This is a preprint version of the article:

Corriero A., Wylie M., Mitsuo N., Zupa R., Mylonas C.C. Reproduction of greater amberjack (*Seriola dumerili*) and other members of the family Carangidae. Reviews in Aquaculture (2021) 13, 1781–1815. doi: 10.1111/raq.12544

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

24 [1] Department of Emergency and Organ Transplantation, Section of Veterinary Clinics and Animal Production, University of Bari Aldo Moro, Valenzano (Bari), Italy

26 [2] The New Zealand Institute for Plant and Food Research Limited, Seafood Production Unit, 293–297 Port Nelson, Nelson 7010, New Zealand

28 [3] Fisheries Resources Institute, Japan Fisheries Research and Education Agency, Yokohama, Japan

30 [4] Institute of Marine Biology, Biotechnology and Aquaculture, Hellenic Center for Marine Research, Heraklion, Crete, Greece

32

34

Table of Contents

1. Introduction

The genus *Seriola* (family Carangidae) includes 12 species that are distributed in all tropical and temperate waters, and some of them have been notable species for aquaculture worldwide, while other carangid species have also been considered as potential cultured species (Table 1). 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, and with new knowledge and methods on reproductive physiology and endocrinology being acquired, 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.* 2017a), 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 have also been studied (Nakada 2002) and this species is currently reared commercially worldwide.

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. 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, in order 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.

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; Kawabe *et al.* 1998; Nyuji *et al.* 2016), from May to July in the Mediterranean Sea (Marino *et al.* 1995b) 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, New Zealand, 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.* 2015a) 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.

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 (*C. 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).

2. Gonad structure and gametogenesis

The ovaries of carangids are paired organs suspended to the dorsal abdominal wall by a mesovarium, and consist of a muscle wall and numerous ovigerous lamellae projecting towards a cavity (Fig. 1). The presence of an internal ovarian cavity where oocytes are released at ovulation (ovarian lumen) is typical of the most evolved teleost fishes and characterizes the so-called cystovarian type (Helfman *et al.* 2009; Piccinno *et al.* 2014). Ovigerous lamellae contains oogonia and oocytes, whose development in fish 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 suspended to the dorsal abdominal wall by a mesorchium, and they belong to the "unrestricted spermatogonial type" of Grier *et al.* (1980) and to the lobular type of Billard (1986), being characterized by the presence of spermatogonia throughout the extension of the seminiferous lobules. 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

The available information on greater amberjack gonadal macroscopic morphology and

164 germ cell developmental stages (Marino *et al.* 1995a; Grau *et al.* 1996; Micale *et al.* 1999; Sley *et al.* 2014) is herein summarized and integrated with more recent observations. The
166 greater amberjack ovaries (Fig. 1) are morphologically similar to those of other large pelagic iteroparous fishes with asynchronous oocyte development, such as the Atlantic bluefin tuna
168 (*Thunnus thynnus*) (Zohar *et al.* 2016). The two ovaries are always different in size, both in immature and mature individuals (Fig. 1a, b) and they join caudally in a common oviduct
170 opening to the exterior in 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.
172 1a); in mature individuals, ovaries occupy 2/3 of the volume of the abdominal cavity (García & Díaz 1995) and show a rich vascular network, which is responsible for their reddish color
174 (Fig. 1b, c). Developing oocytes at the vitellogenic stage provide ovaries with a granular appearance, while in ready-to-spawn ovaries, hydrated oocytes are easily distinguishable as
176 opaque spheres ~1 mm in diameter (Fig. 1c). The ovary wall includes a thick muscle tunica provided with fibers arranged in a circular and in a longitudinal layer and many ovigerous
178 lamellae, containing oogonia and oocytes at different stages of development, immersed in connective tissue (Fig. 1d).

180 The histological appearance of greater amberjack female germ cells has already been described (Marino *et al.* 1995a; Grau *et al.* 1996; Micale *et al.* 1999) and a synthetic
182 description is provided here. Oogonia (diameter 8-15 μm) are present during all phases of the reproductive cycle (Fig. 2). They are often found in small clusters and are rounded cells with
184 a large central euchromatic nucleus (nucleus:cytoplasm ratio, N/C, > 0.7) containing sparse eterochromatic patches and a single nucleolus. Chromatin-nucleolus stage oocytes (diameter
186 15-30 μm) are ovoidal cells at early meiotic prophase (Fig. 2a). They show a slightly basophilic ooplasm, a large eccentric nucleus (N/C≈0.5) showing chromatin strands and
188 sparse eterochromatic patches. Squamous follicular cells are associated with oocytes at this

stage. Perinucleolar stage oocytes (diameter 30-120 μm) are characterized by the presence of several nucleoli adjoining the nuclear envelope (Fig. 2b). Oocytes at chromatin-nucleolus and perinucleolar stages (primary growth) are always observed in the ovaries during all the phases of the reproductive cycle. Lipid/cortical alveoli stage (diameter 120-200 μm) show a reduction of ooplasm basophily, small lipid droplets and the appearance of a thin PAS-positive zona radiata (Fig. 2c). The nucleus contains numerous fattened nucleoli adjoining the nuclear wall. Granulosa and thecal layers are distinguishable, separated by a PAS-positive basal lamina. Oocyte growth is associated with the increase of lipid globules, the appearance of cortical alveoli in the peripheral ooplasm and zona radiata thickening.

Vitellogenesis starts when yolk globules, derived from the precursor protein vitellogenin, start accumulating in the ooplasm. Early vitellogenic oocytes (diameter 200-400 μm) are characterized by the appearance of eosinophilic yolk globules in the peripheral ooplasm and a further increase of the zona radiata thickness (1-3 μm), which appears as a two-layered structure (Fig. 2d). Follicular cells surrounding the oocytes at this stage increase slightly in size and become isoprismatic. Antibodies raised against a partial sequence of Atlantic bluefin tuna vitellogenin were successfully used to label 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 transmission electron microscopy reveals that it is constituted by three layers (Grau *et al.* 1996). Small PAS-positive cortical alveoli are visible at the periphery of the cytoplasm and a few remaining nucleoli are visible in the nucleus. At the end of this stage, the cytoplasm is completely filled with yolk globules.

At the OM stage (Fig. 2g), vitellogenin-derived yolk proteins are hydrolyzed and yolk globules and lipid vesicles coalesce to form the lipid droplet and a homogeneous, translucent, slightly acidophilic yolk mass. The germinal vesicle migrates to the animal pole and its envelope dissolves (germinal vesicle breakdown, GVBD). Oocytes at this stage uptake water

(oocyte hydration) due to the rise of free amino acid concentration, and their diameter increases to 900-1000 µm. The maturing oocytes tend to separate from the now thin and stretched follicular layers. In paraffin-embedded sections, due to the loss of water during tissue processing, hydrated oocytes tend to assume an irregular shape. Eggs released spontaneously from greater amberjack reared at low density in Southern Japan had 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. These POFs are arranged in convoluted cords, consisting of an internal epithelial layer of hypertrophic granulosa cells and external connective layer containing thecal cells, delimiting an irregular lumen (Fig. 2f).

Sparse atretic follicles are always observed in greater amberjack females during vitellogenesis and this is considered as a physiological finding in fish (Agulleiro *et al.* 2007; Brown-Peterson *et al.* 2011). 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.* 2017a; 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).

2.1.2. Testis structure and spermatogenesis

In adult greater amberjack, fully ripe testes (Fig. 3a) occupy 2/3 of the abdominal cavity length (Garcia and Diaz, 1995). As for other teleost fishes (Schulz *et al.* 2010), the greater amberjack testis consists of two structurally and functionally different regions (Fig. 3b): an outer region consisting of a lobular compartment which extends from the periphery towards the inner region. The latter consists of a well-developed sperm duct system in which spermatozoa

240 are conveyed. The lobular compartment represents the testis proliferative region and contains the germinal epithelium made of germ cells at different stage of development, surrounded by 242 cytoplasmic extensions of Sertoli cells to form spermatocysts (Fig. 3c). The greater amberjack testis structure corresponds to the unrestricted spermatogonial type (Grier *et al.* 1980; Billard 244 1986). In this type of testis, which is typical of the fish order Perciformes, spermatogonia and spermatocysts are distributed all along the seminiferous lobules (Parenti & Grier 2004).

246 Different male germ cell types have been described in greater amberjack (Marino *et al.* 1995a; Zupa *et al.* 2017b; Zupa *et al.* 2017a). Zupa *et al.* (2017b) distinguished two types of 248 single A spermatogonia: a small cell type with a diameter of about 8.0 µm (Fig. 3c), and a large cell type with a diameter of about 10.5 µm. Using stemness markers in immunohistochemistry 250 assays, Zupa *et al.* (2017b) identified the small single type A spermatogonia as the only stem spermatogonia. The same authors described also two types of spermatogonia contained in cysts: 252 larger cells about 9 µm in diameter (presumptively type A spermatogonia), and smaller cells, around 5 µm in diameter, (presumptively type B spermatogonia). Primary spermatocytes were 254 around 4.5 µm in diameter and secondary spermatocytes were about 3 µm and their appearance changed according to the different phases of meiosis. Spermatids were described as small cells 256 around 2.5-3 µm in diameter showing a dense and strongly basophilic nucleus, whereas flagellated spermatozoa were characterized by an oval head strongly stained with hematoxylin 258 and were observed within cysts or in the lumen of seminiferous lobules after cyst breakdown (spermiation).

260

2.2. Other *Seriola spp*

262 *Seriola* species are spring and/or summer spawners, exhibiting multiple spawning during their annual spawning season. As with greater amberjack, the ovary of yellowtail 264 shows asynchronous oocyte development (Kagawa 2013). At the completion of

vitellogenesis, the oocytes of yellowtail reach around 700 μm in diameter (Fig. 4a). 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. 4b). 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. 4c). 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. 4d). 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 lobules and the sperm duct are filled with spermatozoa. Spermatozoa disappear from the testis in the post-spawning season.

2.3. Other Carangids

To date, descriptions of ovarian structure, histology or morphology 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.* 1985b). 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.* 1985b), while naturally spawned eggs in captivity ranged between 880-1020 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 colour with primary oocytes. Stage III consisted of vitellogenic oocytes and a yellow coloured 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 colour; hydrated egg diameters ranged between 500-1000 µm. Finally, Stage V

consisted of females that were spent, where the ovary was still large but fluid filled and darker in colour at times. For males, the testes in Stage I were 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 colour. Spent males (Stage IV) had testes that were pink-grey in colour 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 - 860 μm and 200 - 250 μm, respectively (James 1976).

3. Sexual maturity and reproductive cycles

In fishes, both XX/XY (male heterogametic) and ZZ/ZW (female heterogametic) sex-determining systems have been identified (Devlin & Nagahama 2002). 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 SNP in the gene encoding the steroidogenic enzyme 17β-hydroxysteroid dehydrogenase 1 (Hsd17β1) is associated with ZZ/ZW sex determination. Hsd17β 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 Hsh17β1 had lower activity of steroid conversion than W-type Hsh17β1, 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 differentiation of *Seriola* species is considered to be linked to the genetic regulation of steroidogenic enzymes.

3.1. Greater amberjack

3.1.1. Sexual maturity

Marino *et al.* (1995a) reported that the gonads of greater amberjack caught in the Mediterranean at 2-3 months of age and reared in a sea cage started to differentiate after about 2 months (23-26 cm standard length, SL). At 4-5 months of age, ovaries showed 10-11 ovigerous folds containing oogonia and spermatogonial cysts appeared in the testes. A few chromatin nucleolus stage oocytes were visible in the ovaries of 28-32 cm long juveniles (4-5 months old), and seminiferous lobules appeared in the testes at this age. At one year of age, perinucleolar stage oocytes appeared in the ovaries and all the spermatogenesis stages were present in the testes, included luminal spermatozoa. In a recent study on the sex differentiation of hatchery produced greater amberjack (Mylonas, C.C. unpublished data), the ovarian cavity was already formed at 101 days post fertilization (dph) at a total length (TL) of 14.5 ± 6.2 cm, and germ cells were visible 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 differentiation at 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 ± 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 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 (Table 2) (Marino *et al.* 1995b; Marino *et al.* 1995a; Micale *et al.* 1999; Kožul *et al.* 2001; Sley *et al.* 2014) are limited and not always consistent, because they were obtained from studies that made use of fish in different conditions (wild/captive-reared), or adopted different

maturity criteria or biometric parameters (SL, TL or fork length FL). According to a histological study carried out on fish sampled around the Pelagie Islands, Italy (Marino *et al.* 1995b), 50% of the males attain sexual maturity at 109 cm SL; 50% of the females at 113 cm SL; 100% of the fish over 128 cm SL are mature. A quite lower size at median maturity was reported by Sley *et al.* (2014) for greater amberjack sampled in the Gulf of Gabes: 80 and 83 cm SL for females and males, respectively. These data, however, are likely biased due to the fact that specimens with developing gonads (and then still immature), were classified as mature, a mistake that often affects the calculation of size at maturity in fishes due to the difficult discrimination between mature and immature individuals during the resting/early gametogenesis phases of the reproductive cycle. In the southern Adriatic Sea, about 40% of three-years old and 100% of five-years old fish have been found to be sexually mature (Kožul *et al.* 2001). This maturity schedule is confirmed by a recent study carried out on greater amberjack fished commercially around the Pelagie Islands (Corriero A., unpublished data) indicating that 50% of the fish are sexually mature at 3 years of age and 100% at 5 years. 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 4 and 100% at age 6.

3.1.2. Reproductive cycle, spawning areas and fecundity

As mentioned earlier, in general *Seriola* spp spawn in the spring and/or-summer, but differences exist between the temperate, sub-tropical and tropical regions. Timing and duration of greater amberjack reproductive cycle, for example, show variations in the known spawning areas (Mediterranean, north-western Atlantic, Gulf of Mexico and Pacific Ocean/Hawaii), according to local environmental conditions and/or genetic peculiarities. In the Mediterranean Sea (waters around Pelagie Islands, Italy and Gulf of Gabes, Tunisia),

388 greater amberjack gonad 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.* 390 2017a; Pousis *et al.* 2018; Pousis *et al.* 2019) and spermatogenesis is activated in the testes (Mandich *et al.* 2004; Zupa *et al.* 2017b; Zupa *et al.* 2017a). The vitellogenic phase in this 392 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.* 394 2004) so that, 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.* 2017a; Pousis 396 *et al.* 2018; Pousis *et al.* 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 398 greater amberjack females show hydrated oocytes and/or POFs, and males have seminiferous lobules filled with spermatozoa. Fish with post-spawning and resting gonads are found from 400 July to the end of the fishing season in September.

Studies carried out through conventional tagging (McClellan & Cummings 1996), 402 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 404 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, form North Carolina to Florida, 406 and North Gulf of Mexico spawning occurs in April-June, when sea surface temperature is 23°C and above. The comparative analysis of monthly changes of GSI greater amberjack 408 females in different areas (Fig. 5) confirms the presence of different reproductive peaks in the different spawning grounds: June-July in the Mediterranean (Sley *et al.* 2014; Zupa *et al.* 410 2017a), April-May in the northwestern Atlantic and Gulf of Mexico (Thompson *et al.* 1992; Harris *et al.* 2007; Murie & Parkyn 2008) and March-April in the Pacific Ocean (Hawaii) 412 (Kikawwa & Everson 1984). Interestingly, the recorded GSI peaks are higher in specimens

from the Pacific Ocean (peak recorded in 1980: 4.5) than in specimens from the northwestern Atlantic/Gulf of Mexico (peak recorded in the Gulf of Mexico in 1898: 3.3; peak recorded off northwestern Atlantic in 2000-2004: 3.4) and in specimens from the Mediterranean Sea (peak around 2.5, year of sampling not provided). Although the GSI of fish belonging to a single school in spawning condition can reach much higher values, such as 11 in Marino *et al.* (1995b) or > 7 in Zupa *et al.* (2017a), the different average GSI reported during the spawning season in different geographical areas might be indicative of different fecundities in genetically distinct populations.

Regarding the endocrine regulation of gametogenesis, no data on gonadotrophin (GtH) levels during the reproductive cycle of wild greater amberjack have been published yet and the only data on sex steroid plasma concentrations (Table 3) are from fish commercially caught in the Mediterranean Sea around the Pelagie Islands (Mandich *et al.* 2004; Zupa *et al.* 2017b; Zupa *et al.* 2017a). In females, T and E_2 showed a significant increase during the rapid 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 vitellogenins (*vtga, vtgb, vtgc*) (Pousis *et al.* 2018) and the highest vitellogenin plasma concentrations were recorded (Mandich *et al.* 2004), which is in agreement with the widely acknowledged role of E_2 in stimulating liver synthesis of yolk-precursor proteins (Lubzens *et al.* 2010; Lubzens *et al.* 2017). Contrary to E_2, 17,20β-dihydroxypren-4-en-3-one (17,20β-P) showed low plasma concentrations and only slight variations during the different phases of the reproductive cycle of female greater amberjack, with highest levels (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

438 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
440 spawning season (Zupa *et al.* 2017a). A constant increase of 17,20β-P was observed in wild greater amberjack males from the sexual recrudescence phase to the spawning period, in
442 agreement with the role of these hormones in regulating sperm maturation/spermiation. Finally, very low E_2 plasma levels were found during spermatogenesis and a peak of this
444 hormone (1.4 ng ml^{-1}) was associated with the spermatogonial self-renewal concomitant with spermatogenesis cessation (Zupa *et al.* 2017b; Zupa *et al.* 2017a).

446 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
448 observations. The main commercial fishery targeting greater amberjack is purse seining, which makes use of echo sounder to localize schools and of a large circular net to encircle
450 them. According to the available information, in the spawning grounds between Pelagie Islands and Tunisia, during the reproductive period, greater amberjack aggregations are
452 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
454 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
456 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
458 several hours after capture. Courtship behaviour, sign of imminent spawning, was recorded around sunset in Caribbean coral reef of Gladden Spit (Heyman & Kjerfve 2008).

460 A transient multi-species spawning aggregation in the Atlantic tropical waters of Gladden Spit on the Belize Barrier Reef has been reported for greater amberjack adults, along
462 with Samson fish and five other carangids (*Carangoides ruber*, *Carangoides bartholomaei*,

Caranx latus, *Decapterus macarellus* and *Trachinotus falcatus*), occurring between April and June. 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), 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. In fishes with indeterminate fecundity, the total number of eggs produced during a reproductive season (potential annual fecundity) is calculated as the number of eggs released during each spawning event (batch fecundity) multiplied for the estimated total number of spawning events, which in turn is calculated as spawning frequency multiplied for the duration of the spawning season. 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 5 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 4 and 5 later).

3.2. Other *Seriola spp*

The age and size at first maturity (puberty) 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 4 years of age and has a lifespan of 6–7 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 2 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 1 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 1 month before the spawning season, and it was maintained at a high value (>5) during the spawning season. In males, GSI increased about 2 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.

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 sizes of the smallest, 50% and 100% mature females were reported to be 78, 94, and 128 cm FL, while those of males were 75, 81,

and 93 cm, respectively (Poortenaar *et al.* 2001). In southern Australia, females were found to
512 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
514 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,
516 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
518 found to be accelerated to 1 year in male yellowtail kingfish, but females take 4–5 years to reach sexual maturity (Sanchís-Benlloch *et al.* 2017). A rearing study demonstrated that a
520 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
522 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
524 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
526 (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
528 Africa, high GSI values were reported between November and February, consistent with data from Australia and New Zealand (Dunn 2014).

530 Yellowtail kingfish distributed in western Pacific (*Seriola aureovittata*) reaches a body size of around 100 cm FL at 7–8 years of age (Shiraishi *et al.* 2010). In the northern East
532 China Sea off the west coast of Japan, this species was reported to first mature at the age of 2 years, and its size at first maturity was 66 cm FL in females and 62 cm FL in males. In this
534 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

536 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
538 considered to be delayed by about 1 month.

In yellowtail kingfish distributed in eastern Pacific (*S. dorsalis*), research from the late
540 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
542 1960). In addition, larval surveys carried out in southern California between 1954 and 1969 indicates that *S. dorsalis* spawns between April and October, with a peak between July and
544 August (Sumida *et al.* 1985).

Based on high GSI values (>1) in both sexes, it was proposed that longfin yellowtail
546 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.*
548 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
550 1+ year (21 to 22 months of age), while females took 2 complete years (Laidley *et al.* 2004). In the Canary Islands, all male longfin yellowtail that were caught in the wild and reared in
552 captivity for 2 years matured at an average size of 55 cm SL and 3 kg BW (Roo *et al.* 2014; Roo *et al.* 2015). In contrast, 33% of females matured with an average size of 57 cm SL and 4
554 kg after a rearing period of 2 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 3 and 4 years,
556 respectively. This suggests that, under rearing conditions, a sex-dependent difference occurs in the maturity rate of longfin yellowtail.

558 The reproductive biology of Samson fish was analyzed by Rowland (2009), who showed that this species reaches a body size of around 85 cm FL at 5 years of age and around 105 cm

560 FL at 10 years of age. In females, the size and age at first maturity were 70–75 mm FL and 3+ years of age, respectively, while the size at 50% maturity was 83 cm FL. Cortical alveolus-
562 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 maintained
564 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 whose
566 size ranged between 106 and 120 cm FL.

Gene expression profiles of the β subunits of the two gonadotropins (GtH), namely
568 follicle-stimulating hormone (*fshb*) and luteinizing hormone (*lhb*) and of the GtH receptors (*fshr* and *lhr*) during the annual reproductive cycle of yellowtail have demonstrated that there
570 are differences in the 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,
572 while the expression 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
574 testicular *fshr* was high during the early and late phases of testicular development, while the expression of ovarian *lhr* increased gradually during the late phase and peaked during the
576 active spermiation period (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
578 found during the active spermiation period (Higuchi *et al.* 2017b). These studies suggest that, as described in many fishes (Rosenfeld *et al.* 2007; Levavi-Sivan *et al.* 2010), in yellowtail
580 FSH is involved in 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
582 evidence that OM is induced by treatment with human chorionic gonadotropin (hCG), which is an LH-like hormone (Matsuyama *et al.* 1996).

584 Recently, recombinant proteins have been increasingly applied in physiological studies of fish GtH. In *Seriola* species, recombinant FSH produced in the yeast *Pichia pastoris* and its
586 physiological function on gonadal development was analyzed (Sanchís-Benlloch *et al.* 2017). The *in vitro* cultivation of immature ovary and testis showed that FSH induced the production
588 of E_2 and 11-KT, respectively. In teleosts, E_2 is recognized to induce hepatic vitellogenin production in females while 11-KT is the main gonadal steroid controlling spermatogenesis
590 (Lubzens *et al.* 2010; Schulz *et al.* 2010). In yellowtail kingfish, the administration of recombinant FSH in immature fish showed that FSH initiated early secondary growth in the
592 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
594 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-
596 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
598 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
600 FSH secretion.

The synthetic pathway of ovarian steroid hormones has been studied in yellowtail by *in*
602 *vitro* cultivation of ovarian follicles with radiolabeled steroid precursors. During vitellogenesis, E_2 is synthesized from pregnenolone (P5) via 17-hydroxypregnenolone (17-
604 P5), dehydroepiandrosterone (DHEA), AD and T (Rahman *et al.* 2002a). After the completion of vitellogenesis, the steroidogenic pathway shifts from the production of E_2 to 17,20β-P,
606 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;
608 Rahman *et al.* 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 levels 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 levels 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, while 17,20β-P increased only in fish during GVM (Poortenaar *et al.* 2001), while plasma levels of T were also kept high between vitellogenesis and GVM (Poortenaar *et al.* 2001).

As mentioned already, 11-KT is the main androgen in teleosts and plays a role in stimulating spermatogenesis from early to late phases (Schulz *et al.* 2010). In male yellowtail, plasma 11-KT levels were elevated during testicular development and peaked during the active spermiation period (Higuchi *et al.* 2017b). 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 levels 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 in (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.

3.3. Other Carangids

To date, information on the sex differentiation of fishes from the genera *Caranx*, *Gnathanodon* and *Pseudocaranx* remain undescribed or unreported. Descriptions of gonadal development remain limited to data from wild fisheries and limited studies on captive fish (see section 4.3 for details). Furthermore, descriptions of sperm parameters remain unreported for the latter species in the wild and under culture conditions.

The available data on age and/or size at sexual maturity of the carangids considered in the present review 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 2 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 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-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 detail by Sudekum *et al.* (1991), who found that sex ratios were skewed towards females in both species (giant trevally 1M:1.39F; bluefin trevally

1M:1.48F) in coastal waters of the North-western Hawaiian Islands. Generally, both species appeared to spawn during the summer from April to November – with peak spawning during the months of May-August (Sudekum *et al.* 1991). Fecundity estimates for bluefin trevally in the wild range between 65,390 - 657,963 eggs kg^{-1} with an exponential increase in fecundity relative to body weight while fecundity estimates for giant trevally were not reported.

In the Southern Arabian Gulf, peak spawning of golden trevally occurs in spring from 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 and sex ratios (M:F) was 1:1.1 (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) but reported sex ratios of 1:1.5 as well 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 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 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 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) 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.* 1985b).

682 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
684 coast of New South Wales, Australia (Kalish & Johnston 1997; Rowling & Raines 2000). The authors report that silver trevally appear to be partial spawners and proposed that this species
686 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
688 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
690 waters, wild silver trevally have been captured in spawning condition in February, during the summer (James 1976).

692

4. Reproductive function in captivity and spontaneous spawning

694 ### 4.1. Greater amberjack

The first experiments on greater amberjack reproduction in captivity date back to 30
696 years ago, when spawnings were reported in large tanks at the Tokyo Metropolitan Ogasawara Fisheries Center (Kawabe *et al.* 1996). Wild-caught greater amberjack have
698 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
700 from the wild as juveniles and reared for 5 years in outdoor tanks in the Experimental Talassographic Institute of Messina (Italy). Failure of oogenesis completion followed by
702 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.*
704 (2006) reported that a group of 8-kg wild fish took 6 years to overcome the captivity-induced reproductive dysfunction and spawn spontaneously in Tenerife (Spain) in a 500-m^3 outdoor
706 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 and spawning occurring every 4 to 7 days, at night-time, but this was probably the result of only a single female spawning. Finally, Sarih *et al.* (2018) monitored the reproductive maturation of a greater amberjack broodstock of wild origin reared in 10 m^3 thanks in Gran Canaria (Spain) and found that two females out of a total of 19 that completed vitellogenesis and had oocytes > 800 μm in diameter, spawned spontaneously and produced high quality eggs. Finally, fish reared in sea cages for 8 years and transferred to outdoor 70 m^3 tanks in the beginning of the spawning season, spawned spontaneously five times, with an interval of 2-8 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 during the same periods (Zupa *et al.* 2017b; Zupa *et al.* 2017a; Pousis *et al.* 2018; Pousis *et al.* 2019). The captive broodstock consisted of fish caught as young-of-the-year in the Ionian Sea and confined in a sea cage in Salamina Island (Greece) until reproductive maturation. In these captive-reared females, the GSI was lower than in wild females, during the advanced gametogenesis and spawning phases (Zupa *et al.* 2017a). Histological evaluation of the gonads showed that captive-reared females were in the same reproductive state of wild fish at the beginning of the reproductive cycle, showing primary growth and few early vitellogenic oocytes. However, during the active gametogenesis phase

of the wild population, most of the captive-reared females displayed major α atresia of vitellogenic follicles (> 50% vitellogenic follicles), and during the peak of the reproductive season of the wild population 100% of vitellogenic oocytes were atretic, thus indicating a regressed condition related to an impairment of the reproductive cycle (Zupa *et al.* 2017a; 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 throughout the reproductive cycle (Table 3) (Zupa *et al.* 2017b). 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 steroids concentrations of first generation (F_1) hatchery produced greater amberjack reared in tanks (Table 3) were obtained in the framework of an experiment on reproductive control (Jerez *et al.* 2018). In females, plasma sex steroid concentrations showed a limited variability during the sampling period (May-September). These plasma concentrations were comparable to those recorded for the captive-reared greater amberjack in Salamina, Greece and were much lower than those measured in individuals sampled in the wild (Zupa *et al.* 2017a) (Table 3). The valuable data of Jerez *et al.*'s (2018)

experiment confirms the existence of a reproductive impairment in hatchery produced greater amberjack. The observed reproductive impairment, however, did not prevent these 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 during the annual reproductive cycle (from September to August 2011) in captive reared fish in Japan. In the same study, an enzyme-linked immunosorbent assay for FSH and LH was validated and plasma concentrations were measured. Pituitary gene expression of *fshβ* and ovary 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 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 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 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 to enter OM after the completion of vitellogenesis and finally resulted in oocyte atresia and spawning omission. In another experiment (Nyuji *et al.* 2019), the effects of the administration of gonadotropin releasing hormone agonist (GnRHa) at a dose of 600 μg kg^{-1} in cholesterol pellets were analysed on OM and GtH plasma levels in a greater amberjack broodstock of wild origin. Accordingly, the administration of GnRHa in fish whose ovaries contained oocyte at the end of vitellogenesis (oocyte diameter > 600 μm), resulted in a significant increase of plasma concentrations of LH. This plasma elevation occurred 24 h after treatment and after 30-36 h all the treated fish had oocyte > 1000 μm. All the treated fish

782 ovulated after 36-42 h, whereas only two out of five untreated control fish were able to mature oocytes and spawn spontaneously. This experiment confirmed that greater amberjack
784 females undergo reproductive dysfunction even if they are reared in large volumes (sea cages) at sea; however, the reproductive dysfunction can be overcome through the stimulation of LH
786 release from the pituitary by means of GnRHa administration.

Recently, there is an increasing number of studies on the effects of confinement in
788 captivity on greater amberjack spermatogenesis and sperm quality (Table 4). Early experiments with greater amberjack caught as young-of-the-year and confined in captivity in
790 sea cages in the southeastern Adriatic Sea, indicated that fish released sperm after application of abdominal pressure at the age of three years; however, sperm motility was highly variable
792 (Kožul *et al.* 2001). Poor sperm quality was also shown in wild-caught greater amberjack reared in tanks in two different facilities in Greece (Mylonas *et al.* 2004). Sperm motility
794 ranged between 5% and 30% and motility duration between 2.1 and 2.5 min. These findings were interpreted as an effect of a reproductive dysfunction, associated with the confinement in
796 tanks, that affected both spermatogenesis and sperm quality. The treatment of fish with GnRHa controlled-release implants resulted in an increase of sperm motility to 65% and of
798 motility duration to 2.7 min (Mylonas *et al.* 2004).

Two recent studies examined the effects of confinement on the process of greater
800 amberjack spermatogenesis (Zupa *et al.* 2017b; Zupa *et al.* 2017a), involving histological and immunohistochemical analyses of the testes, and determination of sex steroid plasma levels of
802 wild and captive-reared fish sampled in the Mediterranean during three different periods of the reproductive cycle. These studies showed that (a) captive-reared fish had lower GSI and
804 diameter of seminiferous lobules than wild fish, (b) during the phase of active spermatogenesis of the wild population (late May-early June), half of the analyzed captive-
806 reared specimens had precociously ceased their spermatogenic activity showing only residual

sperm cysts and luminal spermatozoa (Fig. 6) and (c) during the spawning phase of the wild fish, all the captive-reared specimens analyzed were in spent (regressed) conditions.

The analysis of germ cell proliferation in immunohistochemical assays, demonstrated a lower capacity of spermatogonia from captive-reared fish to enter meiosis and proceed toward spermatogenesis, which led to the observed precocious cessation of the reproductive activity (Zupa *et al.* 2017b). Moreover, captive-reared greater amberjack exhibited a much higher density of germ cell apoptosis during the early spermatogenesis phase (late April-early May) compared with wild individuals (Zupa *et al.* 2017b). The gametogenesis impairment observed in captive-reared greater amberjack males resulted from an alteration of the sex steroid profile (Zupa *et al.* 2017b; Zupa *et al.* 2017a) (Table 3). In fact, with the exception of 17,20β-P at the beginning of the reproductive cycle, captive-reared fish exhibited lower plasma concentrations of T and 11-KT and 17,20β-P than wild specimens throughout the reproductive cycle (Zupa *et al.* 2017b; Zupa *et al.* 2017a). 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 plasma concentrations (Zupa *et al.* 2017b). The observed abnormal sex steroid profile of captive-reared greater amberjack is likely due to an insufficient GtH (FSH and/or LH) release from the pituitary; unfortunately, GtH plasma levels of those dysfunctional fish are not yet available.

As a consequence of the observed spermatogenesis impairment, a low sperm quality was recorded in captive-reared greater amberjack (Zupa *et al.* 2017b) (Table 4). An abnormally high sperm density was observed, possibly due to the lack of a proper sperm hydration, which in turn might have been caused by the low sex steroid plasma

concentrations. Spermatozoa motility and path velocity were lower compared to other fish species; moreover, both these parameters, as well as sperm motility duration and ATP concentration declined during the spawning phase (Zupa *et al.* 2017b). Finally, the percentage of dead spermatozoa increased significantly during the spawning phase in captive-reared specimens, most probably because the spermatozoa remained in the lumina of the seminiferous lobules without being hydrated and, therefore, released. In another study with wild-caught breeders, no significant differences were observed in sperm quality parameters between greater amberjack reared in tanks and in sea cages in Greece, and most of the fish were in spermiating condition during the spawning season (Fakriadis *et al.* 2020b) (Table 4). Despite the low sperm quality showed by captive-reared greater amberjack compared with other cultured marine species, the large number of fertilized eggs obtained in the same study 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 causing diminished sperm production, but not 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 at Canary Islands (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). Also in this case, the increase in the sperm density during the reproductive season was ascribed to the lack of sperm hydration.

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.* 2017a; 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, included *Boops boops*, *Loligo* spp., *Sardinella aurita*, *Sardina pilchardus* and *Sepia officinalis*, 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.* 2017a; 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.* 2017a; Pousis *et al.* 2019). Sarig *et al.* (2020) confirmed that lipids and highly unsaturated fatty acids with 20 or more carbon atoms (LC-PUFAs) strongly affect greater amberjack spawning performances and suggested to keep dietary DHA and eicosapentaenoic acid 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 optimizes reproductive performance and egg production.

4.2. Other *Seriola spp*

Rearing in captivity leads to an earlier onset of puberty in yellowtail, in which the age at first maturity is 2 years in the wild, while some reared fish reach maturity even at 1 year of age (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.* 2017a; Higuchi *et al.* 2018). A reduction in food intake from an immature stage

882 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
884 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
886 delay in oocyte growth (Higuchi *et al.* 2017a). Food restriction in vitellogenic females showed no effects on plasma proteins and the pituitary gene expression of GtHs. These results
888 indicate that food restriction inhibits the gonadal development of reared yellowtail, while the degree of this inhibition depends on sex and reproductive status.

890 As with greater amberjack, inhibition of OM and ovulation/spawning is the most common type of reproductive dysfunction (Mylonas & Zohar 2007) in other *Seriola* species,
892 although some natural spawning may occur occasionally in yellowtail (Chuda *et al.* 2001b; Hamada & Mushiake 2006). In contrast, spawning in captivity occurs spontaneously in
894 yellowtail kingfish and longfin yellowtail, showing different spawning characteristics (Table 5 and 6). The rearing of wild-caught yellowtail kingfish in New Zealand demonstrated that
896 multiple spawning occurred at water temperatures above 17°C (Moran *et al.* 2007), producing 26 spawning events between November 2002 and January 2003, with a spawning interval of
898 2–4 days. The fish spawned in the early daylight hours before 0600 h at the start of the period, while they spawned around dusk between 2000 and 2200 h towards the end. Observation of
900 the spawning 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
902 kingfish was initiated with increasing day length and temperature, after a period of cooler temperatures with a shorter day length (Symonds *et al.* 2014).

904 Reared yellowtail kingfish in California spawned mainly between April to June (Stuart & Drawbridge 2013; Stuart *et al.* 2020). Monitored for 4 years, a group of 18 females and 17
906 males produced 16 spawning events in the first year and a group of 9 females and 12 males

produced 22 to 43 spawning events in the second to fourth years (Stuart & Drawbridge 2013).
908 The time of spawning ranged from 1600 to 0100 h, and it occurred earlier in the day as the spawning period progressed and total annual fecundity was lower for smaller females (Table
910 5 and 6). It was also demonstrated that egg diameter decreased and was associated with a reduction of fatty acids in the eggs as the spawning season progressed and water temperature
912 increased (Stuart *et al.* 2020). This suggests that the egg quality of yellowtail kingfish decreases in the later phase of the spawning season.

914 The natural spawning of reared longfin yellowtail has been reported in a wide range of locations (Table 5). Reared wild-caught longfin yellowtail in the Ogasawara Islands (southern
916 Japan) for 2 years spawned multiple times between April and November (Kawabe *et al.* 1997). In the first year, 10 fish (unknown sex ratio) with a body size of 68–78 cm FL and
918 weighing 5–10 kg, produced 53 spawns (29,400 $x10^3$ eggs), while in the second year 22 fish (unknown sex ratio) with a body size of 61–82 cm FL and 5–13 kg produced 113 spawns
920 (123,310 $x10^3$ eggs). Assuming that half of the total were females, the total annual fecundity was estimated to be 5,880 $x10^3$ and 11,210 $x10^3$ eggs $female^{-1}$ for each year. During the
922 spawning period, the water temperature ranged from 24 to 27°C, and the time of spawning ranged between 0500 and 0700 h.

924 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
926 Florida (Blacio 2004; Laidley *et al.* 2004; Quiñones-Arreola *et al.* 2015; Patrick *et al.* 2019; Teles *et al.* 2019). When longfin yellowtail were farmed in Hawaii, they spawned naturally all
928 year round with an average of 13 spawns per month under an ambient photoperiod and water temperature (Laidley *et al.* 2004). Meanwhile longfin yellowtail broodstock (20 kg) in
930 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} female

(Blacio 2004). This number is similar to the above maximum estimation of total annual fecundity of longfin yellowtail reared in Japan. 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).

4.3. 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 golden trevally being farmed extensively throughout Asia (Chou 1994; Liao *et al.* 2001; Feng *et al.* 2005), spontaneous spawning of this species in captivity remains unreported or are limited to grey literature such as Sim *et al.* (2007) who solely report the production of fingerlings from spontaneously spawning broodstock influenced by lunar cycles.

The single account by Moriwake *et al.* (2001) highlighted that while bluefin trevally can reach advanced stages of ovarian development during the first year when the broodstock population was established, 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, respectively. However, when the reproductive status of these same two females was re-assessed in early autumn (September), the females either regressed or did not develop further. During the same sampling point eight out of 11 males had motile sperm, thus confirming that males complete spermatogenesis in captivity and produce motile sperm, though sperm production and estimates of quality were

not reported. In the same report, in a follow up experiment commencing in early spring (March), gonadal development of broodstock was assessed every 3-5 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 when gonadal biopsies were collected. 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. 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 were obtained from striped jack 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.* (1985a) after four years of acclimation in captivity under ambient conditions. Egg collection occurred in winter (from 29 December 1984 - 1 March 1985) when water temperatures ranged between 18.5-21.5°C. Spawning occurred 1-2 h after sunset and peaked at three times during the season (in early and late January and late February) 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; Watanabe *et al.* 1998; Vassallo-Agius *et al.* 1999; Vassallo-Agius *et al.* 2001c) where spawning occurred from later winter to early spring (February to May) in Japan (Watanabe & Vassallo-Agius 2003). Prior to spawning in the latter studies, broodstock (both of cultured and wild origin; aged 8-12 years old) were generally conditioned under ambient conditions in sea pens before being transferred to

captivity and maintained in tanks (65 m^3) supplied with flow-through sea water. A study by Vassallo-Agius *et al.* (2001c) proposed a single-step temperature increase from an ambient 17°C to 22°C over a five day period, with 22°C considered to be the optimal spawning temperature (Mushiake 1994).

Studies in Japan during the late 1990's also tested the effects of different diets on the reproductive output of striped jack broodstock. 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). Similarly, 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 to56 $x10^3$ 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 (egg buoyance, fertilization and hatching) 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). While egg hatching occurs within the temperature ranges of 18-26°C, optimum temperature and salinity for hatching is 20°C and between 35-41‰, respectively (Kawabe *et al.* 1991; Murai *et al.* 1992).

In Europe, Nogueira *et al.* (2018) reported quality parameters of eggs from spontaneous spawning wild-caught striped jack after four years of being maintained in captivity under ambient conditions in Portugal. Specifically, broodstocks were maintained under natural

photo-thermal (18-24°C; Madeira, Portugal) conditions at a density of 5 kg m^{-3} in 10-m^3 tanks. The spawning period lasted for two months (May - June) and commenced when the spawning temperature reached 19°C (temperature range 19.5 – 21.9°C) and day length was 16 h of daylight. A total of 20 spawns were detected equating to an estimated 10.8 million eggs for the season – with the number of eggs in each spawn ranging between 15,600 and 1,430,400. The average number of eggs spawned per female was estimated to be 280 $x10^3$. Of the estimated 10.8 million eggs spawned, approximately 57% were buoyant 'viable' and fertilization success of these eggs was consistently greater than 95%. The mean diameter of spawned eggs was 969 ± 27 μm. Both eggs size and hatching decreased towards the end of the spawning season and were negatively correlated with water temperature.

The studies outlined above suggest that while these trevally species are capable of completing vitellogenesis, OM and spawning in captivity – broodstocks of wild-captured origin can take 1-4 years of acclimation before successfully spawning spontaneously. Spawning of striped jack appears to be seasonal and dependent on water temperatures between 19-24°C, while bluefin trevally appears to have multiple spawning seasons within a single year (both in summer and winter). Spermatogenesis and factors affecting sperm quality have yet to be reported in these species as well as information of parental contributions during group-spawning events and the effects of broodstock stocking densities, sex ratios and social interactions, such as dominance hierarchy on spawning.

5. Hormonal manipulations of reproductive function and induced spawning

5.1 Greater amberjack

As reported in 4.1 above, the greater amberjack has a limited capacity to overcome the reproductive dysfunction when wild-caught individuals are reared in captivity, even if the fish

were taken from the wild as young-of-the-year and were reared in aquaculture facilities 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 of greater amberjack has been one of the major bottlenecks preventing its large-scale aquaculture production. Although not experimentally demonstrated in this species, combining the available endocrine research from other fishes and from different studies in 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; Mylonas *et al.* 1998; Mylonas *et al.* 2010). This in turn is caused by a dysfunctional release of GnRH from the hypothalamus (Zohar *et al.* 2010; Zohar 2020). This has been shown in a number of aquaculture fishes and the 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.* 2015b; Nyuji *et al.* 2016; Zupa *et al.* 2017a; Jerez *et al.* 2018; Pousis *et al.* 2018; Sarih *et al.* 2018; Fakriadis *et al.* 2019; Fakriadis *et al.* 2020a; Fakriadis *et al.* 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.* 2015b; Nyuji *et al.* 2016; Jerez *et al.* 2018; Sarih *et al.* 2018; Fakriadis *et al.* 2019; Fakriadis *et al.* 2020a; Fakriadis *et al.* 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 loaded in

controlled-release implants, when fully vitellogenic oocytes (oocyte diameter 650 μm) existed in their ovaries. Two treatments, carried out in June, were effective in inducing 4 spawns (Table 5) producing a total of 50,000 eggs kg^{-1} (Table 6), and in increasing sperm motility and motility duration (Table 4). Later, GnRHa was administered through 15 injections to a wild-caught broodstock (21 fish) reared in Gran Canaria (Spain) in 10 m^3 tanks supplied with surface sea water (Fernández-Palacios *et al.* 2015b). The treatments, at the dose of about 20 μg kg^{-1} fish BW, were applied every 10 days from June to October, at a temperature ranging between 21 and 24°C and resulted in 22 spawns. Spawnings occurred between 33 and 45 h after treatments and the number of spawns per treatment changed during the reproductive season, showing an increase from June (1.3 ± 0.6) to August (2.3 ± 0.6) and decreased to 0.3 ± 0.6 in October, 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 particular, the percentage of fertilized eggs (82-98%) was highest in July and October, the percentage of viable eggs (20-73%) was highest in August, the hatching rate (33-100%) was highest in October, and percentage of larvae that survived 3 days post hatching (dph) (27-90%) was maximum in July.

In another study in the same region, (Sarih *et al.* 2018) reported a comparative study on egg production in greater amberjack after GnRHa administration through injections or implants (Table 5). For this study, 19 fish were caught from the wild as juveniles and were reared at the ECOAQUA Institute (Canary Islands, Spain), until their body weight was 9.5-12 kg. Before starting the experiment, the fish were moved to 40 m^3 tanks under natural photothermal conditions and in late May all males released sperm upon application of abdominal pressure and six females had oocytes > 650 μm and were considered potentially responsive to GnRHa treatments. The fish were then divided in two groups and were given GnRHa injections or GnRHa implants. The injection group was treated from June 3 to

October 31 according to a rotation protocol with 20 μg kg^{-1} every 12 days; the 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} for females and males, respectively. Spawning of treated fish started 43-44 h after each treatment and the number of spawns per treatment was significantly higher for the implanted fish than for the injected ones (2.2 ± 1.9 vs 0.8 ± 0.5). The mean number of eggs produced per spawn was similar between the GnRHa-injected and implanted fish (Table 6), but egg quality was significantly higher in injected than in implanted 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 (Salamina Island, Greece). Females with oocyte > 600 μm and spermiating males were administered either two GnRHa implants (one every two weeks) containing an effective dose of 49-69 and 45-70 μg kg^{-1} for females and males, respectively, or three GnRHa injections (one injection every week) at the dose of 20 μg kg^{-1}. 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, with temperatures ranging between 20 and 24°C. Implanted fish spawned 10 times after the first treatment and four times after the second treatment; injected fish spawned 7 times after the first injection, 3-5 times after the second injection and 1-3 times after the third injection (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 to the respective injection. Egg quality data were good and not significantly different between the two treatments (fertilization rate between 30 and 40%; embryos survival at 24 h between 20 and 80%; hatching rate between 40 and 80%; larval survival at 5 dph between 5 and 30%).

The contradictory results obtained by (Sarih *et al.* 2018) and (Fakriadis *et al.* 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 slow and protracted pituitary stimulation of GtH release is the treatment of choice in this species, because it better fits 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, as well as promoting 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, than Mediterranean ones (Fakriadis *et al.* 2020b).

Based on these difficulties faced with 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). Although rearing in tanks represents the best option for aquaculture broodstock management due to biosecurity reasons, lower environmental impact, ease of handling and egg collection, 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 throughout their life, 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 Greek 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 to 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 spawning was further developed 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). 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} 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} in 11-18 spawns. The eggs quality parameters also did not differ significantly between the two treatments, and based on the previous study that used 50 μg kg^{-1} (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 2-year study at Galaxidi (Greece), between May 30 and July 18 at sea surface temperatures ranging between 20 and 26°C. Selected fish were administered GnRHa implants at a dose of 50 μg kg^{-1} BW at four different times during the studied period with 1-2 weeks 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 years 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 levels in captivity are lower than those observed in wild fish (Zupa *et al.* 2017a; Jerez *et al.* 2018), suggesting that greater amberjack reproduction control and egg production in aquaculture can be further improved.

Finally, F_1 hatchery produced greater amberjack breeders became available in the last decade, and treatments with GnRHa implants were also successful in inducing OM and spawning in (Jerez *et al.* 2018). Fourteen fish (7 females and 7 males; age 6-10 years) were reared at ambient conditions in 50 m^3 outdoor tanks supplied with seawater from a well at the facility of the Centro Oceanográfico de Canarias (Tenerife, Spain). Fish were fed raw fish and, after the first treatment, they were moved to 500 m^3 outdoor raceways. Only females with fully vitellogenic oocytes (oocyte diameter > 650 μm) and spermiating males were considered potentially responsive and were administrated a GnRHa implant at the dose of about 50 mg kg^{-1} in May, June and July. Spawnings begun one-two days after each treatment, at temperature ranging between 20 and 25°C, and a total of 52 spawns occurred over a period

of 72 days: 29 spawns followed the first treatment, 15 were recorded after the second treatment and 8 after the third implantation. The relative fecundity was highest after the first treatment (60 x 10^3 eggs kg^{-1}) and lowest after the third treatment (15 x 10^3 eggs kg^{-1}). Fertilization and hatching were similar after the first two treatments (about 50 and 20%, respectively) and decreased significantly after the third treatment. A similar trend was shown by larval survival 3 days post hatching. This experiment provided also interesting data on hormone concentrations 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 Salamina and much lower than those determined in individuals caught from the wild and sampled soon after capture (Zupa *et al.* 2017a) (Table 3). The observed reproductive impairment, however, did not prevent the production of high amount of eggs, whose quality was adequate for the implementation of larval rearing for commercial purposes, through the administration of GnRHa to individuals that completed vitellogenesis.

5.2. 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 and using a dose of 500–700 IU kg^{-1} (Mushiake *et al.* 1993; Matsuyama *et al.* 1996). After hCG injection, the level of circulating 17,20β-P was elevated after 6 h, but decreased rapidly at 12 h after injection; 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 is 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). Chuta *et al.* (2002) showed that by a single injection of hCG, the number of eggs ovulated was 468 x10^3 eggs female^{-1} at the age of 3 when weighing 8–11 kg, while it was 212 x10^3 eggs female^{-1} at the age of 2 when weighing 6–7 kg. 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 demonstrated 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}) prior to the main injection of hCG (500 IU kg^{-1}) 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}) 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 (600 IU kg^{-1}) 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} female. 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 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}) combined with salmon pituitary extract (0.7 mg kg^{-1}) achieved 16 spawning days at an interval of 1–3 days, between April and May, at a constant water temperature of 21°C. The fertilization success fluctuated (20%–100%) 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

1280 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
1282 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. In contrast,
1284 GnRHa implantation increased the proportion of females contributing to spawning and advanced vitellogenesis in females that had not completed vitellogenesis. However, GnRHa
1286 implantation resulted in reductions in egg buoyancy, fertilization, and viability.

Repeated injection of GnRHa (20 μg kg^{-1}) at an interval of 10–14 days has been shown
1288 to induce multiple spawning for longfin yellowtail reared on the Canary Islands, at a water temperature of 22–24°C (Roo *et al.* 2014; Fernández-Palacios *et al.* 2015b; Roo *et al.* 2015)
1290 (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
1292 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} female (Roo *et al.* 2015). Another group of fish treated
1294 with 15 repeated injections of GnRHa achieved 33 spawning events, with the total number of eggs of 944 $x10^3$ eggs kg^{-1} female (Fernández-Palacios *et al.* 2015b). Combining this result
1296 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
1298 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
1300 (Fernández-Palacios *et al.* 2015b). Unlike the hormonally induced multiple spawning in yellowtail, there were no changes in the fertilization (97–99%), hatching (80–86), and larval
1302 survival (63–78%) among the initial, middle, and final phases of multiple spawning events of longfin yellowtail (Roo *et al.* 2015).

1304

5.3. Other Carangids

A range of hormonal preparations have been used to induce spawning of trevally from the genera *Caranx*, *Gnathanodon* and *Pseudocaranx* either 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 5-7 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}. Fish were left to spawn in 40 m^3 tanks at temperatures and salinities of 27.6-29.25°C and 28-30 parts per thousand (ppt), respectively. Spawned eggs were only observed in hormone-treated fish with ovulation latency times ranging between 24-36 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 to 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 compared to 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, for the production for fertilized eggs to study the digestive ontology of bluefin trevally larvae, fertilized eggs were obtained in summer (May) after hormonal implantation (GnRHa, 70 mg kg^{-1}), 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 (2 females and 6 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}. 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 (2-4 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}.

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}) and CPE (4 mg kg^{-1}). 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 (600 IU kg^{-1}) in addition to a single-step temperature increase to 22°C has been applied on multiple occasions (Mushiake 1994; Vassallo-Agius *et al.* 2001b, a). 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 - 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 300-500 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. Similar 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.

8. Concluding remarks

Reproductive maturation varies among members of the Carangidae family, and ranges between 2 and 4 years of age, with the larger bodied species maturing at a later age. As it 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 and lobular type, being characterized by the presence of spermatogonia and spermatocysts all along the seminiferous lobules. The maturing spermatocysts move towards the center of the lobule, 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, but 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 lobules 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 to 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. Especially for yellowtail kingfish, spawning in captivity takes place spontaneously and, as a result, the species 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 1-3 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 2-3 weeks. Repeated, weekly GnRHa injections or GnRHa implant administrations every 2-4 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 (Jun to October).

In the examined studies, there was no one 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, were comparable to 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 compared to 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.

9. 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.

Agulleiro, MJ, André, M, Morais, S, Cerdà, J & Babin, PJ (2007) High transcript level of fatty acid-binding protein 11 but not of very low-density lipoprotein receptor is correlated to ovarian follicle atresia in a teleost fish (*Solea senegalensis*). *Biology of Reproduction*, **77**, 504-516.

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.

Billard, R (1986) Spermatogenesis and spermatology of some teleost fish species. *Reproduction Nutrition Development*, **26**, 877-920.

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.

Brown-Peterson, NJ, Wyanski, DM, Saborido-Rey, F, Macewicz, BJ & Lowerre-Barbieri, SK (2011) A standardized terminology for describing reproductive development in fishes. *Marine and Coastal Fisheries*, **3**, 52-70.

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 (Japan)*, **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.

da Silva, IM, Hempson, T & Hussey, NE (2014) Giant trevally spawning aggregation highlights importance of community fisheries management no-take zone. *Marine Biodiversity*, **45**, 139-140.

Dale, JJ, Meyer, CG & Clark, CE (2011) The ecology of coral reef top predators in the 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 aggregation of giant trevally *Caranx ignobilis* (Carangidae) on record: implications for management. *African Journal of Marine Science*, **40**, 315-321.

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 thynnus* L.) and the first larval rearing efforts. *Journal of Applied Ichthyology*, **26**, 596-599.

Devlin, RH & Nagahama, Y (2002) Sex determination and sex differentiation in fish: an overview of genetic, physiological, and environmental influences. *Aquaculture*, **208**, 191-364.

Divakaran, S, Kim, BG & Ostrowski, AC (1999) Digestive enzymes present in Pacific threadfin *Polydactylus sexfilis* (Bloch & Schneider 1801) and bluefin trevally *Caranx melampygus* (Cuvier 1833). *Aquaculture Research*, **30**, 781-787.

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.

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. *General and Comparative Endocrinology*, **279**, 78-87.

Fakriadis, I, Miccoli, A, Karapanagiotis, S, Tsele, N & Mylonas, CC (2020a) Optimization of a GnRHa treatment for spawning commercially reared greater amberjack *Seriola dumerili*: Dose response and extent of the reproductive season. *Aquaculture*, **521**, 735011.

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. *Aquaculture*, **519**, 734880.

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 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 marine food fish species, golden trevally *Gnathanodon specious*. *Molecular Ecology Notes*, **5**, 760-761.

Fernández-Palacios, H, Schuchardt, D, Roo, J, Hernández-Cruz, CM & Izquierdo, M (2015a) Multiple GnRHa injections to induce successful spawning of wild caught greater amberjack (*Seriola dumerili*) matured in captivity. *Aquaculture Research*, **46**, 1748-1759.

Fernández-Palacios, H, Schuchardt, D, Roo, J, Hernández-Cruz, C & Izquierdo, M (2015b) Spawn quality and GnRHa induction efficiency in longfin yellowtail (*Seriola rivoliana*) broodstock kept in captivity. *Aquaculture*, **435**, 167-172.

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.

García, A & Díaz, MV (1995) Culture of *Seriola dumerili*. *Cahiers Options Méditerranéennes*, **16**, 103-114.

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 Zealand Journal of Marine and Freshwater Research*, **33**, 457-468.

Grandcourt, EM, Al Abdessalaam, TZ, Francis, F & Al Shamsi, A (2004) Population biology and assessment of representatives of the family Carangidae: *Carangoides bajad* and *Gnathanodon speciosus* (Forsskål, 1775), in the Southern Arabian Gulf. *Fisheries Research*, **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, Yoshida, K, Gen, K, Nyuji, M, Takashi, T, Mushiake, K, *et al.* (2017a) 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.

Higuchi, K, Gen, K, Izumida, D, Kazeto, Y, Hotta, T, Takashi, T, *et al.* (2017b) 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.

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 (Japan)*, **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 (Japan)*, **39**, 211-216.

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 (Japan)*, **46**, 31-36.

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 (Japan)*, **45**, 201-206.

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 (Japan)*, **44**, 151-157.

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.

Lubzens, E, Bobe, J, Young, G & Sullivan, CV (2017) Maternal investment in fish oocytes and eggs: The molecular cargo and its contributions to fertility and early development. *Aquaculture*, **472**, 107-143.

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

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

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

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.

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

Murai, M, Aoki, Y, Nishimura, K & Takashima, F (1985a) 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, Aoki, Y, Nishimura, K & Takashima, F (1985b) 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, Kato, K, Nakano, T & Takashima, F (1987) Egg development and morphological changes of larvae of striped jack *Caranx delicatissimus*. *Suisanzoshoku (Japan),* **34**, 217-226.

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

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, 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.

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 & Zohar, Y (2007) Promoting oocyte maturation, ovulation and spawning in farmed fish. In: *The Fish Oocyte: from Basic Studies to Biotechnological Applications* (ed. by Babin PJ, Cerdà J, Lubzens E). Springer, Dordrecht, The Netherlands, pp. 437-474.

1742 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
1744 maturation. *General and Comparative Endocrinology,* **108**, 223-236.
Mylonas, CC, Fostier, A & Zanuy, S (2010) Broodstock management and hormonal manipulations of
1746 fish reproduction. *General and Comparative Endocrinology,* **165**, 516-534.
Mylonas, CC, Woods, LC, III, Thomas, P & Zohar, Y (1998) Endocrine profiles of female striped bass
1748 (*Morone saxatilis*) in captivity, during post-vitellogenesis and induction of final oocyte maturation via controlled-release GnRHa-delivery systems. *General and Comparative*
1750 *Endocrinology,* **110**, 276-289.
Mylonas, CC, Papandroulakis, N, Smboukis, A, Papadaki, M & Divanach, P (2004) Induction of
1752 spawning of cultured greater amberjack (*Seriola dumerili*) using GnRHa implants. *Aquaculture,* **237**, 141-154.
1754 Mylonas, CC, Bridges, C, Gordin, H, Rios, AB, Garcia, A, de la Gandara, F, *et al.* (2007) Preparation and administration of gonadotropin-releasing hormone agonist (GnRHa) implants for the
1756 artificial control of reproductive maturation in captive-reared Atlantic bluefin tuna (*Thunnus thynnus thynnus*). *Reviews in Fisheries Science,* **15**, 183-210.
1758 Nakada, M (2002) Yellowtail culture development and solutions for the future. *Reviews in Fisheries Science,* **10**, 559-575.
1760 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*
1762 *lalandi*; Perciformes) during the breeding and non-breeding season. *General and Comparative Endocrinology,* **191**, 168-176.
1764 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.
1766 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,*
1768 **95**, 1350-1354.
Nyuji, M, Kazeto, Y, Izumida, D, Tani, K, Suzuki, H, Hamada, K, *et al.* (2016) Greater amberjack
1770 Fsh, Lh, and their receptors: Plasma and mRNA profiles during ovarian development. *General and Comparative Endocrinology,* **225**, 224-234.
1772 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*
1774 *quinqueradiata*. *Fisheries Science,* **68**, 686-689.
Ottolenghi, F, Silvestri, C, Giordano, P, Lovatelli, A & New, MB (2004) *Capture-based Aquaculture.*
1776 *The fattening of eels, groupers, tunas and yellowtails,* Food and Agriculture Organization of the United Nations, Rome, 308 p.
1778 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
1780 yellowtail *Seriola quinqueradiata*. *Bulletin of the Nansei Regional Fisheries Research Laboratory (Japan),* **22**, 1-11.
1782 Parenti, LR & Grier, HJ (2004) Evolution and phylogeny of gonad morphology in bony fishes. *Integrative and Comparative Biology,* **44**, 333-348.
1784 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
1786 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.
1788 *Fish Physiology and Biochemistry,* **26**, 57-70.
Patrick, G, Tarnecki, AM, Rhody, N, Schloesser, R, Main, K, Yanong, R, *et al.* (2019) Disinfection of
1790 almaco jack (*Seriola rivoliana* Valenciennes) eggs: Evaluation of three chemicals. *Aquaculture Research,* **50**, 3793-3801.
1792 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*
1794 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, 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, 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, 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.

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.

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

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.

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.

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

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 (Japan),* **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.

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

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.

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 (Japan),* **50**, 503-506.

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

1958 Zohar, Y & Mylonas, CC (2001) Endocrine manipulations of spawning in cultured fish: from hormones to genes. *Aquaculture*, **197**, 99-136.
1960 Zohar, Y, Muñoz-Cueto, JA, Elizur, A & Kah, O (2010) Neuroendocrinology of reproduction in teleost fish. *General and Comparative Endocrinology*, **165**, 438-455.
1962 Zohar, Y, Mylonas, CC, Rosenfeld, H, de la Gándara, F & Corriero, A (2016) Reproduction, broodstock management, and spawning in captive Atlantic bluefin tuna. In: *Advances in Tuna*
1964 *Aquaculture*. Academic Press, Oxford, UK, pp. 159-188.
Zupa, R, Rodríguez, C, Mylonas, CC, Rosenfeld, H, Fakriadis, I, Papadaki, M, *et al.* (2017a)
1966 Comparative study of reproductive development in wild and captive-reared greater amberjack *Seriola dumerili* (Risso, 1810). *PLoS One*, **12**, e0169645.
1968 Zupa, R, Fauvel, C, Mylonas, CC, Pousis, C, Santamaria, N, Papadaki, M, *et al.* (2017b) Rearing in captivity affects spermatogenesis and sperm quality in greater amberjack *Seriola dumerili*
1970 (Risso, 1810). *Journal of Animal Science*, **95**, 4085-4100.

1972

Figure legends

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)

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).

Figure 3. (a) Testes from a wild adult greater amberjack sampled during the reproductive period. (b) Micrograph of a testis section showing seminiferous lobules converging from the testis periphery to the sperm duct system in the centre. 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). Asterisk: sperm duct system. Arrows: large single type A spermatogonium; arrowheads: small single type A spermatogonium; asterisks: type A spermatogonial cyst; double asterisks: 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.* (2017b).

Figure 4. 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 5. 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 6. 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.* (2017a).

Figure 7. 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 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 being selected and induced to spawn using GnRHa implants (D).