square mesh		84 larvae		April-May	mean = 24.44 ± 1.16	Hunte et al. 1995

than temperature) to build robust models for understanding the ecology of early stages. In the Gulf of Mexico, Kitchens and Rooker (2014) identified a significant association of larvae with frontal areas with higher salinities and (relatively) cooler temperatures, but this kind of information is virtually absent for other areas, including the Mediterranean, and is much needed in the framework of assessing environmental effects on species dynamics.

Diet, competition and predation

The reviewed information regarding the *C. hippurus* diet is summarized in the Table 2. The Pacific Ocean is the richest region for contributions about dolphinfish diet, with a total of 13 publications, while the Atlantic and Mediterranean Sea are represented by six publications, and Indian Ocean (Arabian Sea) is represented by four.

Diet composition

The common dolphinfish is as an active and opportunistic top predator even in early life stages. Finfish were present in 100% of the studies analyzed and represented 63.4–75.1% (either in number or in weight percentage) of the prey present in stomach contents (Figure 2a). The flying fish (Exocoetidae), which was cited in 48.3% of the publications reviewed, is the most commonly ingested finfish and was present in all dolphinfish diets worldwide (Figure 2b), although its presence in the stomach contents of dolphinfish from the Arabian Sea and Mediterranean Sea was considerably lower than that in the other oceans (<5%). The presence of this epipelagic prey confirms the intensive use of surface waters. Despite early studies hypothesizing that the dolphinfish actively selects flying fish (Gibbs and Collette 1959; Rose and Hassler 1974), formal analyses of this selectivity do not exist, and the general consensus is that it is an opportunistic feeder (Oxenford and Hunte 2015a; Varghese et al. 2013; Besbes Benseddik et al. 2015; Varela et al. 2017), although temporal, geographical and size bias may exist (see next subsection). Other relatively frequently consumed fish comprise the order Clupeiforms, mainly the Clupeidae and Engraulidae families (37.9% of reviewed literature), small Carangidae (27.6%) and Scombridae (27.6.0%). These families are almost exclusively pelagic and often represent the penultimate level of the pelagic trophic web (Stergiou and Karpouzi 2001). Their importance in the diet of large pelagic species has been previously reported (Fromentin and Powers 2005; Nikolic et al. 2017). Tetraodontiform fish (mainly Monacanthidae and Balistidae) were are also

represented in 31.0% of reviewed literature. Although individuals of these families are normally necto-benthonic, they are also associated with sargassum mats and with natural or anthropogenic floating objects, such as FAD (Dempster and Taquet 2004; Andaloro et al. 2007; Sinopoli et al. 2011). This led to the hypothesis that dolphinfish forage near the floating objects (Castriota et al. 2007), which has been strengthened by the presence of sargassum in stomach contents (Rose and Hassler 1974; Manooch et al. 1984; Oxenford and Hunte 1999; Varghese et al. 2013; Brewton et al. 2016). Nevertheless, other benthic fish present in the dolphinfish diet could be incorporated during the pelagic stages of their life cycle, including juvenile Mullidae (*Upeneus besasi*) (Sakamoto and Taniguchi 1993) or the flying gurnard (*Dactylopterus volitans*) (Oxenford and Hunte 1999). Adult benthonic fish (Sparidae, Congridae, Mugilidae and Dactylopteridae) found in the stomach contents of Tunisian dolphinfish (Besbes Benseddik et al. 2015) could be attributed to direct foraging on the seabed underneath FAD located in coastal and shallow waters, where dolphinfish have been caught.

Crustaceans appeared in 44.8% of the literature and contributed from 10.9% up to 31.2% (either in number or in weight percentage) of the *C. hippurus* diet, although most individuals could not be identified. These figures are similar in other large pelagic fishes, playing a role in opportunistic feeding (Fromentin and Powers 2005; Torres-Rojas et al. 2014; Nikolic et al. 2017). Cephalopods account for 4.5–13.1% of the dolphinfish diet (either in number or weight percentage), and for crustaceans, a large number of unidentified individuals have been documented. This group appeared in 34.5% of the literature on diet; hence, the relative contribution to the diet is low compared to other pelagic fish predators (see references above). This is probably due to the surface habits of the dolphinfish, which would reduce the probability of encountering cephalopods that tend to live at greater depths.

Variation of diet across scales, ontogeny and sex

The dolphinfish uses different visual and active feeding strategies (Nunes et al. 2015). The data on feeding activity suggest a preference for day-time feeding (Massutí et al. 1998), although a small proportion of night-time feeding was initially suggested based on the presence of some mesopelagic prey species that undergo daily vertical migrations (Massutí et al. 1998; Oxenford and Hunte 1999). This was later confirmed through the analysis of diel feeding periodicity (Olson and Galván-Magaña 2002).

Table 2. Published diet composition of dolphinfish.

Region	Location	Year	Sampling gear	FAD	Sex (M-F)	N	Length range*	Type	Main prey (Type and taxonomic family)	W, N, V**	Size	Sex	Region	Season	References
Mediterranean Sea	Balearic Islands (Spain)							Fish	Exocoetidae, Clupeidae, Engraulidae, Carangidae						Cabo (1961)
Mediterranean Sea	Malta	1974		FAD	169-251	20***	22.2-54.5	Fish	Exocoetidae, Scombridae, Carangidae, Small C. hippurus	NR					Bannister (1976)
Mediterranean Sea	Mallorca Island (Spain)	1990-1991	PS, LL	20-60 FAD		316	14-117	Invertebrates, Fish	Crustaceans, Exocoetidae, Clupeidae	65NI; 45 NI	Yes				Massuti et al. (1998)
Mediterranean Sea	Mallorca Island (Spain)	1995-1997	PS	FAD		235	24.7-70	Invertebrates, Fish	Crustaceans (Decapoda)						Deudero et al. (2001)
Mediterranean Sea	Sicily (Italy)	1994-1995		FAD	138-162	300	11-72 SL	Fish	Myctophidae juveniles, Sparidae, Engraulidae	47N; 44N	Yes	Yes	Yes		Castriota et al. (2007)
Mediterranean Sea	Gulf of Hammamet (Tunisia)	2010		FAD		178	18-82	Invertebrates, Fish, Invertebrates	Crustaceans (Hyperiidae), Clupeidae, Engraulidae, Crustacea (Penaeus kerathurus)	74.1N; 25.0N	Yes				Besbes Benseddik et al. (2015a)
North-Western Atlantic	Hatteras (North Carolina, U.S.)	1961-1964	RR			373	45-127	Fish	Exocoetidae, Scombridae, Carangidae, Monacanthidae	85 W					Rose and Hassler 1974
North-Western Atlantic	Morehead City (North Carolina coast)	2002-2004	RF			527	24-170 TL	Fish	Exocoetidae, Balistidae, C. hippurus	⊠50W; ⊠12W			Yes		Rudershausen et al. (2010)
Central Atlantic	Port Aransas (Texas)	2010-2011	NR		134-205	357	27.6-148.5 TL	Invertebrates, Fish	Crustacean (Portunidae), Carangidae, Tetraodontidae, Balistidae, Monacanthidae, Crustaceans (Malacostraca)	74.8%N, 24.83%N	Yes				Brewton et al. (2016)
Central Atlantic	North Carolina and Texas. Different locations	1980-1981	RR			263	25-153	Invertebrates, Fish	Unidenfieds, Unidentified juvenile, Balistidae, Monacanthus sp.	78N	Yes		Yes	Yes	Manooch et al. (1984)
Central Atlantic	Eastern Caribbean Sea (Barbados)	1981-1982				397	18.5-124 SL	Fish, Invertebrates	Exocoetidae, Dactylopteridae, Crustecea (Mysidacea)	64N; 18 N					Oxenford and Hunte (1999)
Southern Atlantic	Northern coast of Santa Catarina State (Brazil)	2000-2001	HL	Oil Platform	13-15	28	104-141	Fish, Invertebrates	Clupeidae, Cephalopoda (Loliginidae)	82.3 (N%), 13.5 (N%)					Sinopoli et al. (2017)
Northwestern Pacific	Sea of Japan					1103	35-105	Fish	Clupeidae	95 W					Kojima (1961)
Northwestern Pacific	Choci Prefecture (Southwestern of Japan)	1985	PS	FAD		575	40-110	Fish	Clupeidae, Mullidae juvenile	53 N	Yes				Sakamoto and Taniguchi (1993)
Eastern Pacific	Cabo San Lucas (Gulf of California)	1990-1991	RR			500		Fish, Invertebrates	Exocoetidae Balistidae, Scombridae (Auxis spp.), Cephalopoda (Dosidicus gigas), Crustacea (Pleuroncodes planipes)	56.3 (IRI%); 23.1 (IRI%); 20.6 (IRI%)					Aguilar-Palomino et al. (1998)

(Continued)

Table 2. Continued.

Region	Location	Year	Sampling gear	FAD /Fish school	Sex (M-F)	N	Length range*		Main prey (Type and taxonomic family)	W, N, V**	Diet variation according to:				References
											Size	Sex	Region	Season	
Eastern Pacific	Colombia Mexico Panama Venezuela	1992-1994	PS	FAD /Fish school	175-323	545	41.7-177.7	Fish / Invertebrates	Exocoetidae / Cephalopoda (Teutoidea)	57N; 32N			Yes		Olson and Galvan-Magaña (2002)
Central Pacific	Mazatlan (Mexico)	2000-2003	HL			232	45-153	Fish / Invertebrates	Hemiramphus saltator / Crustacea (Hemisquilla californiensis)	80% W; 6.7W	Yes				Tripp-Valdez et al. (2010)
Central Pacific	Oahu (Hawaii)	1951-1955	RR, HL			52	41-121	Fish	Exocoetidae Hemiramphidae	95 V					Tester and Nakamura (1957)
Central Pacific	California Current Extension (CCE)					91		Fish / Invertebrates	Exocoetidae / Crustacea (Pennaeidae)	NR					Rothschild (1964)
Central Pacific	International waters	1994-1997	LL			38	35-129	Fish	Exocoetidae Hemiramphidae	64.9 N					Moteki et al. (2001)
Central Pacific	Peninsula of Baja California	2005-2007	NR		200-218	418	46-137	Fish / Invertebrates	Scombridae (Auxis spp.) Carangidae (Selar crumenophthalmus) / Crustacea (Pleuroncodes planipes) Cephalopoda (Dosidicus gigas)	58.1 (IRI%); 6 (IRI%); both 4 (IRI%)	Yes			Yes	Torres-Rojas et al. (2014)
Central Pacific	Manta (Ecuador)	2014-2015				320	51-149 TL	Fish / Invertebrates	Exocoetidae Scombridae (Auxis sp.) Engraulidae / Cephalopoda (Dosidicus gigas)	79.9W; 16.6W	Yes			Yes	Varela et al. (2017)
Central Pacific	Southern Korea Sea	2015	PS			174	23.8-127	Fish / Invertebrates	Engraulidae (Engraulis japonicas) Scombridae (Scomber japonicus) / Cephalopoda	84 (IRI%); 15.4 (IRI%)					Jeong et al. (2017)
Central Pacific	Baja California Sur (Mexico)		LL			31	58-143	Fish	Cephalopoda (Loligo edulis)	85% W					Young et al. (2018)
Southern Pacific	Sydney, Port Stephens (Tasman Sea, Australia)	2000-2001	RR, HL	FADs		177	32.5-70	Fish	Dactylopteridae Engraulidae Carangidae Monocanthidae Unidentified	77N					Dempster (2004)
Arabian Sea	Indian Exclusive Economic Zone (EEZ)	2006-2009	LL		108-130	238	32-135	Invertebrates / Fish	Crustacea (Megalopa) / Exocoetidae Ballstidae Monacanthus sp.	73,5N; 15.9N	Yes	Yes			Varghese et al. (2013)
Arabian Sea	Karnataka (India)	2013-2015	LL, GN, HL			256	32-128 TL	Invertebrates / Fish	Cephalopoda / Carangidae (Decapturus russelli) Engraulidae (Encrasicholina devisi) Tetraodontidae (Lagocephalus inermis) Unidentified fish	83.3W; 13.6 W					Rajesh et al. (2016)
Arabian Sea	West Coast of India	2005-2015	LL	–	184-164	348	25-135	Invertebrates / Fish	Cephalopoda (Loligo sp.) / Exocoetidae Scombridae Serranidae Carangidae Trichiuridae Clupeidae Nemipteridae Tetraodontidae Syngnathidae	60%	Yes			Yes	Kumar et al. (2017)

(*Continued*)

Table 2. Continued.

Region	Location	Year	Sampling gear	FAD	Sex (M-F)	N	Length range*	Main prey (Type and taxonomic family)		W, N, V**	Size	Sex	Region	Season	References
												Diet variation according to:			
								Invertebrates	Crustaceans (Charybdis cruciate and Charybdis smithi) Cephalopoda (Loligo duvaucelli and octopus)	20; 11%					Saroj et al. (2018)
Arabian Sea	Saurashtra coast (India)	2015-2016	GN		50-78	128	38-125	Fish Invertebrates	Scombridae (tuna) Cephalopoda (Uroteuthis sp.)	47(IRI%); 21.4(IRI%)					

Sampling gears:
RR = Rod and reel.
HL = Hand line.
LL = Long lines.
GN = Gill net.
PS = Purse seine net.
*If there is no specification, length is expressed in furcal length (FL). Otherwise, SL indicates standard length and TL total length.
**W = Weight (%); N = Number (%); V = Volume (%); NI = Not identified; NR = Not reported.
***Bannister 1976 only reported diet information of 20 from 420 individuals sampled.

Early information on the diet of early dolphinfish life stages (Palko et al. 1982 and references therein) showed the relevance of copepods for larvae and early juveniles. Since then, ten contributions have highlighted the variations in diet along with dolphinfish size (Manooch et al. 1984; Sakamoto and Taniguchi 1993; Massutí et al. 1998; Castriota et al. 2007; Tripp-Valdez et al. 2010; Varghese et al. 2013; Torres-Rojas et al. 2014; Besbes Benseddik et al. 2015; Brewton et al. 2016; Varela et al. 2017). The data in these studies comprise dolphinfish sizes ranging from 11 cm in SL to 153 cm in furcal length (FL) and reported substantial dietary changes throughout ontogeny. Four contributions reported a shift from crustacean-based diets in small individuals to fin fish-based diets in larger dolphinfish. The importance of crustaceans, such as hyperiids or megalopas, during the transition from larval feeding strategies to fish-based diets in juveniles has been supported (Manooch et al. 1984; Massutí et al. 1998; Castriota et al. et al. 2007; Tripp-Valdez et al. 2010). Other contributions have reported changes in diet from small fish to larger prey (Sakamoto and Taniguchi 1993; Varghese et al. 2013; Besbes Benseddik et al. 2015; Varela et al. 2017). These changes are expected in the context of a species that needs to maintain very high growth rates and are consistent with other large pelagic fish (Sinopoli et al. 2004; Fromentin and Powers 2005; Nikolic et al. 2017).

The ontogenetic trophic level of the dolphinfish was calculated based on prey items and distinguished among size ranges according to the original sources (Table 3). The mean trophic level increased from 4 ± 0.60 for small individuals to 4.5 ± 0.70 for larger individuals. Smaller individuals from the Mediterranean and Atlantic showed lower trophic levels compared with other oceans and seas (3.6 ± 0.53 and 3.7 ± 0.57, respectively), while larger individuals showed similar values in all regions. These values are comparable to other works and with those that used stable isotopes (Torres-Rojas et al. 2014), but the detected regional differences should be taken into account in potential food-web studies.

The dependence of diet on FAD has been assessed in several areas (Bannister 1976; Sakamoto and Taniguchi 1993; Massutí et al. 1998; Deudero, 2001; Olson and Galván-Magaña 2002; Dempster, 2004; Castriota et al. 2007; Besbes Benseddik et al. 2015), without clear dietary differences between the FAD-associated and non-associated individuals. It seems reasonable that dolphinfish do not use floating objects as their main feeding grounds because food availability would deplete very rapidly. Paradoxically, prey that
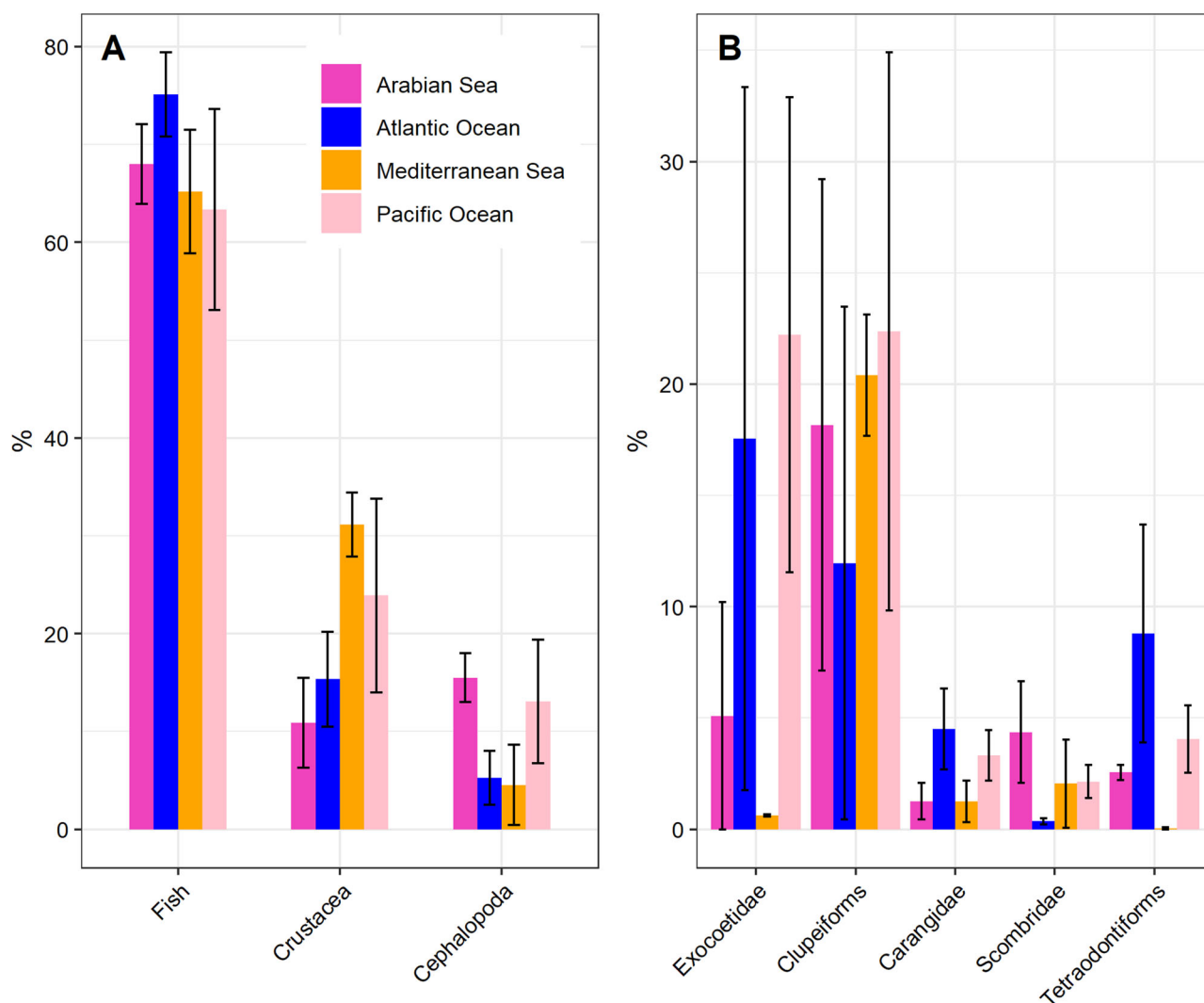
Figure 2. Mean frequency (%, both abundances and biomass are treated the same) of different prey items for each ocean in the surveyed literature summarized in the Table 2. (A) Main prey categories. (B) Main fish families.

Table 3. Prey Items and trophic level (TL ± standard error) calculated from bibliography where differences in diet among small and large dolphinfish individuals are reported. The diet is described according to the original sources (Manooch et al. 1984; Sakamoto and Taniguchi, 1993; Massutí et al. 1998; Castriota et al. 2007; Tripp-Valdez et al. 2010; Varghese et al. 2013; Torres-Rojas et al. 2014; Besbes Benseddik et al. 2015a; Brewton et al. 2016; Varela et al. 2017).

Ocean/Sea	Number of references	Size-range of small dolphinfish (Total length (cm))	Diet of small individuals	Size-range of large dolphinfish (Total length (cm))	Diet of large individuals	Trophic level of small individuals	Trophic level of large individuals
Atlantic	2	25-50	Crustaceans, Carangids, Brachyurans	60-150	Monacanthids, Tetraodontids,	3.7 ± 0.57	4.5 ± 0.8
Pacific	4	40-80	Fish juveniles, Crustaceans, Clupeids	80-150	Mid-sized fish, Cephalopods	4.0 ± 0.67	4.5 ± 0.5
Mediterranean	3	20-40	Amphipods, Decapods, Crustaceans, Clupeids	50-80	Fishes	3.6 ± 0.5	4.5 ± 0.8
Arabic	1	30-115	Fish juveniles	115-135	Cephalopods	4.5 ± 0.8	4.5 ± 0.3
TOTAL	10		–		–	4.0 ± 0.6	4.5 ± 0.7

presumably could be associated with FAD (e.g., Monocanthidae or Balistidae) were present in larger numbers of individuals when not associated with FAD. In any case, the adequacy of the sampling design in some of these studies was sometimes unclear.

Factors other than life stage and time of day can explain the variation in reported dolphinfish diets. Some studies have reported sex-related variation in the Mediterranean Sea, the Atlantic Ocean and the Indian Ocean, but few have reported significant differences. Castriota et al. (2007) reported that females feed on crustaceans in a higher proportion than males, while Varghese et al. (2013) described a higher presence of fish in the diets of female individuals, while males tended to feed on cephalopods. Some of these differences may be attributable to the difference in spatial distribution between the males and females (Rose and Hassler 1974). Furthermore, some effects attributable to seasonality and/or regions could be just the result of a shifting diet throughout life (Manooch et al. 1984; Olson and Galván-Magaña 2002; Castriota et al. 2007; Rudershausen et al. 2010; Varela et al. 2017). Unless they feed close to large productive areas, which is not the case in many populations, a plausible feeding strategy for optimizing high juvenile growth (see the corresponding chapter) is through exploitation of coastal environments where the benthic compartment is close to the surface.

Competition and predation

Interspecific competition for food with many other pelagic predators, such as tunas, marlins or swordfish, may occur, although the effects on the survival of the species remain unknown. On the other hand, a vast number of fish species predate on several stages of the dolphinfish life cycle (Kojima 1961; Beardsley 1967; Shcherbachev 1973; Rose and Hassler 1974; Palko et al. 1982). In Atlantic waters, early stages of dolphinfish were found in the stomach contents of longfin tuna (Murphy 1914), yellow-fin tuna (Sund and Girigorie 1966) and the great blue marlin (Farrington 1949). According to Gorbunova (1969), dolphinfish larvae are an important food source for swordfish larvae in the Indian and Pacific oceans. Takahashi and Mori (1973) reported that in Pacific waters, the main predators are blue marlin, black marlin, yellowfin tuna and sailfish, whereas along the western coast of Africa, the main predators of dolphinfish are yellowfin tuna (Dragovich and Potthoff 1972). In addition, the phenomenon of cannibalism has also been reported by some authors in different regions, such as in the western Atlantic (Rose and Hassler 1974), along the

coasts of the USA (Manooch et al. 1984) and Brazil (Zavala-Camin 1986); along the Japanese coast of the Pacific Ocean (Sakamoto and Taniguchi 1993) and in the Mediterranean Sea (Bannister 1976).

Overall, the literature shows evidence of bias due to the sampling methods/season on diet, although there is a vast amount of dietary data across regions and for different life stages. Scientists should aim for more quantitative data on predation on dolphinfish across stages and seas, to obtain a clearer picture of natural mortality and the role of dolphinfish within food webs.

Age and growth

Dolphinfish present one of the highest growth rates in teleost fish. This fact elicited the interest in this species for aquaculture that enabled the estimation of direct growth rates in laboratory conditions. The analysis of wild populations requires, however, the development of methods to evaluate the age at sub-annual scales (e.g., seasonal or daily growth increments) because many fisheries target age-0 individuals. Available age estimates are based on the reading of rings in calcified structures (CS) (otoliths, scales and vertebrae) as well as from length-frequency analysis. Palko et al. (1982) and Oxenford (1999) conducted early reviews on the growth parameters of dolphinfish. More recently, Chang and Maunder (2012) noted that a significant ageing bias exists that depends on the status and type of the ageing materials/samples used as well as on the regional growth differences.

Ageing methods

In this work, the aging information has been critically reviewed according to the geographical area, method used and validation method applied and is summarized in the Tables 4–6.

Calcified structures: otoliths, vertebrae, scales and dorsal spines.
Sagittal otoliths have a complex shape and are small and fragile. Sagittal and transversal sections were used to identify the daily growth increments (DGI) of juvenile dolphinfish up to fish of 65 cm FL. This method produced a significant underestimation of age when used to age larger fish (Massutí et al. 1999; Benseddik et al. 2011; Chang and Maunder 2012; Gatt et al. 2015). These authors attributed the bias in ageing large individuals from DGI in otoliths to the preparation methodology and the equipment used for the readings. Despite the relevant development of optical equipment in recent years and

Table 4. Von Berttalanfy growth equation parameters estimated for the Atlantic Ocean. ID: identification number used in Figure 3.

Study area	Length range (FL cm)	L∞ (cm)	K (yr⁻¹)	t_0	Phi	Sex	Method	Age validation	ID	References
Strait of Florida	45-132.5	167.00	0.53		4.17	M	Age determination on scales	NO	1	Beardsley (1967)
Strait of Florida	45-132.5	135.00	0.62		4.05	F	Age determination on scales	NO	2	Beardsley (1967)
Strait of Florida	45-132.5	165.00	0.68	0.16	4.27	M + F	Age determination on scales	NO	3	Beardsley (1967)
N Carolina		159.70	0.40	−0.96	4.01		Age determination on scales	NO	4	Rose and Hassler (1968)
Barbados		143.60	2.87		4.77		DGI otoliths	NO	5	Oxenford and Hunte (1983)[1]
St. Lucía	69-167	236.10	0.53	0.17	4.47		Length progression analysis	NO	6	Murray (1985)[2]
Barbados		131.50	3.49		4.78	M + F			7	Oxenford (1985)[3]
Barbados		137.10	5.24		4.99	M			8	Oxenford (1985)[3]
Barbados		132.90	3.43		4.78	F			9	Oxenford (1985)[3]
Gulf of Mexico	27-132	194.00	1.12	0.03	4.62		DGI otoliths	NO	10	Bentivoglio (1988)[3]
Gulf of Mexico	27-132	142.70	3.13		4.80		DGI otoliths	NO	11	Bentivoglio (1988)[3]
S Africa		156.00	1.04		4.40				12	Torres and Pauly (1991)
Barbados		122.10	3.43	0.06	4.71	F	DGI otoliths	NO	13	Oxenford (1999)[4]
Barbados		126.00	5.24	0.09	4.92	M	DGI otoliths	NO	14	Oxenford (1999)[4]
Barbados		120.80	3.49	0.06	4.71	M + F	DGI otoliths	NO	15	Oxenford (1999)[4]
Puerto Rico	38.1-147.9	145.70	2.19	−0.05	4.67	M + F	DGI otoliths	NO	16	Rivera and Appeldoorn (2000)
Puerto Rico	38.1-147.9	138.00	2.55	0.02	4.69	M	DGI otoliths	NO	17	Rivera and Appeldoorn (2000)
Puerto Rico	38.1-147.9	150.60	1.82	−0.09	4.62	F	DGI otoliths	NO	18	Rivera and Appeldoorn (2000)
N Carolina	8.9-145.1	128.60	1.33	−0.02	4.34	M	DGI on sagitta otoliths and scales	NO	19	Schwenke and Buckel (2008)
N Carolina	8.9-145.1	125.00	1.24	−0.06	4.29	F	DGI on sagitta otoliths and scales	NO	20	Schwenke and Buckel (2008)
N Carolina	8.9-145.1	128.90	1.27	−0.03	4.32	M + F	DGI on sagitta otoliths and scales	NO	21	Schwenke and Buckel (2008)
Brasil	7.7-195	194.10	0.91	0.08	4.54	M + F	DGI on sagitta otoliths and scales	NO	22	Lessa and Santana (2016)

[1]Extracted from Rivera and Appeldoorn (2000).
[2]Extracted from Oxenford (1999).
[3]Extracted from Chang et al. (2013).
[4]Extracted from Alejo-Plata, Gómez-Márquez, et al. (2011).

Table 5. Von Berttalanfy growth equation parameters estimated for the Mediterranean Sea. ID: identification number used in Figure 3.

Study area	Length range (FL cm)	L∞ (cm)	K (yr⁻¹)	t_0	Phi	Sex	Method	Age validation	ID	References
Mallorca	16.5-58.5	87.75	1.71	−0.04	4.12	F	DGI on sagitta, lapillus and vertebrae	NO	23	Morales-Nin et al. (1999)
Mallorca	16.5-58.5	81.59	2.45	0.01	4.21	M	DGI on sagitta, lapillus and vertebrae	NO	24	Morales-Nin et al. (1999)
E Sicily	17.2-72	60.84	4.71	0.02	4.24	F	DGI on sagitta, lapillus and vertebrae	NO	25	Morales-Nin et al. (1999)
E Sicily	17.2-72	56.74	7.78	0.07	4.40	M	DGI on sagitta, lapillus and vertebrae	NO	26	Morales-Nin et al. (1999)
W Sicily	17.2-72	48.26	9.94	0.11	4.36	F	DGI on sagitta, lapillus and vertebrae	NO	27	Morales-Nin et al. (1999)
W Sicily	17.2-72	58.25	4.31	0.02	4.17	M	DGI on sagitta, lapillus and vertebrae	NO	28	Morales-Nin et al. (1999)
Mallorca	18-70	72.40	2.50		4.12	M + F	Modal progression analysis	YES*	29	Massutí et al. (1999)
Mallorca	18-70	74.80	2.50		4.15	M + F	Modal progression analysis	YES*	30	Massutí et al. (1999)
Mallorca	14.4-124	110.00	1.56	0.01	4.28	F	DGI otoliths	YES*	31	Massutí et al. (1999)
Mallorca	14.4-124	98.70	2.06	0.02	4.30	M	DGI otoliths	YES*	32	Massutí et al. (1999)
Mallorca	14.4-124	102.40	1.90	0.02	4.30	M + F	DGI otoliths	YES*	33	Massutí et al. (1999)
Tunisia	24-65	100.50	1.42	0.05	4.16	M + F	DGI otoliths	NO	34	Besbes Benseddik et al. (2011)
Tunisia	24-65	97.50	1.50	0.05	4.15	F	DGI otoliths	NO	35	Besbes Benseddik et al. (2011)
Tunisia	24-65	100.50	1.43	0.04	4.16	M	DGI otoliths	NO	36	Besbes Benseddik et al. (2011)
Malta	10.5-131	107.80	1.90		4.34	M	DGI otoliths	NO	37	Gatt et al. (2015)
Malta	10.5-131	120.20	1.56		4.35	F	DGI otoliths	NO	38	Gatt et al. (2015)

*Direct validation by larval culture, modal progression analysis and back calculation of hatch dates.

improvements in reading transversal sections rather than sagittal sections, Chang and Maunder (2012) and Furukawa et al. (2012) still recommend standardizing inter-laboratory methodologies to properly determine the daily age and make it comparable between readers and regions, especially for large individuals.

Lapilli otoliths are flat and oval, with a smaller size than sagittae. Their increments are similar to those of the sagittal otoliths, although their periodicity has not been validated; hence, they are rarely used in aging studies after the larval period (Brothers, 1987). In the dolphinfish, the lapilli are almond-shaped, and their DGI are read in the postrostrum radius. Lapilli were used to age Mediterranean dolphinfish from 26 to 53 cm FL, yielding ages between 74 and 136 increments (Morales-Nin et al. 1999).

Table 6. Von Berttalanfy growth equation parameters estimated for the Pacific and Indian Oceans. ID: identification number used in Figure 3.

Study area	Length range (FL cm)	L∞ (cm)	K yr⁻¹	t_0	Phi	Sex	Method	Age validation	ID	References
SW Sea of Japan		175.00	0.22		3.83		Length progression analysis	NO	39	Kojima (1966)
Hawaii		189.93	1.19	0.08	4.63	M	DGI otoliths	YES (Larvae culture)	40	Uchiyama et al. (1986)
Hawaii		153.27	1.41	0.07	4.52	F	DGI otoliths	YES (Larvae culture)	41	Uchiyama et al. (1986)
Taiwan	40–140	198.00	0.17		3.82	M	Age determination on scales	NO	42	Shung (1987)
Taiwan	40–140	162.00	0.20		3.72	F	Age determination on scales	NO	43	Shung (1987)
Hawaii	10–70SL	185.80	0.72	0.07	4.40	M + F	Aquaculture experiments	NO	44	Benetti et al. (1995)[1]
Colombia, Panamá	29–197	194.00	0.91	−0.10	4.53	M + F	Length progression analysis	NO	45	Lasso and Zapata (1999)
East of Taiwan	38–135	134.60	0.61		4.04	F	Length progression analysis	NO	46	Chen et al. (2006)[2]
East of Taiwan	39–147	143.10	0.71		4.16	M	Length progression analysis	NO	47	Chen et al. (2006)[2]
Taiwan	45–145	172.00	0.70		4.32	M	Length progression analysis	NO	48	Chang (2006)[2]
Taiwan	30–140	160.00	0.56		4.16	F	Length progression analysis	NO	49	Chang (2006)[2]
Gulf of Tehuantepec	20.5–152	126.03	0.95	−0.03	4.18	M + F	Age determination on scales	NO	50	Alejo-Plata, Gómez-Márquez, et al. (2011)
Gulf of Tehuantepec	20.5–129	125.83	1.00	−0.04	4.20	F	Age determination on scales	NO	51	Alejo-Plata, Gómez-Márquez, et al. (2011)
Gulf of Tehuantepec	25.5–152	126.28	1.00	−0.39	4.20	M	Age determination on scales	NO	52	Alejo-Plata, Gómez-Márquez, et al. (2011)
Gulf of Tehuantepec	20.5–129	135.51	1.03	0.06	4.28	F	Length progression analysis (EDKs)	NO	53	Alejo-Plata, Gómez-Márquez, et al. (2011)
Gulf of Tehuantepec	25.5–152	139.98	1.02	0.05	4.30	M	Length progression analysis (EDKs)	NO	54	Alejo-Plata, Gómez-Márquez, et al. (2011)
Gulf of Tehuantepec	20.5–129	166.50	1.10	−0.05	4.48	F	Length progression analysis (ELEFAN I)	NO	55	Alejo-Plata, Gómez-Márquez, et al. (2011)
Gulf of Tehuantepec	25.5–152	166.70	1.30	−0.05	4.56	M	Length progression analysis (ELEFAN I)	NO	56	Alejo-Plata, Gómez-Márquez, et al. (2011)
Gulf of Tehuantepec		67.20	1.84	−0.07	3.92	M + F	Length progression analysis (ELEFAN I)	NO	57	Alejo-Plata, Gómez-Márquez, et al. (2011)
Japan	0.95–112.4	104.90	0.84		3.96	M	DGI on sagitta otoliths and age determination on scales	NO but little individuals used	58	Furukawa et al. (2012)
Japan	0.95–112.4	93.80	1.03		3.96	F	DGI on sagitta otoliths and age determination on scales	NO but little individuals used	59	Furukawa et al. (2012)
Taiwan	38–140	149.40	0.72		4.21	M + F	Length progression analysis	NO	60	Chang et al. (2013)
Pacific	37–135	231.65	0.87	0.07	4.67	M + F	DGI otoliths	NO	61	Solano-Fernández et al. (2015)
Pacific	37–135	L∞ =7.02	G = 3.04	g = 2.89		M + F	DGI otoliths	NO		Solano-Fernández et al. (2015)[3]
Perú	79–141TL	148.92	1.08	−0.08	4.38	F	DGI otoliths	NO	62	Solano et al. (2015)
Perú	100–157 TL	169.75	0.89	−0.12	4.45	M	DGI otoliths	NO	63	Solano et al. (2015)
Panamá	35.3–184 TL	171.50	0.36		4.61		Length progression analysis	NO	64	Guzman et al. (2015)
SW Coast of India	55–185 TL	194.25	0.40		4.18		Length progression analysis	NO	65	Benjamin and Kurup (2012)
West Coast of India	25–135	135	0.35	0.124	3.80	M + F	Length progression analysis	NO	66	Kumar et al. (2017)

[1] L∞ data corrected by Chang et al. (2013).
[2] Extracted from Chang and Maunder (2012).
[3] Parameters of the Gompertz growth equation.

Table 7. Dolphinfish age-size classes determined by scale interpretation. When not indicated, values are for both sexes combined.

Region	Length measure	Age 0+	Age 1	Age 2	Age 3	Age 4	References
Mediterranean Sea	FL range cm		F65-110	73-120	92-124		Massutí
	Mean cm (SD)		87.95 (10.15)	97.54 (10.95)	108.73 (10.17)		et al. (1999)
N Carolina (W Atlantic)	FL range cm		57.5-143.5	92.5-145.1	109.5-133.4		Schwenke and
	Mean cm (SE)		93.8 (0.98)	119.7 (17.3)	124.9 (17.9)		Buckel (2008)
N Carolina (W Atlantic)	Mean cm		65.3	92.4	118.7		Rose and
							Hassler (1968)
Strait of Florida (W Atlantic)	Mean cm		72.5	117.5	142.4 (1 ind.)	152.5 (1 ind.)	Beardsley (1967)
Gulf of Tehuantepec (E Pacific)	**Male:** FL range cm	37-54	57-84	89-114	96-124	120-135	Alejo-Plata
	Mean cm (SD)	43 (6.71)	57.7 (12.19)	103.9 (10.49)	118.8 (6.94)	125.9 (4.91)	et al. (2011a)
	Female: FL range cm	26-59	46-76	91-114	104-120	120-135	
	Mean cm (SD)	46.9 (10.58)	58.4 (9.46)	103.7 (7.32)	114.4 (3.97)	125.5 (3.97)	
NE China Sea (W Pacific)	FL range (cm)	41.2-112.4	41.2-112.4	41.2-112.4			Furukawa et al. (2012)

Vertebrae from the tail have been used in the Mediterranean to ascertain the presence of DGI in juvenile fish and compared with lapillus and sagittal otoliths. The statistical analysis of the ages determined using otoliths and vertebrae showed that the vertebrae of fish over 45 cm FL yielded younger ages than the otoliths. Therefore, Morales-Nin et al. (1999) considered vertebrae unsuitable for ageing juvenile dolphinfish. Although the formation of the growth increments in vertebrae does not seem to be daily, it is likely that seasonal marks appear in fish older than one year, similar to other fishes like Atlantic bluefin tuna (*T. thynnus*) (Neilson and Campana 2008), but this has not been demonstrated for dolphinfish.

The factors involved in the regulation of growth marks in scales are the same as in other CS; they show annual growth rhythms, although no accurate infra-annual cycles have been validated directly. Beardsley (1967) and Rose and Hassler (1968) performed the first works on dolphinfish scales and assumed the check marks on scales to be true annuli. Beardsley (1967) determined four age groups for dolphinfish in the Straits of Florida (size range from 45 to 132.5 cm FL), but from the 511 dolphinfish examined, only one individual corresponded to age group III and one to age group IV. Rose and Hassler (1968) determined 3 age classes for the dolphinfish in North Carolina waters, with only 8 individuals belonging to age class III (Table 7).

The seasonal marks in the cycloid scales of Mediterranean adult fish (size range 65–124 cm FL) resulted in the identification of three age classes with interpretable scales in 93% of the fish examined (Massutí et al. 1999). These authors concluded that scales are the best method for aging adult fish because the DGI in the otoliths caused age underestimates. Schwenke and Buckel (2008), for the dolphinfish in North Carolina waters, also described three age classes and had a consistent interpretation of the scales, with

69% agreement in three readings. They validated the nature of the seasonal growth increments using the marginal growth progression, with maximum growth during summer. In Brazilian waters, Lessa and Santana (2016) found no clear seasonal growth patterns in the scale marginal increments, which led to the conclusion that they were not adequate for age estimation. Similarly, Gatt et al. (2015) did not find any clear seasonal growth in Maltese dolphinfish scales and concluded that they underestimate age. In addition, Shung (1987) and Lessa and Santana (2016) found up to eight macro-increments in scales. These age estimations are above the data detailed in the Table 7. Lessa and Santana (2016) mentioned that the periodicity of increment deposition was inconclusive, and this maximum number of increments may be an overestimation of the "non-validated ages".

Only one study in the central Mediterranean Sea (Gatt et al. 2015) used dorsal spines to age adult dolphinfish (>65 cm FL). The longest dorsal spine offered the best results. The authors clearly identified broad and narrow bands radiating outwards from the central core and assigned annual annuli to the narrow bands that were visible around the entire circumference of the spine. Two independent readers identified identical counts in 90% of the cases. They estimated 3-year classes, but as they did not apply marginal increment radius analysis, they could not validate the age.

Age validation. The methods applied for age validation depended on the age range considered, and it was somewhat biased because most studies analyzed juveniles through daily growth increments. Direct validation using mark and recaptured individuals is lacking, due to the high sensitivity of the species to manipulation. Only two studies used fish reared in captivity to assign the number of DGI to the real age. Both studies validated the daily nature of DGI in larvae and juvenile fish and determined the start of the

formation of the increments from the hatching day (Uchiyama et al. 1986; Massutí et al. 1999). The rest assumed the daily periodicity of the DGI.

The daily formation of otolith increments enables the back-calculation of the hatch-date distributions of dolphinfish by subtracting the age in days from the date of capture (Uchiyama et al. 1986; Massutí et al. 1999). Hatch dates determined from the otolith reading can be compared with the known spawning period and may be an indirect age validation method (Massutí et al. 1999). The application of the method may be limited to some locations, because reports of multiple spawning behaviors exist, mainly near the tropics (Oxenford 1999; see reproduction section). In addition, this kind of validation should consider the expected interannual variations in spawning (Dempster 2004).

The monthly growth progression of the annuli laid in the edge can be followed when using seasonal structures on CS. This indirect validation method must show a period of maximum growth of the annuli followed by a decreasing growth or change in the nature of the increment deposited (i.e., discontinuities in the circulii, changes in opacity of the spines). If these growth rhythms are seasonal, the periodicity is determined. Various approaches can be followed: measuring the last increment width against the previous increment (Beardsley 1967) or applying marginal increment analysis (MI) (Alejo-Plata, et al. 2011; Furukawa et al. 2012; Gatt et al. 2015) using the following equation (Lai and Liu 1979):

$$MI = \frac{R - r_n}{r_n - r_{n-1}} \quad (1)$$

where R is the overall radius from the focus to the outer edge of the CS, r_n is the radius from the focus to the outer edge of each annulus and r_{n-1} is the radius from the focus to the previous r_n annulus. This method, however, was not successful for spines due to their irregular shape (Gatt et al. 2015).

Several studies have examined the use of the growth increments in pairs of CS (i.e., scales and otoliths; scales and spines) to corroborate the determined ages. These approximations do not validate the temporal meaning of the growth structures, so they are not true validation methods (Panfili and Morales-Nin 2002).

Length-based studies. The works using cohort analysis to determine growth are included in the Tables 4–6. The two studies from the Indian Ocean used length progression analysis. In the Pacific, 53.8% of the literature reviewed used length-frequency analysis or a combination of similar methods instead of otolith

interpretation (38.5%), while in the Atlantic and Mediterranean, there was a predominance of studies based on the DGI on otoliths (72.7 and 100% of the bibliography, respectively). Length-based methods work well for dolphinfish, particularly in the Mediterranean, where the spawning period is relatively short (2–3 months), as reported in the reproduction section, which results in discrete modes in their size distributions. This method is limited due to the high mobility of the species after maturation, which poses difficulties in correcting the assignment of cohorts.

Growth rates and growth parameters

Many studies report daily (linear) estimates of growth ranging from 0.49 mm SL d^{-1} to 9.66 mm SL d^{-1} and are highly dependent on the length (age) range considered (Table 8). Oxenford (1999) reviewed growth rates for first-year dolphinfish from the western central Atlantic and reported rates from 1.43 to 4.71 mm d^{-1}, similar to data from the Pacific, ranging from 2 mm FL d^{-1} to 5.9 mm FL d^{-1} (Table 8). Newer data yielded comparable values, with an expected slowing in the growth rates after maturity (Gatt et al. 2015; Lessa and Santana 2016). Furthermore, differences between male and female growth existed, with males generally growing faster (Oxenford 1999). In the Mediterranean Sea, linear growth for immature fish ranged from 2.11 mm FL d^{-1} for fish from 24–65 cm FL to 5.1 mm FL d^{-1} for fish from 36 to 60 cm FL (Table 8). The highest growth rates were reported for captive fish (data extracted from Oxenford (1999)), which is an unusual observation for pelagic fish and suggests possible food-limited growth in the wild.

The typical method for inferring patterns of fish growth relies on a sample of a broad size range of individuals from the population, for which the age is determined from their CS. Numerous studies have applied this approach using the von Bertalanffy growth equation (Tables 4–6). Although this widely applied equation has a strong physiological basis (Longhurst and Pauly 1987), it should be applied only if most of the life span is covered, which is not accomplished in most dolphinfish studies, where the fished population consists of age-0 individuals. Solano-Fernández et al. (2015) showed that the Gompertz model better fits the growth pattern for juvenile individuals of this species.

Some known biases related to the estimation of growth parameters include sex (often pooled) and length units; in this species, the tail is curved, and body length is reported either as standard length (SL), fork length (FL), or total length (TL). These aspects

Table 8. Published daily growth rates of dolphinfish.

Ocean/Sea	Study area	Length range (FL cm)	Length grow estimation	Sex	References
Atlantic	Florida		4.8 mmSL/d		Herald (1961)[1]
Atlantic	Strait of Florida	45-132.5	1.82 mmSL/d	M + F	Beardsley (1967)[1]
Atlantic	Strait of Florida	40-106	2.65 mmFL/d		Beardsley (1967)
Atlantic	N Carolina		1.64 mmSL/d		Rose and Hassler (1968)
Atlantic	Strait of Florida		5.28 mmSL/d		Beardsley (1971)[1]
Atlantic	N Carolina	1.5-10.1TL	1.07 mmTL/d		Hassler and Rainville (1975)[1]
Atlantic	N Carolina	juvenile (0.5-5.6Kg)	5.88 mmSL/d		Hassler and Hogarth (1977)[1]
Pacific	Hawaii	35-50 TL	123 cmTL/7-8months		Soichi (1978)[2]
Pacific	Taiwan	50-100	2.96 mmSL/day		Wang (1979)[3]
Pacific	Hawaii		3.56 mmSL/d		Hagood et al. (1981)[1]
Atlantic	Florida	juvenile	9.66 mmSL/d		Shekter (1982)[4]
Atlantic	Florida	juvenile	2.73 mmSL/d		Shekter (1982)[4]
Atlantic	Barbados	70-110SL	1.43 mmSL/d		Oxenford and Hunte (1983)
Atlantic	Barbados	60-120SL	1.53 mmSL/d		Oxenford and Hunte (1983)
Atlantic	St. Lucía	69-167	1.78 mmFL/d		Murray (1985)[4]
Pacific	Hawaii		3.19 mmSL/d	M	Uchiyama et al. (1986)
Pacific	Hawaii		2.82 mmSL/d	F	Uchiyama et al. (1986)
Atlantic	Gulf of Mexico	27-132	4.15 mm/d		Bentivoglio (1988)[4]
Atlantic	Gulf of Mexico	27-132	4.15 mm/d		Bentivoglio (1988)[4]
Atlantic	Gulf of Mexico	850-1210mmSL	0.49 SL mm/d		Bentivoglio (1988)[5]
Atlantic	Gulf of Mexico	25-121SL	3.88 mmSL/d		Bentivoglio (1988)[5]
Atlantic	Puerto Rico	55-132.5	2.52		Rivera-Betancourt (1994)[4]
Pacific	Hawaii	10-70SL	0.227cm/d	M + F	Benetti et al. (1995)
Pacific	Hawaii		2 mm/day		Kraul (1999)
Pacific	Australia, New Guinea and New Zeland	10-140	Mass growth = 2.5Kg/6months; Growth/d= 0.014 x FL-0.455		Kingsford and Defries (1999)
Atlantic	Puerto Rico	38.1-147.9	2.52 mm/d for M + F. Cumulative L-G for 1st year= 6 mm/d with a max observed of 9.5 mm/d. Extrapolating L-G from VBGM cumulative growth= 3.59 mm/d for 1st year.	M + F	Rivera and Appeldoorn (2000)
Pacific	E Australia	10.9-56.7	3-5.9 mm/d		Dempster (2004)
Atlantic	N Carolina	8.9-145.1	3.78 mm/d	M	Schwenke and Buckel (2008)
Atlantic	N Carolina	8.9-145.1	3.78 mm/d	F	Schwenke and Buckel (2008)
Atlantic	N Carolina	8.9-145.1	3.78 mm/d	M + F	Schwenke and Buckel (2008)
Mediterranean	Tunisia	24-65	2.11 mm/d	M + F	Besbes Benseddik et al. (2011)
Mediterranean	Tunisia	24-65	2.11 mm/d	F	Besbes Benseddik et al. (2011)
Mediterranean	Tunisia	24-65	2.11 mm/d	M	Besbes Benseddik et al. (2011)
Mediterranean	Malta	16-35	5.1 mm/d	M + F	Gatt et al. (2015)
Atlantic	Brasil	7.7-195	0.29 cm/d	M + F	Lessa and Santana (2016)
Atlantic	Florida		3.03 mmSL/d		Schekter pers comm. [1]

[1]Extracted from Oxenford & Hunte (1983).
[2]Extracted from Uchiyama et al. (1986).
[3]Extracted from Rivera and Appeldoorn (2000).
[4]Extracted from Chang et al. (2013).
[5]Extracted from Oxenford (1999).

are included in the Tables 4–6. These tables compile growth parameters derived from populations ranging from 0.95 cm TL to 197 cm FL, but the majority of the lengths considered were of intermediate sizes, which was probably related to the fishing technique. Larger sizes have been reported for the Pacific and Atlantic Oceans (197 cm and 195 cm FL, respectively), probably due to captures using long lines and hand lines. In the Mediterranean, the length range is more restricted (10.5–131 cm FL). These length ranges

would yield estimated ages varying from one month to a maximum of approximately five years (Furukawa et al. 2012). This is higher than four years, which is the maximum life span suggested for this species (Benetti et al. 1995; Lessa and Santana, 2016; Massutí et al. 1999; Oxenford 1999 and references therein; Palko et al. 1982 and references therein; Schwenke and Buckel 2008), and contrasts with the average estimated longevity of less than two years (Oxenford 1999).

The reported growth curves in the four regions were compared using the phi (ø) growth performance index (Munro and Pauly 1983) (Equation 2), which is based on the high inverse correlation of the von Bertalanffy growth parameters L∞ and k as follows:

$$\emptyset = 2\ln(L\infty) + \ln(k) \tag{2}$$

Plots of ø vs L∞ showed a large dispersion for the ø of Atlantic data calculated using CS (Figure 3a). L∞ showed a wide variation from 48.26 to 236.1 cm FL regardless of the estimation method. The dependence of the parameters on the length range was clear in the lower estimates of L∞ in the Mediterranean studies.

The simultaneous 95% confidence region (SCR) for the growth parameters, which was calculated as in Chang et al. (2013), showed different ellipses in the plot of negative ln K against L∞ (Figure 3b). Therefore, there was notable differentiation in the growth patterns for the different regions, which was more pronounced in the Mediterranean than in
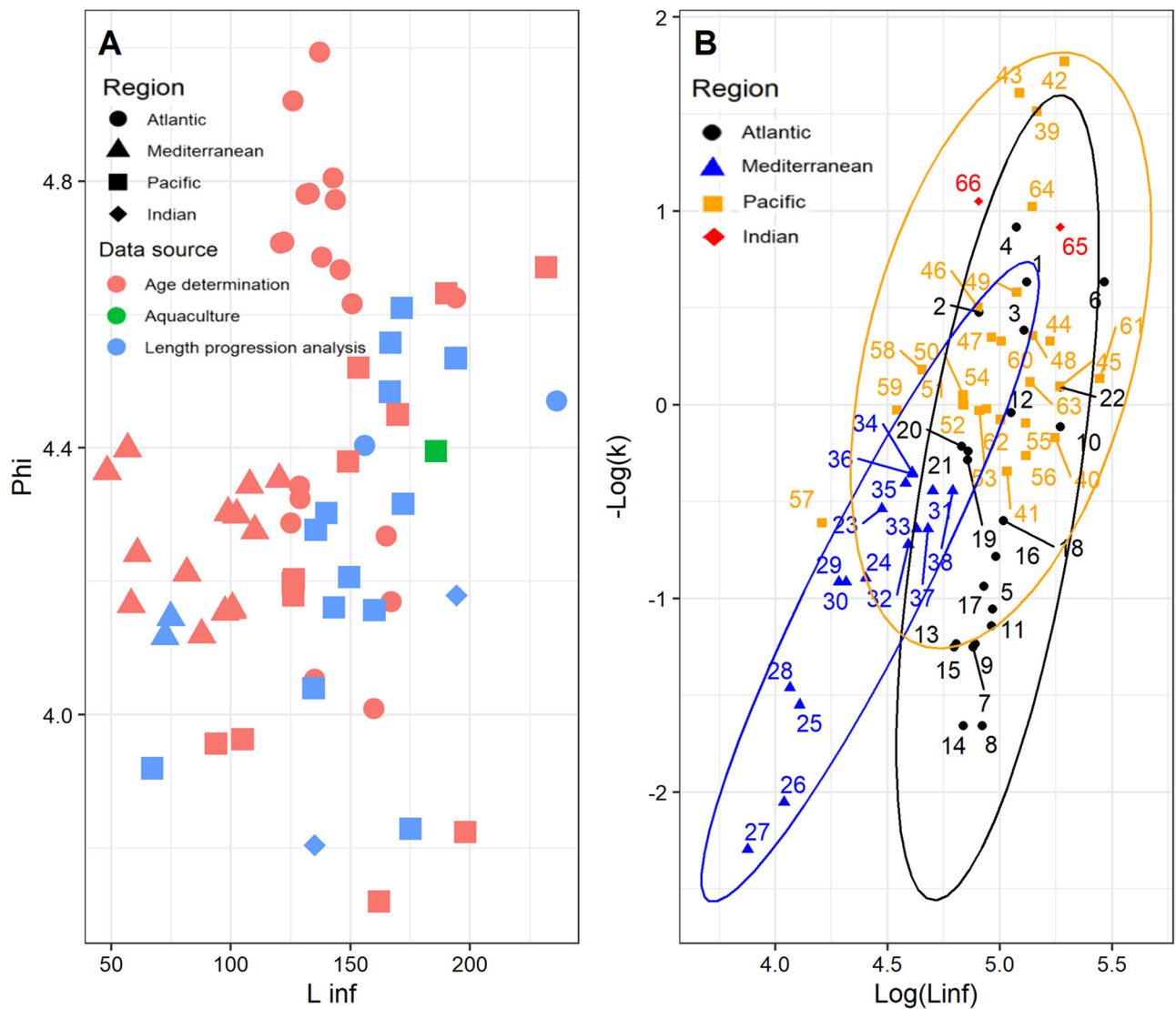
Figure 3. (A) Relationship between ø (phi) and L∞ (Linf) depending on the dolphinfish geographic area (shapes) and the method used to calculate the von Bertalanffy parameters (colours). (B) Relationship between log(L∞) and − log(K) of the von Bertalanffy growth equation parameters provided in the Tables 4–6, with the 95% confidence ellipses. The points lying outside of the SCR could be considered to be beyond the credible range of growth index (Chang et al. 2013). Numbers correspond to the ID column indicated in the corresponding tables. No confidence ellipse is given for the Indian Ocean (only two records).

Table 9. Published length-weight relationships for dolphinfish.

Ocean/Sea	Study area	Length range (FL cm)	Length-weight parameters	Sex	References
Atlantic	Strait of Florida	45-132.5	$W = 2.62 \times 10^{-4} FL^{2.64570}$	M	Beardsley (1967)
Atlantic	Strait of Florida	45-132.5	$W = 2.35 \times 10^{-4} FL^{2.42795}$	F	Beardsley (1967)
Atlantic	N Carolina		$W = 0.5 \times 10^{-7} L^{2.75}$ (L in mm)	M	Rose and Hassler (1968)
Atlantic	N Carolina		$W = 1.27 \times 10^{-7} L^{2.59}$ (L in mm)	F	Rose and Hassler (1968)
Mediterranean	Malta	22.2 – 54.3	$W = 1.637 \times 10^{-5} FL^{2.952}$	M	Bannister (1976)
Mediterranean	Malta	22.4 – 54.5	$W = 2.094 \times 10^{-5} FL^{2.919}$	F	Bannister (1976)
Pacific	Taiwan	40-140	$W = 1.638 \times 10^{-5} FL^{2.934}$	M	Shung (1987)
Pacific	Taiwan	40-140	$W = 1.844 \times 10^{-5} FL^{2.918}$	F	Shung (1987)
Atlantic	S Africa	FL max = 180	$W = 6.23 \times 10^{-5} FL^{2.53}$	?	Torres (1991)
Atlantic	Puerto Rico	35.8-132.3	$W = 1.39 \times 10^{-5} FL (mm)^{2.919}$	M + F	Pérez and Sadovy (1991)
Pacific	Hawaii	10-70SL	$W = 8.36 \times 10^{-3} FL^{3.07}$	M + F	Benetti et al. (1995)
Atlantic	Cuba	50-120	$W = 3.21 \times 10^{-2} FL^{2.67}$		García-Arteaga et al. (1997)
Pacific	Colombia, Panamá	29-197	$W = 0.0224 \times FL^{2.78}$	M + F	Lasso and Zapata (1999)
Pacific	Colombia, Panamá	29-197	$W = 0.0406 \times FL^{2.6588}$		Lasso and Zapata (1999)
Pacific	Colombia, Panamá	29-197	$W = 0.042 \times FL^{2.6328}$		Lasso and Zapata (1999)
Mediterranean	Mallorca	14.4-124	$W = 0.0139 \times FL^{2.8983}$	F	Massutí et al. (1999)
Mediterranean	Mallorca	14.4-124	$W = 0.0092 \times FL^{3.0187}$	M	Massutí et al. (1999)
Mediterranean	Mallorca	14.4-124	$W = 0.0113 \times FL^{2.9605}$	M + F	Massutí et al. (1999)
Atlantic	Canary Islands	76.5-103	$W = 0.00095 \times FL^{3.527}$	M + F	Castro et al. (1999)
Atlantic	Canary Islands	76.5-99	$W = 0.01656 \times FL^{2.873}$	F	Castro et al. (1999)
Atlantic	Canary Islands	80.5-103	$W = 0.00398 \times FL^{3.222}$	M	Castro et al. (1999)
Atlantic	Gulf of Mexico		$W = 2.98 \times 10^{-4} FL^{2.71}$	M + F	Thompson (1999)
Atlantic	Puerto Rico	38.1-147.9	$W = 3.8 \times 10^{-5} FL^{2.78}$	M + F	Rivera and Appeldoorn (2000)
Pacific	Los Cabos	40-192	$W = 7 \times 10^{-5} FL^{3.031}$	M + F	Madrid and Beltrán-Pimienta (2001)
Pacific	Mazatlán	40-192	$W = 2.8 \times 10^{-5} FL^{2.706}$	M + F	Madrid and Beltrán-Pimienta (2001)
Pacific	Nayarit	40-192	$W = 2.1 \times 10^{-7} FL^{2.71}$	M + F	Madrid and Beltrán-Pimienta (2001)
Atlantic	N Carolina	8.9-145.1	$W = 2.25 \times 10^{-8} FL^{2.87}$	M	Schwenke and Buckel (2008)*
Atlantic	N Carolina	8.9-145.1	$W = 9.42 \times 10^{-8} FL^{2.64}$	F	Schwenke and Buckel (2008)*
Pacific	Gulf of Tehuantepec	20.5-129	$W = 1.2 \times 10^{-5} FL^{2.8482}$	F	Alejo-Plata, Gómez-Márquez, et al. (2011)
Pacific	Gulf of Tehuantepec	25.5-152	$W = 4 \times 10^{-6} FL^{3.1435}$	M	Alejo-Plata, Gómez-Márquez, et al. (2011)
Pacific	Gulf of Tehuantepec	20.5-129	$W = 1.2 \times 10^{-5} FL^{2.8482}$	F	Alejo-Plata, Gómez-Márquez, et al. (2011)
Pacific	Gulf of Tehuantepec	25.5-152	$W = 4 \times 10^{-6} FL^{3.1435}$	M	Alejo-Plata, Gómez-Márquez, et al. (2011)
Pacific	Gulf of Tehuantepec	20.5-129	$W = 1.2 \times 10^{-5} FL^{2.8482}$	F	Alejo-Plata, Gómez-Márquez, et al. (2011)
Pacific	Gulf of Tehuantepec	25.5-152	$W = 4 \times 10^{-6} FL^{3.1435}$	M	Alejo-Plata, Gómez-Márquez, et al. (2011)
Mediterranean	Tunisia	24-65	$W = 0.0081 \times FL^{3.0669}$	M + F	Besbes Benseddik et al. (2011)
Mediterranean	Tunisia	24-65	$W = 0.0091 \times FL^{3.0281}$	F	Besbes Benseddik et al. (2011)
Mediterranean	Tunisia	24-65	$W = 0.0077 \times FL^{3.0893}$	M	Besbes Benseddik et al. (2011)
Pacific	Pacific	37-135	$W = 2.45 \times 10^{-5} FL^{2.75}$	M + F	Solano-Fernández et al. (2015)
Pacific	Pacific	37-135	$W = 4.608 \times 10^{-5} FL^{2.586}$	F	Solano-Fernández et al. (2015)
Pacific	Pacific	37-135	$W = 2.154 \times 10^{-5} FL^{2.788}$	M	Solano-Fernández et al. (2015)
Mediterranean	Malta	11-142	$W = 0.0178 \times FL^{2.8551}$	M	Gatt et al. (2015)
Mediterranean	Malta	11-142	$W = 0.0216 \times FL^{2.7903}$	F	Gatt et al. (2015)
Pacific	Perú	79-141TL	$W = 0.019 \times TL^{2.645}$	F	Solano et al. (2015)
Pacific	Perú	100-157TL	$W = 0.099 \times TL^{2.331}$	M	Solano et al. (2015)
Indian	West coast of India	35 – 125	$W = 0.2059 \times FL^{2.234}$	F	Kumar et al. (2017)
Indian	West coast of India	27.5 – 135	$W = 0.3227 \times FL^{2.1286}$	M	Kumar et al. (2017)
Indian	West coast of India	27.5 - 135	$W = 0.2701 \times FL^{2.1707}$	M + F	Kumar et al. (2017)
Pacific	Cabo San Lucas, Baja California Sur, Mexico	33-137	$W = 132 \times 10^{-5} FL^{2.886}$	F	Ortega-García et al. (2018)
Pacific	Cabo San Lucas, Baja California Sur, Mexico	37-149	$W = 606 \times 10^{-6} FL^{3.075}$	M	Ortega-García et al. (2018)
Pacific	Cabo San Lucas, Baja California Sur, Mexico	33-149	$W = 455 \times 10^{-6} FL^{3.130}$	M + F	Ortega-García et al. (2018)

*Extracted from Solano-Fernandez et al. (2015). Not in the original.

Table 10. Sex ratio values reported from dolphinfish catches.

Region	Study area	Sex ratio M:F	References
Western Central Atlantic	Virgin Island	1:1.9	Mather and Day (1954)
Western Central Atlantic	North Carolina	1:1.9	Rose and Hassler (1974)
Western Central Atlantic	Barbados	1:3	Oxenford (1985)
Western Central Atlantic	Puerto Rico	1:2.3	Pérez et al. (1992)
Western Central Atlantic	Gulf of Mexico	1:1.2	Bentivoglio (1988)
Western Central Atlantic	Florida Current	1:1.8	Oxenford (1985)
Western Atlantic	Brazil	1:1.9	Dos Santos et al. (2014)
Eastern Atlantic	Canary Islands	1:1.4	Castro et al. (1999)
Eastern Atlantic	Ivory Coast	1:2.18	Kouame et al. (2017)
South Central Pacific	Coast of Colombia and Panama	0.96:1	Lasso and Zapata (1999)
Central Pacific	Gulf of Tehuantepec	1:1	Alejo-Plata, Díaz-Jaimes, et al. (2011)
Central Pacific	Hawaii	1:2	Tester (1957)
Eastern Pacific	Costa Rica	2:1	Campos et al. (1993)
Eastern Pacific	Southern Golf of California	1:1	Zúñiga-Flores et al. (2011)
Eastern Pacific	Perú	1:2	Solano et al. (2015)
Eastern Pacific	Panamá	1:1.5	Guzman et al. (2015)
Western Indian	East Africa	1:4	Williams and Newell (1957)
North Indian	South-West coast of India	1:2.05	Rajesh et al. (2016)
North Indian	West coast of India	1.12:1	Kumar et al. (2017)
North Indian	North-West coast of India	1:1.75*	Saroj et al. (2018)
Western and Central Mediterranean	Balearic Islands	1:1*	Massutí and Morales-Nin (1997)
Western and Central Mediterranean	Western & Central Mediterranean	1:2	Potoschi et al. (1999)
Western and Central Mediterranean	Malta FAD fishery	1:1.54	Gatt et al. (2015)
Western and Central Mediterranean	Malta longline fishery	1:0.76	Gatt et al. (2015)
Mediterranean Sea	Mediterranean Sea**	1:1.16	Maroso et al. (2016)
Western and Central Mediterranean	Tunisia	1:2	Benseddik et al (2019)

*Overall proportions of the whole length ranges and seasons studied. For sex ratio information by different length ranges see the original paper.
**For sex ratio information by sampling location see the original paper.

the other regions. This could be related to different environmental conditions, and/or physiological traits attributable to hypothetical subpopulations from those regions (Díaz-Jaimes et al. 2010).

Length-weight relationships

Dolphinfish show a negative allometric growth in weight in relation to fish length (Table 9). The negative b value is consistent when adult fish are included in the estimation (29–197 cm FL range), whereas b becomes positive only for juvenile fish (10–70 cm FL range). Most studies report larger mean length and greater weight-at-length for males than for females, and there are small differences in the length-weight relationships between locations (Oxenford 1999). Males are closer to isometric than females. This allometric growth may be related to the elongated body shape required to achieve the fast swimming characteristic of the species.

Reproductive biology and maturity

Sexual dimorphism

In addition to the sex-related physiological or behavioral differences, the dolphinfish is a gonochoric species with very marked external sexual dimorphism that is visible in the head profile, which allows visual discrimination of sex starting in the late juvenile stages. The characteristic bone crest on the top of the head ("bullhead") is particularly evident in large

males in some regions (Beardsley 1967; Massutí and Morales-Nin 1997), whereas females exhibit more slender head profiles. This dimorphism appears at a size of approximately 40–50 cm in furcal length (FL) (Beardsley 1967; Shcherbachev 1973; Palko et al. 1982; Massutí and Morales-Nin 1997; Besbes Benseddik et al. 2015). Noticeably, a recent case of hermaphroditism has been reported in the tropical southeastern Arabian Sea (Retheesh et al. 2017), where one individual with male external appearance of 45 cm FL showed oocytes in different developmental stages and a spermatozoa mass in the same gonad.

Sex ratio

The sex ratio generally shows female dominance in most locations (Table 10). Only in Costa Rica and the western coast of India was the ratio favorable to males (Campos et al. 1993; Vinod Kumar et al. 2017). Many works have reported a sex ratio close to 1:1, but when the ratio is examined by different size classes, there is a bias toward females of smaller sizes (<90 cm FL), whereas males are predominant at larger sizes (>90 cm FL) (Kojima 1966; Arocha et al. 1999; Castro et al. 1999; Alejo-Plata, Díaz-Jaimes, et al. 2011; Zúñiga-Flores et al. 2011). Other studies have reported females outnumbering males at small size classes but an equal ratio for larger sizes (Kojima, 1966; Dos Santos et al. 2014). The same trend has been reported for the Mediterranean Sea, where in the western and central Mediterranean, catches from FAD (mainly

Table 11. Summary of dolphinfish length at first maturity by regions. Length is expressed in furcal length (FL) unless other unit specified, being SL standard length and TL total length.

Region	Study area	Sex	L_{50} (FL cm)	Age of maturity (months)	References
Western Atlantic	Straits of Florida	F	35–55		Beardsley (1967)
		M	45		
Western Atlantic	Gulf of Mexico	F	49-52	3–4	Bentivoglio (1988)
		M	53	4	
Western Atlantic	Puerto Rico		>60		Perez and Sadovy (1991); Perez et al. (1992)
Western Atlantic		F	84		Oxenford (1999)
		M	80.50		
Western Atlantic	North Carolina	F	46		Schwenke and Buckel (2008)
		M	47.50		
Western Atlantic	Florida		41.90		McBride et al. (2012)
Western Atlantic	Brazil	F	68.60		Dos Santos et al. (2014)
		M	70.66		
Eastern Pacific	Mexican coast	F	48.38		Alejo-Plata, Díaz-Jaimes, et al. (2011)
		M	50.57		
Eastern Pacific	Costa Rica		130TL		Campos et al. (1993)
Eastern Pacific	Southern Gulf of California	F	50.50		Zúñiga-Flores et al. (2011)
		M	45		
Eastern Pacific	Southern Gulf of California	F population mean	93		Zúñiga-Flores et al. (2011)
		M population mean	77		
Western Pacific	Taiwan coast		51		Wu et al. (2001)
Western Pacific	Northeastern China Sea	F	51.40		Furukawa et al. (2012)
		M	52.40		
Western Indian	East Africa		<53.50 cm SL		Williams and Newell (1957)
North Indian	Southwestern coast of India	F	49		Rajesh et al. (2016)
		M	47		
North Indian	West coast of India		35		Kumar et al. (2017)
North Indian	Northwestern coast of India	F	59.3		Saroj et al. (2018)
Western and Central Mediterranean			<60	5–6	Massutí and Morales-Nin (1997)
Western and Central Mediterranean	Balearic Islands	F	54.50		Massutí and Morales-Nin (1997)
		M	61.80		
Western and Central Mediterranean	Tunisian coast	F	53.50	5–6	Besbes Benseddik et al. (2019)
		M	60.50	6–7	
Western and Central Mediterranean	Malta	F	62.60		Gatt et al. (2015)
		M	58.90		

juveniles) show female predominance (2:1), whereas longline catches, which are dominated by larger individuals on average, show a 1:1 ratio (Lozano-Cabo 1961; Bannister 1976; Massutí and Morales-Nin 1997; Gatt et al. 2015; Besbes Benseddik et al. 2019).

The tendency for female-biased sex ratio at small sizes is believed to result from inadvertent selection for females by the fishery due to behavioral differences between sexes rather than a real population difference in sex ratio (Nakamura 1971; Rose and Hassler 1974; Oxenford 1999). Oxenford (1999) suggested that small males and all sizes of females spent more time associated with floating objects than large males, which tend to spend more time in open water, possibly traveling between female-dominated schools below rafts. Hence, catches of small fish are likely to have a sex ratio of approximately 1:1, while catches of large fish will be biased in favor of females if taken in association with floating objects. Given that reproduction occurs in pairs, the sex ratio of the adult captures during the spawning season approaches 1:1.

Maturity

According to most studies worldwide, the common dolphinfish reaches sexual maturity within its first year of life (3-7 months and a mean of approximately 55 cm FL), with females doing so at a smaller size than males (Table 11). Some extreme values exist: Oxenford (1999) reported maturity estimates of 84 cm FL for females and 80.5 cm FL for males in the western Atlantic. The L_{50} value provided for Costa Rica was 130 cm (Campos et al. 1993), which largely departed from the other reported values. The Mediterranean values aligned with the data obtained for the other oceans: in the western and central Mediterranean, dolphinfish reach sexual maturity at a size of less than 60 cm FL and at ages from 5 to 6 months. In the Balearic Islands, estimates of maturity have shown L_{50} values of 54.5 and 61.8 cm FL for

Table 12. Dolphinfish reproductive season by region. Dark gray represents the spawning peak and light gray the spawning period.

	January	February	March	April	May	June	July	August	September	October	November	December	References
Atlantic Ocean													
North Carolina						▨	▨	▨	▨	▨	▨	▨	Rose (1966)
Florida Current	▨	■	■	■	■								Beardsley (1967)
Puerto-Rico	■	▨	■	■	■								Pérez and Sadovy (1991), Perez et al. (1992)
Gulf of Mexico						▨				▨			Ditty et al. (1994)
Canary Islands							▨	▨	▨				Castro et al. (Ret al. 1999)
Venezuela													Arocha et al. (1999)
Pacific Ocean													
Western Japan Sea						▨	▨	▨					Kojima (1955)
East Coast of Taiwan			▨	▨	▨	▨	▨	▨	▨	▨	▨		Wu et al. (2001)
Colombia-Panama													Lasso and Zapata (1999)
Mexico					■	■	■	■	■	■	■	■	Alejo-Plata, Díaz-Jaimes, et al. (2011)
Indian Ocean													
Eastern Africa													Williams and Newel (1957)
Southwestern (Karnataka)	■		▨	▨	▨	▨	■	■	■	■		■	Rajesh et al. (2016)
Western coast of India	■	▨			▨	■	■	■			■	■	
Northwestern (Saurashtra)													Saroj et al. (2018)
Mediterranean Sea													
Balearic Islands					▨	▨	▨						Massutí et al. (1997)
Malta						■	■						Gatt et al. (2015)
Tunisia						■	■						Besbes Benseddik et al. (2015b)

females and males, respectively (Massutí and Morales-Nin 1997). In Tunisia, Besbes Benseddik et al. (2019) reported L_{50} values of 53.5 cm for females and 60.5 cm for males based on macroscopic and microscopic examinations of the gonads. The maturity values estimated in Malta by Gatt et al. (2015) were slightly different, with higher values for females than males (62.6 and 58.9 cm FL, respectively).

Reproduction

Dolphinfish shows early sexual maturity, high fecundity, and an asynchronous reproductive strategy. Spawning events occur in surface waters with external fertilization. As noted for many pelagic species, there is a clear relationship between latitude and spawning seasonality. Cheung et al. (2008) modeled the spawning distribution of the species and showed regular spawning throughout the year in the tropics, whereas a gradual separation into strong spring-spawning activity and weaker autumn spawning activity occurred at higher latitudes. This aligns with dolphinfish reproductive activity, which is relatively constant throughout the year (at the population level) in the tropics, while in subtropical and temperate regions individuals tend to synchronize spawning to the warm period of the year (Table 12). An inspection of the gonadosomatic index (as a proxy of population reproductive activity), temperature and latitude illustrate this trend (Figure 4).

Temperature seems to be the key factor triggering spawning events, either by stimulation of physiological mechanisms or in association to with mixing processes conducive to trophic enrichment of the environment. Several studies conducted in the Atlantic Ocean (Mather and Day 1954; Erdman 1956; Beardsley 1967), Pacific Ocean (Kojima 1955, 1964; Wang 1979; Sánchez 2008; Zúñiga-Flores et al. 2011), Indian Ocean (Rajesh et al. 2016; Vinod Kumar et al. 2017), and Mediterranean Sea (Lozano-Cabo 1961; Massutí and Morales-Nin 1997; Besbes Benseddik et al. 2015) agree that the optimal minimum temperature triggering *C. hippurus* spawning is approx. 21 °C, whereas the maximum is reported at approx. 30 °C. The spawning season in the Mediterranean Sea is from May to September (Massutí and Morales-Nin 1997; Besbes Benseddik et al. 2015, 2019; Gatt et al. 2015) and it is considerably shorter in comparison with other regions, in accordance with the shorter time window when the optimal temperatures for spawning occur.

The global data, including those for the Mediterranean, show that dolphinfish present multiple and intermittent spawning events, occurring 2–3 times in

each breeding period. This is justified by the presence of several sizes of oocytes (in different maturity stages) in the ovaries (Beardsley 1967; Shcherbachev 1973; Pérez and Sadovy 1996; Massutí and Morales-Nin 1997; Oxenford 1999; Alejo-Plata, Díaz-Jaimes, et al. 2011; Besbes Benseddik et al. 2019). This reproductive behavior is typical of tropical and sub-tropical fishes (Burt et al. 1988) and is considered an adaptation to minimize the risk of poor larval survival from a single expulsion during the spawning season (Ditty et al. 1994).

The oocyte diameters in mature ovaries (Table 13) and fecundity values (Table 14) have been estimated for different regions. Mature ovaries present oocytes ranging from 0.2 to almost 2 mm, while hydrated oocytes, which are ready to be emitted, present diameters over 0.9 mm. In the central Mediterranean Sea, the estimated mean fecundity (eggs/female) was 660,000 in females ranging from 64 to 106 cm FL (Besbes Benseddik et al. 2019). This value is comparable to that reported by Massutí and Morales-Nin (1997) in the western Mediterranean, which was approximately 764,000 for females ranging from 67 to 117 cm FL. In other regions, relative fecundity varies from approximately 30,000 to more than two million eggs, depending on the size of females, but there are large differences for a given size (Table 14). Variations in the abiotic (temperature, salinity, others) and/or biotic (trophic) factors, may condition the balance between the environmental and the population reproductive potential, and could explain these differences in fecundity values.

Mediterranean dolphinfish fisheries

The common dolphinfish has been an exploited resource since ancient times in the Mediterranean Sea (Massutí et al. 1997). This is a key species for the fisheries of western Mediterranean coastal countries, yielding important local incomes due to the elevated number of catches (Cannizzaro et al. 1999; Morales-Nin et al. 2000, 2010; Battaglia et al. 2010; Quetglas et al. 2016; Palmer et al. 2017). There is high gastronomical appreciation for this species where it is present, and it is exploited by recreational fishers, acquiring an elevated socio-economic relevance for the populations in these countries. In the eastern Mediterranean, a large gap of knowledge on all aspects of its exploitation exists; this species is present, but there is not a specific fishery targeting it, and official data on catches are not available. In summary, dolphinfish is an emblematic species for artisanal and recreational Mediterranean fisheries in several countries, and it is considered a part of the cultural heritage in countries such as Malta (Copemed II 2016). The last updates on all aspects of the fisheries in the Mediterranean Sea are shown below.

FAD fishery

This is the main dolphinfish fishery in the Mediterranean. It is a small-scale commercial fishery based on a large fleet of small artisanal boats targeting age-0 juveniles from late summer to autumn when this life stage is abundant in Mediterranean waters (Massutí and Morales-Nin 1995; Morales-Nin et al. 2000; Grau and Camiñas 2011). This artisanal fishery takes place in the western and central Mediterranean, particularly in Spain (Balearic Islands), Italy (Sicily), Malta and Tunisia (Massutí and Morales-Nin 1995; Potoschi et al. 1999; Vella 1999; Zaouali and Missaoui 1999; Morales-Nin et al. 2000; Sinopoli et al. 2012).

Fishing gears. The FAD used in this fishery has changed little since ancient times. Locally known as "capcers" in Spain (Balearic Islands), "cannizzi" in Sicily, "kannizzati" in Malta and "ghanatsi" or "jrid" in Tunisia, FAD have been exhaustively described in previous articles (Morales-Nin et al. 2000). In summary, they are moored floats with some palm fronds or bush branches tied on top to allow fishers to locate them and to increase their surface and expand shadows underwater. The float is usually made of cork, wood or, in some cases, a group of tires due to the floating characteristics of these materials and their low prices. Fishers anchor the FAD to the bottom with limestone blocks over depths ranging less than a hundred to over 1000 m; they are disposed seasonally along transects or swaths within the fishing regions.

Fish aggregated under FAD are collected with a specifically designed surrounding net without purse lines or purse rings (called "llampuguera" in the Balearic Islands, "lampuki" in Malta, "lampugara" or "caponara" in Sicily and "lamboukara" in Tunisia). The nets have been extensively described in the past (Massutí et al. 1999; Potoschi et al. 1999; Zaouali and Missaoui 1999; Morales-Nin et al. 2000; Morales-Nin 2003; Sinopoli et al. 2012) and have some particularities for the different regions (Table 15). Only some regions have the maximum dimensions regulated (Spain: Orden OAA/1688/2013; Malta: Council Regulation 1967/2006). The most developed net is the Maltese "lampuki", which consists of four main sections: two wings (the setting wing and the second wing), the body and a landing bag (Galea 1961). Modifications to this net are made throughout the fishing season by different fishers, including changes
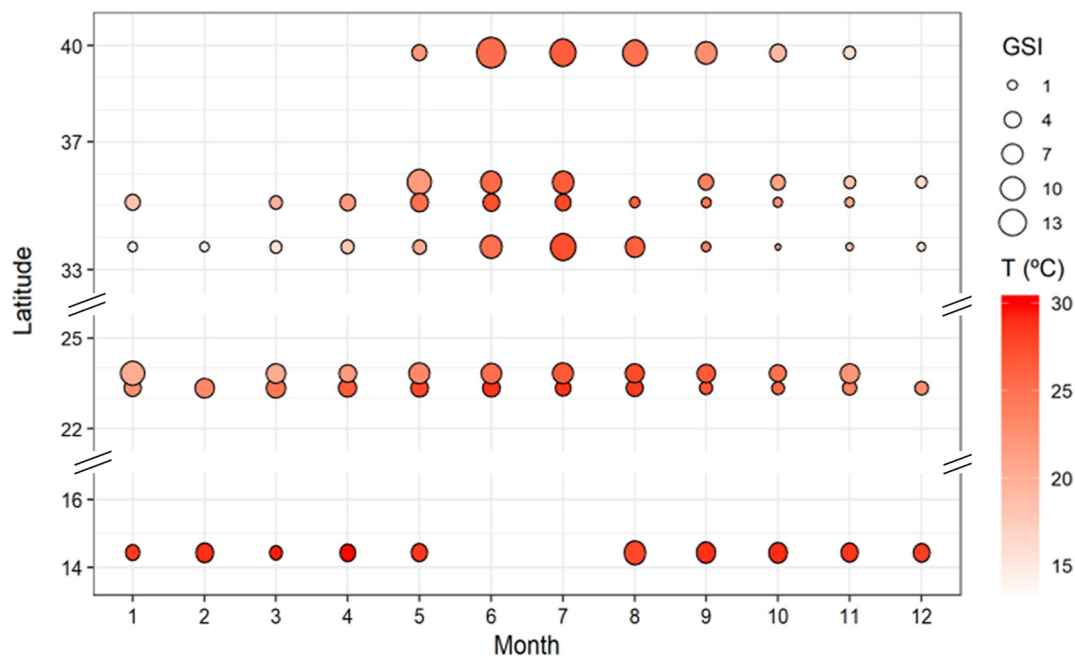
Figure 4. Relationship between Gonadosomatic Index values, latitude (N and S are treated equally) and temperature for each month. Data obtained from Oxenford 1985; Pérez et al. 1992 (in Oxenford, 1999); Massutí and Morales-Nin (1997); Wu et al. (2001); Schwenke and Buckel (2008); Alejo-Plata, Díaz-Jaimes, et al. (2011); Zúñiga-Flores et al. (2011); Furukawa et al. (2012); Gatt et al. (2015); Dos Santos et al. (2014); Rajesh et al. (2016).

Table 13. Reported oocyte diameters (mm) in mature ovaries of dolphinfish.

Region	Oocytes ∅ (mm)	Hydrated oocytes ∅ (mm)	References
Mediterranean	0.2–1	>1.2	Besbes Benseddik et al. (2015b)
Mediterranean	0.2–1.4	>0.8	Besbes Benseddik et al. (2019)
Mediterranean	0.2–1.5; two batches at 0.4 and 0.8 mm		Massutí and Morales-Nin (1997)
Eastern Atlantic	0.2–1.8	>1.2	Beardsley (1967)
Eastern Atlantic	0.72	>0.9	McBride et al. (2012)
Eastern Atlantic	0.75–1	–	Arocha et al. (1999)
Eastern Pacific	0.1–1.99	>1.3; mode at 1.42	Alejo-Plata, Díaz-Jaimes, et al. (2011)
Eastern Pacific	0.72	>0.9	Zúñiga-Flores et al. (2011)
Western Pacific	0.3–1.6	>1	Wu et al. (2001)
West-central Indian	0.25–1.58	0.96–1.03	Chatterji and Ansari (1982)
Northwest Indian	0.3–1.96	–	Saroj et al. (2018)

in the total length, which can be accomplished by changing the length of the wings, and can be made depending on the size, maneuverability of the vessel and the number of meshes (Darmanin et al. 2002).

Fleet and fishing operations. The whole regulated Mediterranean fleet using FAD and purse seines is approximately 700 boats, with a total length below 15 meters and engine power of less than 100 hp (details of fleet in each country can be found in the appendix). The number of boats per country has remained relatively stable and has oscillated between approx. 45 in the Balearic Islands to 300 in Tunisia in the last decade, with some interannual variability. The boat capacity varies between regions (from approx. 8 m length and 5.6 Gt in the Balearic Islands, to approx. 13 m and 17 Gt in some regions of Malta). The fishing methodology is

similar among Mediterranean countries. It consists on visiting the FAD swath at sunrise, and once the fish are detected visually or using a hand line, a quick haul is conducted close to or around the FAD if the weather is calm and there is no current. If the hand line is used, fishers use the hooked fish to attract the school and carry the haul around it. The catches obtained in the first fishing operations of the day determine the number of FAD visited. If the catch is sufficient, especially in Mallorca where TAC are self-imposed (see drivers of the *C. hippurus* harvesting chapter), the fishing day concludes without visiting all FAD. Otherwise, if the catches are not sufficient once all FAD have been visited, they can search for floating objects where dolphinfish could be found, or return to visit the FAD again at sunset (Besbes Benseddik et al. 1999; Zaouali and Missaoui 1999; Morales-Nin et al. 2000).

Table 14. Dolphinfish fecundity values.

Region	Length range (FL cm)	Min. Fecundity	Max. Fecundity	Mean Fecundity	References
Atlantic Ocean					
Western Atlantic	55–120			80000–1000000	Beardsley (1967)
West-central Atlantic	55–93	58000	1500000		Pérez et al. (1992)
Central Atlantic	49–129	45022	1930245	466410	Alejo-Plata, Díaz-Jaimes, et al. (2011)
Indian Ocean					
West-central Indian	55–80	139636	549540	300878	Chatterji and Ansari (1982)
Northwest Indian		107813	1550400	575391	Saroj et al. (2018)
Pacific Ocean					
Central Pacific	42–121	278413	2348463	1313438	Wu et al. (2001)
Eastern Pacific	61–114	33022	730555	279383	Zúñiga-Flores et al. (2011)
Eastern Pacific				324416	Solano et al. (2015)
Mediterranean Sea					
Western Mediterranean	65–117	195000	1381000	763857	Massutí and Morales-Nin (1997)
Central Mediterranean	64–106	385000	1134500	$660 \times 10^3 \pm 224 \times 10^3$	Besbes Benseddik et al. (2019)

Fishery regulations. The exploitation of this species in the Mediterranean Sea is subjected to different normative, based on technical measures and effort from the European to the regional level (Appendix). European legislation must be passed by all European countries involved in this fishery. In Tunisia, the legislation is based on association agreements. European legislation regulates special fishing permits (EC n1627/94), and management plans (EC n1343/2011 and EC n1967/2006), such as the closing period between January and August imposed by the FAO GFCM (Recommendation GFCM/30/2006/2). In some countries, the fishing season is opened later depending on the national legislation.

In the three European countries (Italy, Malta, Spain), the data collection normative established by the EU Regulation 199/08, Reg. EC 1004/2017 and Reg. EU 1251/2016 applies. In countries where dolphinfish is a priority species, the GFCM Data Collection Reference Framework and ICCAT data collection requirements must be complied. Only Malta has the obligation to record data on size due to the high percentage of dolphinfish catches in relation to the total catches of all species. Further details of the normative and restrictions at the regional level are provided in the appendix. It is worth mentioning that the only existing total allowable catch (TAC) is set in the Balearic Islands (Spain), where it is self-imposed by the associations of fishers resulting from a local agreement in 2012. Fishers have adopted individual landing quotas of a maximum of 300 kg per boat per day. This common agreement aims to avoid the drop in the market price during the period of maximum catches (Grau and Camiñas 2011; Maynou et al. 2013). As this is not a legal measure, it has varied over the years and can even change within a given year, thus hampering the estimation of proxies for abundance.

Pelagic longline fishery

In addition to the FAD fishery, dolphinfish can be captured by a specific type of longline in Malta alone, although this method is not widely used in the present days. This gear has a mainline of 60 mm monofilament, where a number of snooded hooks (approximately 350) baited with squid are set at approximately 12 m intervals. The line is attached to floats, allowing it to drift with the current (Galea 1961). There is also a variation of this longline used from land that is held afloat or pulled out to the sea by a sail attached to a triangular float (Darmanin et al. 2002).

Dolphinfish are also caught as by-catch of commercial Mediterranean surface longline fisheries that target swordfish (*Xiphias gladius*), Atlantic bluefin tuna (*Thunnus thynnus*) and albacore (*Thunnus alalunga*) (Massutí and Morales-Nin 1995; Macías et al. 2012, 2016). This fishery captures both juveniles and adults; catches are spread throughout the year but are extremely low in winter. The longline bycatches reported by Italy, Malta and Spain to ICCAT constitute less than 25% of the total dolphinfish catches when pooling small-scale fishers and longliners together. Estimates show low CPUE for dolphinfish, at approximately 1.08 fishes/1000 hooks. The longline targeting albacore operates closer to the coast with smaller hooks and bites, and captures mainly juveniles, with values up to 1.77 fish/1000 hooks (Macías et al. 2016). On the other hand, longlines targeting other large pelagic fish have a higher incidence of large specimens of dolphinfish (Macías et al. 2012, 2016). Recent studies have indicated that dolphinfish catchability in surface longline could be influenced by the north Atlantic oscillation (Báez et al., 2020).

Recreational fishery

The sport or recreational fisheries in the Mediterranean are important in Spain, Italy or Malta
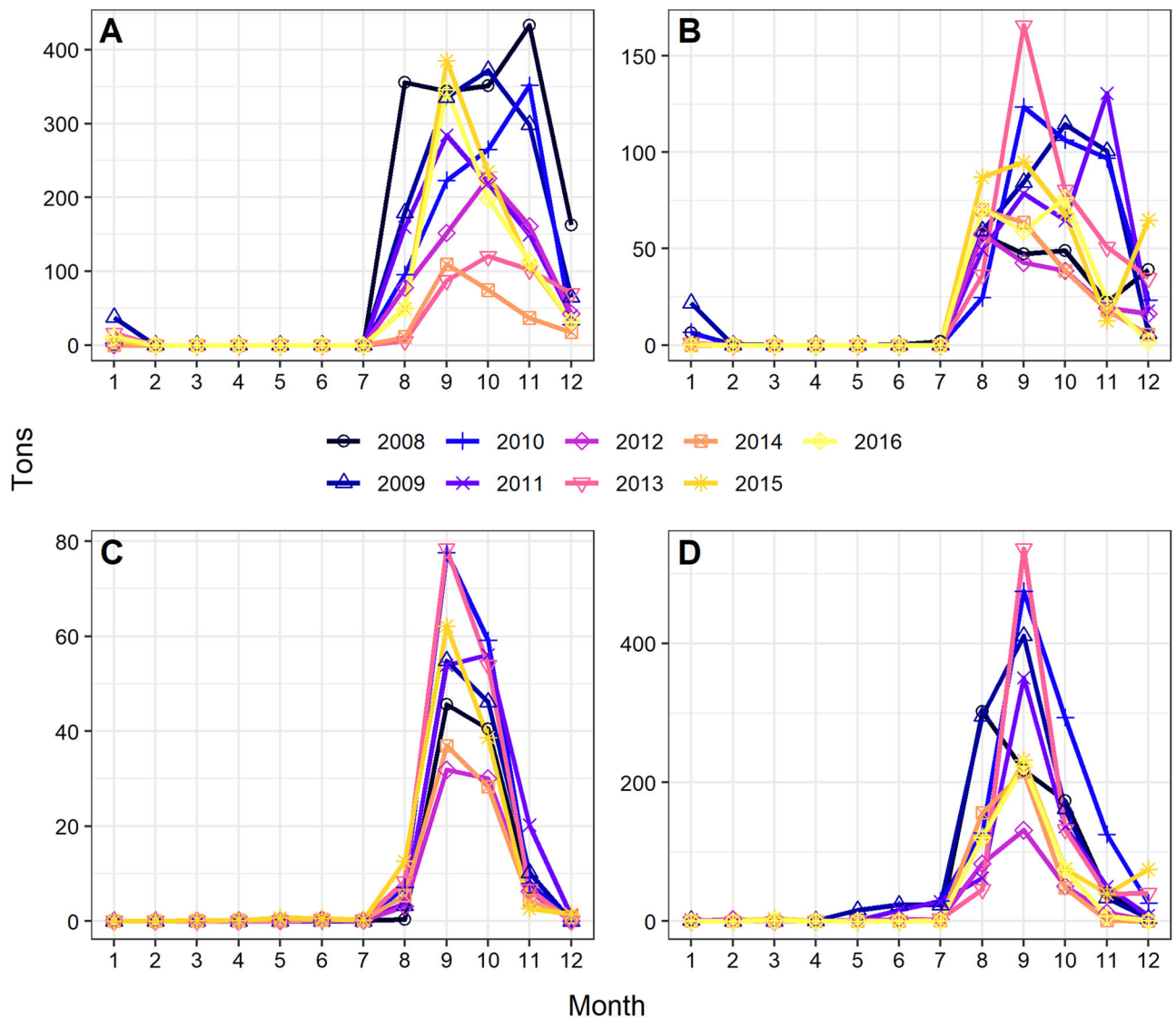
Figure 5. Seasonality of landings reported in each Mediterranean country between 2008 and 2016. (A) Italy, (B) Malta, (C) Spain, (D) Tunisia.

and exploit dolphinfish at different stages of development (Massutí and Morales-Nin 1995; Morales-Nin et al. 2010), from juveniles captured from the seashore to large adults captured in fishing game competitions. Anglers also capture dolphinfish from the seashore through "spinning", which consists of throwing a lure, generally a fish imitation, and picking it to mimic the movement of a fish. Fishing from sport vessels is carried out in very different ways, from "spinning" and "jigging" (similar to spinning but vertical) to the more usual trolling, which they also conduct from kayaks near the shore. Coastal trolling, known as "rixa" in Maltese or "fluixa" in Catalan, is practiced from August to September, although it has also been reported in November in Mallorca. It consists of a line with one or more hooks with a lure attached to each hook. A boat drags the lines from the stern sides at speeds varying from 2.5 to 5 knots. Usually, the line is hand-held and pulled forward and backwards to imitate the movement of an injured fish. In the past, these lures were usually feathers, but currently, plastic decoys are commonly used, varying from plastic pulpits to fish lures that simulate the swimming of an injured fish; natural baits, such as small pelagic fishes or squids, are also used.

Recreational fishers also look for floating objects, including marine debris, fattening cages or even FAD, which creates conflicts between commercial and recreational sectors. Some fishers bait the water with small pelagic fishes or squids to attract dolphinfish; as in the commercial FAD fishery, a hooked fish left in the water will attract new specimens, thus increasing boat
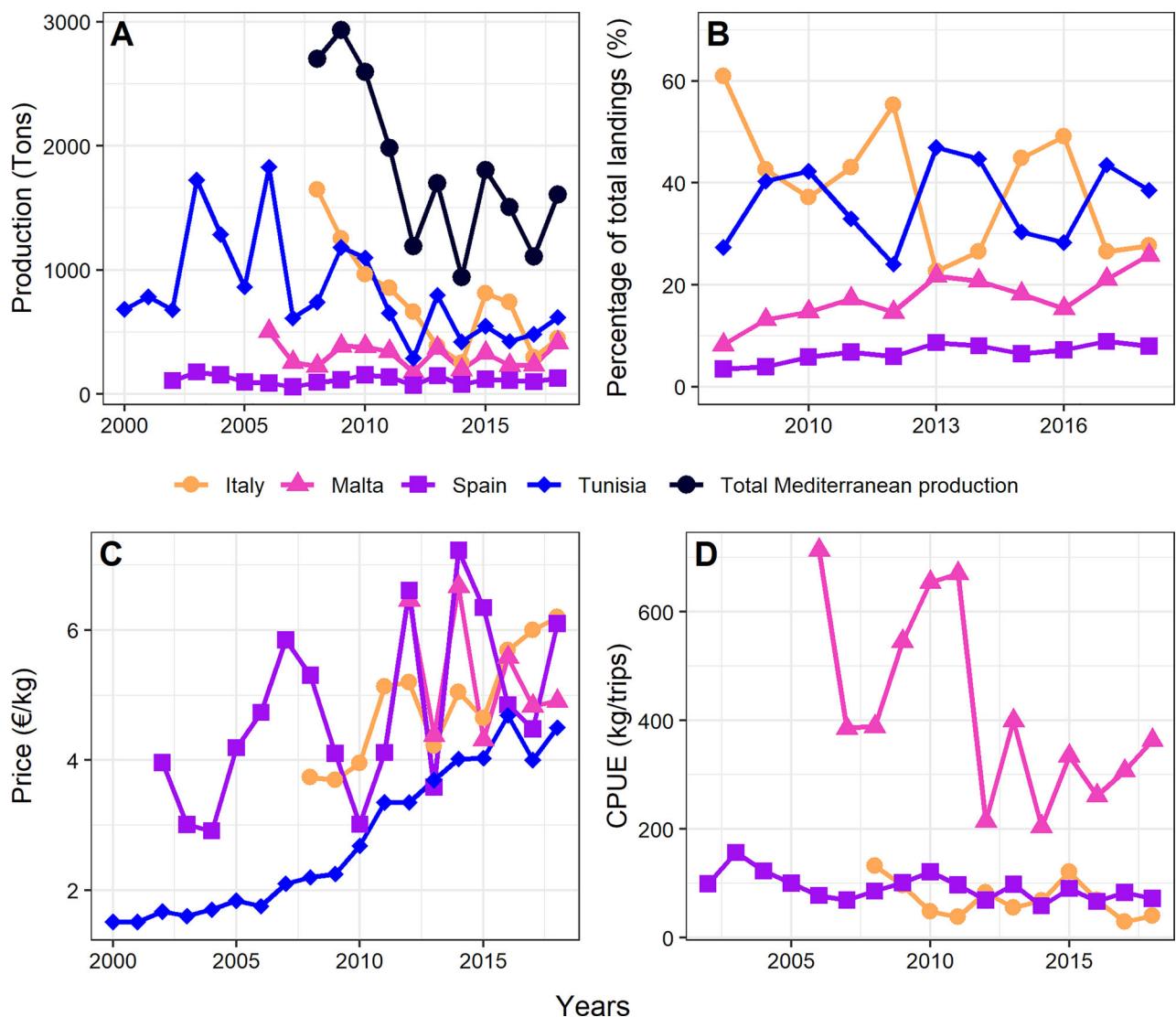
Figure 6. Historical series of Mediterranean fishery data per country. (A) Total annual production (in tons) for different countries, as well as for the entire Mediterranean; (B) Percentage with respect to the total landed by each country; (C) Evolution of price in €/kg and (D) Estimated CPUE in kg/trips.

catches. There is another type of trolling carried out in open waters, that mainly targets large pelagic species such as albacore (*T. alalunga*), or white marlin (*Tetrapturus* spp.) that also captures dolphinfish, which are generally adult spawners. Information on the number of anglers and catches involved in the dolphinfish recreational fishery is scarce and uncertain, as most data come from sport contests that are not recorded in a systematic and regular way and are not always available to scientists.

Drivers of harvesting

This section only refers to the FAD fishery, as no data exist for the other modalities. The monthly distribution of landings in the different Mediterranean countries shows the maximum annual production in September

or October and a progressive decrease toward January, with some interannual synchrony in the monthly harvest among countries (Figure 5). Since 2006, under a recommendation issued by GFCM, the fishery has been legally open from August 15th until December 31st, although an extension can be requested up to the end of January if a country can demonstrate that, due to bad weather, fishers were unable to utilize their assigned fishing days. The seasonal presence and exploitation of this resource allow the artisanal fleet to rotate target species and gears, such as longline or trammel nets, throughout the year (e.g., Palmer et al. 2017).

Despite the dolphinfish FAD fishery being highly selective, small amounts of bycatch (< 5% of total captures) are reported and are sold in the market. These species are pilotfish (*Naucrates ductor*) and

Table 15. Mean dimensions of the surrounding net used in different countries, MLA = Maximum Legal Allowed.

Country	Length (m)	Height (m)	Mesh diameter (mm)
Spain	180 (200 MLA)	16 (22 MLA)	50 in wings 30 in cod-end
Malta	180–200	36	35–43 mm in landing bag
Italy	180	45	–
Tunisia	200–400	15–35	30–40 in wings 20 in cod-end

juvenile greater amberjack (*Seriola dumerlii*). In the case of Malta, the bycatch also includes the chub mackerel (*Scomber japonicus*) and horse mackerel (*Trachurus trachurus*) and, in some rare cases, juvenile albacore (*T. alalunga*) and Atlantic bluefin tuna (*T. thynnus*), but these are not retained since they are below the minimum allowed landings size. Due to the key economic role of FAD fishery for the artisanal fleet (Lleonart et al. 1999; Quetglas et al. 2016; Palmer et al. 2017), the temporal evolution of the key parameters of the fishery reported by official statistics from each country are discussed below.

Spain. The fishery almost exclusively operates from Mallorca island (Balearic region), where this species ranks first in disembarked captures (tons) and is one of the most economically relevant species (Morales-Nin et al. 2010; Quetglas et al. 2016; Palmer et al. 2017). Therefore, the data presented in the Figure 6 are only for the Balearic region.

Morales-Nin et al. (2000) analyzed the annual landings of dolphinfish in the 1980s and 1990s for Mallorca, Malta, Italy and Tunisia. In the case of the Balearic region, the historical data were characterized by wide fluctuations, especially during the 1980s, with a general increasing trend until 1996 reaching more than 120 tons (Morales-Nin et al. 2000). Since 2002, landings have fluctuated by approximately 100 tons per year (maximum of approximately 177 tons in 2003, a minimum of approximately 57 tons in 2007, Figure 6a). The catches are the lowest of all countries due to the small fleet, but the percentage contribution to total dolphinfish catch has slightly increased in the last 10 years (Figure 6b).

In terms of the prices per kilogram (Figure 6c), there was an ascending trend from 2004 to 2007 followed by a marked decrease during the second half of the 2000s (2007–2010), when the prices decreased from near 6 €/kg to 3 €/kg. This led fishers to establish a series of agreed upon measures to revert this trend so that the revenues and profitability of the fishery remained stable or increased. Those measures included the reduction of working hours (fishing effort) and the establishment of an individual daily

quota. Regarding the working time, a rest period of 24 consecutive hours (from 12:00 on Saturday to 12:00 on Sunday) was set in July 2001. Subsequently, in July 2002, the authorities extended the resting time to 30 h (Orden APA/52/2002) and finally, in July 2005, to 48 consecutive hours during the weekend. On the other hand, fishers self-imposed a quota of 300 kg per boat and day in 2012 (by an agreement among fisher associations), to avoid the low prices in years of high captures. Price fluctuated greatly after the establishment of the quota, suggesting that the quota did not stabilize the prices (Grau and Camiñas 2011; Camiñas et al. 2016). In any case, the trend in average price/kg is inversely proportional to the landings (Figure 6a, d), suggesting an inverse harvest-price relationship.

Malta. Historical data show an increasing trend in catch from the beginning of the 1980s to a peak of more than 520 tons in 1984 followed by a decrease; since then, catches have fluctuated around 350 tons (Morales-Nin et al. 2000; Figure 6a). The contribution of Malta to total Mediterranean catches has, however, progressively increased from approximately 10% to more than 20% during the last decade due to the decline in the overall Mediterranean catches (Figure 6b). The interannual price oscillations from 2012 are synchronous with the prices in Mallorca and Italy, with similar values to those in Mallorca (Figure 6c), showing the same harvest-price relationship.

Italy. Dolphinfish exploitation is concentrated along the Sicilian coasts, where 80% of captures occur, mainly along the southeastern Ionian and northern Tyrrhenian coasts. Together with Tunisia, Italy catches a large proportion of the dolphinfish in the Mediterranean (Figure 6a, b). The annual landings of this species showed a sharp decreasing trend from 1646 tons in 2008 to 250 tons in 2014. Since 2014, landings have fluctuated according to the total catches reported in the Mediterranean Sea. The approximate number of boats decreased from 350 to 200 in 2015, a fact that could contribute to the reduction in catches (Copemed II 2016). Interestingly, the interannual importance of this country in the total dolphinfish landings in the Mediterranean was inverse to that of Tunisia ($R = -0.90$, Figure 6b), suggesting a spatial displacement of the species in some years: northern displacements would favor Italian FAD fisheries, and southern displacements would explain increases in the Tunisian contribution to the total catch. In terms of the market price, there was a general upward trend throughout the years analyzed, reaching average values

of approximately 6 €/kg since 2016, which was the highest with respect to those of the other countries (Figure 6c). Cannizzaro et al. (1999) and Morales-Nin et al. (2000) concluded that dolphinfish can be considered a profitable resource in Sicily, where it ensures one of the highest profit rates, ranging from 30 to 46% in the fishery market.

Tunisia. Until the 1980s, the catches did not exceed 300 tons and were limited to the eastern region. Since then, fishers in the north and south have taken interest in the lucrative fishery and now contribute 25% and 18% of the national production, respectively. The Tunisian national production underwent a spectacular increase starting in 1992, reaching peaks of more than 1500 tons in 2003 and 2006 (Figure 6a). This increase could be explained by a relative abundance of the resource along the Tunisian coasts, the government incentives and the technological upgrading undertaken during this period (fleet renovation, modernization of fishing and navigation equipment and upgrading of personnel), and the strong interest of professionals in this seasonal and remunerative artisanal activity (Besbes Benseddik 2017). From 2010, the average recorded catches dropped by half, with a minimum record of 288 tons in 2012 (Figure 6a). Some causes of this decline could be related to an (unassessed) drop in the resource (see total Mediterranean production in the same figure), the fishing effort exerted by other countries (in 2012, the Sicilian fleet had a much higher proportional catch than Tunisia in nearby waters, Figure 6b) or/and the transitional socio-economic situation suffered by this country since January 2011 (lack of monitoring and control of fishing activity, unreliability of statistical data, discouragement of professionals, etc.). The market price constantly increased from 1.5 €/kg in 2000 until reaching 4.6 €/kg in 2016 (Figure 6c). This is probably attributable to the reduction in catches and in part to the continued fall of the Tunisian dinars against the euro. This situation may cause serious impacts on the consumption of this product and to this traditional fishery (Besbes Benseddik, pers. comm.).

Catch per unit effort. The currently available information on fishing effort is restricted to the number of catches landed (in tons) in reference to the number of fishing trips per month and is collected in European countries (hence is not available for Tunisia) within the data collection framework (Reg.EC 1004/17, 1639/00 and 199/08). Malta shows a higher CPUE than Mallorca and Italy, which are more or less similar

(Figure 6d). The high CPUE values in Malta are probably due to a high number of FAD visited per trip; the CPUE in terms of landings by operated FAD were approximately 20 kg/FAD in 2011 and approximately 11 kg/FAD in 2014. This was the first indication that CPUE were not comparable among countries as proxies for abundance. The CPUE values for Mallorca have remained relatively constant, with slight fluctuations over time (Figure 6d).

The Mediterranean dolphinfish FAD fishery, contrary to other FAD fisheries, such as those for tropical tunas, operates almost exclusively on moored FAD. During a fishing journey, fishers may not necessarily visit all FAD, and there may be no fish at any visited FAD. Moreover, it is not possible to routinely collect parameters such as searching time, vessel power or fish hold volume for CPUE estimation, as all boats are artisanal, of reduced dimension and power and not subject to mandatory monitoring. In the case of Spain, the dolphinfish fishery is monospecific, and the use of other gear or the exploitation of other species during the fishing season is forbidden. In other countries, this fishery is multi-specific and the fleet can fish other species in the same fishing trip, posing further difficulties to the estimation of CPUE, which is also affected by the changing market price as the season progresses.

Another important factor that affects the CPUE in this fishery is the weather conditions, as small vessels cannot operate FAD in strong currents or on rough sea. Hence, the relationship between a bad weather indicator and landings should be explored to improve CPUE estimates (Copemed II 2016). Furthermore, in some years, the number of FAD initially deployed can decrease by 50% due to meteorological damage. The high vulnerability of the fishery to weather conditions explains the modification of the GFCM recommendation extending the fishing season when fishing operations have not been possible due to bad weather conditions.

The proper estimation of effort is complex and is currently under discussion (Copemed II 2016, 2019). That group proposed that a more precise estimate of effort should account for (i) the number of FAD fished by vessels in each fishing trip; (ii) the number of FAD assigned to each vessel and (iii) the fishing time. Although fishing effort is defined by the GFCM data collection reference framework (DCRF) as the total number of FAD, total number of fishing trips, number of FAD targeted per fishing trip, average number of FAD fished per fishing trip where a net was deployed to catch aggregated fish and average number of FAD visited per fishing trip (regardless of

whether they have been fished), there is no obligation to report any of those figures, and it has not been established whether they are complementary or exclusive.

Stock assessment

Despite the relevant commercial interest in this species in these Mediterranean countries and the long history of this traditional fishery, few attempts to quantitatively assess the status of the stocks have been undertaken thus far. The difficulties inherent to the population dynamics of this highly migratory, fast-growing and short-lived fish, together with the fact that the fishery is targeting only the young-of-the-year as well as the complexity of measuring fishing effort have hampered the application of classical analytical models.

Previous attempts in the Mediterranean date back to the late 1990s. Lleonart et al. (1999) conducted a virtual population analysis (VPA) of the Mallorca FAD for two separate years, 1995 and 1996, adapted to a single year pseudo-cohort with the time units in fortnights rather than years. This analysis allowed the identification of the evolution of recruitment pulses, although it did not provide a picture at the population level. The work could not provide conclusive reference points but rather insight into the evolution of cohorts that exhibited fast depletion over five months. The activity occurs from August to November when the temperature is higher, and the weekly fishing mortality rates are extremely high, reaching values of approximately $14 \, y^{-1}$. The weekly and monthly CPUE were estimated using different effort units: number of vessels, fishing days, fishing hours and the number of operated FAD. The number of fished FAD was the most stable and representative unit of effort (Lleonart et al. 1999). A second assessment exercise was carried out in 2004 by the CORY-WG, which assessed different models: The non-equilibrium production model IFOX with the CPUE data for the 1984–2001 period from Malta and Spain resulted in very poor goodness of fit (below 4%) which prevented the estimation of the maximum sustainable yield (MSY) or other reference points. The Jones LCA, which was applied to the annual average catch length composition from 2000-2001, yielded no better results due to the short and incomplete data series, and the restrictive equilibrium assumptions given the wide and complex dynamics of the Mediterranean dolphinfish. A separable VPA applied to the catch-at-age data (on a monthly basis) for 2001 (Tunisia, Malta, Majorca and Sicily) yielded some reference points ($F = 14.5 \, y^{-1}$ (average for sizes

30–50 cm) and $F = 11.7 \, y^{-1}$ (average for sizes 17–65 cm)) but was not considered reliable due to model sensitivity problems.

On the southwestern coast of India, Benjamin and Kurup (2012) used one-year data (2008–2009) from the longlines, purse seiners and troll fisheries of three ports in the Kerala region to conduct a length-based VPA. It resulted in fishing mortality rates of approximately $12–16 \, y^{-1}$ for the length range between 145 and 175 cm (TL), which was similar to that obtained in the Mediterranean Sea (Lleonart et al. 1999; FAO-GFCM 2004). The exploitation rate in SW India was 0.38, which was well below the optimum for the maximum Y/R, showing that the species was not overexploited and suggesting the potential for an increase in fishing effort.

There are some recent trials that have applied data-limited methods: in the eastern Pacific Ocean, where dolphinfish is by-catch of the tuna fishery through different gears, the Inter-American Tropical Tuna Commission (IATTC) has developed a method based on the depletion of an annual cohort based on the negative exponential decay on a monthly basis. The method, called the monthly depletion estimator, is similar to the catch-curve analysis. It measures the relative abundance of a cohort as it ages throughout its first year of life, using the CPUE (Aires-da-Silva et al. 2014). Further modifications with standardized indices of CPUE have led to the improvement in the model (Aires-da-silva et al. 2016). No reference points, targets or limits could be defined, and therefore, conclusions on stock status have not been drawn thus far. Notwithstanding, according to these authors, recent catches are near the estimates of MSY and there are no signs of risk for the population in the eastern Pacific.

The stock-recruitment relationship of this species is poor, and the recruitment dynamics are probably highly dependent on environmental conditions (Aires-da-silva et al. 2016). The available information on stock assessments, coupled to the great capacity of recovery of this species, with several spawning pulses during the year even at very young ages (one year), suggests that the species is not at risk of overexploitation in the areas studied.

Conclusions and future lines of research

This review summarizes and expands the knowledge of the biological parameters of dolphinfish in a global context, synthesizing the information on distribution, habitat of the different life stages, diet, age and growth

and reproduction, with specific emphasis on the Mediterranean region and its fisheries.

Despite the global distribution of this species and its migratory behavior, genetic studies covering wide regions (Díaz-Jaimes et al. 2010; Maggio et al. 2018) suggest that there are separate populations in different regions. These populations present different biological traits such as growth (Chang and Maunder 2012; Chang et al. 2013) or reproductive biology (this work), in response to the different environmental conditions of those regions. There is a lack of knowledge on the mobility of this species among these regions on an ecological scale. This knowledge is crucial in terms of fisheries management, stock assessments, and the calculation of potential environmental effects on the distribution shifts of the species. Further research focused on collaborative tagging programs, such as the dolphinfish research program in the western Atlantic (Merten et al. 2014a) would improve the existing knowledge about the migratory patterns of this species.

Biological traits, such as growth and reproduction, are strongly influenced by environmental parameters and food availability (Lorenzen 2016; Ashworth et al. 2017), which can explain the observed regional/seasonal differences in the biological traits of this species between and within regions (Furukawa et al. 2012). In the future, modeling approaches should be adopted to integrate extrinsic and intrinsic factors into predictable patterns of distribution or traits. For highly mobile species such as C. hippurus, new tagging technologies, computer capabilities and modeling approaches aid the transition into the new era of spatial ecology (Lowerre-Barbieri et al. 2019). These efforts are even more needed at the limits of the species distribution, such as the Mediterranean Sea, where the effects of projected increasing temperatures may crucially impact this thermophilic species and the communities exploiting it.

Knowledge of dolphinfish larval ecology is scarce. Physiological thresholds derived from laboratory experiments have been recently collated (Perrichon et al. 2019), but better field estimates of optimal environmental windows for spawning and recruitment are still needed. Understanding the recruitment variability in this species is a key element because its fisheries depend on the young of the year, particularly in areas such as the Mediterranean Sea. In fact, interannual variations in the catches from the Mediterranean, which cannot be explained by changes in the exploitation rates, could be attributed to variations at the recruitment level, although this point has not been confirmed quantitatively. Even basic information on C. hippurus spawning grounds and the larval distribution in the Mediterranean is scarce, partly due to the reproductive behavior of the species (reproductive specimens tend to be caught in pairs of males and females, which probably explains the dilution of reproductive outputs) and to the larval characteristics. Their quick swimming, rapid growth and offshore surface distribution make them difficult to capture within the standard ichthyoplankton surveys conducted through oblique tows. There is also a need for the determination and comparison of trophic requirements in the earliest life stages in reproductive areas that may differ in the structure of the first trophic levels.

Concerning the Mediterranean fisheries, clear improvements are possible in terms of fisheries operation. A conservative estimate suggests that approx. 60,000 FAD targeting the species are anchored every year in the Mediterranean Sea, representing approximately 30% of the FAD worldwide (including those not anchored) and 90% of those anchored (Morales-Nin 2011). Improving the profitability of the fisheries might rely on the reduction in the number of FAD visited before the desired quota per trip is attained. The use of eco-sounder buoys could be a potential solution to reduce the number of anchored FAD (Cillari et al. 2018). Several authors have suggested that a large number of FAD impacts the distribution of epipelagic fish species (Dempster and Taquet 2004; Sinopoli et al. 2007, 2011, 2015, 2019), and in some places even the benthic community (Pace et al. 2007; Deidun et al. 2014). These aspects should be further evaluated.

In terms of stock assessments and fisheries management in the Mediterranean, there is a growing interest in evaluating the population under the hypotheses of a stock shared by different countries. International regulation (GFCM-DCRF and EU Reg 199 (08)) set the fishing season and data collection obligations. The latter differs for the different countries depending on the share of the dolphinfish landings compared with other commercial species. In addition, national regulations affect the fishing gear, the area where FAD are deployed and the time at sea. A more detailed definition of data collection (and enforcement) is needed, including the effort units in the number of FAD operated by fishing trips. Market drivers and weather conditions have relevant effects, further suggesting the inadequacy of catch series as potential indicators of stock status. A novel abundance index for FAD fisheries target species has been proposed based on the acoustic estimation of biomass

from eco-sounders attached to FAD (López et al. 2016; Santiago et al. 2016). These methods could be experimentally applied to the Mediterranean dolphinfish FAD fishery. This should be coupled to movement and behavior information around the FAD to avoid hyperstability biases (Ehrhardt et al. 2017), as no information from free schools is available for this fishery to be compared with FAD catches. A thorough analysis of the standardization of CPUE through statistical approaches (e.g. GLM or GAMs) is also proposed to properly apply production (or depletion) methods.

With all these considerations in mind at the Mediterranean level, new attempts to assess the current status of the dolphinfish fishery are amongst the research priorities of the four main Mediterranean countries exploiting this resource. The GFCM, FAO and in particular the *ad hoc* working group (Cory-WG), should work in the uncovered research directions in the near future to improve the existing quantitative tools to better understand and improve scientific advice to manage this complex living resource.

Acknowledgments

Disclosure statement

No potential conflict of interest is reported by the authors.

ORCID

Vicenç Moltó http://orcid.org/0000-0002-9918-2216

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Appendix

This section contains the extended information regarding the fleet, fishing gears and the management regulations for the Mediterranean dolphinfish FAD fishery.

Fleet

The Spanish fleet is composed of artisanal boats, locally known as "llauts", traditionally built in local shipyards, offering a traditional job in this region since the beginning of the last century. The active fleet fluctuate around 50 vessels. Although these boats operate in established regions near their base harbors, the landings must be disembarked at the Mallorca central fish auction wharf, due to the commercial requirements and for a better control of landings.

In Italy, most of the vessels are concentrated along the Sicilian coasts (mainly in the southeastern Ionian and the northern Tyrrhenian coasts). There is an estimated number of 150 vessels plus another 30–50 vessels in other Italian regions such as Calabria, and other areas of the Tyrrhenian Sea, such as Campania and Liguria. In the case of Sicily, there are differences between the western and eastern fleet. These differences are related with the different fishing methods carried out throughout the year. In the western Sicily, the boats generally operate near the coast, and are engaged in fishing dolphinfish from September to December, while the rest of the year they fish using "trammel-net", bottom long-line or gill-nets. On the other hand, the eastern Sicily fleet is involved in the dolphinfish fishery only a limited period of the year, when this species is present. Then, they engage in other fisheries, some of them farther away from the coast, where the length and power of the boats take considerable importance, reaching 14–15 m in some cases. As a result, from the end of the dolphinfish fishery until March they fish with hand lines or bottom long lines. From March to August, they are involved in the swordfish (*Xiphias gladius*) fishery using pelagic long lines, or fishing small and medium-sized pelagic species with purse-seine nets (Potoschi et al. 1999; Morales-Nin et al. 2000).

Tunisia has the largest fleet dedicated to this fishery, with almost 300 fishing boats from 20 different harbors. Most of them (approximately 200 boats, 72% of the fleet) are located througout the eastern coast, while the rest is distributed througout the northern coast (approximately 100 boats, 24% of the fleet) and the southern coast (approximately 20 boats, 6% of the fleet) (Besbes Benseddik et al. 2000; Besbes Benseddik and Besbes, 2005). The elevated number of boats operating in the eastern coast reflects the importance of this traditional activity and the relative abundance of this resource in that region. Nonetheless, the fishing activity in the northern and southern regions has incrased the recent years (Besbes Benseddik and Besbes, 2005).

The technical specifications of the fleets operating in different countries are summarized in the following table:

Table A1. Characteristics of the Mediterranean artisanal small-scale fleet.

Region / Strata	Length (m)	Gross tonnage (Gt)	Power (Kw)	Number
Spain (Mallorca island)	8.3	5.6	64*	45
Malta 1**	9.9 ± 3.42	6.±7.66	97.8 ± 70.7	45
Malta 2**	11.6 ± 4.37	9.0 ± 8.14	113.7 ± 76.5	19
Malta 3**	13.3 ± 4.82	17.5 ± 14.66	188.8 ± 107.8	27
Sicily West	9.9	5.8	–	150
Sicily East	11.4	10.4	–	
Tunisia North	9.8 ± 1.60	8.3 ± 3.2	54.8 ± 23.6	71
Tunisia East	10.2 ± 1.50	8.4 ± 3.3	57.4 ± 27.5	205
Tunisia South	12.3 ± 1.70	15.5 ± 4.8	118.4 ± 64.4	18

*Data in hp units.
**Fleet data based on 2000 data.

Fishery legislation

Spain

This fishery is managed by the agriculture, food and environment ministry of Spain, advised by the fisheries directorate of the Balearic Islands regional government (Orden OAA/1688/2013).

Briefly, each boat involved in the fishery is provided with a mooring area that is raffled among all fishermen at the beginning of the fishing season. This raffle is conducted by the representative entities of the fishing sector before the July 15th. Afterward, the ministry is informed of the assignated mooring areas. To participate in the raffle, each boat owner or boat master must prove the ownership of a "llampuguera" and a minimum of two crew members enrolled in the boat. The boats authorized to fish dolphinfish can not fish with other fishing gears or target other species during the fishing season (Orden OAA/1688/2013).

Malta

The importance of this fishery led to the development of a management plan for the lampuki FAD fishery in 2013 (DFA 2013), with two main objectives: (i) to ensure the sustainability of the dolphinfish stock, with the target of maintaining stable the trends of the local annual catches, which are around 350 tons on average; and (ii) to ensure the financial stability of the fishers, considering landing data of local catches and socio-economic data (the gross profit per vessel) as indicators.

Other measures indicated in the management plan are that no more than 130 vessels will be authorized to take part in the FAD fishery and all the vessels, including those smaller than 10 m, would be forced to land in the designated ports and annotate their landings in catch logbooks (DFA, 2013). Apart from these national measures, the management plan emphasizes that, to ensure the sustainability and stability of Maltese catches, a regional management plan is required to manage the stock, as dolphinfish could be considered a shared stock among other Mediterranean regions.

Italy

The boats involved in the FAD fishery must be specifically authorized. The fishing operations are always conducted

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Table A2. Summary of legislation applicable to dolphinfish fishery for each region.

Region	Regulation	Period to deploy FAD	FAD Positioning	Fishing period permitted	Number of FAD per boat	FAD technical measures	Obligation to remove FAD after fishing season	Obligation to report biological data of landings
Spain	Orden AAA/1688/2013	–	Maximum distance of 18nm from the base harbour; Between 70 and 1200m depth; Obligation to remove FAD after fishing season	August 25th –December 31st. 48h resting period per week.	30 approx. 50 max. per boat	• 1.5 x 1.2 max. dimensions; Soft materials such as cork or polystyrene. Hard materials are banned; Identified with the boat ID; Signalling buoy equipped with one or two flags (not white colour) and a yellow light projecting visible flashes at a distance of 2nm every 5s	Yes	NO
Malta	Chapter 425 and its subsidiary legislation	–	• Assigned swaths FAD separated 1 nm from each other 7 nm from the coast	August 15th – December. It can be extended up to January	–	Identified with the boat ID	–	• Date of captures; Length frequency distributions; Weight; Sex distributions; Maturity stages; N boats operating FAD; N fishing trips and FAD visited in each trip; • N of fishing days; N captures
Italy	–	Mid August		Mid August - November/December, depending on meteorological conditions	Depends on local tradition, regional legislation and the size of the boat. From 20 to 90/boat. 40 in average	See regional regulation	See regional regulation	
Italy - Portorosa	Ordinance CG Milazzo 40/2013	–		Sept 15th - Dec 31st	–	• Net no longer than 300m; FAD materials must be biodegradable	yes	–
Italy - Augusta	Ordinance CG Augusta 87/2013	Aug 1st		Aug 16th - Dec 31st	20	• FAD materials must be biodegradable; Long line forbidden 500m around	Yes, within 100m deep **	–
		Aug 1st		Aug 16th - Dec 31st	–			–

Italy -Capo Passero	Ordinance CG Siracusa 116/2013				• FAD materials must be biodegradable Long line forbidden 500m around	Yes within 100m deep**
Italy -Palermo	Ordinance CG Palermo 51/2013	Aug 15th		Sept 1st - Dec 31st	–	Yes within 100m deep **
Italy -Trapani	Ordinance CG Trapani 51/2013	Aug 20th		Sept 1st - Dec 31st	–	Yes within 100m deep **
Italy - Isole Eolie	Ordinance CG Milazzo 40/2013	Sept 15th		Sept 30th - Dec 31st	FAD materials must be biodegradable.	Yes
North Tunisia	Law 94 -13 of 31 January 1994 Decree 95-252 of 13 February 1995 Decree of 28 September 1995 Annual decree	According to the annual decree	30 - 60m depth At least 500m between FAD swaths	August 15th to December 31st, but it could be restricted by the annual decree	According to the annual decree	–
Centre Tunisia	Law 94 -13 of 31 January 1994 Decree 95-252 of 13 February 1995 Decree of 28 September 1995 Annual decree	According to the annual decree	120 – 180m depth At least 500m between FAD swaths	August 15th to December 31st, but it could be restricted by the annual decree	According to the annual decree	–
South Tunisia	Law 94 -13 of 31 January 1994 Decree 95-252 of 13 February 1995 Decree of 28 September 1995 Annual decree	According to the annual decree	120 – 180m depth At least 500m between FAD swaths	August 15th to December 31st, but it could be restricted by the annual decree	According to the annual decree	–

by a multi-gear fleet that can use different gears throughout the fishing season. The fishing activity commonly starts in the Ionian (eastern part of Sicily) and progressively extends to the other areas.

The number of FAD deployed in Sicily is regulated by local agreements, set up by 7 different COGEPA (fishers associations). These agreements are part of a local management plan supported by the EU Fisheries Funds to implement local regulations.

Tunisia

This fishery is regulated by annual ministerial decrees issued by a national steering committee. The committee is constituted by researchers from the Institut National des Sciences et Technologies de la Mer (INSTM), professionals of the fishing sectors (fishers or fishers unions), the regional delegate of fishers, the heads of ports, health authorities and the supervisory authorities (defense and national security). This committee meets as many times as needed until the end of July or early August, through the proposal of the general director of fisheries and aquaculture.

At the end of July, exploratory surveys are conducted by scientists of the INSTM in the framework of the steering committee, to detect the presence of dolphinfish and determine the length distribution of the dolphinfish beneath the FAD. If the size of the dolphinfish do not reach the minimum regulated size, which is established in 30 cm FL, the opening of the fishery can be delayed.

The ministry of agriculture publishes an annual decree before the fishing season opening considering the measures described above, which fixes the restrictions for the current fishing season. The boats must have a special authorization; however, the dolphinfish fishery is not exclusive during the season. Vessels are allowed to fish dolphinfish in a multi-gear fishery context. Thus, depending on the weather conditions, or on the success of the first hauls, they can also fish other species on the same trip.

Additional details of regional regulations are summarized in the table A2.