Reproduction of greater amberjack (Seriola dumerili) and other members of the family Carangidae

Journal:	*Reviews in Aquaculture*
Manuscript ID	RAQ-11-20-0300.R3
Manuscript Type:	Review
Date Submitted by the Author:	n/a
Complete List of Authors:	Corriero, Aldo; University of Bari Aldo Moro, Emergency and Organ Transplantation, Section of Veterinary Clinics and Animal Production Wylie, Matthew; New Zealand Institute for Plant and Food Research Ltd, Seafood Production Unit Nyuji, Mitsuo ; Japan Fisheries Research and Education Agency, Fisheries Resources Institute Zupa, Rosa; University of Bari Aldo Moro, Emergency and Organ Transplantation, Section of Veterinary Clinics and Animal Production Mylonas, Constantinos ; Hellenic Center for Marine Research, Institute of Marine Biology, Biotechnology and Aquaculture
Keywords:	fish reproduction, fish rearing in captivity, fish reproductive dysfunction, fish gametogenesis, fish reproduction control, Carangidae

Reproduction of greater amberjack (*Seriola dumerili*) and other members of the family Carangidae

Corriero Aldo[1], Wylie Matthew J.[2], Nyuji Mitsuo[3], Zupa Rosa[1] and Mylonas Constantinos C.[4]

[1] Department of Emergency and Organ Transplantation, Section of Veterinary Clinics and Animal Production, University of Bari Aldo Moro, Valenzano (Bari), Italy

[2] The New Zealand Institute for Plant and Food Research Limited, Seafood Production Unit, 293–297 Port Nelson, Nelson 7010, New Zealand

[3] Fisheries Resources Institute, Japan Fisheries Research and Education Agency, Yokohama, Japan

[4] Institute of Marine Biology, Biotechnology and Aquaculture, Hellenic Center for Marine Research, Heraklion, Crete, Greece

Correspondence: Constantinos C. Mylonas, Institute of Marine Biology, Biotechnology and Aquaculture, Hellenic Center for Marine Research, P.O. box 2214, Heraklion, 71003, Crete, Greece. Email: mylonas@hcmr.gr

Table of Contents

Abstract

The family Carangidae contains several species of aquaculture interest, including the amberjacks, yellowtails and trevallies. Among them, the greater amberjack (*Seriola dumerili*), the Japanese amberjack or yellowtail (*Seriola quinqueradiata*) and the yellowtail kingfish (*Seriola lalandi*) are considered the species with the highest potential for commercial aquaculture. Understanding the reproductive physiology-biology, spawning kinetics and production characteristics in captivity is of utmost importance for the domestication of any animal, and developing broodstock management methods and therapies to optimize egg production and overcome potential reproductive dysfunctions are essential. The present article reviews the available literature on the reproductive biology of the Carangidae species of interest for the aquaculture industry, both in the wild and under farming conditions. The reproductive traits of wild and farmed fish, whenever available, were compared in order to improve the understanding of the reproductive dysfunctions occurring in captivity. Finally, the hormonal maturation and spawning induction protocols examined so far to ameliorate the reproductive dysfunctions and obtain fertile gametes are summarized, and their effectiveness in the different rearing conditions are discussed.

1. Introduction

The genus *Seriola* (family Carangidae) includes 12 species that are distributed in all tropical and temperate waters (Table 1). Some of them have been notable species for aquaculture worldwide, while other carangid species have also been considered as potential cultured species. Among them, the greater amberjack (*Seriola dumerili*) has attracted significant interest in Europe and Japan since the 1990s, because of its fast growth and cosmopolitan distribution and appreciation. However, failure to control reproduction in captivity has prevented its commercial production (Ottolenghi *et al.* 2004). With the need to diversify aquaculture worldwide, a renewed interest in studying the reproductive biology of greater amberjack and developing methods to control egg production in captivity has emerged (Nyuji *et al.* 2016; Zupa *et al.* 2017b), and a significant body of information has been produced in recent years for this species. For other members of the *Seriola* family, such as the Japanese amberjack or yellowtail (*S. quinqueradiata*), which is a very important fishery resource in Japan, aquaculture research had already begun in the 1970s (Kagawa 1992; Nakada 2002; Yamazaki *et al.* 2002). Following the work on yellowtail, more recently the reproductive biology and physiology of yellowtail kingfish (*S. lalandi*) have also been studied (Nakada 2002) and this species is currently reared commercially worldwide.

The greater amberjack is a cosmopolitan species found throughout the temperate zone, where it spawns naturally from February to April in the Gulf of Mexico (Wells & Rooker 2004), from April to June in Japan (Kawabe *et al.* 1996, 1998; Nyuji *et al.* 2016), from May to July in the Mediterranean Sea (Marino *et al.* 1995a) and from April to October in the Canary Islands (Jerez *et al.* 2006). Yellowtail kingfish has been considered to exist as geographically separate populations and its aquaculture has spread from Japan to Australia, Chile, Mexico, and California (Sicuro & Luzzana 2016). However, Martinez-Takeshita *et al.* (2015) recently proposed that these different populations are actually genetically distinct

species and named them using the following names: yellowtail kingfish has been reserved for fish in the Southern Hemisphere, *S. aureovittata* has been used for those in Asian waters (western Pacific) and *S. dorsalis* for those off the coast of California (eastern Pacific). As regards other members of the *Seriola* genus, longfin yellowtail or almaco jack (*S. rivoliana*) is distributed widely in the Eastern and Western Pacific (Fernández-Palacios *et al.* 2015b) and it has been cultured recently in Ecuador, Hawaii and the Canary Islands (Spain) and studies on its reproduction have been published (Roo *et al.* 2012). In contrast, the Samson fish (*S. hippos*), which is distributed in coastal waters around Australia and New Zealand, is a target species for sport fishing only and its reproduction has been studied in Western Australia (Rowland 2009). The other *Seriola* species, Guinean amberjack (*S. carpenteri*), fortune jack (*S. peruana*), lesser amberjack (*S. fasciata*), blackbanded trevally (*S. nigrofasciata*) and banded rudderfish (*S. zonata*), are of limited fishery interest and they are not under investigation for aquaculture purposes.

In addition to members of the genus *Seriola*, there is a large diversity of other species belonging to the family Carangidae, and some of them have also attracted some interest for aquaculture production. The giant trevally (*Caranx ignobilis*) is a large reef-associated pelagic species (Meyer *et al.* 2007; Dale *et al.* 2011) found throughout much of the Indo-Pacific tropics and subtropics (Sudekum *et al.* 1991). It has been identified as a potential aquaculture species in Asia (Liao *et al.* 2001; Alaira *et al.* 2014; Mutia *et al.* 2015; Kappen *et al.* 2018; Albasri *et al.* 2020; Rostika *et al.* 2020) and is known to tolerate low salinities in estuaries and rivers (Alaira *et al.* 2014; Kappen *et al.* 2018; Rostika *et al.* 2020). Based on wild fisheries, this species can reach a body weight (BW) of 5.5 and 16.8 kg at one and two years of age, respectively (Abdussamad *et al.* 2008). Despite this species being cultured as early as the late 1990s in Taiwan (Liao *et al.* 2001), control of its reproduction under culture conditions is still necessary to ensure seed supply for farmers (Kappen *et al.* 2018). The bluefin trevally

(*Caranx melampygus*), a close relative of giant trevally that shares a similar habitat (Sudekum *et al.* 1991; McKenzie *et al.* 2014), has attracted aquaculture interest due to its relatively high market value in Hawaii (Leber 1994; Divakaran *et al.* 1999; Kim *et al.* 2001; Moriwake *et al.* 2001) and parts of Asia (Liao *et al.* 2001; Suprayudi *et al.* 2014; Albasri *et al.* 2020). Golden trevally (*Gnathanodon speciosus*) is farmed extensively throughout Asia (Chou 1994; Liao *et al.* 2001; Feng *et al.* 2005) and more recently the USA (Broach *et al.* 2015). In addition to being an important sport fish and food source, this species is a valued ornamental species for the aquarium trade (Chou & Lee 1997; Grandcourt *et al.* 2004; Feng *et al.* 2005; Broach *et al.* 2015; Chen *et al.* 2019). The distribution of the golden trevally ranges from the tropical Indo-Pacific eastward to the Americas (Randall 1995). Among the carangids, striped jack or white trevally (*Pseudocaranx dentex*) is the most expensive fish due to its high value as a sashimi species in Japan (Watanabe & Vassallo-Agius 2003). This species has also been identified as a potential aquaculture species in Europe (Socorro *et al.* 2005; Roo *et al.* 2012; Nogueira *et al.* 2018) and has an anti-tropical distribution throughout the Atlantic, Mediterranean and Indo-Pacific (Smith-Vaniz 1999). Finally, the silver trevally (*P. georgianus*), also known by its indigenous Māori name “araara” is of aquaculture interest in New Zealand. This is the only *Pseudocaranx* species found in New Zealand and its distribution also extends into neighboring waters of southern Australia (Kemp 2019).

Incorporating a new species in aquaculture requires a good knowledge of its reproductive physiology and control of reproduction in captivity. In the instance where reproductive dysfunctions occur, which is very common in cultured fishes (Zohar & Mylonas 2001; Mylonas *et al.* 2010), there is a need to optimize methods to hormonally induce maturation and spawning to obtain adequate numbers of good quality eggs for commercial hatchery production. The present manuscript is the first one attempting to review the available literature on the reproductive physiology of various members of the family Carangidae and

the control of fertilized egg production in captivity. Our objective is to facilitate both the advancement of the study of reproductive physiology of these important fishes, but also the implementation of the acquired knowledge for the development of commercial production.

2. Reproductive biology of the family Carangidae

Genetic linkage analysis using fertilized eggs obtained by pair-breeding in yellowtail demonstrated a ZZ/ZW sex-determining system (Fuji *et al.* 2010). Furthermore, Koyama *et al.* (2019) provided intriguing evidence that in three *Seriola* spp. (yellowtail kingfish, greater amberjack and yellowtail), a missense single nucleotide polymorphism in the gene encoding the steroidogenic enzyme 17β-hydroxysteroid dehydrogenase 1 (HSD17β1) is associated with ZZ/ZW sex determination. HSD17β1 catalyzes the interconversion of 17-ketosteroids to 17β-hydroxysteroids, such as androstedione (AD) to testosterone (T) and estrone to 17β-estradiol (E_2). In *Seriola* spp., Z-type HSD17β1 had lower activity of steroid conversion than W-type HSD17β1, resulting in lower production of E_2 (Koyama *et al.* 2019). These authors supposed that the higher production of E_2 in ZW fish may act as an inducer of female sex. Thus, the sex determination of *Seriola* species is considered to be linked to the genetic regulation of steroidogenic enzymes.

The gonads of carangids are paired organs suspended to the dorsal abdominal wall by a mesogonad. The ovary consists of a muscle wall and numerous ovigerous lamellae projecting towards a cavity (Fig. 1), where oocytes are released at ovulation (ovarian lumen) in the most evolved teleost fishes of the so-called cystovarian type (Helfman *et al.* 2009; Piccinno *et al.* 2014). Ovigerous lamellae contains oogonia and oocytes, whose development has been broadly divided into three phases: primary growth, secondary growth, and oocyte maturation (OM) (Patiño & Sullivan 2002). The testes are also paired elongated organs and belong to the

"unrestricted spermatogonial type" of Grier *et al.* (1980), being characterized by the presence of spermatogonia along the germinal compartment throughout the testis (Schulz *et al.* 2010). Spermatogenesis is divided into three phases: proliferative phase, meiotic phase, and spermiogenic phase (Schulz *et al.* 2010).

2.1. Greater amberjack

2.1.1. Ovary structure and oogenesis

Information on greater amberjack ovarian morphology and germ cell developmental stages has been reported earlier (Marino *et al.* 1995b; Grau *et al.* 1996; Micale *et al.* 1999; Sley *et al.* 2014) and is herein summarized. The greater amberjack ovaries (Fig. 1) are similar to other iteroparous fishes with asynchronous oocyte development. The two ovaries are always different in size (Fig. 1a, b) and they join caudally in the oviduct leading to the urogenital pore. The ovary size changes according to the maturity stage: in immature individuals, ovaries appear as a few-cm long pinkish sacks (Fig. 1a); in mature individuals, ovaries occupy 2/3 of the volume of the abdominal cavity (García & Díaz 1995) and show a rich vascular network (Fig. 1b, c). Developing vitellogenic oocytes provide ovaries with a granular appearance, while in ready-to-spawn ovaries, hydrated oocytes are easily distinguishable as opaque spheres ~1 mm (Fig. 1c). The ovary wall includes a thick muscle tunica provided with fibers arranged in a circular and a longitudinal layer and many ovigerous lamellae, containing oogonia and oocytes at different stages of development (Fig. 1d).

Oogonia (diameter 8–15 μm) (Fig. 2) are rounded cells with a large central euchromatic nucleus, containing sparse eterochromatic patches and a single nucleolus. Chromatin-nucleolus stage oocytes (diameter 15–30 μm) are ovoidal cells at early meiotic prophase (Fig. 2a) show a slightly basophilic ooplasm, a large eccentric nucleus, chromatin strands and sparse eterochromatic patches. Squamous follicular cells are associated with oocytes at this

stage. Perinucleolar stage oocytes (diameter 30–120 μm) have several nucleoli adjoining the nuclear envelope (Fig. 2b). Lipid/cortical alveoli stage oocytes (diameter 120–200 μm) have small lipid droplets and a thin PAS-positive zona radiata (Fig. 2c). Granulosa and thecal layers are distinguishable, separated by a PAS-positive basal lamina. Early vitellogenic oocytes (diameter 200–400 μm) are characterized by eosinophilic yolk globules in the peripheral ooplasm and a further increase of the zona radiata thickness (1–3 μm) (Fig. 2d). Follicular cells surrounding the oocytes at this stage increase slightly in size and become isoprismatic. Antibodies raised against Atlantic bluefin tuna (*Thunnus thynnus*) vitellogenin labelled follicular cells and the zona radiata (Fig. 2e). In late vitellogenic oocytes (diameter 400–550 μm), the zona radiata increases further in thickness (Fig. 2f) and the cytoplasm is completely filled with yolk globules.

At the OM stage (Fig. 2g) yolk globules and lipid vesicles coalesce to form the lipid droplet and a homogeneous yolk mass. The germinal vesicle migrates to the animal pole before germinal vesicle breakdown (GVBD). Oocytes at this stage hydrate by uptake of water and their diameter increases to 900–1000 μm. The maturing oocytes tend to separate from the now thin and stretched follicular layers. Eggs have a mean diameter of 1.1 mm and an oil droplet of 0.27 mm (Kawabe *et al.* 1996). In active spawning individuals, post-ovulatory follicles (POFs) are found for a few days after spawning (Fig. 2f).

Sparse atretic follicles are always observed in greater amberjack females during vitellogenesis; however, extensive atresia of advanced vitellogenic follicles has been often reported in captive-reared, reproductively dysfunctional individuals (Micale *et al.* 1999; Mylonas *et al.* 2004; Zupa *et al.* 2017b; Pousis *et al.* 2018; Passantino *et al.* 2020). Alpha atretic vitellogenic follicles displayed zona radiata fragmentation, coalescence of yolk globule and nucleus disintegration; in beta atretic follicles zona radiata and yolk globules were completely reabsorbed (Fig. 2h).

214 ***2.1.2. Testis structure and spermatogenesis***

In adult greater amberjack, fully ripe testes (Fig. 3a) occupy 2/3 of the abdominal cavity
216 length (García and Diaz, 1995). As in other teleost fishes (Schulz *et al.* 2010), the greater amberjack testis consists of two structurally and functionally different regions (Fig. 3b): an
218 outer region consisting of a lobular compartment and an inner region consisting of the sperm duct system in which spermatozoa are conveyed. The lobular compartment represents the testis
220 proliferative region and contains the germinal epithelium made of germ cells at different stage of development, surrounded by cytoplasmic extensions of Sertoli cells to form spermatocysts
222 (Fig. 3c).

Different male germ cell types have been described in greater amberjack (Marino *et al.*
224 1995b; Zupa *et al.* 2017a, b). Zupa *et al.* (2017a) distinguished two types of single A spermatogonia: a small cell type with a diameter of about 8.0 µm (Fig. 3c), and a large cell type
226 with a diameter of about 10.5 µm. Using stemness markers in immunohistochemistry assays, Zupa *et al.* (2017a) identified the small single type A spermatogonia as the only stem
228 spermatogonia. Primary spermatocytes were around 4.5 µm in diameter and secondary spermatocytes were about 3.0 µm and their appearance changed according to the different
230 phases of meiosis. Spermatids were described as small cells around 2.5–3.0 µm in diameter showing a dense and strongly basophilic nucleus, whereas flagellated spermatozoa were
232 characterized by an oval head strongly stained with hematoxylin and were observed within cysts or in the lumen of seminiferous tubules after cyst breakdown (spermiation).

234

2.1.3. Sex differentiation, sexual maturity and reproductive cycles

236 Marino *et al.* (1995b) reported that the gonads of greater amberjack caught in the Mediterranean started to differentiate about two-three months of age (23–26 cm standard

238 length, SL). At four–five months of age, ovaries showed ovigerous folds containing oogonia, and spermatogonial cysts appeared in the testes. A few chromatin nucleolus stage oocytes were
240 visible in the ovaries of 28–32 cm long juveniles (four–five months old), and seminiferous tubules appeared in the testes at this age. At one year of age, perinucleolar stage oocytes
242 appeared in the ovaries and all the spermatogenesis stages were present in the testes, including luminal spermatozoa. In a recent study on the sex differentiation of hatchery produced greater
244 amberjack (Mylonas, C.C. unpublished data), the ovarian cavity was already formed at 101 days post hatching (dph) at a total length (TL) of 14.5 ± 6.2 cm, and germ cells were visible
246 around the cavity. The typical ovarian structure with ovarian lamellae and occasional presence of primary oocytes was apparent at 260 dph (27.8 ± 1.9 cm TL), while complete ovarian
248 differentiation occurred at 408 dph (41.2 ± 3.8 cm TL). In the same study, at 101 dph the testes contained mostly somatic cells and connective tissue and no germ cells were observed (14.5 ±
250 6.6 cm TL). The first germ cells were apparent at 150 dph, when spermatocytes could be found in the gonads (24.1 ± 3.1 cm TL), while the typical testicular structure featuring all types of
252 male germ cells, including spermatozoa, was observed at 260 dph (28.6 ± 2.9 cm TL).

The available data on greater amberjack sexual maturity in the Mediterranean Sea
254 (Table 2) are limited and not always consistent (Marino *et al.* 1995a, b; Micale *et al.* 1999; Kožul *et al.* 2001; Sley *et al.* 2014). According to a histological study of fish sampled around
256 the Pelagie Islands, Italy (Marino *et al.* 1995a), sexual maturity was attained by 50% of the males at 109 cm SL; 50% of the females at 113 cm SL; 100% of the fish over 128 cm SL. A
258 quite lower size at median maturity was reported by Sley *et al.* (2014) for fish sampled in the Gulf of Gabes: 80 and 83 cm SL for females and males, respectively. These data, however,
260 are likely biased due to the fact that specimens with developing gonads (and then still immature), were classified as mature. In the southern Adriatic Sea, about 40% of three-year-
262 old and 100% of five-year-old fish have been found to be sexually mature (Kožul *et al.* 2001).

A similar maturity schedule has been proposed for greater amberjack from the Gulf of Mexico by Murie and Parkyn (2008) who reported that 86% of females mature at age four and 100% at age six.

In general, *Seriola* spp. spawn in the spring and/or summer; however, differences in timing and duration of reproductive cycles show variations in the known spawning areas according to local environmental conditions and/or genetic peculiarities. In the Mediterranean Sea, greater amberjack reproductive recrudescence starts in early May when secondary growth oocytes appear in the ovaries (Mandich *et al.* 2004; Sley *et al.* 2014; Zupa *et al.* 2017b; Pousis *et al.* 2018, 2019) and spermatogenesis is activated in the testes (Mandich *et al.* 2004; Zupa *et al.* 2017a, b). The vitellogenic phase in this species appears to be quite rapid compared with other large pelagic teleosts such as the Atlantic bluefin tuna (Corriero *et al.* 2003) and the swordfish *Xiphias gladius* (Corriero *et al.* 2004). Therefore, by the end of May, when the sea surface temperature is around 19–20°C, part of the population has already started spawning (Mandich *et al.* 2004; Zupa *et al.* 2017b; Pousis *et al.* 2018, 2019). The peak of the reproductive season in the Mediterranean Sea, however, occurs in June–July, when sea surface temperature is 23–24°C and most of the greater amberjack females show hydrated oocytes and/or POFs, and males have seminiferous tubules filled with spermatozoa. Fish with post-spawning and resting gonads are found from July to the end of the fishing season in September.

Studies carried out through conventional tagging (McClellan & Cummings 1996), histological analysis of the gonads (Thompson *et al.* 1992; Harris *et al.* 2007; Murie & Parkyn 2008), the gonadosomatic index (GSI) (Murie & Parkyn 2008) or the count of daily growth increments on sagittal otoliths of the young-of-the-year (Wells & Rooker 2004) indicate that in the temperate and sub-tropical waters off eastern US coast, spawning occurs in April–June, when sea surface temperature is ≥ 23°C. The comparative analysis of monthly changes of GSI

in greater amberjack females from different areas (Fig. 4) confirms the presence of different reproductive peaks in the different spawning grounds: June–July in the Mediterranean (Sley *et al.* 2014; Zupa *et al.* 2017b), April–May in the northwestern Atlantic and Gulf of Mexico (Thompson *et al.* 1992; Harris *et al.* 2007; Murie & Parkyn 2008) and March–April the Pacific Ocean (Hawaii) (Kikawwa & Everson 1984). Interestingly, the recorded GSI peaks are higher in specimens from the Pacific Ocean than in specimens from the northwestern Atlantic/Gulf of Mexico and in specimens from the Mediterranean Sea, and they might be indicative of different fecundities in genetically distinct populations.

Greater amberjack spawning events in the wild have never been documented and information on the depth at which spawning occurs comes mainly from fisheries-based observations. In the spawning grounds between Pelagie Islands and Tunisia, during the reproductive period, greater amberjack aggregations are mainly localized at about 20–35 m depth (Lazzari & Barbera 1989; Andaloro & Pipitone 1997). In the north-western Atlantic Ocean, from North Carolina to Florida, greater amberjack in spawning condition were sampled mostly in the shelf break between 20 and 100 m (Harris *et al.* 2007). No precise information is available regarding the preferential spawning hour; however, on the basis of oocyte stage of maturation, the authors hypothesised that fish caught in the north-western Atlantic Ocean in the morning would have likely released eggs several hours after capture. Courtship behaviour, a sign of imminent spawning, was recorded around sunset in the Caribbean coral reef of Gladden Spit (Heyman & Kjerfve 2008).

Between April and June, a transient multi-species spawning aggregation, including greater amberjack, Samson fish (*Seriola hippos*) and five other carangids (*Carangoides ruber*, *Carangoides bartholomaei*, *Caranx latus*, *Decapterus macarellus* and *Trachinotus falcatus*), has been reported in the Atlantic tropical waters of Gladden Spit on the Belize Barrier Reef. All greater amberjack captured during these times had ripe gonads and courtship behaviour

was documented underwater (Heyman & Kjerfve 2008). In the tropical waters of the Pacific Ocean (Hawaii), the greater amberjack spawning season extends from November to June with peaks in March and April (Kikawwa & Everson 1984).

As for all *Seriola* species, greater amberjack is a multiple spawner with indeterminate fecundity (Harris *et al.* 2007), *i.e.* vitellogenic oocytes are continuously recruited during the reproductive season from the primary growth oocyte reservoir. Based on the proportion of females with oocyte in maturation or POFs less than 24 h old, it was calculated that greater amberjack from the north-western Atlantic Ocean spawn every five days during a 73-day spawning season, which corresponds to approximatively 14 spawning events (Harris *et al.* 2007). Statistically significant relationships were developed between estimated batch fecundity and size (or age) for north-western Atlantic (Harris *et al.* 2007) and Pacific (Kikawwa & Everson 1984) greater amberjack populations. According to these relationships, greater amberjack females with FL ranging between 83 and 130 cm release 1.3–4.2 million eggs per spawning event and 18–59 million eggs per reproductive season. It must be noted that these values are extremely high when compared to actual fecundity values obtained in captivity (See section 3 and 4 later).

2.1.4. Endocrine control of reproduction

Limited information is available on the hormonal regulation of reproduction in greater amberjack in the wild, and is limited to sex steroid plasma concentrations (Table 3) collected from fish commercially caught in the Mediterranean Sea (Mandich *et al.* 2004; Zupa *et al.* 2017a, b). In females, T and E_2 showed a significant increase during vitellogenic oocyte growth between late May–early June (T peak: 5.0 ng ml^{-1}; E_2 peak: 6.6 ng ml^{-1}) followed by a decrease during the spawning peak in late June–July. Concomitantly with the E_2 peak, the highest transcription levels of liver vitellogenin (Pousis *et al.* 2018) and the highest

vitellogenin plasma concentrations were recorded (Mandich *et al.* 2004). Contrary to E_2, 17,20β-dihydroxypren-4-en-3-one (17,20β-P) showed low plasma concentrations and only slight variations during the reproductive cycle of female greater amberjack, with highest concentrations (1.0–1.3 ng ml^{-1}) recorded at the onset and during the peak of the spawning season (Table 3).

As for most fish species, 11-Ketotestosterone (11-KT) is the main androgen in greater amberjack, its plasma concentrations in males being higher than those of T throughout the reproductive cycle (Table 3). Both T and 11-KT concentrations were highest during the active gametogenesis phase (T peak: 4.3 ng ml^{-1}; 11-KT: 6.3 ng ml^{-1}) and then decreased during the spawning season (Zupa *et al.* 2017b). A constant increase of 17,20β-P was observed in wild greater amberjack males from the sexual recrudescence phase to the spawning period, in agreement with the role of these hormones in regulating spermiation and sperm maturation. Finally, very low E_2 plasma levels were found during spermatogenesis and a peak of this hormone (1.4 ng ml^{-1}) was associated with the spermatogonial self-renewal concomitant with spermatogenesis cessation (Zupa *et al.* 2017a, b).

2.2. Other Seriola spp.

2.2.1. Oogenesis and spermatogenesis

In terms of ovarian function, yellowtail shows asynchronous oocyte development, as the greater amberjack, indicative of multiple spawning (Kagawa 2013). At the completion of vitellogenesis, the oocytes of yellowtail reach around 700 µm in diameter (Fig. 5a). At the beginning of OM, during germinal vesicle migration (GVM), the oocyte diameter of the spawning batch increases to 750–900 µm, but this clutch is not clearly distinct from other oocytes in terms of the diameter (Fig. 5b). At the end of OM, the diameter of hydrated oocytes ranges from 950 to 1200 µm, which is clearly distinct from the size of other oocytes

(Fig. 5c). In the ovary just after spawning, when newly formed POFs are present, the oocyte diameter of the subsequent spawning batch reaches 700 μm, indicating that vitellogenesis has already been completed (Fig. 5d). The oocyte development of yellowtail kingfish is similar to that of yellowtail, with slight differences. For example, in yellowtail kingfish the diameter of fully vitellogenic oocytes is larger at 850 μm (Poortenaar *et al.* 2001), and the diameter of spawned eggs ranges from 1.2 to 1.5 mm (Moran *et al.* 2007; Setiawan *et al.* 2016), while it is around 1.2 mm in yellowtail (Vassallo-Agius *et al.* 2002). In addition, the oocyte size-frequency distribution of yellowtail kingfish shows that the spawning batch is more clearly distinct from other oocytes in the mature ovary, showing one or two group-synchronous modes (Gillanders *et al.* 1999; Poortenaar *et al.* 2001). The subsequent spawning batch completes vitellogenesis when the spawning batch is ovulated, which is similar to oocyte development in yellowtail.

The onset of testicular development in yellowtail and yellowtail kingfish is recognized histologically by the appearance of type B spermatogonia and spermatocytes (Poortenaar *et al.* 2001; Shiraishi *et al.* 2010, 2011). During active testicular development the testis contains spermatocysts at various stages of development, while during the breeding season, seminiferous tubules and the sperm duct are filled with spermatozoa. Spermatozoa disappear from the testis in the post-spawning season.

2.2.2. Sexual maturity and reproductive cycles

Puberty (the age and size at first maturity) have been examined in several *Seriola* species for wild and/or reared fish (Table 2). Yellowtail reaches a body size of 75–85 cm in FL and 7–8 kg in weight at four years of age and has a lifespan of six–seven years (Tian *et al.* 2012; Sassa *et al.* 2020). In the northern East China Sea off the west coast of Japan, yellowtail first matures at the age of two years, and the reported size of the smallest mature female and

male is 63 and 61 cm FL, respectively (Shiraishi *et al.* 2011). In farming, some yellowtail mature even at the age of one year (Kagawa 1992; Miura *et al.* 2014). Survey data on the occurrence of eggs and larvae in the wild indicated that spawning occurs mainly from 19 to 21°C (Yamamoto *et al.* 2007). The spawning period of yellowtail ranges from February to May in the southern East China Sea, while it begins in March in the northern area, with the main activity occurring between April and May (Shiraishi *et al.* 2011; Sassa *et al.* 2020). The gonadal changes during the annual reproductive cycle in the northern East China Sea (Shiraishi *et al.* 2011), showed that the GSI remained low (< 1.0) between summer and winter in both sexes. In females, the GSI increased at the onset of vitellogenesis, about one month before the spawning season, and it was maintained at a high value (> 5) during the spawning season. In males, GSI increased about two months before the spawning season with the appearance of type B spermatogonia and spermatocytes, indicating the onset of active testicular development, and it was maintained at a high value (> 7.5) during the breeding season (Shiraishi *et al.* 2011).

Yellowtail kingfish reaches a body size of more than 170 cm FL and 60 kg, although fish of this size are rare (Gillanders *et al.* 1999; Symonds *et al.* 2014). Off the coast of northern New Zealand, the body size of yellowtail kingfish ranges from 55 to 147 cm FL at ages of 4–23 years (McKenzie *et al.* 2014). In this region, the size of the smallest mature female, the median size at first maturity (L_{50}) and the size at which all females are mature (L_{100}) were reported to be 78, 94, and 128 cm FL, respectively. As regards males, the size of the smallest mature, L_{50} and L_{100} were 75, 81, and 93 cm, respectively (Poortenaar *et al.* 2001). In southern Australia, females were found to first mature at 70 cm FL at the age of 3+ years and the size at 50% maturity was 83 cm FL, while males first matured at 36 cm FL at the age of 0+ years and the size at 50% maturity was 47 cm FL (Gillanders *et al.* 1999). In waters around South Africa, the estimated size at maturity was smaller than that in Australia and

New Zealand, and the sizes of the smallest, 50%, and 100% mature females were 52, 55, and 78 cm FL, while those of males were 52, 59, and 82 cm FL, respectively (Dunn 2014). In farming in Australia, the age at puberty was found to be accelerated to one year in male yellowtail kingfish, but females take four–five years to reach sexual maturity (Sanchís-Benlloch *et al.* 2017). A rearing study demonstrated that a water temperature above 17°C is required for the spawning of yellowtail kingfish (Moran *et al.* 2007) and the spawning period ranges from November to February (austral spring to summer) in waters around Australia and New Zealand (Gillanders *et al.* 1999; Poortenaar *et al.* 2001). Gonadal analysis of the reproductive cycle of wild yellowtail kingfish in northern New Zealand showed that the GSI was maintained at high values between October and January, in association with the appearance of fish in OM/ovulation and spermiation (Poortenaar *et al.* 2001). In Southern Australia, the highest gonadal weight of both sexes was observed in December and January (Gillanders *et al.* 1999). In yellowtail kingfish from South Africa, high GSI values were reported between November and February, consistent with data from Australia and New Zealand (Dunn 2014).

Yellowtail kingfish distributed in western Pacific (*S. aureovittata*) reaches a body size of around 100 cm FL at seven–eight years of age (Shiraishi *et al.* 2010). In the northern East China Sea off the west coast of Japan, this species was reported to first mature at the age of two years, and its size at first maturity was 66 cm FL in females and 62 cm FL in males. In this region, vitellogenesis starts in March and spermatids appear in the testis in April. This research further showed that the GSI increased from April, peaked in May, and decreased in June. Accordingly, compared with the reproductive cycle of yellowtail in the same region (Shiraishi *et al.* 2011), the gonadal development and spawning season of *S. aureovittata* are considered to be delayed by about one month.

In yellowtail kingfish distributed in eastern Pacific (*S. dorsalis*), research from the late 1950s in waters off Southern California showed that oocyte growth starts in March and it is completed in late June, and the spawning period occurs between July and October (Baxter 1960). In addition, larval surveys carried out in southern California between 1954 and 1969 indicate that *S. dorsalis* spawns between April and October, with a peak between July and August (Sumida *et al.* 1985).

Based on high GSI values (> 1) in both sexes, it was proposed that longfin yellowtail spawns in waters around Ogasawara Islands (southern Japan) of the Western Pacific mainly between May and September, at sea surface temperature between 23 and 28°C (Kato *et al.* 1990). The size of the smallest mature female was 63 cm FL and 4 kg, while that of male was 60 cm FL and 3 kg. In longfin yellowtail farmed in Hawaii, males first matured at the age of 1+ year (21 to 22 months of age), while females took two complete years (Laidley *et al.* 2004). In the Canary Islands, all wild-caught male longfin reared in captivity for two years matured at an average size of 55 cm SL and 3 kg BW (Roo *et al.* 2014, 2015). In contrast, 33% of females matured with an average size of 57 cm SL and 4 kg after a rearing period of two years, and the proportion of mature females increased to 66% (66 cm SL, 6 kg) and 83% (70 cm SL, 8 kg) after rearing periods of three and four years, respectively. This suggests that, under rearing conditions, a sex-dependent difference occurs in the maturity rate of longfin yellowtail.

Information on the reproductive biology of Samson fish, has been provided by Rowland (2009). This species reaches a body size of around 85 cm FL at five years of age and around 105 cm FL at 10 years of age. In females, the size and age at first maturity were 70–75 cm FL and 3+ years of age, respectively, while the size at 50% maturity was 83 cm FL. Cortical alveolus-stage oocytes appeared in September and vitellogenesis progressed in October, while ovulated eggs and POFs were found between November and March. A high GSI value was

462 maintained between November and January, but it gradually decreased from January to May. This research further showed that the batch fecundity was 51–1,472 x10^3 eggs in females
464 whose size ranged between 106 and 120 cm FL.

466 ***2.2.3. Endrocrine control of reproduction***

Recent studies in the endocrine control of reproduction of yellowtail have provided
468 important information for the first time in any carangid species. Gene expression profiles of the β subunits of the two gonadotropins (GtHs), namely follicle-stimulating hormone (*fshb*)
470 and luteinizing hormone (*lhb*) and of the GtH receptors (*fshr* and *lhr*) during the annual reproductive cycle of yellowtail, have demonstrated that there are differences in the
472 physiological roles of FSH and LH in reproduction. In females, the expression of pituitary *fshb* and ovarian *fshr* was high during the early phase of vitellogenesis, while the expression
474 of pituitary *lhb* and ovarian *lhr* was high during the late phase of vitellogenesis (Rahman *et al.* 2003). In males, the expression of pituitary *fshb* and *lhb* and testicular *fshr* was high during
476 the early and late phases of testicular development, while the expression of ovarian *lhr* increased gradually during the late phase and peaked during the active spermiation period
478 (Rahman *et al.* 2003). A recent study showed similar expression patterns of *fshb* and *lhb* in male yellowtail, but high expression of pituitary *fshb* was also found during the active
480 spermiation period (Higuchi *et al.* 2017a). These studies suggest that, as described in many fishes (Rosenfeld *et al.* 2007; Levavi-Sivan *et al.* 2010), in yellowtail FSH is involved in
482 vitellogenesis and in the whole process of spermatogenesis, while LH acts at the late phase of gametogenesis and maturation in both sexes. This is in agreement with the evidence that OM
484 is induced by treatment with human chorionic gonadotropin (hCG), which is an LH-like hormone (Matsuyama *et al.* 1996).

Also recently, the physiological function of recombinant FSH on gonadal development was examined in *Seriola* species (Sanchís-Benlloch *et al.* 2017). *In vitro,* FSH induced the production of E_2 and 11-KT by immature ovarian and testicular tissue, respectively. In teleosts, E_2 is recognized to induce hepatic vitellogenin production in females while 11-KT is the main gonadal steroid controlling spermatogenesis (Lubzens *et al.* 2010; Schulz *et al.* 2010). In yellowtail kingfish, the administration of recombinant FSH in immature fish initiated early secondary growth in the ovary, while in the testis it resulted in the appearance of spermatozoa (Sanchís-Benlloch *et al.* 2017). These results suggest that FSH acts on the early phase of oogenesis in females, while it may be involved both in the early and late phases of spermatogenesis in males. It has also been shown in yellowtail kingfish that the administration of kisspeptins (Kiss1-10 and Kiss2-10) stimulated gonadal development in prepubertal male yellowtail kingfish, in association with the upregulation of pituitary *fshb* and *lhb* (Nocillado *et al.* 2013). This suggests that Kisspeptins may act as the upstream regulator of the brain–pituitary–gonadal axis as recognized in mammals (Taranger *et al.* 2010), and thus modulate the onset of puberty via FSH secretion.

The synthetic pathway of ovarian steroid hormones has been studied in yellowtail by *in vitro* cultivation of ovarian follicles. During vitellogenesis, E_2 is synthesized from pregnenolone (P5) via 17-hydroxypregnenolone (17-P5), dehydroepiandrosterone (DHEA), androstenedione (AD) and T (Rahman *et al.* 2002a). In yellowtail, estrogen-responsive elements were found in three vitellogenin subtypes (*vtgAa*, *vtgAb*, and *vtgC*) and estrogen receptor α (*erα*) (Mushirobira *et al.* 2020). In addition, the hepatic expression of *vtgAa*, *vtgAb*, *vtgC*, and *erα* were synchronously activated during vitellogenesis. After the completion of vitellogenesis, the steroidogenic pathway shifts from the production of E_2 to 17,20β-P, which has been identified as the maturation-inducing hormone (MIH) since it is very effective at inducing OM and binds specifically to the ovarian membrane (Rahman *et al.* 2001, 2002b). In

contrast, 17,20β,21-trihydroxy-4-pregnen-3-one (20β-S), which has been identified as an MIH in some marine fishes is not synthesized in ovarian follicles of yellowtail (Rahman *et al.* 2001). Analysis of the circulating concentrations of steroid hormones supports the notion that a shift of the production of E_2 to 17,20β-P occurs in ovarian follicles of *Seriola* species, such as yellowtail and yellowtail kingfish. In yellowtail, serum concentrations of E_2 increased during vitellogenesis, accompanied by an increase of serum vitellogenin level, while the serum level of 17,20β-P increased just before the onset of GVM, which was induced by the administration of hCG (Ouchi *et al.* 1989; Matsuyama *et al.* 1996). Likewise, in female yellowtail kingfish, plasma levels of E_2 were high during vitellogenesis, 17,20β-P increased only in fish during GVM (Poortenaar *et al.* 2001) and T was also high between vitellogenesis and GVM (Poortenaar *et al.* 2001).

As mentioned already, 11-KT is the main androgen in teleosts (Schulz *et al.* 2010). In male yellowtail, plasma 11-KT levels were elevated during testicular development and peaked during spermiation (Higuchi *et al.* 2017a). While the physiological mechanisms regulating the maturation of male gametes in fish are still not defined, 17,20β-P has been suggested to play a role (Schulz *et al.* 2010). Yellowtail showed high concentrations of serum 17,20β-P during the spermiation period (Miura *et al.* 2020). *In vitro* cultivation of testicular tissues with radiolabeled 17,20β-P also demonstrated that specific binding to 17,20β-P in spermiating tissues was more potent than that in non-spermiating tissues (Ohta *et al.* 2002). These results suggest a specific role of 17,20β-P in sperm maturation. Conversely, in yellowtail kingfish plasma 17,20β-P remained low throughout the reproductive cycle, although plasma levels of 11-KT were high from late spermatogenesis to the spermiation period (Poortenaar *et al.* 2001). Therefore, there may be some species differences in the physiological function of 17,20β-P in spermatogenesis among *Seriola* species.

2.3. Other Carangids

2.3.1. Oogenesis and spermatogenesis

To date, descriptions of ovarian structure and germ cell development for giant trevally, bluefin trevally and golden trevally remain unreported. However, detailed histological accounts of the gonadal development have been described in wild striped jack from the coastal waters of the Canary Islands (Socorro *et al.* 2005) and from Japan (Murai *et al.* 1985a). In the Southern Hemisphere, descriptions of gonadal development have been made for wild silver trevally off the coast of New South Wales, Australia (Rowling & Raines 2000) and more recently, descriptions of ovarian development from cultured first generation (F_1) silver trevally undergoing their maiden spawning cycle in captivity have been made in New Zealand (M.J. Wylie, unpublished data). Oogenesis and spermatogenesis, where described, follows the paradigm of the better studied *Seriola* spp., although the size of oocytes at the completion of vitellogenesis and at ovulation may differ slightly.

In striped jack, oocytes that had completed vitellogenesis had diameters of approximately 400 µm (Murai *et al.* 1985a), while naturally spawned eggs in captivity ranged between 880 and 1020 µm and averaged 953 µm in diameter (Murai *et al.* 1987). A similar mean diameter of eggs (969 ± 27 µm) was reported from spontaneous spawning captive striped jack in Europe (Nogueira *et al.* 2018). For the description of silver trevally stocks off the coast of New South Wales, Rowling and Raines (2000) categorized the reproductive cycle by microscopic examination into five stage for females and four stages for males. For females in Stage I, the ovary was fully reduced and contained clear fluid with no visible eggs or oocytes. Stage II consisted of a developing ovary, orange in color with primary oocytes. Stage III consisted of vitellogenic oocytes and a yellow colored ovary; oocyte diameters were mostly 400 µm accompanied by a small number of hydrating oocytes with diameters exceeding 500 µm. Ripe females were classed as stage IV as these had ‘mature eggs’ and the

ovary was golden in color; hydrated egg diameters ranged between 500 and 1000 µm. Finally, Stage V consisted of females that were spent, where the ovary was still large but fluid filled and darker in color at times. For males, Rowling and Raines (2000) again described the testes in Stage I as thin and sinew-like. As testis development progressed, lobes become apparent and some milt was present (Stage II). Stage III consisted of 'ripe'/ spermiating males; testes were large in size, multi-lobed and white in color. Spent males (Stage IV) had testes that were pink-grey in color and had a 'loose texture'. In a different study were ripe gametes were strip-spawned from wild silver trevally in New Zealand and fertilized *in vitro*, egg and oil globule diameters were reported to range between 760 and 860 µm, and 200 and 250 µm, respectively (James 1976).

2.3.2. Sexual maturity and reproductive cycles

The available data on age and/or size at sexual maturity of the carangids are reported in Table 2. Ages at first maturity of giant trevally and bluefin trevally were estimated at 3.5 years (~60 cm SL) and two years (~35 cm SL), respectively (Sudekum *et al.* 1991). In the wild, giant trevally form seasonal mating aggregations with a peak spawning period during the summer months (Sudekum *et al.* 1991; Meyer *et al.* 2007; da Silva *et al.* 2014; Daly *et al.* 2018). Studies suggest that these spawning aggregations are influenced by lunar cycles (Johannes 1978; Meyer *et al.* 2007; da Silva *et al.* 2014; Daly *et al.* 2018). In spawning aggregations of giant trevally observed in the Western Indian Ocean during mid-December (da Silva *et al.* 2014), more than 1000 fish were observed two days before the full moon. Prior to spawning, fish migrated from the deep-water reef channels to depths of approximately 15–20 m near the shelf edge where courtship behaviors such as pair chasing and body color morphing were observed. The latter color changes were also noted in other studies (Meyer *et al.* 2007; Daly *et al.* 2018). Based on recruitment patterns and the abundance of young giant

586 trevally along the Tuticorin Coast of India, findings indicate that this species is also capable of spawning throughout most of the year with a peak spawning period in November–
588 December followed by a second smaller peak in March–April (Abdussamad *et al.* 2008). The life history and ecology of both the giant trevally and bluefin trevally was described in greater
590 detail by Sudekum *et al.* (1991). Generally, both species appeared to spawn during the summer from April to November – with peak spawning during the months of May–August
592 (Sudekum *et al.* 1991). Fecundity estimates for bluefin trevally in the wild range between 65,390 and 657,963 eggs kg^{-1} with an exponential increase in fecundity relative to body
594 weight while fecundity estimates for giant trevally were not reported.

In the Southern Arabian Gulf, peak spawning of golden trevally occurs in spring from
596 April to May (Grandcourt *et al.* 2004). Based on the wild fisheries data obtained from the Southern Arabian Gulf, an estimate for mean body size at first maturity was 32.5 cm FL
598 (Grandcourt *et al.* 2004). Wild fisheries data from a similar study by Farrag *et al.* (2019) in the same region support the spawning period as that described by Grandcourt *et al.* (2004) and
600 median size and age at first maturity of 34.5 cm FL and 1.4 years, respectively.

Reproduction and spawning of striped jack has been described in the central north
602 Atlantic by Afonso *et al.* (2008) and the coastal waters of the Canary Islands (Socorro *et al.* 2005). In the central north Atlantic, fish showed a clear annual summer spawning season from
604 June to September where mature individuals were observed aggregating near summits of offshore reefs, when temperatures reached approximately 19°C. Median size at first maturity
606 was 27.8 cm FL for males and 30 cm FL for females. A lengthy spawning period for wild striped jack in the coastal waters of the Canary Islands was suggested by Socorro *et al.* (2005)
608 who observed oocytes in the advanced stages of vitellogenesis from late spring until the end of autumn (May to November). In Japan, the spawning season was estimated to be from

December to February – as evidenced by high GSI values of nearly 3 for females and 7 for males during this time (Murai *et al.* 1985a).

In the Southern Hemisphere, a similar size at maturity (26–28 cm, but occasionally as small as 18–20 cm) has been reported from wild fisheries data from silver trevally off the coast of New South Wales, Australia (Kalish & Johnston 1997; Rowling & Raines 2000). The authors report that silver trevally appears to be a partial spawner with several batches of eggs and proposed that this species is likely to release several batches of eggs over a wide period from spring to autumn (September of March) with GSI peaking around November to December. Individual batch fecundity estimates were up to 220 x10^3 eggs for a 37 cm fish; however, estimates for the majority of females measuring 23–37 cm in length were 30–100 x10^3 eggs. In New Zealand waters, wild silver trevally have been captured in spawning condition in February, during the summer (James 1976).

3. Reproductive function in captivity and spontaneous spawning

3.1. Greater amberjack

The first experiments on greater amberjack reproduction in captivity date back to 30 years ago, when spawnings were reported in large tanks in Japan (Kawabe *et al.* 1996). Wild-caught greater amberjack have proven difficult to adapt to captivity. Oocyte atretic degeneration following failure to complete vitellogenesis and enter OM was reported by Micale *et al.* (1999) in fish caught as juveniles and reared for five years in outdoor tanks in Messina (Italy). Failure of oogenesis completion followed by atresia was also reported by Mylonas *et al.* (2004) in wild females reared in 30–40-m^3 tanks under ambient photothermal conditions, in a mixture of surface and well-water. Jerez *et al.* (2006) reported that a group of 8-kg wild fish took six years to overcome the captivity-induced reproductive dysfunction and

spawn spontaneously in Tenerife (Spain) in a 500-m^3 outdoor tank under natural environmental conditions. Repeated spawnings (n = 38) were reported to occur between the end of April to October (19.7 and 24.5°C), with the spawning peak between July and September. Spawning occurred every four to seven days, at night-time, but this was probably the result of only a single female spawning. Also in Spain, Sarih *et al.* (2018) monitored the reproductive maturation of a greater amberjack broodstock of wild origin reared in 10 m^3 tanks in Gran Canaria and found that two females out of a total of 19 spawned spontaneously and produced high quality eggs. Finally, in Greece, fish reared in sea cages for eight years and transferred to outdoor 70 m^3 tanks in the beginning of the spawning season (Fig. 6) spawned spontaneously five times, with an interval of two–eight days at sundown (C.C. Mylonas, unpublished data).

The above data testify that wild greater amberjack can potentially spawn when reared in captivity. However, their capacity to adapt and reproduce spontaneously under captive conditions, even in large volume tanks under natural environmental conditions, is rather limited, since the reproductive axis takes several years to partially overcome the stress-induced dysfunction and only a small fraction of captive-reared females is able to mature eggs and spawn spontaneously. In order to gain further insights on the reproductive dysfunctions occurring in captivity, the reproductive status of captive-reared greater amberjack was examined during three periods of the reproductive cycle, and compared with fish caught commercially in the wild in the Mediterranean (Zupa *et al.* 2017a, b; Pousis *et al.* 2018, 2019). In captive-reared females, the GSI was lower than in wild females, during the advanced gametogenesis and spawning phases (Zupa *et al.* 2017b). During the active gametogenesis phase of the wild population, most of the captive-reared females displayed major α atresia of vitellogenic follicles (> 50% were atretic), and during the peak of the reproductive season, 100% of vitellogenic oocytes were atretic, thus indicating a regressed

condition related to an impairment of the reproductive cycle (Zupa *et al.* 2017b; Pousis *et al.* 2018). In these reproductive dysfunctional greater amberjack females, an alteration of the sex steroids profile was also observed with plasma T, E_2, and 17,20β-P being lower than wild fish (Table 3) (Zupa *et al.* 2017a). The observed reproductive dysfunctions were not related to an impairment of the vitellogenic process, because liver expression of the three vitellogenins (*vtga, vtgb and vtgc*), as well as yolk uptake in vitellogenic oocytes did not differ between captive-reared and wild greater amberjack (Pousis *et al.* 2018). However, captive-reared females showed a reduced gene expression of vitellogenin receptors (*vtgr* and *lrp13*) at the beginning of the reproductive cycle, associated with a reduced number of vitellogenic oocytes during the vitellogenesis phase (Pousis *et al.* 2019). These findings suggested that the observed reproductive dysfunctions in greater amberjack females arose during the early phase of oogenesis and, ultimately, resulted in a reduced reproductive potential (fecundity) (Pousis *et al.* 2019). Similar results were obtained from wild-caught greater amberjack reared in tanks in different aquaculture facilities (Fakriadis *et al.* 2020b).

Interesting data on plasma sex steroid concentrations of first generation (F_1) hatchery produced greater amberjack reared in tanks (Table 3) recently (Jerez *et al.* 2018). In females, plasma sex steroid concentrations were low and showed a limited variability during the sampling period (May–September) (Table 3), confirming the existence of a reproductive impairment in hatchery produced greater amberjack. This impairment, however, did not prevent the fish from producing high numbers of high-quality eggs through hormonally induced spawning (see later).

The cDNAs encoding FSHβ, LHβ of greater amberjack and their ovarian receptors were cloned (Nyuji *et al.* 2016) and *fhsβ*, *lhβ*, *fsh* receptor (*fshr*) and *lh* receptor (*lhr*) transcripts were measured from September to August 2011 in captive reared fish in Japan. In the same study, FSH and LH was measured in the plasma. Pituitary gene expression of *fshβ* and ovary

684 expression of *fshr* showed a significant increase from January to March and reached a peak in April–June. This peak was followed by a significant increase of FSH plasma level at the end
686 of the reproductive season in August, which was possibly related to the role of FSH in preparing the gonad to the next reproductive cycle (Nyuji *et al.* 2016). A similar peak in
688 pituitary *lhβ* gene expression was reported in April–June; however, this peak was not followed by any significant surge in LH plasma concentration. These data indicate that greater
690 amberjack confined in captivity do have a normal capacity to synthesize pituitary GtHs; however, the capacity to release LH from the pituitary is altered. This prevented oocytes from
692 entering OM after the completion of vitellogenesis and finally resulted in oocyte atresia and spawning omission. The effects of the administration of gonadotropin releasing hormone
694 agonist (GnRHa) on OM and GtH plasma levels were examined in a greater amberjack broodstock of wild origin (Nyuji *et al.* 2019). In fish whose ovaries contained oocyte at the
696 end of vitellogenesis (oocyte diameter > 600 μm), a significant increase of plasma concentrations of LH was observed 24 h after treatment, and all treated fish ovulated after 36–
698 42 h, whereas only two out of five untreated control fish spawn spontaneously. This experiment confirmed that greater amberjack females undergo reproductive dysfunction even
700 if they are reared in large volumes (sea cages) at sea; however, the reproductive dysfunction was overcome through the GnRHa stimulation of LH release from the pituitary.

702 Recently, there is an increasing number of studies on the effects of confinement in captivity on greater amberjack spermatogenesis and sperm quality (Table 4). Early
704 experiments with wild young-of-the-year confined in sea cages, indicated that fish released sperm after application of abdominal pressure at the age of three years; however, sperm
706 motility was highly variable (Kožul *et al.* 2001). Poor sperm quality was also shown in wild-caught greater amberjack reared in tanks (Mylonas *et al.* 2004), as well as in sea cages
708 through the year (Fakriadis & Mylonas 2021). Sperm motility ranged between 5% and 30%

and motility duration between 2.1 and 2.5 min in tanks (Mylonas *et al.* 2004). When breeders were maintained in sea cages, sperm motility ranged between 30% and 60% and motility duration between 1.2 and 5.3 min (Fakriadis & Mylonas 2021). The treatment of fish in tanks with GnRHa controlled-release implants resulted in an increase of sperm motility to 65% and of motility duration to 2.7 min (Mylonas *et al.* 2004), whereas the GnRHa treatment of fish reared in sea cages increased sperm motility from 24% to 45%, while motility duration was unchanged (Fakriadis & Mylonas 2021). In more recent studies (Zupa *et al.* 2017a, b) it was shown that (a) captive-reared males had lower GSI and diameter of seminiferous tubules than wild fish, (b) half of the analyzed captive-reared specimens had precociously ceased their spermatogenic activity during the phase of active spermatogenesis of the wild population (late May–early June) (Fig. 7) and (c) all captive-reared fish were in spent (regressed) condition during the spawning phase of the wild fish. A lower capacity of spermatogonia from captive-reared fish to enter meiosis and proceed toward spermatogenesis was noted, which led to the observed precocious cessation of the reproductive activity (Zupa *et al.* 2017a). Moreover, captive-reared greater amberjack exhibited a much higher density of germ cell apoptosis during the early spermatogenesis phase compared with wild individuals (Zupa *et al.* 2017a). The gametogenesis impairment of the captive-reared greater amberjack males resulted from an alteration of the sex steroid profile (Zupa *et al.* 2017a, b) (Table 3). In fact, these fish exhibited lower plasma concentrations of T, 11-KT and 17,20β-P than wild specimens throughout the reproductive cycle (Zupa *et al.* 2017a, b). Moreover, a very high plasma concentration of E_2 was detected in captive-reared fish during the early phase of spermatogenesis and it was hypothesized that the observed low spermatogonial capacity to enter meiosis and the high density of apoptotic germ cells at the onset of spermatogenesis may represent the results of the combined effects of abnormally high E_2 and low 11-KT/T concentrations (Zupa *et al.* 2017a).

As a consequence of the observed spermatogenesis impairment, a low sperm quality was recorded in captive-reared greater amberjack (Zupa *et al.* 2017a) (Table 4). Despite this, the large number of fertilized eggs obtained from fish reared in sea cages and then moved to land-based tanks for spawning after GnRHa treatment, suggested that captivity affected spermatogenesis to some extent (Fakriadis & Mylonas 2021), but did not result in a failure to spawn and fertilize eggs (Fakriadis *et al.* 2020b). Finally, in the only available study with hatchery produced males (F_1) reared in tanks (Jerez *et al.* 2018), mean sperm motility was > 50% and remained unchanged throughout the reproductive season (May–September); a gradual reduction of sperm motility duration was observed from May to June and mean sperm density increased from May to September (Jerez *et al.* 2018) (Table 4), likely due to the lack of sperm hydration (Zupa *et al.* 2017a).

The gametogenesis impairment observed in both male and female captive-reared greater amberjack was proposed to be exacerbated by a nutritional deficiency (Zupa *et al.* 2017b; Pousis *et al.* 2019). The diet of adult greater amberjack caught during the spawning season is mainly constituted by pelagic and benthic teleosts and a small amount of molluscs and crustaceans (Sley *et al.* 2016). During the spawning period, however, greater amberjack diet was reported to be limited to fewer species, with a clear prevalence of demersal preys (Andaloro & Pipitone 1997). The diet of wild greater amberjack breeders results in specific polar lipids and fatty acid profiles (Zupa *et al.* 2017b; Pousis *et al.* 2019) and common commercial broodstock diets might not fit their nutritional requirements. In fact, differences in the gonad composition of wild fish *vs* captive-reared individuals fed a commercial broodstock diet were found. In particular, significant differences were observed in total polar lipid contents, as well as in essential fatty acids, arachidonic acid (ARA) and docosahexaenoic acid (DHA), which play a pivotal role in oocyte membrane structure including receptor domains, egg quality, as well as in sperm motility and testosterone

production (Zupa *et al.* 2017b; Pousis *et al.* 2019). Sarih *et al.* (2020) confirmed that highly unsaturated fatty acids (LC-PUFAs) strongly affect greater amberjack spawning performances and suggested to keep dietary DHA and eicosapentaenoic acid (EPA) in the range of 1–1.7% dry weight of feed. Moreover, according to another study by the same authors (Sarih *et al.* 2019), increased histidine and taurine content in broodstock feed optimized reproductive performance and egg production.

3.2. Other Seriola spp.

Rearing in captivity leads to an earlier onset of puberty in yellowtail, in which the age at first maturity is two years in the wild (Kagawa 1992; Shiraishi *et al.* 2011; Miura *et al.* 2014). High feeding under captive conditions causes high growth rates and enhanced lipid storage, leading to the early onset of puberty (Taranger *et al.* 2010). It has been demonstrated that, in reared yellowtail, food restriction results in a delay and inhibition of gonadal development (Miura *et al.* 2014; Higuchi *et al.* 2017b, 2018). A reduction in food intake from an immature stage showed the inhibition of E_2 production and vitellogenesis in females, while in males, it resulted in a decrease of GSI, but an increase of plasma 11-KT levels and the completion of spermatogenesis (Miura *et al.* 2014; Higuchi *et al.* 2018). In contrast, a reduction in food intake during the vitellogenic phase resulted in the inhibition of E_2 production but only in a delay in oocyte growth (Higuchi *et al.* 2017b). Food restriction in vitellogenic females showed no effects on plasma proteins and the pituitary gene expression of GtHs. These results indicate that food restriction inhibits the gonadal development of reared yellowtail, while the degree of this inhibition depends on sex and reproductive status.

As with greater amberjack, inhibition of OM and ovulation/spawning is the most common type of reproductive dysfunction in yellowtail, although some natural spawning may occur occasionally (Chuda *et al.* 2001b; Hamada & Mushiake 2006). In contrast, spawning in

784 captivity occurs spontaneously in yellowtail kingfish and longfin yellowtail, showing different spawning characteristics (Table 5 and 6). The rearing of wild-caught yellowtail
786 kingfish in New Zealand demonstrated that multiple spawning occurred at water temperatures above 17°C (Moran *et al.* 2007), with a spawning interval of two–four days. The fish spawned
788 in the early daylight hours before 06:00 h at the start of the period, while they spawned around dusk between 20:00 and 22:00 h towards the end. Observation of the spawning
790 behavior showed that only one female and two males were involved in 50% of the recorded spawning events. In another study, it was shown that spawning of yellowtail kingfish was
792 initiated with increasing day length and temperature, after a period of cooler temperatures with a shorter day length (Symonds *et al.* 2014).

794 Reared yellowtail kingfish in California spawned mainly between April to June (Stuart & Drawbridge 2013; Stuart *et al.* 2020). Monitored for four years, a group of 18 females and
796 17 males produced 16 spawning events in the first year and a group of nine females and 12 males produced 22 to 43 spawning events in the second to fourth years (Stuart & Drawbridge
798 2013). The time of spawning ranged from 16:00 to 01:00 h, and it occurred earlier in the day as the spawning period progressed (Table 5 and 6). It was also demonstrated that egg diameter
800 decreased and was associated with a reduction of fatty acids in the eggs as the spawning season progressed and water temperature increased (Stuart *et al.* 2020). This suggests that the
802 egg quality of yellowtail kingfish decreases in the later phase of the spawning season.

The natural spawning of reared longfin yellowtail has been reported in a wide range of
804 locations (Table 5). Reared wild-caught longfin yellowtail in the Ogasawara Islands (southern Japan) for two years spawned multiple times between April and November (Kawabe *et al.*
806 1997). In the first year, 10 fish (unknown sex ratio) with a body weight of 5–10 kg, produced 53 spawns (29.4 x10^6 eggs), while in the second year 22 fish (unknown sex ratio) with a body
808 weight of 5–13 kg produced 113 spawns (123.3 x10^6 eggs). During the spawning period, the

water temperature ranged from 24 to 27°C, and the time of spawning ranged between 05:00 and 07:00 h.

On the other hand, several studies have demonstrated that longfin yellowtail has a longer spawning period at a water temperature of 26°C in Ecuador, Hawaii, Mexico, and Florida (Blacio 2004; Laidley *et al.* 2004; Quiñones-Arreola *et al.* 2015; Patrick *et al.* 2019; Teles *et al.* 2019). In Hawaii, longfin yellowtail spawned naturally all year round with an average of 13 spawns per month under an ambient photoperiod and water temperature (Laidley *et al.* 2004). Meanwhile longfin yellowtail in Ecuador started spawning when the water temperature reached 26°C, and a single female spawned once or twice a week, and the total annual fecundity was 600 $x10^3$ eggs kg^{-1} (Blacio 2004). Observation of the spawning of longfin yellowtail reared at constant water temperatures in Mexico showed that spawning continued between May and December (Quiñones-Arreola *et al.* 2015). Taken together, natural spawning of reared longfin yellowtail occurs at higher temperatures than in other farmed *Seriola* species, and rearing at relatively constant temperatures results in more spawning events (Table 5) and higher annual fecundity in captivity (Table 6).

3.3. Other Carangids

Acclimation and spontaneous spawning has been reported for bluefin trevally (Moriwake *et al.* 2001), and striped jack in Europe (Nogueira *et al.* 2018) and Japan on several occasions (Table 5 and 6). Despite the fact that golden trevally has been farmed extensively throughout Asia (Chou 1994; Liao *et al.* 2001; Feng *et al.* 2005), spontaneous spawning of this species in captivity remains unreported or is limited to a report by Sim *et al.* (2007) of fingerling production from spontaneously spawning broodstock.

The single account by Moriwake *et al.* (2001) highlighted that while bluefin trevally reached advanced stages of ovarian development during the first year when the broodstock population was established, but it was not until the second year that spontaneous spawning was observed. During the first year of acclimation of the broodstock, the largest size-class of oocyte diameters of two females were 375 and 425 µm, but did not progress further. During the same sampling point males had motile sperm, thus confirming that males complete spermatogenesis in captivity. In the same report by Moriwake *et al.* (2001), in a follow up experiment commencing in early spring (March), gonadal development of broodstock was assessed every three–five months over a two-year period while maintained in a 35-m^3 tank. All females had reached advanced stages of oocyte development by early summer (June) and remained 'mature' for the duration of the study. Spontaneous spawning was observed in both years during the summer (May to August) and to a lesser extent in the winter (Table 5). Spawning occurred at night and during the new moon and third lunar quarter. Findings indicated that bluefin trevally is also a multiple spawning species – a female is able to spawn at least eight times each year and at least two times within a five-day period (Moriwake *et al.* 2001). The mean diameter of spawned eggs ranged between 721 and 787 µm and fecundity per female was estimated at 1,545 x10^3 eggs per kg^{-1} (Table 6). Mean fertilization from the two years were 65 and 58%, respectively.

The first fertilized eggs and hatched larvae from striped jack were obtained in Japan in 1973 (Harada *et al.* 1984a, b). In subsequent years, natural spawning of wild-caught striped jack was reported by Murai *et al.* (1985b) after four years of acclimation in captivity. Egg collection occurred in winter (18.5 and 21.5°C). Spawning occurred 1–2 h after sunset and peaked at three times during the season with an estimated total annual egg production of 3,895 x10^3 eggs $female^{-1}$. The spontaneous spawning of striped jack has been prompted by means of a single-step temperature increase (Vassallo-Agius *et al.* 1998, 1999, 2001c;

Watanabe *et al.* 1998) where spawning occurred from later winter to early spring in Japan (Watanabe & Vassallo-Agius 2003). Prior to spawning in the latter studies, broodstock were generally conditioned under ambient conditions in sea pens before being transferred to tanks. Vassallo-Agius *et al.* (2001c) proposed a single-step temperature increase from an ambient 17°C to 22°C over a five-day period, and 22°C was considered to be the optimal spawning temperature (Mushiake 1994).

Studies in Japan during the late 1990s also tested the effects of different diets on the reproductive output of striped jack. Generally, the number of spawning events was higher from broodstock maintained on a raw fish diet, with total egg production being 2.5–3 times higher than that from broodstock maintained on test formulated/commercial soft dry pellets (Watanabe *et al.* 1998; Vassallo-Agius *et al.* 1999). While buoyancy, fertilization and hatching were higher in spawns from the raw fish diet group, larval survival was comparable between the different diets (Watanabe *et al.* 1998; Vassallo-Agius *et al.* 1999). Estimates of total egg production from each of the studies ranged from 114 to 213 $x10^3$ eggs $female^{-1}$ day^{-1} (Watanabe *et al.* 1998) and from 37 to 56 $x10^3$ eggs kg^{-1} female day^{-1} (Vassallo-Agius *et al.* 1999). In a similar study testing the effect of raw fish and formulated/commercial soft dry pellet diets on reproductive output of striped jack subsequent to a single-step temperature increase, both groups spawned 18 times and no differences in the mean total egg production and egg quality were observed (Vassallo-Agius *et al.* 2001c). The egg diameters from the latter studies on striped jack were within the 880–1020 μm range reported elsewhere from naturally spawning eggs in captivity (Murai *et al.* 1987). Optimum temperature and salinity for hatching is 20°C and between 35–41‰, respectively (Kawabe *et al.* 1991; Murai *et al.* 1992).

Nogueira *et al.* (2018) reported wild-caught striped jack broodstocks spawning spontaneously after four years in captivity in Madeira (Portugal). The broodstocks were

reared in tanks under natural photo-thermal conditions (18–24°C). Spawning occurred in May and June (19.5 and 21.9°C). A total of 20 spawns were recorded (mean egg diameter: 969 ± 27 µm; range of number of eggs in each spawn: 15.6 x10^3 - 1.4 x10^6; average number of eggs spawned per female: 280 x10^3). Approximately 57% of the spawned eggs were buoyant 'viable' and fertilization success was consistently greater than 95%. Both eggs size and hatching decreased towards the end of the spawning season and were negatively correlated with water temperature.

The data above reported on the reproduction in captivity of trevally species, indicate that broodstocks of wild origin are capable of completing vitellogenesis, OM and spawning in captivity; however, they can take one to four years to acclimatize before spawning spontaneously. Spawning of striped jack appears to be seasonal and dependent on water temperatures between 19 and 24°C, while bluefin trevally appears to have multiple spawning seasons within a single year (both in summer and winter).

4. Hormonal manipulations of reproductive function and induced spawning

4.1. Greater amberjack

As reported in 3.1 above, the greater amberjack has a limited capacity to overcome reproductive dysfunctions in captivity, even if the fish were taken from the wild as young-of-the-year and were reared for many years. As a result, females fail to undergo complete gametogenesis and/or OM and males produce reduced amount of sperm and of variable quality. The failure to control reproduction has been the major bottleneck for this species' aquaculture production (Ottolenghi *et al.* 2004). Although not experimentally demonstrated, combining the available endocrine research from other fishes and greater amberjack, one can hypothesise that the reproductive dysfunction is related to an insufficient release of LH from

the pituitary at the conclusion of oogenesis (Mylonas *et al.* 1997, 1998, 2010). This in turn is caused by a dysfunctional release of GnRH from the hypothalamus (Zohar *et al.* 2010; Zohar 2020). This hypothesis is in agreement with (a) the evidence that both liver vitellogenin gene expression and oocyte yolk accumulation are not impaired (Pousis *et al.* 2018) and fully vitellogenic oocytes are commonly found in the ovary of captive-reared fish (Mylonas *et al.* 2004; Fernández-Palacios *et al.* 2015a; Nyuji *et al.* 2016; Zupa *et al.* 2017b; Jerez *et al.* 2018; Pousis *et al.* 2018; Sarih *et al.* 2018; Fakriadis *et al.* 2019, 2020a, 2020b), (b) the absence of a peak in LH plasma concentration following the increase in pituitary *lhβ* gene expression (Nyuji *et al.* 2016) and (c) the low capacity of females to complete oogenesis and spawn spontaneously (Jerez *et al.* 2018; Sarih *et al.* 2018). Another empirical evidence is the effectiveness of even a single GnRHa administration in inducing oocyte maturation and spawning (Mylonas *et al.* 2004; Fernández-Palacios *et al.* 2015a; Nyuji *et al.* 2016; Jerez *et al.* 2018; Sarih *et al.* 2018; Fakriadis *et al.* 2019, 2020a, 2020b).

The first successful attempt to hormonally induce spawning in wild-caught greater amberjack reared in captivity was carried out by Mylonas *et al.* (2004), who treated a pair of fish, reared in a mixed surface and well water in 30–40 m^3 tanks, with GnRHa implants, when fully vitellogenic oocytes (oocyte diameter 650 μm) existed in their ovaries (Table 5), producing a total of 50,000 eggs kg^{-1} (Table 6), and increasing sperm motility and duration (Table 4). Later, GnRHa was administered through 15 consecutive injections to a wild-caught broodstock reared in Gran Canaria (Spain) in 10 m^3 tanks supplied with surface sea water (Fernández-Palacios *et al.* 2015a). Spawnings occurred between 33 and 45 h after each treatment and the number of spawns per treatment changed during the reproductive season, with an average of 1.5 ± 0.8. The mean fecundity was about 339 x 10^3 eggs kg^{-1} female BW and the egg quality parameters showed an overall increase during the reproduction period.

In the same region, another study (Sarih *et al.* 2018) reported on egg production after GnRHa administration of wild-caught fish reared until their body weight was 9.5 – 12 kg and were moved to 40 m^3 tanks under natural photothermal conditions (Table 5). In late May, all males produced releasable sperm and six females had oocytes > 650 µm (potentially responsive to GnRHa treatments). The GnRHa injection group was treated from June 3 to October 31 according to a rotation protocol with 20 µg kg^{-1} BW every 12 days; the GnRHa implantation group was treated every 27 ± 7 days from June 3 to October 14 with GnRHa implants, to produce an effective dose of 50 and 25 µg kg^{-1} BW for females and males, respectively. The number of spawns per treatment was significantly higher for the implanted than for the injected fish (2.2 ± 1.9 vs 0.8 ± 0.5). The mean number of eggs produced per spawn was similar between treatments (Table 6), but egg quality was significantly higher in injected fish, so it was concluded that GnRHa administration through injections was more effective in inducing high quality spawns.

Different results were reported by Fakriadis *et al.* (2019) in wild caught greater amberjack reared in sea cages during the year (Fig. 8a), selected during the spawning season (Fig. 8b and c) and treated with GnRHa to induce spawning (Fig. 8d). Females with oocyte > 600 µm and spermiating males were administered either two GnRHa implants (one every two weeks), or three GnRHa injections (one injection every week). The fish were then moved to four 23-m^3 indoor tanks provided with surface sea water under ambient photo-thermal conditions. Spawning started one day after the first treatment (possibly because some fish had already oocytes in maturation that were spontaneously spawned) and two days after the second and third treatments (20 and 24°C) (Table 5). At the end of the experiment, more implanted than injected females were still reproductively active and potentially eligible for further spawning. Both egg production per spawn and total egg production were significantly higher in GnRHa implanted than in injected fish (Table 6). In particular, the total number of

eggs produced after the first and second implantation were more than double compared with the respective injection. Egg quality data were good and not significantly different between the two treatments.

The contradictory results obtained by Sarih (2018) and Fakriadis (2019) were explained through differences in the environmental conditions (surface sea water vs borehole seawater) and in the genetic origin of the used greater amberjack populations (Fakriadis *et al.* 2019). Genetic studies suggested that Atlantic and Mediterranean greater amberjack populations are genetically different (Šegvić-Bubić *et al.* 2016). In addition, greater amberjack reproductive activity in the wild is strongly affected by the environmental conditions and the reproductive season is much extended in tropical than in temperate waters (Kikawwa & Everson 1984). The higher number of spawns obtained through GnRHa administration by means of implants confirms that the sustained pituitary stimulation of GtH release is the treatment of choice in this species, because it fits better the reproductive physiology of fishes with asynchronous (or group-synchronous) oocyte development. In fact, the prolonged GnRHa stimulation likely induces both LH and FSH release from the pituitary and it prompts both meiosis resumption in oocytes that have completed vitellogenesis and vitellogenesis of successive oocyte batches, so assuring more cycles of OM and spawning (Fakriadis *et al.* 2019). Another noticeable difference between Atlantic and Mediterranean greater amberjack broodstocks is represented by the different tank adaptation capacity, as Atlantic stocks seem to be more capable of complete gametogenesis when reared in tanks (even relatively small ones), than Mediterranean ones (Fakriadis *et al.* 2020b).

Based on these difficulties in vitellogenesis of greater amberjack maintained in tanks, a method has been developed for inducing spawning of fish reared in sea cages during the year, and then placed in tanks after GnRHa treatment (Fakriadis *et al.* 2020b). Rearing in tanks represents the best option for aquaculture broodstock management due to biosecurity reasons,

lower environmental impact, ease of handling and egg collection. However, rearing in sea cages offers the opportunity to maintain broodstocks at the right environmental conditions for reproduction and minimizes stress. Maintaining broodstocks in sea cages, and collecting eggs in the sea using curtain-type egg collection devices has been implemented successfully in Atlantic bluefin tuna in the Mediterranean after GnRHa induction (Mylonas *et al.* 2007; De Metrio *et al.* 2010). A similar broodstock management and spawning induction method for greater amberjack was attempted in three fish farms over a three-year period (Fakriadis *et al.* 2020b). All males were in spermiating condition, and most of the females had fully vitellogenic oocytes (oocyte diameter > 650 μm) or oocytes in OM at the beginning of the reproductive season in June. Unfortunately, a very low quantity of eggs was collected after GnRHa implantation of fish in sea cages, indicating a low efficiency of the egg collectors applied to the cages (Fakriadis *et al.* 2020b). The failure to implement efficient egg collection for greater amberjack in sea cages — compared with Atlantic bluefin tunas — was probably related to the lower buoyancy of greater amberjack eggs and the time of spawning in relation to when egg collection was attempted. On the contrary, large numbers of eggs were obtained from the females moved to land-based tanks after GnRHa implantation.

This cage-to-tank broodstock management and spawning induction method for greater amberjack was further optimized by comparing GnRHa injections vs implants (Fakriadis *et al.* 2019), examining the effect of GnRHa re-implantation (Fakriadis *et al.* 2020b), and determining the most effective GnRHa dose to be administrated through implants and the extent of the spawning season (Fakriadis *et al.* 2020a). More recently, an evaluation was also made on the effect of the GnRHa implantations on sperm production and quality parameters, over the whole reproductive season and in different facilities (Fakriadis & Mylonas 2021). As mentioned earlier, the GnRHa implants were shown to be more effective than repeated injections in Mediterranean greater amberjack (Table 5 and 6). As regards the GnRHa implant

dose-response treatments, an effective dose of 25 or 75 μg kg^{-1} BW was examined. The two GnRHa doses proved to be equally effective, resulting in a total relative fecundity of 185 to 199 ± 17 x 10^3 eggs kg^{-1} BW in 11–18 spawns. The egg quality parameters also did not differ significantly between the two treatments, and based on the previous study that used 50 μg kg^{-1} BW (Fakriadis *et al.* 2019), this was concluded to be the most cost-effective dose. In order to determine the extent of the reproductive season in greater amberjack reared in sea cages in the eastern Mediterranean and to identify the best timing for GnRHa induction, two experiments were carried out in a two-year study at Galaxidi (Greece), between May 30 and July 18 at 20 - 26°C (Fakriadis *et al.* 2020a). Selected fish were administered GnRHa implants at four different times during the studied period with a one– or two-week interval. No significant differences in the mean diameter of the largest vitellogenic oocyte population of females treated at these different times were observed, indicating that all the females were potentially responsive to GnRHa treatment throughout the examined period. Spawning frequency was higher after the first two treatments during both years. Daily relative fecundity did not change significantly during the experimental period in either year and no significant differences in egg quality parameters was observed. The authors concluded that it is possible to take portions of a broodstock from a sea cage at any time from the end of May to the end of July to successfully induce them to spawn in onshore tanks.

The bulk of data produced by spawning induction experiments in greater amberjack indicates that the response to GnRHa administration is different between broodstocks in the Mediterranean and the Canary Islands (eastern Atlantic, Spain), due to genetic peculiarities of the two populations and/or different environmental conditions. GnRHa administration via injections or implants successful induces high quality spawns, and repeated administrations of both injections and implants support a reproductive season prolonged from May to July in the Mediterranean and from May to October in the subtropical water of the Canary Islands.

Reproductive maturation of female greater amberjack reared in tanks assures the production of fully vitellogenic oocytes responsive to GnRHa administration in the eastern Atlantic, but not in the Mediterranean, where only rearing in cages allowed producing high amount of good quality eggs. In order to optimize egg collection from fish reared in sea cages, fish should be moved to land-based tanks after hormonal induction, because egg collection is inefficient in sea cages. The egg production from GnRHa-treated fish is adequate for commercial purposes, provided that the proper rearing conditions, hormone doses and timing of treatment are optimized; however, daily and total annual fecundity usually recorded in captive conditions are at least 2 orders of magnitude lower than those reported for wild fish (Harris *et al.* 2007), possibly because oocyte recruitment into vitellogenesis is limited due to a reduced expression of vitellogenin receptors during the phase of ovarian recrudescence (Pousis *et al.* 2019) and reproductive hormone concentrations in captivity are lower than those observed in wild fish (Zupa *et al.* 2017b; Jerez *et al.* 2018), suggesting that greater amberjack reproduction control and egg production in aquaculture can be further improved.

Finally, hatchery produced greater amberjack breeders became available in the last decade, and treatments with GnRHa implants were also successful in inducing OM and spawning (Jerez *et al.* 2018). Fourteen F_1 hatchery produced fish (seven females and seven males; age 6–10 years) were reared at ambient conditions in 50-m^3 outdoor tanks supplied with seawater from a well in Tenerife (Spain). Females with fully vitellogenic oocytes (oocyte diameter > 650 μm) and spermiating males were administrated a GnRHa in May, June and July. Spawnings begun one–two days after each treatment (at 20 - 25°C), and a total of 52 spawns occurred over a period of 72 days. The relative fecundity was highest after the first treatment (60 x 10^3 eggs kg^{-1} BW) and lowest after the third treatment (15 x 10^3 eggs kg^{-1} BW). Fertilization and hatching were similar after the first two treatments and decreased significantly after the third treatment. A similar trend was shown by larval survival three days

post hatching. This experiment also provided interesting data on sex steroid hormone concentrations in the plasma of fish sampled before treatments (Table 3). Sex steroid plasma concentrations of hatchery produced greater amberjack were comparable to those recorded for wild-caught greater amberjack reared in captivity in Greece and much lower than those determined in individuals caught from the wild and sampled soon after capture (Zupa *et al.* 2017b) (Table 3). These low plasma levels, however, did not prevent the production of a large number of good quality eggs through the administration of GnRHa to individuals that completed vitellogenesis.

4.2. Other Seriola spp.

The first successful efforts to hormonally induce spawning in yellowtail involved an injection of hCG of females having oocytes greater than 700 μm in diameter (Mushiake *et al.* 1993; Matsuyama *et al.* 1996). The level of circulating 17,20β-P was elevated after 6 h from hCG injection, but decreased rapidly after 12 h; then, GVM begun at 24 h after injection (Matsuyama *et al.* 1996). In another study, it was demonstrated that after hCG injection ovulation occurred at 36–48, 42–48, and 48–54 h in females having oocytes of 750–800, 700–750, and 650–700 μm in diameter, respectively (Chuda *et al.* 2005). Thus, the time elapsed from hCG injection to ovulation was inversely related to the oocyte diameter at the time of injection. The number of eggs produced by a single injection of hCG was 300–1,000 $x10^3$ eggs $female^{-1}$ weighing 8–10 kg (Kagawa 1992; Mushiake *et al.* 1993; Vassallo-Agius *et al.* 2002; Yamazaki *et al.* 2002) (Table 6). Chuda *et al.* (2002) showed that by a single injection of hCG, the number of eggs ovulated was 468 $x10^3$ eggs $female^{-1}$ for fish of three years of age and 8–11 kg BW, while it was 212 $x10^3$ eggs $female^{-1}$ for fish of two years of age and 6–7 kg BW. Between these two age groups, there were no differences in fertilization and hatching

success. Therefore, the number of ovulated eggs varies depending on the age and size of females, but there does not appear to be any age-related differences in egg quality.

A comparison of a single injection of hCG and other hormonal treatments suggested that the former approach is a better method for inducing ovulation in yellowtail (Chuda *et al.* 2001a). This experiment showed that a priming injection of hCG (50 and 100 IU kg^{-1} BW) prior to the main injection of hCG (500 IU kg^{-1} BW) resulted in a delay in ovulation and lower rates of fertilization and hatching. The same study further showed that the implantation of GnRHa-containing cholesterol pellet (200 and 400 µg GnRHa kg^{-1} BW) resulted in a reduction in the number of ovulated eggs. Chuda *et al.* (2001a) concluded that a single injection of hCG produces eggs in large numbers and of good quality in yellowtail, as the batch fecundity obtained by hCG injection is generally higher than that obtained by natural spawning and GnRHa-induced ovulation/spawning.

Nevertheless, other studies demonstrated that both hCG and GnRHa can be effective at inducing multiple spawning of yellowtail (Kagawa 1992; Mushiake *et al.* 1995) (Table 5). Groups of five females and four to five males treated with a single injection of hCG showed multiple spawning for 14 consecutive days (Mushiake *et al.* 1995). In that experiment, the highest number of eggs was recorded in the first spawning (500–1,150 $x10^3$ eggs per group), after which the number of spawned eggs decreased (< 100 $x10^3$ eggs per group after the fifth day). The total number of eggs spawned was 125–199 $x10^3$ eggs kg^{-1} BW. In contrast, a group of seven females and males implanted with GnRHa-containing cholesterol pellet (1000 µg $fish^{-1}$) showed multiple spawning for more than 11 consecutive days (Kagawa 1992). The total number of eggs spawned was 172 $x10^3$ eggs kg^{-1} female. These two studies suggest that GnRHa implantation stimulates the recruitment of oocytes to vitellogenesis, leading to the constant production of eggs, but hCG does not, resulting in a reduction in the number of

spawned eggs. A similar conclusion for the function of GnRHa implants was reached recently in greater amberjack (Fakriadis *et al.* 2019). In the GnRHa implantation-induced spawning, there was, however, a decrease in the fertilization and hatching success from 71% at the first spawning to about 10% at the ninth spawning (Kagawa 1992). Similarly, the survival of hatched larvae obtained from hCG-injected spawning was reduced with repeated spawning (Mushiake *et al.* 1995). It is unclear whether egg or sperm quality are associated with the reduction in the quality of fertilized eggs in the hormonally induced multiple spawning of yellowtail.

Multiple spawning induced by hCG treatment has also been reported for yellowtail kingfish (*S. aureovittata*) (Tachihara *et al.* 1997) (Table 5). In that experiment, a group of 35 fish (8.5 kg) injected with hCG (500 IU kg^{-1} BW) combined with salmon pituitary extract (0.7 mg kg^{-1} BW) achieved 16 spawning days at an interval of one–three days, between April and May (21°C). The fertilization success fluctuated during the multiple spawning period, but there was no trend toward a decrease of it in association with repeated spawning, unlike what has been observed in the yellowtail (Mushiake *et al.* 1995). Sustained release of GnRHa (from a GnRHa implant) has been applied to induce multiple spawning in yellowtail kingfish as well, and the results were compared with those from spontaneous spawning (Setiawan *et al.* 2016) (Table 5). In this experiment, a group of seven females (10 kg) and males (9 kg) was implanted with GnRHa (500 μg $fish^{-1}$), while another group of seven females (11 kg) and males (10 kg) underwent mock implantation. From the spawning observations, similar results were obtained in the numbers of spawning events (23 and 22 for the GnRHa and control groups), intervals (1.1 and 1.3 days), and eggs produced per batch (3,880 and 4,270 eggs kg^{-1} female) between the two groups. However, GnRHa implantation (a) increased the proportion of females contributing to spawning and (b) advanced vitellogenesis in females that had not

completed the process at the time of treatment. However, GnRHa implantation resulted in reductions in egg buoyancy, fertilization, and viability.

Repeated injection of GnRHa at an interval of 10–14 days has been shown to induce multiple spawning for longfin yellowtail reared on the Canary Islands, at a water temperature of 22–24°C (Roo *et al.* 2014, 2015; Fernández-Palacios *et al.* 2015a) (Table 5). Each GnRHa injection was shown to induce spawning at 32 h post-injection (Roo *et al.* 2015). A group of fish (4–7 kg) treated with such injection for three spawning seasons achieved 10, 17, and 9 spawning events for each year, with the number of eggs per batch in the range of 19,000–22,000 eggs kg^{-1} BW (Roo *et al.* 2015). Another group of fish treated with 15 repeated injections of GnRHa achieved 33 spawning events, with the total number of eggs of 944 $x10^3$ eggs kg^{-1} BW (Fernández-Palacios *et al.* 2015a). Combining this result with the data obtained from natural spawning (Kawabe *et al.* 1997; Blacio 2004), longfin yellowtail is supposed to possess an ability to spawn a number of eggs about five times higher than that of yellowtail and yellowtail kingfish (Table 6). Longfin yellowtail egg production showed an increase from June to July, peaked in September, and decreased in October (Fernández-Palacios *et al.* 2015a). Unlike the hormonally induced multiple spawning in yellowtail, there were no changes in the fertilization, hatching, and larval survival among the initial, middle, and final phases of multiple spawning events of longfin yellowtail (Roo *et al.* 2015).

4.3. Other Carangids

A range of hormonal preparations have been used to induce spawning of trevally by intramuscular (IM) injections (either singular or in a series) or the administration of sustained-release delivery systems containing GnRHa. For example, Mutia *et al.* (2015) tested the effect of hCG, GnRHa or Carp Pituitary Extract (CPE) on spawning performance of giant trevally. Broodstock aged five–seven years old with oocyte diameters of at least 500 µm and 60% of

the oocytes undergoing GVM were injected twice IM with either hCG (1000 IU kg^{-1}), GnRHa (100 µg kg^{-1}) or CPE at a dose of 5 mg kg^{-1} and the fish were left to spawn in 40 m^3 tanks (27.6–29.3°). Spawned eggs were only observed in hormone-treated fish with ovulation latency times ranging between 24 and 36 h after the second injection in hCG-treated females and 25–52 h after treatment with GnRHa. Treatment with CPE appeared to be the less effective, as only one of five females ovulated and eggs were not fertilized. While egg production (mean number of spawned eggs) was higher in the hCG-treated fish (223,068 eggs kg^{-1}) when compared with GnRHa-treated fish (176,524 eggs kg^{-1}), the fertilization and hatching success, as well as the number of larvae produced, were higher from fish treated with GnRHa than those treated with hCG. There are additional reports of giant trevally eggs being produced by induced spawning to study early and behavioral ontology of larvae; however, the protocol to induce spawning was not reported (Leis *et al.* 2006). Likewise, in order to produce fertilized eggs for the study of bluefin trevally digestive system ontogenesis, fertilized eggs were obtained in summer (May) after hormonal implantation with GnRHa, but further details were not reported by Kim *et al.* (2001).

In a single report on the induced spawning of golden trevally, one population of broodstock (two females and six males) was implanted IM with a single Ovaplant® implant (sGnRHa; an estimated dose of 31 µg kg^{-1}) while another broodstock was left untreated to determine if spawning occurred spontaneously (Broach *et al.* 2015). Broodstock tanks were 4.5 m^3 in volume and were maintained on a simulated-natural photoperiod and ambient temperature (26°C) and both females had vitellogenic oocytes of 300–500 µm in diameter. Spawning activity was only detected in the GnRHa-treated group over the two-week monitoring period of the study at 48, 72 and 96 h post-implantation. All eggs from the first spawn were unfertilized, while subsequent spawns were all fertilized. Based on the three spawns, the authors suggest the batch fecundity estimates may exceed 15,900 eggs kg^{-1} BW.

The same authors also report that repeated injections of Ovaprim® (sGnRHa + dopamine inhibitor) at a dose of 0.35–0.51 ml kg^{-1} has proven useful as a therapy to inducing multiple spawning events (two–four spawns per weekly injection) in the same species. As golden trevally spawned on multiple occasions throughout the spawning seasons, the authors estimate that the total seasonal fecundity may be greater than 225 $x10^3$ eggs kg^{-1} BW.

As a measure to increase the production of striped jack in the late 1980s, broodstock were induced to spawn using IM injections of hCG (500 IU kg^{-1} BW) and CPE (4 mg kg^{-1} BW). While specific latency times and egg production parameters between the two different hormone treatments were not reported, spawning was detected 40–50 h post-injection. A total of 12,6 x 10^6 million eggs were produced with an average hatching of 17% (Arakawa *et al.* 1987). Furthermore, in order to spawn a virgin striped jack broodstock, an injection of hCG in addition to a single-step temperature increase to 22°C has been applied on multiple occasions (Mushiake 1994; Vassallo-Agius *et al.* 2001a, b). Spawning was observed 36–48 h post-injection with egg production generally being higher within the first two days of spawning. In a study by Vassallo-Agius *et al.* (2001a) investigating the effect of astaxanthin supplementation of the reproductive output of hCG-treated virgin broodstock, total egg production ranged between 68 and 203 x 10^3 eggs $female^{-1}$ per day, with egg production being higher from broodstock maintained on the raw fish and the astaxanthin-supplemented pellet diets relative to production from broodstock fed the standard pellet diet. Egg buoyancy, fertilization and hatching rates were also higher in the latter groups when compared to those from broodstock maintained on the standard pellet diet. In a similar study, Vassallo-Agius *et al.* (2001b) reported that when the diet of hCG-treated females was supplemented with squid meal or equal portions of squid meal and krill meal, egg production was highest from broodstock maintained on the raw fish diet (233 x 10^3 eggs $female^{-1}$ per day) when compared to the supplemented diets with either squid meal (114 $x10^3$ eggs $female^{-1}$ per day) or squid

meal and krill meal (122 x 10^3 eggs female^{-1} per day). Despite the lower egg production from females supplemented with squid meal, egg quality buoyancy, fertilization and hatching were higher in this group. In general, reproductive output of hCG-treated females maintained on the raw fish diets from both studies was comparable to fecundity estimates described earlier from spontaneously spawning striped jack broodstock maintained on a similar diet.

Sustained-release GnRHa implants have also been used to induce spawning in striped jack with a target dose of 20 µg kg^{-1} (Roo *et al.* 2012), and most recently silver trevally with a target dose of 100 µg kg^{-1} (M.J. Wylie, unpublished data). In the study by Roo *et al.* (2012), females with oocyte diameters > 500 µm were selected for spawning induction. Of the estimated 4 million eggs produced from a total of three spawns, 98% of these were buoyant and fertilized while only 53% of these hatched. Based on these reports, it appears that broodstock with oocyte diameters > 500 µm can be successfully induced to spawn for giant trevally (Mutia *et al.* 2015) and striped jack (Roo *et al.* 2012), while spawning can be induced in golden trevally with oocytes ranging between 300 and 500 µm in diameter (Broach *et al.* 2015). Latency times in trevallies, regardless of species, vary from 36–50 h after a single injection of hCG (500–600 IU kg^{-1}) to 24–36 h after a second injection (dose 1000 IU kg^{-1}) when two injections are applied. Somewhat longer latency times are reported (48, 72 and 96 h post-implantation) in fish administered GnRHa implants (Broach *et al.* 2015). The effects of hormonal preparations on sperm quality and parental contributions during mass spawning events have yet to be reported for the latter trevally/jack species.

5. Concluding remarks

Reproductive maturation varies among members of the Carangidae family, and ranges between two and four years of age, with the larger bodied species maturing at a later age. As is

common in many fishes, males may mature at an earlier age and smaller size, and fish reared in captivity may also mature earlier, presumably due to higher food availability and faster growth. All carangids examined here have a paired, cystovarian type ovary with ovulated eggs being released into an ovarian cavity, and from there to the environment during spawning via a common oviduct, leading to the urogenital pore. The testis (also a paired organ) belongs to the unrestricted spermatogonial type, being characterized by the presence of spermatogonia along the germinal compartment throughout the testis. The maturing spermatocysts move towards the center of the tubule, and during spermiation the spermatozoa are released into the lumen from where they reach the sperm duct system. From there, the capacitated spermatozoa are released to the environment through a common sperm duct, which leads to the urogenital pore.

The examined carangids are iteroparous with asynchronous oocyte development and spawn multiple times during an annual reproductive season, whose extend depends on ambient water temperature. In general, these fishes spawn in the spring and/or summer, but differences exist between the temperate, sub-tropical and tropical regions in the duration of the spawning period, which is usually longer in the sub-tropical and tropical regions, where environmental conditions are more stable. Spawning takes place between 19 and 24°C, but in populations close to the tropics may spawn at even higher temperatures (28°C).

Acclimation to captivity is relatively easy for carangids, in terms of feeding and growth, but reproductive development and maturation has been quite variable both among species, and among populations of certain species, from different geographical regions. For example, greater amberjack and yellowtail rarely undergo spontaneous maturation, ovulation and spawning in captivity, while yellowtail kingfish, longfin yellowtail and striped jack spawn readily in captivity when exposed to the appropriate photothermal cycles. In greater amberjack, which has been the most extensively studied species in this aspect, vitellogenesis takes place normally in captivity when fish are maintained in sea cages during the year, or in large-volume tanks

supplied with surface seawater, as opposed to borehole sea water. However, oocyte maturation and spontaneous spawning is inconsistent and unreliable for commercial production. Furthermore, when females are maintained in tanks during the year and are exposed to borehole sea water, vitellogenesis is also affected and only a small number of females may reach advanced stages and undergo maturation. Similarly, male greater amberjack also exhibit reproductive dysfunctions when reared in captivity, resulting in reduced volume of sperm and variable quality. Recent studies showed that captive-reared males had lower GSI and smaller diameter of seminiferous tubules than wild fish, and they had ceased their spermatogenic activity precociously, exhibiting low germ cell proliferation capacity and enhanced apoptosis. Furthermore, these changes appeared to be associated with altered sex steroid profiles compared with wild fish, but this reproductive dysfunction did not prevent males from spawning and fertilizing eggs when treated with GnRHa. In contrast to yellowtail and greater amberjack, spawning in captivity occurs spontaneously in yellowtail kingfish, longfin yellowtail and striped jack and, as a result, species such yellowtail kingfish is cultured commercially in many countries, including Australia, the U.S.A., Chile, the Netherlands, Germany and Denmark, among others.

In all species, hormonal methods to induce maturation of females and enhance spermiation in males have been examined, and successful results have been obtained. The hormonal therapies include injections of hCG or GnRHa, and more recently controlled release implants loaded with GnRHa. Hormonal treatments are effective when given to females with fully vitellogenic oocytes, and fish start spawning 36–48 h after treatment and may continue to spawn with a spawning interval of one–three days for a few days or weeks, depending on the treatment. For example, in greater amberjack a GnRHa injection may induce spawning for only a few days, while a GnRHa implant may induce spawning for two–three weeks. Repeated, weekly GnRHa injections or GnRHa implant administrations every two–four weeks may extent

the spawning activity for several weeks, and in the case of the sub-tropical Canary Islands, Spain, where photoperiod and temperature do not exhibit wide annual variations, spawning may extend for many months (June to October).

In the examined studies, there was no type of hormonal treatment that worked best in all carangid species examined so far. A single injection of hCG worked very well for yellowtail, yellowtail kingfish and striped jack; multiple almost-weekly injections of GnRHa worked best for greater amberjack and longfin yellowtail in the sub-tropical Canary Islands; while GnRHa implants worked best in greater amberjack in the Mediterranean region, and were comparable with all other treatments tested in yellowtail and yellowtail kingfish, and were also effective in striped jack and golden trevally. Administration of GnRHa via a sustained release implant has the advantage of a long-term release of GnRHa in the blood, and a stimulation of the appropriate release of GtHs from the pituitary, thus stimulating not only the maturation of the fully vitellogenic oocytes, but also the recruitment of further oocytes into vitellogenesis, leading to a longer and higher production of eggs in response to a single application.

The egg production and quality from hormone-treated carangids is adequate for commercial purposes, provided that the proper rearing conditions, hormone doses and timing of treatment are optimized. In the species where it was examined, however, the resulting fecundity was always lower than spontaneously spawning broodstocks, suggesting that further optimization can be made in the developed methods for reproduction control and egg production for greater amberjack, other species of the genus *Seriola* and other members of the family Carangidae.

Less attention has been given to male carangid broodstocks, since spermiation and spawning does occur in captivity and so far, has not be identified as a bottleneck to the expansion of the industry. However, significant reductions in sperm production have been identified in at least one species that has been examined more thoroughly — namely the greater

amberjack — when reared in captivity. A hormonal therapy with GnRHa implants has been shown to provide some improvement in sperm production and quality, but significantly more research effort has to be allocated to male reproductive physiology as well, in order to enhance our knowledge on the process of spermatogenesis and spermiation in captivity, and in optimizing hormonal control methods.

As more carangids enter the commercial production phase, we expect more knowledge will be acquired on their reproductive requirements, both from aquaculturists and researchers, and broodstock management methods will be optimized to produce high fecundity and quality eggs, to establish these species in the global aquaculture industry.

6. References

Abdussamad EM, Kasim HM & Balasubramanian TS (2008) Distribution, biology and behaviour of the giant trevally, *Caranx ignobilis* - a candidate species for mariculture. *Bangladesh Journal of Fisheries Research,* **12**, 89-94.

Afonso P, Fontes J, Morato T, Holland KN & Santos RS (2008) Reproduction and spawning habitat of white trevally, *Pseudocaranx dentex*, in the Azores, central north Atlantic. *Scientia Marina,* **72**, 373-381.

Alaira SA, Rebancos CM, Banyaga OI & Bato BP (2014) Maliputo (*Caranx ignobilis* Forsskål) fish cage farming practices among selected operators in the Taal Lake, Batangas, Philippines *Journal of Nature Studies,* **13**, 25-40.

Albasri H, Sagala SL, Pratama I & Sammut J (2020) An improved prioritization framework for selecting new finfish mariculture candidates for research and development in Indonesia. *Aquaculture Research,* **51**, 1464-1479.

Andaloro F & Pipitone C (1997) Food and feeding habits of the amberjack, *Seriola dumerili* in the Central Mediterranean Sea during the spawning season. *Cahiers de Biologie Marine,* **38**, 91-96.

Arakawa T, Takaya M, Kitajima C, Yoshida N, Yamashita K, Yamamoto H*, et al.* (1987) Some problems in the mass production of striped jack *Caranx delicatissimus*. *Bulletin of Nagasaki Prefectural Institute of Fisheries* **13**, 31-37.

Baxter JL (1960) A Study of The Yellowtail *Seriola dorsalis* (Gill). *Fish B-Noaa,* **110**, 1-91.

Blacio E (2004) Outdoor tank culture of almaco jacks in Ecuador. *Global Aquaculture Advocate,* **7**, 38-39.

Broach JS, Ohs CL, Palau A, Danson B & Elefante D (2015) Induced spawning and larval culture of golden trevally. *North American Journal of Aquaculture,* **77**, 532-538.

Chen JY, Zeng C, Jerry DR & Cobcroft JM (2019) Recent advances of marine ornamental fish larviculture: broodstock reproduction, live prey and feeding regimes, and comparison between demersal and pelagic spawners. *Reviews in Aquaculture,* **12**, 1518-1541.

Chou R (1994) Seafarming and searanching in Singapore. In: *Workshop on aquaculture development in Southeast Asia and prospects for seafarming and searanching* (eds Lacanilao F, Coloso RM, Quinitio GF). Aquaculture Department, Southeast Asian Fisheries Development Center, Iloilo City, Philippines*,* pp. 115-121.

Chou R & Lee HB (1997) Commercial marine fish farming in Singapore. *Aquaculture Research,* **28**, 767-776.

Chuda H, Imayoshi T, Arakawa T & Matsuyama M (2001a) Hormonal treatment for induction of oocyte maturation and ovulation in cultured yellowtail, *Seriola quinqueradiata*. *Science Bulletin of the Faculty of Agriculture-Kyushu University,* **2**, 169-177.

Chuda H, Nakao T, Arakawa T & Matsuyama M (2001b) Relationship between post-ovulation time and fertilization rate of eggs in artificial insemination of yellowtail, *Seriola quinqueradiata*. *Nippon Suisan Gakkaishi,* **67**, 874-880.

Chuda H, Nakao T, Arakawa T & Matsuyama M (2002) Effects of hCG injection on oocyte maturation and ovulation in cultured two-year-old yellowtail, *Seriola quinqueradiata*. *Suisanzoshoku,* **50**, 235-236.

Chuda H, Nakao T, Arakawa T & Matsuyama M (2005) Effects of oocyte diameter on ovulation time, quantity and quality of eggs in yellowtail *Seriola quinqueradiata* in inducing ovulation with HCG. *Nippon Suisan Gakkaishi* **71**, 942-946.

Corriero A, Desantis S, Deflorio M, Acone F, Bridges CR, de la Serna JM*, et al.* (2003) Histological investigation on the ovarian cycle of the bluefin tuna in the western and central Mediterranean. *Journal of Fish Biology,* **63**, 108-119.

Corriero A, Acone F, Desantis S, Zubani D, Deflorio M, Ventriglia G*, et al.* (2004) Histological and immunohistochemical investigation on ovarian development and plasma estradiol levels in the swordfish (*Xiphias gladius* L.). *European Journal of Histochemistry,* **48**, 413-422.

1362 da Silva IM, Hempson T & Hussey NE (2014) Giant trevally spawning aggregation highlights importance of community fisheries management no-take zone. *Marine Biodiversity,* **45**, 139-
1364 140.
Dale JJ, Meyer CG & Clark CE (2011) The ecology of coral reef top predators in the
1366 Papahānaumokuākea Marine National Monument. *Journal of Marine Biology,* **2011**, 1-14.
Daly R, Daly CAK, Bennett RH, Cowley PD, Pereira MAM & Filmalter JD (2018) Quantifying the largest
1368 aggregation of giant trevally *Caranx ignobilis* (Carangidae) on record: implications for management. *African Journal of Marine Science,* **40**, 315-321.
1370 De Metrio G, Bridges CR, Mylonas CC, Caggiano M, Deflorio M, Santamaria N*, et al.* (2010) Spawning induction and large-scale collection of fertilized eggs in captive Atlantic bluefin tuna (*Thunnus*
1372 *thynnus* L.) and the first larval rearing efforts. *Journal of Applied Ichthyology,* **26**, 596-599.
Divakaran S, Kim BG & Ostrowski AC (1999) Digestive enzymes present in Pacific threadfin
1374 *Polydactylus sexfilis* (Bloch & Schneider 1801) and bluefin trevally *Caranx melampygus* (Cuvier 1833). *Aquaculture Research,* **30**, 781-787.
1376 Dunn K (2014) The diet, reproductive biology age and growth of yellowtail, *Seriola lalandi*, in South Africa. University of Cape Town, Cape Town, South Africa.
1378 Fakriadis I, Lisi F, Sigelaki I, Papadaki M & Mylonas CC (2019) Spawning kinetics and egg/larval quality of greater amberjack (*Seriola dumerili*) in response to multiple GnRHa injections or implants.
1380 *General and Comparative Endocrinology,* **279**, 78-87.
Fakriadis I, Miccoli A, Karapanagiotis S, Tsele N & Mylonas CC (2020a) Optimization of a GnRHa
1382 treatment for spawning commercially reared greater amberjack *Seriola dumerili*: Dose response and extent of the reproductive season. *Aquaculture,* **521**, 735011.
1384 Fakriadis I, Sigelaki I, Papadaki M, Papandroulakis N, Raftopoulos A, Tsakoniti K*, et al.* (2020b) Control of reproduction of greater amberjack *Seriola dumerili* reared in aquaculture facilities.
1386 *Aquaculture,* **519**, 734880.
Fakriadis I & Mylonas CC (2021) Sperm quality of greater amberjack *Seriola dumerili* throughout the
1388 reproductive season and in response to GnRHa treatment with controlled release implants. *Fish Physiology and Biochemistry (in press)* https://doi.org/10.1007/s10695-020-00910-9
1390 Farrag E, Al-Zaaby A, Alyafei E & Alshaer M (2019) Population dynamics and assessment of golden trevally, *Gnathonodon speciosus* (Forsskål, 1775), in the Southern Arabian Gulf off the United
1392 Arab Emirates. *International Journal of Fisheries and Aquaculture Research* **5**, 1-11.
Feng F, Lo LC, Lin G, Zhu ZY & Yue GH (2005) Isolation and characterization of microsatellites in a
1394 marine food fish species, golden trevally *Gnathanodon speciou*s. *Molecular Ecology Notes,* **5**, 760-761.
1396 Fernández-Palacios H, Schuchardt D, Roo J, Hernández-Cruz C & Izquierdo M (2015a) Spawn quality and GnRHa induction efficiency in longfin yellowtail (*Seriola rivoliana*) broodstock kept in
1398 captivity. *Aquaculture,* **435**, 167-172.
Fernández-Palacios H, Schuchardt D, Roo J, Hernández-Cruz CM & Izquierdo M (2015b) Multiple
1400 GnRHa injections to induce successful spawning of wild caught greater amberjack (*Seriola dumerili*) matured in captivity. *Aquaculture Research,* **46**, 1748-1759.
1402 Fuji K, Yoshida K, Hattori K, Ozaki A, Araki K, Okauchi M*, et al.* (2010) Identification of the sex-linked locus in yellowtail, *Seriola quinqueradiata*. *Aquaculture,* **308**, S51-S55.
1404 García A & Díaz MV (1995) Culture of *Seriola dumerili*. *Cahiers Options Méditerranéennes,* **16**, 103-114.
1406 Gillanders BM, Ferrell DJ & Andrew NL (1999) Size at maturity and seasonal changes in gonad activity of yellowtail kingfish (*Seriola lalandi*: Carangidae) in New South Wales, Australia. *New*
1408 *Zealand Journal of Marine and Freshwater Research,* **33**, 457-468.
Grandcourt EM, Al Abdessalaam TZ, Francis F & Al Shamsi A (2004) Population biology and
1410 assessment of representatives of the family Carangidae: *Carangoides bajad* and *Gnathanodon speciosus* (Forsskål, 1775), in the Southern Arabian Gulf. *Fisheries Research,*
1412 **69**, 331-341.

Grau A, Crespo S, Riera F, Pou S & Sarasquete C (1996) Oogenesis in the amberjack *Seriola dumerilii* Risso, 1810. An histological, histochemical and ultrastructural study of oocyte development. *Scientia Marina,* **60**, 391-405.

Grier HJ, Linton JR, Leatherland JF & De Vlaming VL (1980) Structural evidence for two different testicular types in teleost fishes. *American Journal of Anatomy,* **159**, 331-345.

Hamada K & Mushiake K (2006) Advanced spawning of yellowtail *Seriola quinqueradiata* as early as December by manipulations of both photoperiod and water temperature. *Nippon Suisan Gakkaishi,* **72**, 186–192.

Harada T, Murata O & Miyashita S (1984a) Maturation and egg yield of reared striped jack, *Caranx delicatissimus*. *Kinki Daigaku Suisan Kenkyujou Nenpo,* **2**, 143–149.

Harada T, Murata O & Miyashita S (1984b) Artificial hatching and rearing of striped jack, *Caranx delicatissimus*. *Kinki Daigaku Suisan Kenkyujou Nenpo* **2**, 151–160.

Harris PJ, Wyanski DM, White DB, Mikell PP & Eyo PB (2007) Age, growth, and reproduction of greater amberjack off the Southeastern U.S. Atlantic Coast. *Transactions of the American Fisheries Society,* **136**, 1534-1545.

Helfman G, Collette BB, Facey DE & Bowen BW (2009) *The Diversity of Fishes: Biology, Evolution, and Ecology,* Wiley-Blackwell, Hong Kong, 736 p.

Heyman WD & Kjerfve B (2008) Characterization of transient multi-species reef fish spawning aggregations at Gladden Spit, Belize. *Bulletin of Marine Science,* **83**, 531-551.

Higuchi K, Gen K, Izumida D, Kazeto Y, Hotta T, Takashi T*, et al.* (2017a) Changes in plasma steroid levels and gene expression of pituitary gonadotropins, testicular steroidogenesis-related proteins and insulin-like growth factors during spermatogenesis of the yellowtail *Seriola quinqueradiata*. *Fisheries Science,* **83**, 35-46.

Higuchi K, Yoshida K, Gen K, Nyuji M, Takashi T, Mushiake K*, et al.* (2017b) Effect of timing of restricted feeding on sexual maturation in female yellowtail, *Seriola quinqueradiata*. *Aquaculture,* **479**, 609-615.

Higuchi K, Yoshida K, Gen K, Matsunari H, Takashi T, Mushiake K*, et al.* (2018) Effect of long-term food restriction on reproductive performances in female yellowtail, *Seriola quinqueradiata*. *Aquaculture,* **486**, 224-231.

James GD (1976) Eggs and larvae of the trevally *Caranx georgianus* (Teleostei: Carangidae). *New Zealand Journal of Marine and Freshwater Research,* **10**, 301-310.

Jerez S, Samper M, Santamaría FJ, Villamados JE, Cejas JR & Felipe BC (2006) Natural spawning of greater amberjack (*Seriola dumerili*) kept in captivity in the Canary Islands. *Aquaculture,* **252**, 199-207.

Jerez S, Fakriadis I, Papadaki M, Martín MV, Cejas JR & Mylonas CC (2018) Spawning induction of First-Generation (F1) greater amberjack *Seriola dumerili* in the Canary Islands, Spain using GnRHa delivery systems. *Fishes,* **3**, 35.

Johannes RE (1978) Reproductive strategies of coastal marine fishes in the tropics. *Environmental Biology of Fishes,* **3**, 65-84.

Kagawa H (1992) Reproductive physiology and induced spawning of yellowtail (*Seriola quinqueradiata*). In: *NOAA Technical Report NMFS,* pp. 15-18.

Kagawa H (2013) Oogenesis in teleost fish. *Aqua-BioScience Monographs,* **6**, 99-127.

Kalish JM & Johnston MB (1997) Validation of age and growth in silver trevally *Pseudocaranx dentex* from Australian waters. Australian National University, Canberra.

Kappen DC, Kumar D & Divya ND (2018) Pioneer attempt on cage culture of giant trevally, *Caranx Ignobilis* through farmer participatory approach in Thiruthipuram backwaters, Kochi, Kerala, India. *Ambient Sci,* **5**, 6-8.

Kato K, Okamura Y, Kimura J, Yoshida K, Takenouchi T & Miki M (1990) Gonadal maturation of carangid *Seriola rivoliana* from Ogasawara Islands waters, southern Japan. *Suisanzoshoku,* **38**, 81-87.

Kawabe K, Murai M, Kato K & Takashima F (1991) The effect of water temperature on egg development of striped jack, *Caranx delicatissimus*. *Suisanzoshoku,* **39**, 211-216.

Kawabe K, Kato K, Kimura J, Okamura Y, Ando K, Saito M*, et al.* (1996) Rearing of broodstock fish and egg-taking from amberjack *Seriola dumerili* in Chichijima, Ogasawara Islands, southern Japan. *Suisanzoshoku,* **44**, 151-157.

Kawabe K, Kato K, Kimura J, Okamura Y, Takenouchi T & Yoshida K (1997) Rearing of brood fish and egg-taking from the carangid fish *Seriola rivoliana* in Chichi-Jima, Ogasawara Islands, southern Japan. *Suisanzoshoku,* **45**, 201-206.

Kawabe K, Kimura J, Ando K & Kakiuchi K (1998) Natural spawning from 2-year-old reared amberjack, *Seriola dumerili* in Chichijima Ogasawara Islands, Southern Japan. *Suisanzoshoku,* **46**, 31-36.

Kemp L (2019) A first investigation into the evolutionary relationships, population structure and demographic history of New Zealand Trevally (*Pseudocaranx georgianus*) and its implications for fisheries management. Victoria University of Wellington, Wellington.

Kikawwa BS & Everson AR (1984) Gonadal maturation, fecundity, and spawning of the greater amberjack, *Seriola dumerili* (Risso), in Hawaiian waters with references to ciguatoxin incidences. In: *Proceedings of the second Symposium on Resource Investigations in the Northwestern Hawaiian Islands*. UNIHI-SEAGRANT-MR-84-01, Campus Center Ballroom, University of Hawaii, Honolulu, Hawaii, May 25-27, 1983*,* pp. 161-178.

Kim BG, Divakaran S, Brown CL & Ostrowski AC (2001) Comparative digestive enzyme ontogeny in two marine larval fishes: Pacific threadfin *(Polydactylus sexfilis)* and bluefin trevally *(Caranx melampygus)*. *Fish Physiology and Biochemistry,* **24**, 225-241.

Koyama T, Nakamoto M, Morishima K, Yamashita R, Yamashita T, Sasaki K*, et al.* (2019) A SNP in a steroidogenic enzyme is associated with phenotypic sex in *Seriola* Fishes. *Current Biology,* **29**, 1901-1909.

Kožul V, Skaramuca B, Glamuzina B, Glavić N & Tutman P (2001) Comparative gonadogenesis and hormonal induction of spawning of cultured and wild Mediterranean amberjack (*Seriola dumerili*, Risso 1810). *Scientia Marina,* **65**, 215-220.

Laidley CW, Shields RJ & Ostrowski AC (2004) Amberjack culture progresses at Oceanic Institute. *Global Aquaculture Advocate,* **7**, 42-43.

Lazzari A & Barbera G (1989) Prime osservazioni sulla pesca di riproduttori di ricciola, *Seriola dumerili*, nelle Isole Pelagie. *Oebalia,* **XV**, 645-652.

Leber KM (1994) *Prioritizing marine fishes for stock enhancement in Hawaii,* The Oceanic Institute, Honolulu, Hawaii.

Leis JM, Hay AC, Clark DL, Chen I & Shao K (2006) Behavioral ontogeny in larvae and early juveniles of the giant trevally *(Caranx ignobilis)*(Pisces: Carangidae). *Fish B-Noaa,* **104**, 401-414.

Levavi-Sivan B, Bogerd J, Mañanós EL, Gómez A & Lareyre JJ (2010) Perspectives on fish gonadotropins and their receptors. *General and Comparative Endocrinology,* **165**, 412-437.

Liao IC, Su HM & Chang EY (2001) Techniques in finfish larviculture in Taiwan. *Aquaculture,* **200**, 1-31.

Lubzens E, Young G, Bobe J & Cerdá J (2010) Oogenesis in teleosts: how fish eggs are formed. *General and Comparative Endocrinology,* **165**, 367-389.

Mandich A, Massari A, Bottero S, Pizzicori P, Goos H & Marino G (2004) Plasma sex steroid and vitellogenin profiles during gonad development in wild Mediterranean amberjack (*Seriola dumerili*). *Marine Biology,* **144**, 127-138.

Marino G, Mandich A, Massari A, Andaloro F, Porrello S, Finoia MG*, et al.* (1995a) Aspects of reproductive biology of the Mediterranean amberjack (*Seriola dumerilii* Risso) during the spawning period. *Journal of Applied Ichthyology,* **11**, 9-24.

Marino G, Porrello S, Andaloro F, Massari A & Mandich A (1995b) Aspects of reproductive biology of Mediterranean amberjack (*Seriola dumerilii* Risso, 1810): gonadal development. *Cahiers Options Méditerranéennes,* **16**, 115-124.

Martinez-Takeshita N, Purcell CM, Chabot CL, Craig MT, Paterson CN, Hyde JR*, et al.* (2015) A tale of three tails: cryptic speciation in a globally distributed marine fish of the genus *Seriola*. *Copeia,* **103**, 357-368.

Matsuyama M, Kagawa H, Arimoto M, Maruyama K, Hirotsuji H, Kashiwagi M*, et al.* (1996) Changes of ovarian maturity in the yellowtail *Seriola quinqueradiata* induced by a human chorionic gonadotropin. *Aquaculture Science,* **44**, 189-195.

McClellan DB & Cummings NJ (1996) Preliminary analysis of tag and recapture data of the greater amberjack, *Seriola dumerili*, in the southeastern United States. In: *Proceedings of the Gulf and Caribbean Fisheries Institute*. GCFI, Christ Church, Barbados, pp. 25-45.

McKenzie J, Smith M, Watson T, Francis M, Maolagáin CÓ, Poortenaar C*, et al.* (2014) Age, growth, maturity and natural mortality of New Zealand kingfish (*Seriola lalandi lalandi*). Ministry of Primary Industries, New Zealand.

Meyer CG, Holland KN & Papastamatiou YP (2007) Seasonal and diel movements of giant trevally *Caranx ignobilis* at remote Hawaiian atolls: implications for the design of marine protected areas. *Marine Ecology Progress Series,* **333**, 13-25.

Micale V, Maricchiolo G & Genovese L (1999) The reproductive biology of the amberjack, *Seriola dumerilii* (Risso 1810): I. Oocyte development in captivity. *Aquaculture Research,* **30**, 349-355.

Miura C, Yoshihara Y, Shimizu-Yamaguchi S, Hayashi D, Hamada K, Takeda Y*, et al.* (2014) Controlled feeding alleviates the reduced growth associated with spawning in farmed yellowtail (*Seriola quinqueradiata*). *Aquaculture,* **424**, 10-17.

Miura C, Hayashi D & Miura T (2020) Relationship between gonadal maturation and kyphosis in cultured yellowtail (*Seriola quinqueradiata*). *Aquaculture,* **520**, 734667 (734661-734669).

Moran D, Smith CK, Gara B & Poortenaar CW (2007) Reproductive behaviour and early development in yellowtail kingfish (*Seriola lalandi* Valenciennes 1833). *Aquaculture,* **262**, 95-104.

Moriwake AM, Moriwake VN, Ostrowski AC & Lee C (2001) Natural spawning of the bluefin trevally *Caranx melampygus* in captivity. *Aquaculture,* **203**, 159-164.

Murai M, Aoki Y, Nishimura K & Takashima F (1985a) Studies on the artificial seedling production of *Caranx delicatissimus* in the Chichijima, Bonin Islands (Japan), 1: Gonad maturation and spawning season through the histological studies. *The Aquiculture,* **33**, 76-81.

Murai M, Aoki Y, Nishimura K & Takashima F (1985b) Studies on the artificial seedling production of *Caranx delicatissimus* in the Chichijima, Bonin Island (Japan), 2: Rearing of brood fish and egg taking. *The Aquiculture,* **33**, 82-87.

Murai M, Kato K, Nakano T & Takashima F (1987) Egg development and morphological changes of larvae of striped jack *Caranx delicatissimus*. *Suisanzoshoku,* **34**, 217-226.

Murai M, Kawabe K & Takashima F (1992) Optimum salinity and temperature for hatching of striped jack eggs. *Suisanzoshoku,* **40**, 261-268.

Murie DJ & Parkyn DC (2008) Age, growth and sex maturity of greater amberjack (*Seriola dumerili*) in the Gulf of Mexico. In: *SEDAR33-RD13, SEDAR*, North Charleston, SC, USA, pp. 41.

Mushiake K, Arai S, Matsumoto A, Shimma H & Hasegawa I (1993) Artificial insemination from 2 year-old cultured yellowtail fed with moist pellets. *Nippon Suisan Gakkaishi,* **59**, 1721-1726.

Mushiake K (1994) Studies on the technical development of broodstock management in striped jack and yellowtail. Hiroshima University Hiroshima.

Mushiake K, Kawano K, Verakunpiriya W, Watanabe T & Hasegawa I (1995) Egg collection from broodstocks of yellowtail fed commercial soft dry pellets. *Nippon Suisan Gakkaishi,* **61**, 540-546.

Mushirobira Y, Niida M, Hotta T, Fujinami Y & Soyano K (2020) Hepatic expression profiles of three subtypes of vitellogenin and estrogen receptor during vitellogenesis in cultured female yellowtail. *General and Comparative Endocrinology,* **299**, 113612.

Mutia M, Theresa M, Muyot FB & Magistrado ML (2015) Induced breeding of giant trevally, maliputo *(Caranx ignobilis)*. In: *Proceedings of the International Workshop on Resource Enhancement and Sustainable Aquaculture Practices in Southeast Asia 2014*. Aquaculture Department, Southeast Asian Fisheries Development Center, Tigbauan, Iloilo, Philippines, pp. 311.

Mylonas CC, Bridges C, Gordin H, Rios AB, García A, de la Gandara F*, et al.* (2007) Preparation and administration of gonadotropin-releasing hormone agonist (GnRHa) implants for the artificial

control of reproductive maturation in captive-reared Atlantic bluefin tuna (*Thunnus thynnus thynnus*). *Reviews in Fisheries Science,* **15**, 183-210.

Mylonas CC, Fostier A & Zanuy S (2010) Broodstock management and hormonal manipulations of fish reproduction. *General and Comparative Endocrinology,* **165**, 516-534.

Mylonas CC, Papandroulakis N, Smboukis A, Papadaki M & Divanach P (2004) Induction of spawning of cultured greater amberjack (*Seriola dumerili*) using GnRHa implants. *Aquaculture,* **237**, 141-154.

Mylonas CC, Scott AP & Zohar Y (1997) Plasma gonadotropin II, sex steroids, and thyroid hormones in wild striped bass (*Morone saxatilis*) during spermiation and final oocyte maturation. *General and Comparative Endocrinology,* **108**, 223-236.

Mylonas CC, Woods LC, III, Thomas P & Zohar Y (1998) Endocrine profiles of female striped bass (*Morone saxatilis*) in captivity, during post-vitellogenesis and induction of final oocyte maturation via controlled-release GnRHa-delivery systems. *General and Comparative Endocrinology,* **110**, 276-289.

Nakada M (2002) Yellowtail culture development and solutions for the future. *Reviews in Fisheries Science,* **10**, 559-575.

Nocillado JN, Zohar Y, Biran J, Levavi-Sivan B & Elizur A (2013) Chronic kisspeptin administration stimulated gonadal development in pre-pubertal male yellowtail kingfish (*Seriola lalandi*; Perciformes) during the breeding and non-breeding season. *General and Comparative Endocrinology,* **191**, 168-176.

Nogueira N, Ferreira M, Cordeiro N & Canada P (2018) Quality parameters of wild white trevally (*Pseudocaranx dentex*) natural spawn kept in captivity. *Aquaculture,* **495**, 68-77.

Nyuji M, Kazeto Y, Izumida D, Tani K, Suzuki H, Hamada K*, et al.* (2016) Greater amberjack Fsh, Lh, and their receptors: Plasma and mRNA profiles during ovarian development. *General and Comparative Endocrinology,* **225**, 224-234.

Nyuji M, Yamamoto I, Hamada K, Kazeto Y & Okuzawa K (2019) Effect of GnRHa on plasma levels of Fsh and Lh in the female greater amberjack *Seriola dumerili*. *Journal of Fish Biology,* **95**, 1350-1354.

Ohta K, Rahman MA, Chuda H, Yoshikuni M, Nagahama Y & Matsuyama M (2002) Maturation-inducing hormone and its membrane receptor in gonads of Japanese yellowtail, *Seriola quinqueradiata*. *Fisheries Science,* **68**, 686-689.

Ottolenghi F, Silvestri C, Giordano P, Lovatelli A & New MB (2004) *Capture-based Aquaculture. The fattening of eels, groupers, tunas and yellowtails,* Food and Agriculture Organization of the United Nations, Rome, 308 p.

Ouchi K, Hara A, Adachi S, Arimoto M, Mizuta Y & Nagahama Y (1989) Changes in serum concentrations of steroid hormones and vitellogenin during the period of vitellogenesis in the yellowtail *Seriola quinqueradiata*. *Bulletin of the Nansei Regional Fisheries Research Laboratory,* **22**, 1-11.

Passantino L, Zupa R, Pousis C, Mylonas CC, Hala E, Jirillo E*, et al.* (2020) Increased melanomacrophage centres in the liver of reproductively dysfunctional female greater amberjack *Seriola dumerili* (Risso, 1810). *Journal of Fish Diseases,* **43**, 503-514.

Patiño R & Sullivan CV (2002) Ovarian follicle growth, maturation, and ovulation in teleost fish. *Fish Physiology and Biochemistry,* **26**, 57-70.

Patrick G, Tarnecki AM, Rhody N, Schloesser R, Main K, Yanong R*, et al.* (2019) Disinfection of almaco jack (*Seriola rivoliana* Valenciennes) eggs: Evaluation of three chemicals. *Aquaculture Research,* **50**, 3793-3801.

Piccinno M, Zupa R, Corriero A, Centoducati G, Passantino L, Rizzo A*, et al.* (2014) In vitro effect of isotocin on ovarian tunica albuginea contractility of gilthead seabream (*Sparus aurata* L.) in different reproductive conditions. *Fish Physiology and Biochemistry,* **40**, 1191-1199.

Poortenaar CW, Hooker SH & Sharp N (2001) Assessment of yellowtail kingfish (*Seriola lalandi lalandi*) reproductive physiology, as a basis for aquaculture development. *Aquaculture,* **201**, 271-286.

Pousis C, Mylonas CC, De Virgilio C, Gadaleta G, Santamaria N, Passantino L*, et al.* (2018) The observed oogenesis impairment in greater amberjack *Seriola dumerili* (Risso, 1810) reared in captivity is not related to an insufficient liver transcription or oocyte uptake of vitellogenin. *Aquaculture Research,* **49**, 243-252.

Pousis C, Rodríguez C, De Ruvo P, De Virgilio C, Pérez JA, Mylonas CC*, et al.* (2019) Vitellogenin receptor and fatty acid profiles of individual lipid classes of oocytes from wild and captive reared greater amberjack (*Seriola dumerili*) during the reproductive cycle. *Theriogenology,* **140**, 73-83.

Quiñones-Arreola MF, Arcos-Ortega GF, Gracia-López V, Casillas-Hernández R, Weirich C, Morris T*, et al.* (2015) Reproductive broodstock performance and egg quality of wild-caught and first-generation domesticated *Seriola rivoliana* reared under same culture conditions. *Latin American Journal of Aquatic Research,* **43**, 953-962.

Rahman MA, Ohta K, Chuda H, Nakano S, Maruyama K & Matsuyama M (2001) Gonadotropin-induced steroidogenic shift towards maturation-inducing hormone in Japanese yellowtail during final oocyte maturation. *Journal of Fish Biology,* **58**, 462-474.

Rahman MA, Ohta K, Chuda H, Yamaguchi A & Matsuyama M (2002a) Steroid hormones and their synthetic pathways in the vitellogenic ovarian follicles of yellowtail, *Seriola quinqueradiata*. *Journal of the Faculty of Agriculture, Kyushu University,* **46**, 311-319.

Rahman MA, Ohta K, Yamaguchi A, Chuda H, Hirai T & Matsuyama M (2003) Gonadotropins, gonadotropin receptors and their expressions during sexual maturation in yellowtail, a carangid fish. *Fish Physiology and Biochemistry,* **28**, 81-83.

Rahman MA, Ohta K, Yoshikuni M, Nagahama Y, Chuda H & Matsuyama M (2002b) Characterization of ovarian membrane receptor for 17,20β-dihydroxy-4-pregnen-3-one, a maturation-inducing hormone in yellowtail, *Seriola quinqueradiata*. *General and Comparative Endocrinology,* **127**, 71-79.

Randall JE (1995) *Coastal fishes of Oman,* Crawford House Publishing., Bathurst, Australia.

Roo J, Izquierdo MS, Mesa-Rodriguez A, Guirao R, Hernández-Cruz CM & Fernández-Palacios H (2012) Current status and recent advances in striped jack *Pseudocaranx dentex* culture in Europe. In: *Aquaculture Europe 2012*. European Aquaculture Society, Prague, Czech Republic.

Roo J, Fernández-Palacios H, Hernández-Cruz CM, Mesa-Rodriguez A, Schuchardt D & Izquierdo M (2014) First results of spawning and larval rearing of longfin yellowtail *Seriola rivoliana* as a fast-growing candidate for European marine finfish aquaculture diversification. *Aquaculture Research,* **45**, 689-700.

Roo J, Fernández-Palacios H, Schuchardt D, Hernández-Cruz CM & Izquierdo MS (2015) Influence of hormonal induction and broodstock feeding on longfin yellowtail *Seriola rivoliana* maturation, spawning quality and egg biochemical composition. *Aquaculture Nutrition,* **21**, 614-624.

Rosenfeld H, Meiri I & Elizur A (2007) Gonadotropin regulation of oocyte development. In: *The Fish Oocyte: from Basic Studies to Biotechnological Applications*. Kluwer Academic Publishers, Dordrecht, The Netherlands, pp. 171-198.

Rostika R, Fauzan MI & Lili W (2020) The use of various proportions of rough fish on giant trevally (*Caranx* sp.) culture in the floating net cages, Pangandaran, West Java. *Asian Journal of Fisheries and Aquatic Research,* **5**, 1-7.

Rowland AJ (2009) The biology of Samson fish *Seriola hippos* with emphasis on the sportfishery in Western Australia. In: *Murdoch University*, Australia.

Rowling KR & Raines LP (2000) Description of the biology and an assessment of the fishery for silver trevally *Pseudocaranx dentex* off New South Wales. NSW Fisheries Research Institute Cronulla, New South Wales, Australia.

Sanchís-Benlloch PJ, Nocillado J, Ladisa C, Aizen J, Miller A, Shpilman M*, et al.* (2017) In-vitro and in-vivo biological activity of recombinant yellowtail kingfish (*Seriola lalandi*) follicle stimulating hormone. *General and Comparative Endocrinology,* **241**, 41-49.

Sarih S, Djellata A, La Barbera A, Fernández-Palacios Vallejo H, Roo J, Izquierdo M*, et al.* (2018) High-quality spontaneous spawning in greater amberjack (*Seriola dumerili*, Risso 1810) and its comparison with GnRHa implants or injections. *Aquaculture Research,* **49**, 3442-3450.

Sarih S, Djellata A, Fernández-Palacios H, Ginés R, Fontanillas R, Rosenlund G*, et al.* (2020) Adequate n-3 LC-PUFA levels in broodstock diets optimize reproductive performance in GnRH injected greater amberjack (*Seriola dumerili*) equaling to spontaneously spawning broodstock. *Aquaculture,* **520**, 735007.

Sarih S, Djellata A, Roo J, Hernández-Cruz CM, Fontanillas R, Rosenlund G*, et al.* (2019) Effects of increased protein, histidine and taurine dietary levels on egg quality of greater amberjack (*Seriola dumerili*, Risso, 1810). *Aquaculture,* **499**, 72-79.

Sassa C, Takahashi M, Konishi Y, Aonuma Y & Tsukamoto Y (2020) The rapid expansion of yellowtail (*Seriola quinqueradiata*) spawning ground in the East China Sea is linked to increasing recruitment and spawning stock biomass. *ICES Journal of Marine Science,* **77**, 581-592.

Schulz RW, de França LR, Lareyre JJ, LeGac F, Chiarini-Garcia H, Nóbrega RH*, et al.* (2010) Spermatogenesis in fish. *General and Comparative Endocrinology,* **165**, 390-411.

Šegvić-Bubić T, Marrone F, Grubišić L, Izquierdo-Gomez D, Katavić I, Arculeo M*, et al.* (2016) Two seas, two lineages: How genetic diversity is structured in Atlanticand Mediterranean greater amberjack *Seriola dumerili* Risso, 1810 (Perciformes, Carangidae). *Fisheries Research,* **179**, 271-279.

Setiawan AN, Muncaster S, Pether S, King A, Irvine GW, Lokman PM*, et al.* (2016) The effects of gonadotropin-releasing hormone analog on yellowtail kingfish *Seriola lalandi* (Valenciennes, 1833) spawning and egg quality. *Aquaculture Reports,* **4**, 1-9.

Shiraishi T, Ohshimo S & Yukami R (2010) Age, growth and reproductive characteristics of gold striped amberjack *Seriola lalandi* in the waters off western Kyushu, Japan. *New Zealand Journal of Marine and Freshwater Research,* **44**, 117-127.

Shiraishi T, Ohshimo S & Yukami R (2011) Age, growth and reproductive characteristics of yellowtail (*Seriola quinqueradiata*) caught in the waters off western Kyushu. *Bulletin of the Japanese Society of Fisheries and Oceanography,* **75**, 1-8.

Sicuro B & Luzzana U (2016) The state of *Seriola* spp. other than yellowtail (*S. quinqueradiata*) farming in the world. *Reviews in Fisheries Science & Aquaculture,* **24**, 314-325.

Sim SY, Suwirya K & Rimmer M (2007) Update: Marine finfish research and development at the Research Institute for Mariculture, Gondol, Bali, Indonesia. In: *Asia-Pacific Marine Finfish Aquaculture Network*

Sley A, Hadj Taeib A, Jarboui O, Ghorbel M & Bouain A (2014) Reproductive biology of greater amberjack *Seriola dumerili* (Risso, 1810) from the Eastern Mediterranean Sea (Tunisia, Gulf of Gabes). *Cahiers de Biologie Marine,* **55**, 421-430.

Sley A, Hadj Taeib A, Jarboui O, Ghorbel M & Bouain A (2016) Feeding behaviour of greater amberjack *Seriola dumerili* (Risso, 1810) from Central Mediterranean (Gulf of Gabes, Tunisia). *Journal of the Marine Biological Association of the United Kingdom,* **96**, 1229-1234.

Smith-Vaniz WF (1999) Carangidae. Jacks and scads (also trevallies, queenfishes, runners, amberjacks, pilotfishes, pompanos, etc.). In: *The Living Marine Resources of the Western Central Pacific* (ed. by Carpenter KE, Niem VH). Food and Agriculture Organization of the United Nations Rome, pp. 2659-2756.

Socorro J, Roo J, Fernández-Palacios H, Izquierdo MS, Guirao R & Reyes T (2005) Gonadal development in striped jack *Pseudocaranx dentex* (Bloch and Schneider, 1801) in Canary Islands coastal waters. *Boletín - Instituto Español de Oceanografía,* **21**, 271-282 (in Spanish with English abstract).

Stuart KR & Drawbridge MA (2013) Captive spawning and larval rearing of California yellowtail (*Seriola lalandi*). *Aquaculture Research,* **44**, 728-737.

Stuart KR, Armbruster L, Johnson R & Drawbridge MA (2020) Egg diameter as a predictor for egg quality of California yellowtail (*Seriola dorsalis*). *Aquaculture,* **522**, 735154 (735151-735156).

Sudekum AE, Parrish JD, Radtke RL & Ralston S (1991) Life-history and ecology of large jacks in undisturbed, shallow, oceanic communities. *Fish B-Noaa,* **89**, 493-513.

Sumida BY, Moser HG & Ahlstrom EH (1985) Descriptions of larvae of California yellowtail, *Seriola lalandi*, and three other carangids from the eastern tropical Pacific: *Chloroscombrus orqueta*, *Caranx caballus*, and *Caranx sexfasciatus*. *CalCOFI Reports,* **26**, 139-159.

Suprayudi MA, Ihu MZ, Utomo NP & Ekasari J (2014) Protein and energy: protein ratio in diets for juvenile bluefin trevally *Caranx melampygus*. *Journal of Applied Aquaculture,* **26**, 187-196.

Symonds JE, Walker SP, Pether S, Gublin Y, McQueen D, King A*, et al.* (2014) Developing yellowtail kingfish (*Seriola lalandi*) and hāpuku (*Polyprion oxygeneios*) for New Zealand aquaculture. *New Zealand Journal of Marine and Freshwater Research,* **48**, 371-384.

Tachihara K, El-Zibdeh MK, Ishimatsu A & Tagawa M (1997) Improved seed production of goldstriped amberjack *Seriola lalandi* under hatchery conditions by injection of triiodothyronine (T3) to broodstock fish. *Journal of the World Aquaculture Society,* **28**, 34-44.

Taranger GL, Carrillo M, Schulz RW, Fontaine P, Zanuy S, Felip A*, et al.* (2010) Control of puberty in farmed fish. *General and Comparative Endocrinology,* **165**, 483-515.

Teles A, Salas-Leiva J, Alvarez-Gonzalez CA & Tovar-Ramirez D (2019) Changes in digestive enzyme activities during early ontogeny of *Seriola rivoliana*. *Fish Physiology and Biochemistry,* **45**, 733-742.

Thompson BA, Wilson CA, Render JH, Beasley M & Cauthron C (1992) Age, growth, and reproductive biology of greater amberjack and cobia from Louisiana waters. In: *SEDAR28-RD26, SEDAR*, St. Petersburg, FL, USA*,* pp. 77.

Tian YJ, Kidokoro H, Watanabe T, Igeta Y, Sakaji H & Ino S (2012) Response of yellowtail, *Seriola quinqueradiata*, a key large predatory fish in the Japan Sea, to sea water temperature over the last century and potential effects of global warming. *Journal of Marine Systems,* **91**, 1-10.

Vassallo-Agius R, Watanabe T, Mushiake K, Kawano K & Satoh S (1998) Chemical components of eggs and yolksac larvae obtained from striped jack broodstock fed on a raw fish mix or dry pellets. *Fisheries Science,* **64**, 759-765.

Vassallo-Agius R, Mushiake K, Imaizumi H, Yamazaki T & Watanabe T (1999) Spawning and quality of eggs of striped jack fed raw fish or dry pellets with 2% spirulina. *Suisanzoshoku,* **47**, 415-422.

Vassallo-Agius R, Imaizumi H, Watanabe T, Yamazaki T, Satoh S & Kiron V (2001a) The influence of astaxanthin supplemented dry pellets on spawning of striped jack. *Fisheries Science,* **67**, 260-270.

Vassallo-Agius R, Imaizumi H, Watanabe T, Yamazaki T, Satoh S & Kiron V (2001b) Effect of squid meal in dry pellets on the spawning performance of striped jack *Pseudocaranx dentex*. *Fisheries science,* **67**, 271-280.

Vassallo-Agius R, Watanabe T, Imaizumi H, Yamazaki T, Satoh S & Kiron V (2001c) Effects of dry pellets containing astaxanthin and squid meal on the spawning performance of striped jack *Pseudocaranx dentex*. *Fisheries Science,* **67**, 667-674.

Vassallo-Agius R, Watanabe T, Imaizumi H & Yamazaki T (2002) Spawning performance of yellowtail *Seriola quinqueradiata* fed dry pellets containing paprika and squid meal. *Fisheries Science,* **68**, 230-232.

Watanabe T, Vassallo-Agius R, Mushiake K, Kawano K, Kiron V & Satoh S (1998) The first spawn-taking from striped jack broodstock fed soft-dry pellets. *Fisheries Science,* **64**, 39-43.

Watanabe T & Vassallo-Agius R (2003) Broodstock nutrition research on marine finfish in Japan. *Aquaculture,* **227**, 35-61.

Wells RJD & Rooker JR (2004) Distribution, age, and growth of young-of-the-year greater amberjack (*Seriola dumerili*) associated with pelagic Sargassum. *Fish B-Noaa,* **102**, 545-554.

Yamamoto T, Ino S, Kuno M, Sakaji H, Hiyama Y, Kishida T*, et al.* (2007) On the spawning and migration of yellowtail *Seriola quinqueradiata* and research required to allow catch forecasting. *Bull. Fish. Res. Agen.,* **21**, 1-29 (in Japanese with English abstract).

Yamazaki H, Shiozawa S & Fujimoto H (2002) Present status of seed production techniques for yellowtail *Seriola quinqueradiata* in Japan Sea-Farming Association. . *Suisanzoshoku,* **50**, 503-506.

Zohar Y (2020) Fish reproductive biology - reflecting on five decades of fundamental and translational research. *General and Comparative Endocrinology*, 113544.

Zohar Y, Muñoz-Cueto JA, Elizur A & Kah O (2010) Neuroendocrinology of reproduction in teleost fish. *General and Comparative Endocrinology,* **165**, 438-455.

Zohar Y & Mylonas CC (2001) Endocrine manipulations of spawning in cultured fish: from hormones to genes. *Aquaculture,* **197**, 99-136.

Zupa R, Fauvel C, Mylonas CC, Pousis C, Santamaria N, Papadaki M*, et al.* (2017a) Rearing in captivity affects spermatogenesis and sperm quality in greater amberjack *Seriola dumerili* (Risso, 1810). *Journal of Animal Science,* **95**, 4085-4100.

Zupa R, Rodríguez C, Mylonas CC, Rosenfeld H, Fakriadis I, Papadaki M*, et al.* (2017b) Comparative study of reproductive development in wild and captive-reared greater amberjack *Seriola dumerili* (Risso, 1810). *PLoS One,* **12**, e0169645.

Table 1 Common and scientific names, distribution and maximum body size of various members of the Carangidae family, reviewed in the present article. Data were obtained from fishbase.org.

Common name	Scientific name	Distribution	Max length	Max weight
greater amberjack	*Seriola dumerili*	Mediterranean Sea, Worldwide	190 cm TL[1]	80 kg
yellowtail or Japanese amberjack	*Seriola quinqueradiata*	Japan	150 cm TL[1]	40 kg
yellowtail kingfish	*Seriola lalandi*	Australia, New Zealand	250 cm TL[1]	97 kg
yellowtail kingfish	*Seriola aureovittata*	Japan	n/a	n/a
yellowtail kingfish	*Seriola dorsalis*	California USA	n/a	n/a
Samson fish	*Seriola hippos*	Australia	150 cm TL[1]	53 kg
giant trevally	*Caranx ignobilis*	Philippines, Hawaii USA	170 cm TL[1]	80 kg
bluefin trevally	*Caranx melampygus*	Hawaii USA		
golden trevally	*Gnathanodon speciosus*	Arabian Gulf, USA	120 cm TL[1]	15 kg
striped jack or white trevally	*Pseudocaranx dentex*	Japan, Portugal	122 cm TL[1]	18 kg
silver trevally	*Pseudocaranx georgianus*	Australia		

[1] TL Total length
[2] FL Fork length
n/a: data not available

1794 **Table 2** Age and size at maturity of the species from the family Carangidae reported in this review.

Common name	Region	Fish origin	Age at first maturity (year)		Size at smallest maturity (fork length, mm)[a]		Size at 50% maturity (fork length, mm)[a]		Reference
			Female	Male	Female	Male	Female	Male	
greater amberjack	Mediterranean Sea (Pelagie Island, Sicily, Italy)	Wild	4	4	800^{SL}	610^{SL}	1130^{SL}	1090^{SL}	Marino *et al.* (1995a)
	Mediterranean Sea (Gulf of Gabes, Tunisia)	Wild	-	-	814	930	953	937	Sley *et al.* (2014)
	Gulf of Mexico	Wild	4	-	-	-	800	-	Murie & Parkyn (2008)
yellowtail or Japanese amberjack	Northern East China Sea	Wild	2	2	632	605	-	-	Shiraishi *et al.* (2011)
	Japan	Captive	1	1	-	-	-	-	Kagawa (1992); Miura *et al.* (2014)
yellowtail kingfish	Southern Australia	Wild	3+	0+	698	360	834	470	Gillanders *et al.* (1999)
	Northern New Zealand	Wild	-	-	775	750	944	812	Poortenaar *et al.* (2001)
	South Africa	Wild	-	-	520	520	550	585	Dunn (2014)
	Australia	Captive	4–5	1+	-	-	-	-	Sanchís-Benlloch *et al.* (2017))
	Northern East China Sea	Wild	2	2	662	624	-	-	Shiraishi *et al.* (2010)
longfin yellowtail	Southern Japan	Wild	-	-	634	595	-	-	Kato *et al.* (1990)
	Hawaii	Captive	2	1+	-	-	-	-	Laidley *et al.* (2004)
Samson fish	Western Australia	Wild	3+	-	700–750	-	831	-	Rowland (2009)
giant trevally	Hawaii	Wild	3.5	-	550-650^{SL}	-	-	-	Sudekum *et al.* (1991)
bluefin trevally	Hawaii	Wild	2	-	325-375^{SL}	-	-	-	Sudekum *et al.* (1991)
golden trevally	Southern Arabian Gulf	Wild	-	-	-	-	325	-	Grandcourt *et al.* (2004)
	Southern Arabian Gulf	Wild	1.4	-	-	-	345	-	Farrag *et al.* (2019)
striped jack or white trevally	Central North Atlantic	Wild	-	-	-	-	300	278	Afonso *et al.* (2008)
silver trevally	Australia	Wild	-	-	210	220	~190	-	Rowling & Raines (2000)

[a] When not specified, fish fork length is reported. SL, standard length.

1796

Table 3 Plasma concentrations of sex steroids in wild, wild-caught captive-reared and hatchery produced greater amberjack (*Seriola dumerili*).

Sex	Fish origin	Period	E_2 (ng ml^{-1})	T (ng ml^{-1})	11-KT (ng ml^{-1})	17,20β-P (ng ml^{-1})	Reference
FEMALES	Wild	April–May	1.8±0.7	0.7±0.3	nd	0.4±0.1	Zupa *et al.* (2017b)
		May–June	6.6±0.5	5.0±0.4	nd	1.3±0.1	
		June–July	3.4±0.6	2.3±0.3	nd	1.0±0.2	
	Wild caught	April–May	0.7±0.1	0.3±0.1	nd	0.1±0.1	
		May–June	2.0±0.5	0.7±0.2	nd	0.3±0.1	
		June–July	0.4±0.2	0.2±0.1	nd	0.4±0.1	
	Hatchery produced	May	≈1.8*	≈0.4*	nd	≈0.4*	Jerez *et al.* (2018)
		June	≈1.1*	≈0.6*	nd	≈0.4*	
		July	≈0.8*	≈0.2*	nd	≈0.4*	
		September	≈1.2*	≈0.7*	nd	≈0.8*	
MALES	Wild	April–May	0.1±0.1	1.4±0.4	2.7±0.5	0.2±0.1	Zupa *et al.* (2017a, b)
		May–June	0.2±0.1	4.3±0.4	6.3±0.3	0.4±0.1	
		June–July	0.6±0.4	2.4±0.7	3.1±1.1	1.4±0.6	
	Wild caught	April–May	5.4±2.0	0.8±0.2	2.3±0.6	0.4±0.4	
		May–June	0.7±0.3	0.4±0.1	0.8±0.1	0.1±0.1	
		June–July	1.1±0.7	0.2±0.1	0.2±0.1	0.5±0.1	
	Hatchery produced	May	nd	≈0.8*	≈0.2*	≈0.2*	Jerez *et al.* (2018)
		June	nd	≈0.6*	≈0.2*	≈0.3*	
		July	nd	≈0.1*	<0.1*	≈0.2*	
		September	nd	≈2.1*	≈0.5*	≈0.6*	

Hormone concentrations are expressed as mean ± standard deviation.
*Hormone concentrations extrapolated from graphics. nd = not determined.

Table 4 Sperm quality parameters of greater amberjack (*Seriola dumerili*) reared in captivity in different locations.

Farm location	Fish origin	Sampling period	Hormonal treatment before sperm sampling	Density (spz/mL)	Motility (% of motile spz)	Average path velocity† (μm/s)	Motility duration (min)	Reference
South-Eastern Adriatic Sea (Croatia)	Wild caught	June	No	-	50–90	-		Kožul *et al.* (2001)
Crete/ Nafpaktos (Greece)	Wild caught	June	No	-	5–30	-	2.1–2.5	Mylonas *et al.* (2004)
		July	GnRHa implant (≈30 μg kg^{-1} body mass) in June	12 x 10^{10}	65%	-	2.7	
Salamina Island (Greece)	Wild caught	April	No	2.3 ± 0.5 × 10^{10}	46.3 ± 17.7	79.0 ± 3.0	8.3 ± 1.5	Zohar & Mylonas (2001)
		June	No	3.6 ± 0.4 × 10^{10}	58.5 ± 16.9	102.7 ± 6.9	5.0 ± 0.4	
		July	No	4.6 ± 0.6 × 10^{10}	21.0 ± 9.7	36.5 ± 3.3	0.6 ± 0.3	
Canary Islands, Spain	Hatchery produced (F1 generation)	May	No	30.8 ± 6.8 x 10^{9}	54 ± 10.0	-	4.35 ± 1.12	Jerez *et al.* (2018)
		June	GnRHa implant (50 μg kg^{-1} body mass) in May	45 x 10^{9}	68 ± 7.0	-	2.44 ± 0.24	
		July	GnRHa implant (50 μg kg^{-1} body mass) in May and June	55 x 10^{9}	54 ± 10.0	-	3.50 ± 0.40	
		September	GnRHa implant (50 μg kg^{-1} body weight) in May, June and July	78.0 ± 72.2 x 10^{9}	58 ± 12.0	-	3.80 ± 0.20	
Ionian and Aegean Sea, Greece	Wild caught	June	No	-	80 ± 7.0 (tanks) ----- 81 ± 3.0 (sea cages)	-	3.7 ± 0.4 (tanks) ----- 3.6 ± 0.5 (sea cages)	Fakriadis *et al.* (2020b)

Data are expressed as mean, mean ± standard deviation or range, according to the source of information.
Motility data represent the highest percentage of spermatozoa motility, which was reached within the first 10 Jerez *et al.* (2018; Fakriadis *et al.* (2020a) or 20 s Zupa *et al.* (2017a) after sperm activation †Path velocity data represent the highest average path velocity, which was reached within 10 s from sperm activation Zupa *et al.* (2017a). spz = spermatozoa.

1810 **Table 5** Representative characteristics of spontaneous or hormonally-induced spawnings in the species reported in this review.

Common name	Location	Year	Number of fish[a]	Treatment[b]	Spawning period	Water temperature (°C)	Number of spawning events	Spawning interval (days)	Spawning time	Reference
greater amberjack	Greece	2016	3–4 (F), 3–4 (M)	GnRHa implants	Jun	20.3–24.0	14	1–3	17:00–20:00 h or 06:00–08:00 h	Fakriadis *et al.* (2019)
			3–4 (F), 3–4 (M)	GnRHa injections	Jun	20.3–24.0	13	1–3	18:00–21:00 h or 06:00–08:00 h	
	Greece	2020	4 (F), 5 (M)	Natural	Jun	19–22	5	2–8	18:00–21:00 h	Mylonas CC (unpublished data)
	Canary Islands (Spain)	2015	7 (F), 7 (M)	GnRHa implants	May–Aug	20–24	52	1–15	-	Jerez *et al.* (2018)
	Spain (Canary Islands)	2002	11	Natural	Apr–Oct	1–-25	38	4–7	early daylight hrs	Jerez *et al.* (2006)
	Greece	2003	1 (F), 1 (M)	GnRHa implant	Jun	21–25	4	1	-	Mylonas *et al.* (2004)
	Canary Islands (Spain)	2012	2 (F), 4 (M)	GnRHa multiple injection	Jun–Oct	22–24	22	-	-	Fernández-Palacios *et al.* (2015b)
	Canary Islands (Spain)	2014	3 (F), 3 (M)	GnRHa implant	Jun–Oct	19–26	38	6	-	Sarih *et al.* (2018)
			3 (F), 3 (M)	GnRHa injection			29			
			2 (F), 2 (M)	Natural			23			
yellowtail or Japanese amberjack	Japan	-	7 (F), 7 (M)	GnRHa implant	May	-	> 11[c]	1	-	Kagawa (1992)
	Japan	1994	4–5 (F), 5 (M)	hCG injection	Apr	-	14[c]	1	-	Mushiake *et al.* (1995)
yellowtail kingfish	New Zealand	2002–2003	14	Natural	Nov–Feb	≥17	26[d]	2–4	early daylight hrs (Dec), 20:00–22:00 h (Jan)	Moran *et al.* (2007)
	New Zealand	2012	7 (F), 5 (M)	Natural	Jan–Feb	20–22	22	1.34	-	Setiawan *et al.* (2016)
			7 (F), 5 (M)	GnRHa implant	Feb	20–22	23	1.10	-	
	Japan	1992	35	hCG+SPE injection	Apr–May	21	16[c]	1–3		Tachihara *et al.* (1997)

	California	2007	18 (F), 17 (M)	Natural	Apr–Jul	16-22	16	-	16:00–01:00 h	Stuart & Drawbridge (2013)
		2008–2010	9 (F), 12 (M)	Natural	Apr–Aug	16–22	22–43	-	16:00–01:00 h	
longfin yellowtail	Japan	1988	10	Natural	May–Nov	23–28	53[c]	-	05:00–13:00 h (mainly, 05:00–07:00 h)	Kawabe *et al.* (1997)
		1989	22	Natural	Apr–Oct	21–27	113[c]	-	05:00–13:00 h (mainly, 05:00–07:00 h)	
	Ecuador	2002	11	Natural	Jun–Sep	≥26	-	3–7	-	Blacio (2004)
	Hawaii	2001–2002	20	Natural	Year round	25–27	13 month^{-1}	-	-	Laidley *et al.* (2004)
	Mexico	2012	28–30	Natural	May–Dec	26–27	28–57[c]	-	-	Quiñones-Arreola *et al.* (2015)
	Canary Islands	2009–2011	6 (F), 5 (M)	GnRHa injections	Jun–Oct	21–24	9–17	-	-	Roo *et al.* (2015)
	Canary Islands	2012	2 (F), 4 (M)	GnRHa injections	Jun–Oct	22–24	33	-	-	Fernández-Palacios *et al.* (2015a)
giant trevally	Philippines	-	5 (F), unknown (M)	hCG injections	March–July	27.6–29.3	-	-	-	Mutia *et al.* (2015)
		-	5 (F), unknown (M)	GnRHa injections	March–July	27.6–29.3	-	-	-	
bluefin trevally	USA (Hawaii)	1996	5 (F), 5 (M)	Natural	Aug	26.3–27.2	8	-	neurula to mid-embryo stages between 07:50–10:00 h	Moriwake *et al.* (2001)
		1997	5 (F), 5 (M)	Natural	Jan–Nov	24.8–26.7	37	-	neurula to mid-embryo stages between 06:45–10:10 h	
golden trevally	USA	2014	2 (F), 6 (M)	GnRHa Implant (Ovaplant)	April	26	3	1	-	Broach *et al.* (2015)
striped jack or white trevally	Japan	-	5 (F), 5 (M)	hCG injection	Feb–May[a]	22	10–17	1	-	Vassallo-Agius *et al.* (2001b) Watanabe & Vassallo-Agius (2003)
	Japan	-	4–5 (F), 5 (M)	hCG injection	Feb–May[a]	22	18–24	1	-	Vassallo-Agius *et al.* (2001a) Watanabe & Vassallo-Agius (2003)
	Japan	-	7 (F), 7 (M)	Natural	Feb–May[a]	22	18	-	-	Vassallo-Agius *et al.* (1999)
	Japan	-	4 (F), 6 (M)	Natural	Feb–May[a]	22	37–69	-		Vassallo-Agius *et al.* (1999)

	Japan	-	4–5 (F), 7 (M)	Natural	Feb–May[a]	22	27–37	-	morula stage at 09:00 h	Watanabe *et al.* (1998)
	Japan	1984–1985	14 (F), 3 (M)	Natural	Dec–March	18.5–21.5	-	-	1–2 h after sunset	Murai *et al.* (1985b)
	Portugal	-	5 (F), 4 (M)	Natural	May–June	19.5–21.9	20	1	-	Nogueira *et al.* (2018)

[a] Female (F) and male (M) are indicated.
[b] hCG, human chorionic gonadotropin; GnRHa, gonadotropin-releasing hormone agonist; SPE, salmon pituitary extract.
[c] Spawning days were counted.
[d] Spawnings were recorded only between Nov and Jan.

1816 **Table 6** Batch fecundity and total annual fecundity of captive-reared species reported in this review.

Common name	Body size of females		Treatment[b]	Batch fecundity (eggs kg^{-1} female, x10^3)*	Total annual fecundity (eggs kg^{-1} female, x10^3)*	Reference
	Length (fork length, cm)*,[a]	Weight (kg)*				
greater amberjack	-	17–22	GnRHa implants (2 tanks)	15±2	204±20 (mean±SD)	Fakriadis *et al.* (2019)
	-	15–24	GnRHa injections (2 tanks)	6±1	80±12 (mean±SD)	
	-	27–31	natural	23	113	unpublished data
	-	9–43	GnRHa implants	2	118	Jerez *et al.* (2018)
	-	25	Natural	3	115	Jerez *et al.* (2006)
	89^{TL}	12.5	GnRHa implant	4-30	54	Mylonas *et al.* (2004)
	73	≈7	GnRHa injections	15	339	Fernández-Palacios *et al.* (2015b)
	82	≈11	GnRHa implant	25	327	Sarih *et al.* (2018)
	84	≈12	GnRHa injection	37	364	
	79	10	Natural	57	1,305	
yellowtail or Japanese amberjack	-	9	hCG injection	58	-	Kagawa (1992)
	73–78	8–9	hCG injection	36-81	-	Mushiake *et al.* (1993)
	-	9	hCG injection	89–107	-	Vassallo-Agius *et al.* (2002)
	82–85	13	hCG injection	-	125-199	Mushiake *et al.* (1995)
	-	8	GnRHa implant	-	172	Kagawa (1992)
yellowtail kingfish	83	11	Natural	4.3	-	Setiawan *et al.* (2016)
	82	10	GnRHa implant	3.9	-	
	-	16–18	Natural	-	45-57	Stuart & Drawbridge (2013)
	-	20–21	Natural	-	199-227	

longfin yellowtail	-	20	Natural	-	600	Blacio (2004)
	57–70[SL]	4–8	GnRHa injections	19–22	170–360	Roo *et al.* (2015)
	86[TL]	11	GnRHa injections	-	944	Fernández-Palacios *et al.* (2015a)
giant trevally	-		hCG injections	-	223	Mutia *et al.* (2015)
	-		GnRHa injections	-	176	
bluefin trevally	52	3.4	Natural	-	1,545	Moriwake *et al.* (2001)
golden trevally	49	2.4	GnRHa Implant (Ovaplant)	> 16	> 225	Broach *et al.* (2015)
striped jack or white trevally	52–54	3.5–3.8	hCG injection	-	539–1,133	Vassallo-Agius *et al.* (2001b) Watanabe & Vassallo-Agius (2003)
	52–56	3.3–3.4	hCG injection	-	3081,044	Vassallo-Agius *et al.* (2001a) Watanabe & Vassallo-Agius (2003)
	54	3.8	Natural	49–52	873–928	Vassallo-Agius *et al.* (2001c)
	-	4.7–5.4	Natural	37–56	-	Vassallo-Agius *et al.* (1999)
	59	5.3	Natural	-	-	Watanabe *et al.* (1998)
	68	6.3	Natural	-	-	Murai *et al.* (1985b)
	-	-	Natural	-	-	Nogueira *et al.* (2018)

*Data are expressed as mean, mean ± standard deviation or range, according to the source of information.

[a] When not otherwise indicated, fish length is reported as fork length. SL, standard length; TL, total length.

[b] hCG, human chorionic gonadotropin; GnRHa, gonadotropin-releasing hormone agonist.

1824 **Figure Legends**

1826 **Figure 1.** Immature (a), maturing (b) and mature (c) ovaries from greater amberjack females sampled in the Mediterranean Sea. (d) Histological section of the ovary from a wild
1828 greater amberjack sampled on 01 May 2015 during the early phase of oogenesis showing a thick muscle wall and ovigerous lamellae containing oocytes at the primary growth
1830 stage. Hematoxylin-eosin staining. Magnification bars: 5 cm in (a); 10 cm in (b) and (c); 300 μm in (d). Micrographs (a), (b), and (c) are authors' unpublished photos; micrograph
1832 (d) has been taken and modified from Zupa *et al.* (2017b).

1834 **Figure 2.** Micrographs of ovary sections from different greater amberjack sampled in the Mediterranean Sea. a) Oogonia (asterisk) and chromatin-nucleolus stage oocytes
1836 (arrowhead). b) Perinucleolar stage oocytes. c) Cortical alveoli stage oocytes. d) Early vitellogenic oocytes. e) Particular of an early vitellogenic oocyte showing anti-
1838 vitellogenin positive granules in the peripheral ooplasm (arrow) and anti-vitellogenin positive granulosa cells (double arrow). f) Ovary section showing late vitellogenic (lv)
1840 oocytes and post-ovulatory follicles (dashed arrow) simultaneously. g) Hydrated oocyte (ho) from a wild fish in active spawning. h) α and β atretic vitellogenic follicles. All
1842 micrographs have been taken from sections stained with hematoxylin-eosin, except in (e) which has been taken from an ovary section immunostained with antibodies against anti
1844 Atlantic bluefin tuna vitellogenin (Pousis *et al.* 2019). Magnification bars = 10 μm in (a) and (e), 50 μm in (b), 100 μm in (c) and (h), 200 μm in (d), and 150 μm in (f), (g).
1846 Micrographs (a), (b), (c), (d) and (h) are authors' unpublished photos; micrograph (e) has been taken and modified from Pousis *et al.* (2019), micrographs (f) and (g) have been
1848 taken and modified from Zupa *et al.* (2017b).

Figure 3. (a) Testes from a wild adult greater amberjack sampled during the reproductive period. (b) Micrograph of a testis section showing seminiferous tubules converging from the testis periphery to the sperm duct system in the center. Hematoxylin-eosin staining. (c) Micrograph of a testis section in active spermatogenesis showing different germ cell types. Hematoxylin-eosin staining. Magnification bars: 10 cm in (a), 2000 μm in (b) and 25 μm in (c). Arrow: large single type A spermatogonium; arrowhead: small single type A spermatogonium; asterisk: type A spermatogonial cyst; double asterisk: type B spermatogonial cyst. sd = spermatid cyst; scI = primary spermatocyte cyst; scII = secondary spermatocyte cyst; sz = spermatozoa. Micrographs (a) and (b) are authors' unpublished photos; micrograph (c) has been taken and modified from Zupa *et al.* (2017a).

Figure 4. Monthly trend of gonadosomatic index (GSI) of greater amberjack (*Seriola dumerili*) females captured in different reproductive areas. GSI of greater amberjack from the Gulf of Mexico (GOM) has been calculated by pooling data from Thompson *et al.* (1992) and Murie and Parkyn (2008). Data for the north-western Atlantic Ocean (NW Atlantic), Pacific Ocean (Hawaii) and Mediterranean Sea have been taken from Harris *et al.* (2007), Kikawwa and Everson (1984) and Sley *et al.* (2014), respectively.

Figure 5. Oocyte size-frequency (≥200 μm) in yellowtail (*Seriola quinqueradiata*) ovaries at different stages of the spawning cycle. The frequency distribution is shown for individual fish (a to d) caught around the Pacific coast of Japan in 2005 and 2006 were used. Fork length (FL) and gonadosomatic index (GSI) are indicated for each individual. Ovarian developmental stages are as follows: LV, late vitellogenesis (a); GVM, germinal vesicle

migration (b); HY, hydration (c); LV+POF, late vitellogenesis with newly-formed post-ovulatory follicles (d).

Figure 6. Tanks of 70 m^3 volume (A) for the spawning of greater amberjack (*Seriola dumerili*) (B) maintained in sea cages during the year (see Fig. 8A) at the Argosaronikos Fishfarms S.A., Salamina Island, Greece. The fish spawned spontaneously after transfer from the sea, without any hormonal induction (C.C. Mylonas, unpublished data).

Figure 7. Micrographs of testis sections from males caught during the active phase of the reproductive cycle (late May–early June) in the Mediterranean Sea. (a) Testis section from a wild fish caught around Pelagie Islands (Sicily, Italy) showing all stages of spermatogenesis and large number of luminal spermatozoa; (b) Testis section from a captive-reared fish sampled in a commercial farm in Salamina Island (Greece) showing arrested spermatogenesis, with residual sperm cysts in the germinal epithelium and large number of luminal spermatozoa. Hematoxylin-eosin staining. Magnification bars = 100 μm in (a) and 200 μm in (c). sp: luminal spermatozoa. Micrographs has been taken and modified from Zupa *et al.* (2017b).

Figure 8. Evaluation and selection for spawning induction of greater amberjack (*Seriola dumerili*) maintained in sea cages at Galaxidi Marine Farms, S.A., Greece (A). Biopsies were obtained from the gonads using a catheter (B) and the oocytes were evaluated for size, morphology and stage of development (C) before fish selection and spawning induction using GnRHa implants (D).

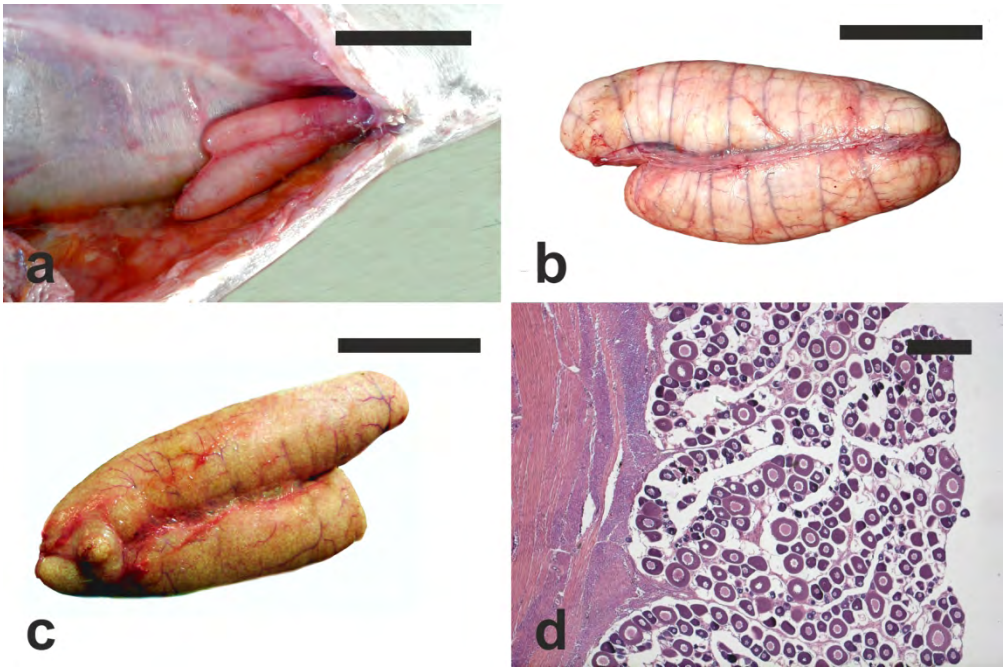

Figure 1. Immature (a), maturing (b) and mature (c) ovaries from greater amberjack females sampled in the Mediterranean Sea. (d) Histological section of the ovary from a wild greater amberjack sampled on 01 May 2015 during the early phase of oogenesis showing a thick muscle wall and ovigerous lamellae containing oocytes at the primary growth stage. Hematoxylin-eosin staining. Magnification bars: 5 cm in (a); 10 cm in (b) and (c); 300 μm in (d). Micrographs (a), (b), and (c) are authors' unpublished photos; micrograph (d) has been taken and modified from Zupa et al. (2017a).

149x99mm (300 x 300 DPI)

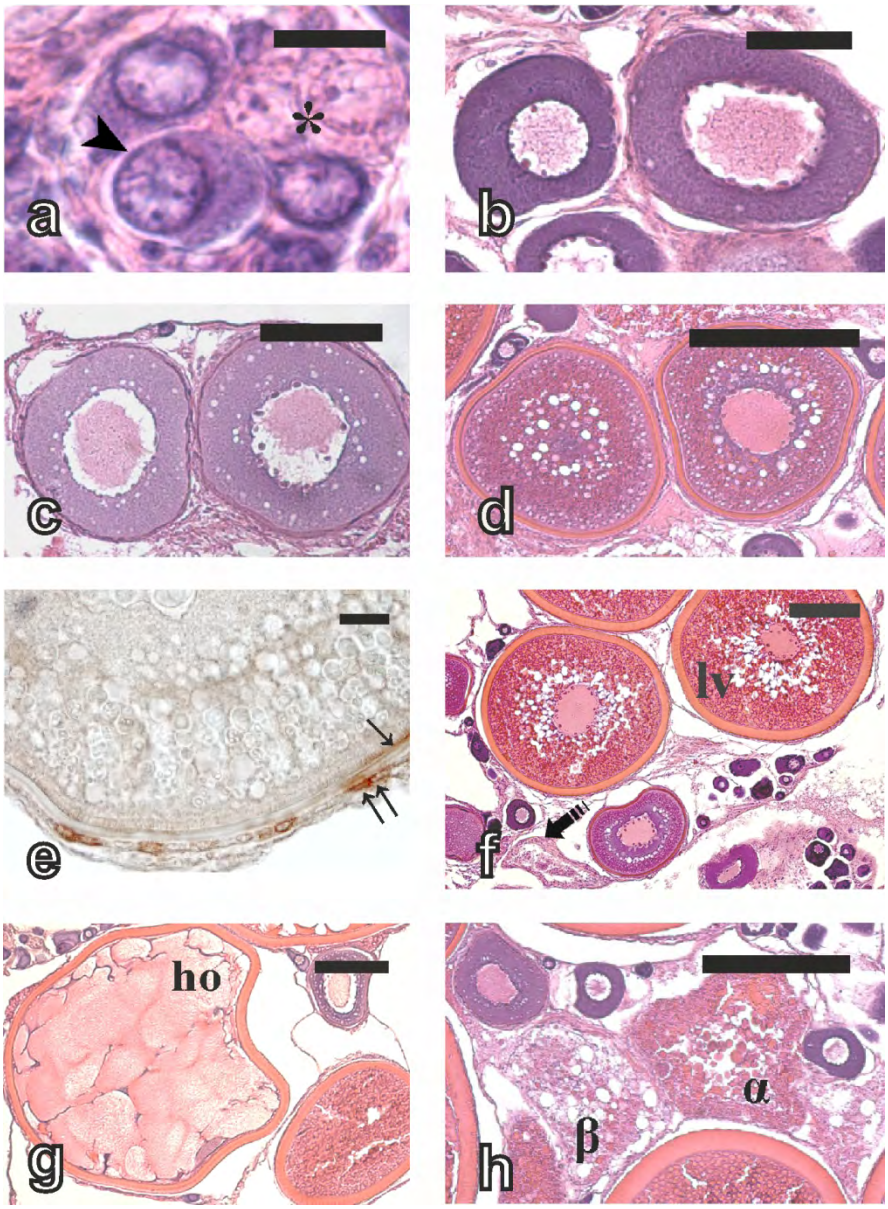

Figure 2. Micrographs of ovary sections from different greater amberjack sampled in the Mediterranean Sea. a) Oogonia (asterisk) and chromatin-nucleolus stage oocytes (arrowhead). b) Perinucleolar stage oocytes. c) Cortical alveoli stage oocytes. d) Early vitellogenic oocytes. e) Particular of an early vitellogenic oocyte showing anti-vitellogenin positive granules in the peripheral ooplasm (arrow) and anti-vitellogenin positive granulosa cells (double arrow). f) Ovary section showing late vitellogenic (lv) oocytes and post-ovulatory follicles (dashed arrow) simultaneously. g) Hydrated oocyte (ho) from a wild fish in active spawning. h) α and β atretic vitellogenic follicles. All micrographs have been taken from sections stained with hematoxylin-eosin, except in (e) which has been taken from an ovary section immunostained with antibodies against anti Atlantic bluefin tuna vitellogenin (Pousis et al. 2019). Magnification bars = 10 μm in (a) and (e), 50 μm in (b), 100 μm in (c) and (h), 200 μm in (d), and 150 μm in (f), (g). Micrographs (a), (b), (c), (d) and (h) are authors' unpublished photos; micrograph (e) has been taken and modified from Pousis et al. (2019), micrographs (f) and (g) have been taken and modified from Zupa et al. (2017a).

120x163mm (300 x 300 DPI)

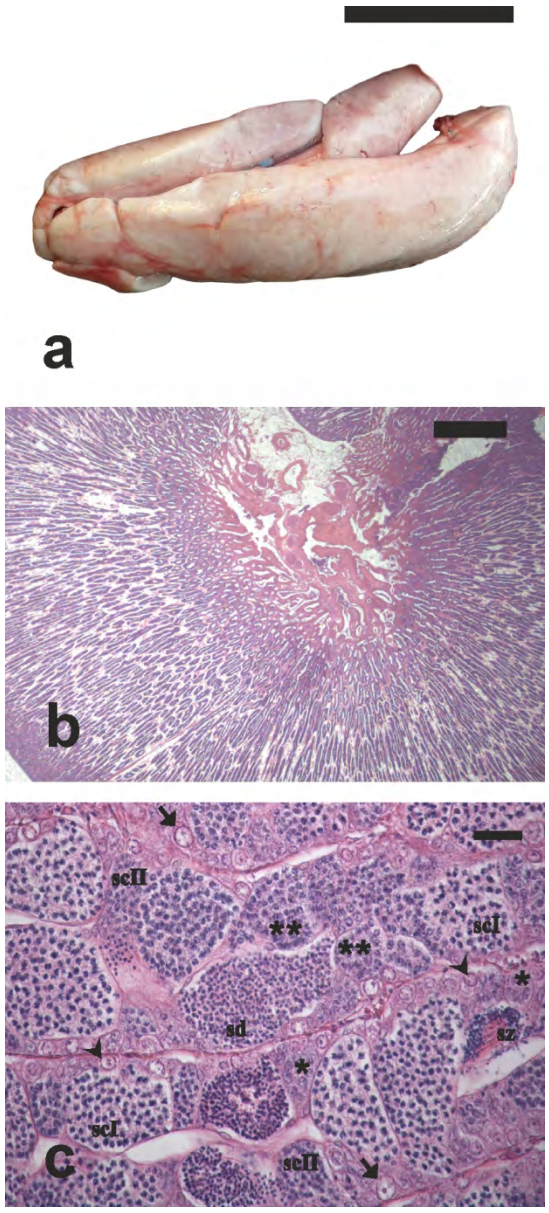

Figure 3. (a) Testes from a wild adult greater amberjack sampled during the reproductive period. (b) Micrograph of a testis section showing seminiferous tubules converging from the testis periphery to the sperm duct system in the center. Hematoxylin-eosin staining. (c) Micrograph of a testis section in active spermatogenesis showing different germ cell types. Hematoxylin-eosin staining. Magnification bars: 10 cm in (a), 2000 µm in (b) and 25 µm in (c). Arrow: large single type A spermatogonium; arrowhead: small single type A spermatogonium; asterisk: type A spermatogonial cyst; double asterisk: type B spermatogonial cyst. sd = spermatid cyst; scI = primary spermatocyte cyst; scII = secondary spermatocyte cyst; sz = spermatozoa. Micrographs (a) and (b) are authors' unpublished photos; micrograph (c) has been taken and modified from Zupa et al. (2017a).

74x164mm (300 x 300 DPI)

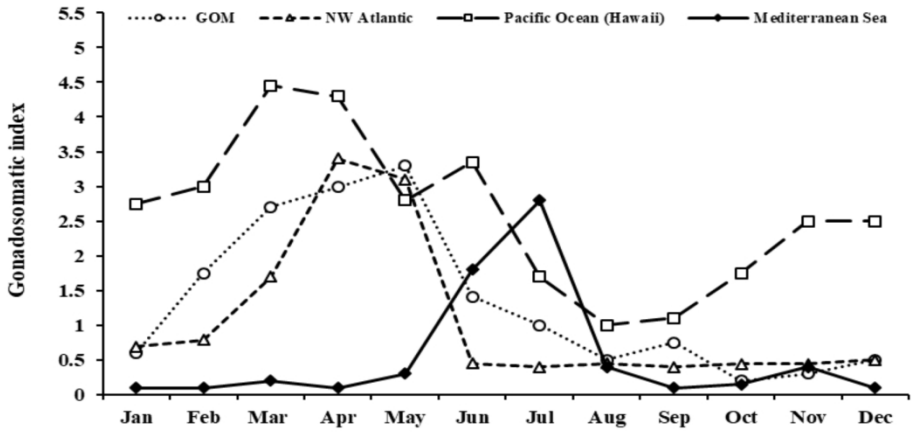

Figure 4. Monthly trend of gonadosomatic index (GSI) of greater amberjack (Seriola dumerili) females captured in different reproductive areas. GSI of greater amberjack from the Gulf of Mexico (GOM) has been calculated by pooling data from Thompson et al. (1992) and Murie and Parkyn (2008). Data for the north-western Atlantic Ocean (NW Atlantic), Pacific Ocean (Hawaii) and Mediterranean Sea have been taken from Harris et al. (2007), Kikawwa and Everson (1984) and Sley et al. (2014), respectively.

161x93mm (300 x 300 DPI)

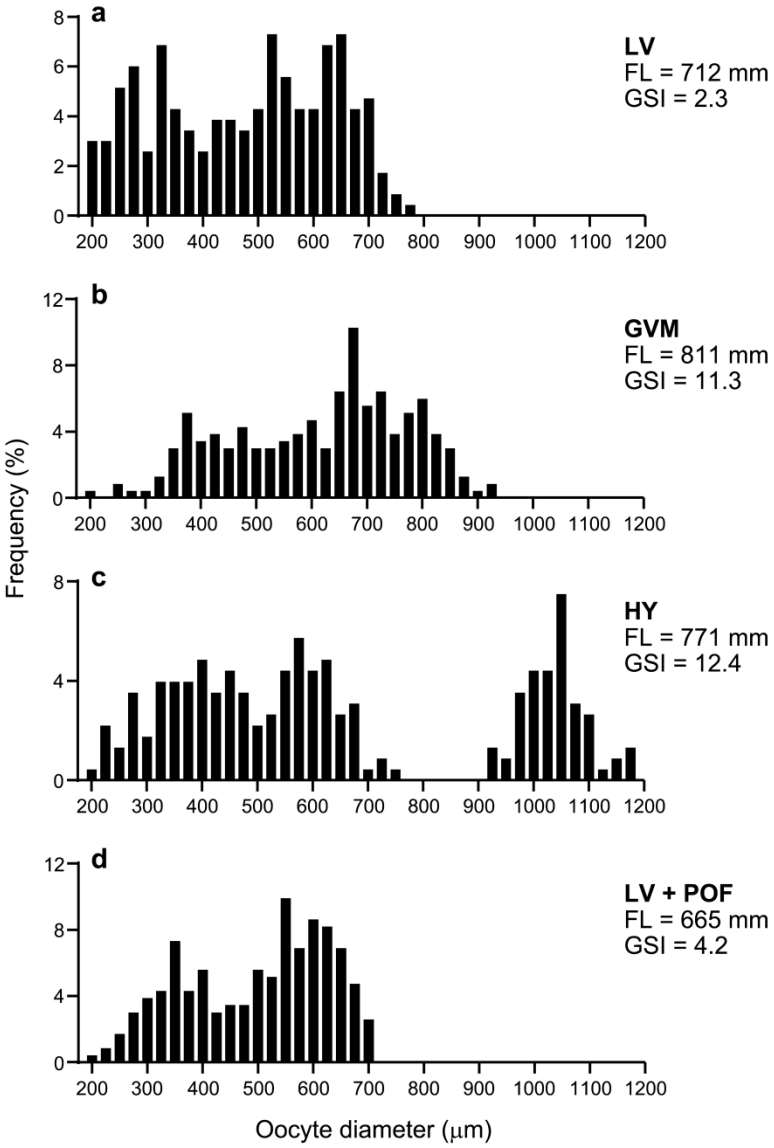

Figure 5. Oocyte size-frequency (≥ 200 μm) in yellowtail (Seriola quinqueradiata) ovaries at different stages of the spawning cycle. The frequency distribution is shown for individual fish (a to d) caught around the Pacific coast of Japan in 2005 and 2006 were used. Fork length (FL) and gonadosomatic index (GSI) are indicated for each individual. Ovarian developmental stages are as follows: LV, late vitellogenesis (a); GVM, germinal vesicle migration (b); HY, hydration (c); LV+POF, late vitellogenesis with newly-formed post-ovulatory follicles (d).

Figure 6. Tanks of 70 m3 volume (A) for the spawning of greater amberjack (Seriola dumerili) (B) maintained in sea cages during the year (see Fig. 8A) at the Argosaronikos Fishfarms S.A., Salamina Island, Greece. The fish spawned spontaneously after transfer from the sea, without any hormonal induction (C.C. Mylonas, unpublished data).

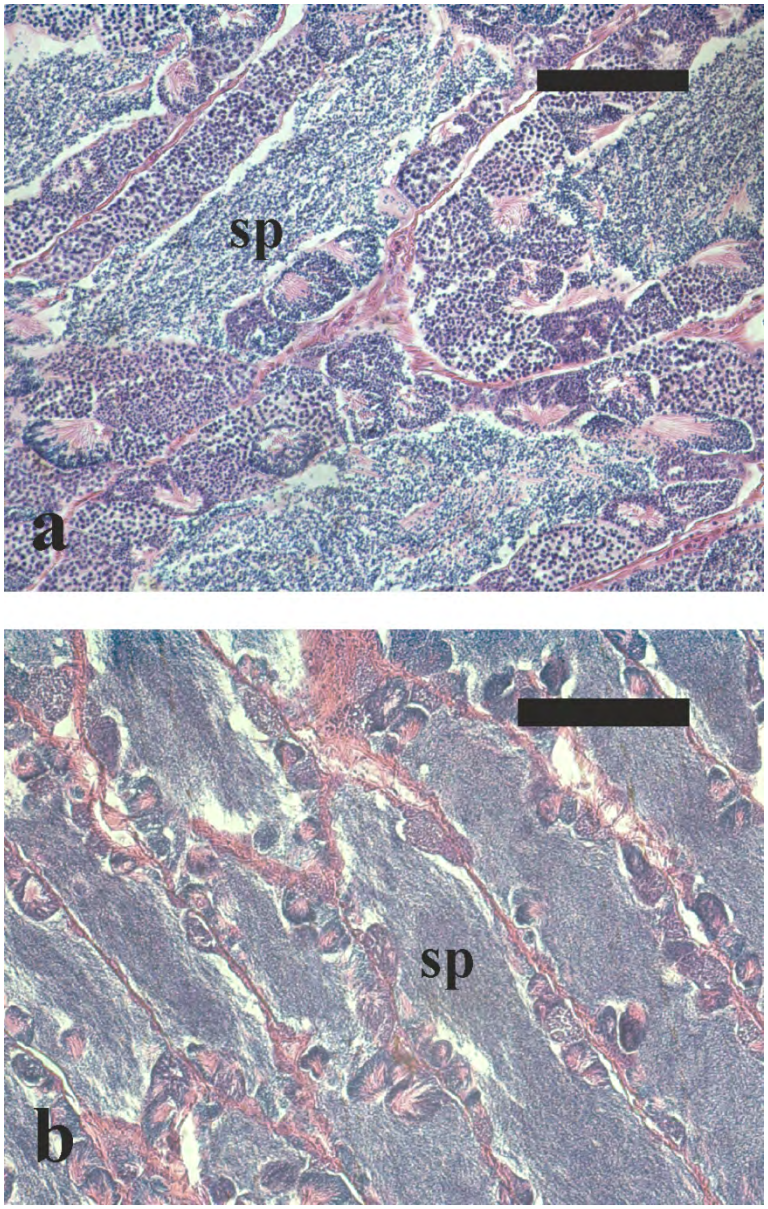

Figure 7. Micrographs of testis sections from greater amberjack caught during the active phase of the reproductive cycle (late May–early June) in the Mediterranean Sea. (a) Testis section from a wild fish caught around Pelagie Islands (Sicily, Italy) showing all stages of spermatogenesis and large number of luminal spermatozoa; (b) Testis section from a captive-reared fish sampled in a commercial farm in Salamina Island (Greece) showing arrested spermatogenesis, with residual sperm cysts in the germinal epithelium and large number of luminal spermatozoa. Hematoxylin-eosin staining. Magnification bars = 100 μm in (a) and 200 μm in (c). sp: luminal spermatozoa. Micrographs has been taken and modified from Zupa et al. (2017b).

80x126mm (300 x 300 DPI)

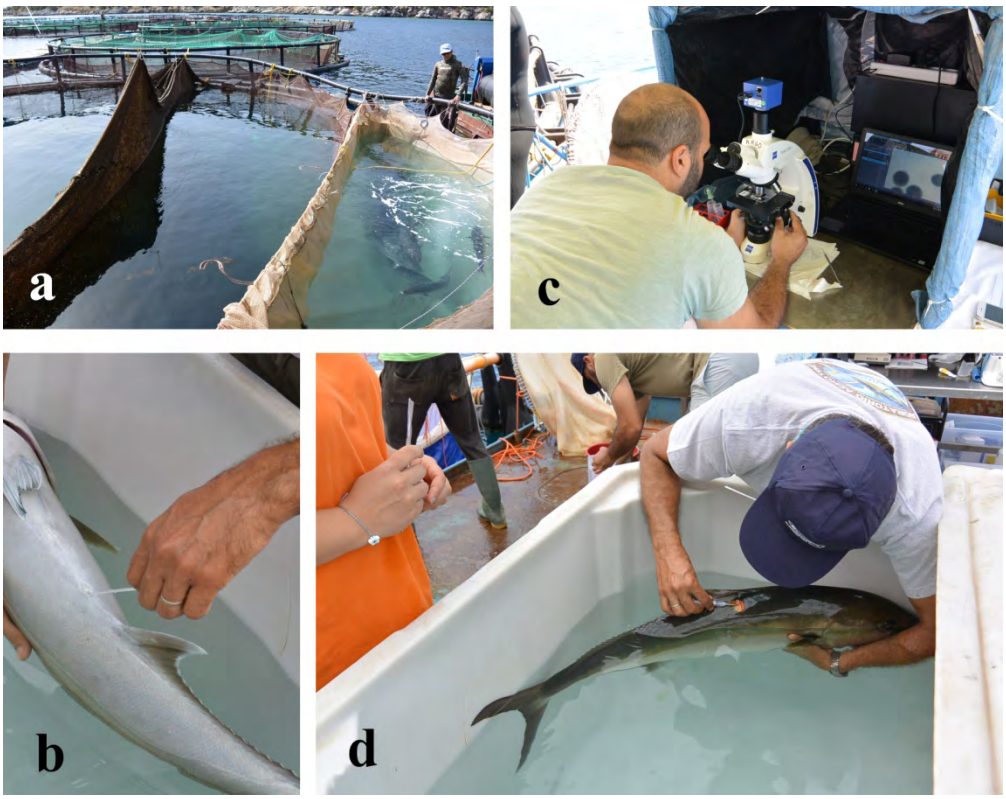

Figure 8. Evaluation and selection for spawning induction of greater amberjack (Seriola dumerili) maintained in sea cages at Galaxidi Marine Farms, S.A., Greece (A). Biopsies were obtained from the gonads using a catheter (B) and the oocytes were evaluated for size, morphology and stage of development (C) before fish selection and spawning induction using GnRHa implants (D).