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Infectious diseases and treatment solutions of farmed greater amberjack *Seriola dumerili* with particular emphasis in Mediterranean region

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Abstract

Greater amberjack (*Seriola dumerili*) is a very promising candidate for the diversification of the Mediterranean aquaculture due to its high demand, excellent flesh quality and high market prices. Its production expansion has, however, failed so far, due to several bottlenecks mainly related to pathology. This review addresses the major pathogens, which hinder the culture of greater amberjack with special focus in the Mediterranean region, and highlights possible treatment solutions. Among the important recorded pathogens of caged greater amberjack in the Mediterranean, the gill monogenean *Zeuxapta seriolae* seems to be the most problematic, causing significant losses. While formalin immersions are inefficient to combat this parasite, baths with hydrogen peroxide are extremely effective and praziquantel administration could be a more practical in-feed treatment solution. The digenean blood flukes, *Paradeontacylix* spp., also account for important losses in greater amberjack farms in the same region. Dietary administration of praziquantel constitutes an effective therapeutic measure against those infections. *Vibrio harveyi* is also a bacterial pathogen severely affecting fish maintained both in land-based facilities and in cages, whereas Epitheliocystis is a disease reported frequently that can be fatal when it occurs at early stages. Skin flukes such as *Benedenia seriolae* and *Neobenedenia girellae* as well as other parasites bacteria and viruses mentioned herein, which have caused substantial losses in Asian enterprises, but have not been identified yet in greater amberjack farmed in the Mediterranean, should be considered as potential threats.

Key words: diseases, greater amberjack, pathogens, Seriola dumerili, treatment.

Introduction

Greater amberjack (*Seriola dumerili*) (Risso, 1810) is an important fish for farming and game fishing with a cosmopolitan distribution in the subtropical and tropical seas, where is highly appreciated due to its high meat quality and commercial value (Andaloro & Pipitone 1997). Greater amberjack is a very promising candidate for aquaculture diversification and development of value-added products since its tremendous growth in captivity is associated with efficient feed utilization (Mazzola *et al.*, 2000), high demand, excellent flesh quality and high market prices (Nijssen *et al.*, 2019). Remarkably, the big market size of greater amberjack (3–5 kg) is achieved as early as 2–3 years (FAO 2018).

Global production leader of greater amberjack is Japan (38 770 tons in 2013) where its farming was initiated in the 70s, while it was later developed in European countries such as Spain, Italy, Malta, Croatia (Sicuro & Luzzana, 2016) and Greece. In recent years, greater amberjack has gained additional interest in the Mediterranean area and is now considered as one of the most important species for the diversification of conventional marine farmed finfish production, which is currently suffering from product limitation and market stagnation. However, recent and clear production volumes of greater amberjack on a country level are not available.

Since the greater amberjack farming in Japan has been based largely on wild and/or imported juveniles from China, most of the scientific effort regarding reproduction, larval rearing and grow-out has been generated from Mediterranean countries (Sicuro & Luzzana, 2016), although the same bottlenecks were initially faced in the region (Kožul *et al.*, 2001). Progress made in hormonally induced spawning with the use of GnRHa-delivery systems (Mylonas *et al.*, 2004) has led to advances in juvenile production (Mazzola *et al.*, 2000). Controlled reproduction, along with breeding selection, made it possible to expand the commercial production of greater amberjack (Jerez *et al.*, 2018). However, disease outbreaks induced by parasites, bacteria and viruses (Table 1) have become a significant limiting factor for the further expansion of greater amberjack farming, both in the Mediterranean region and elsewhere (Crespo *et al.*, 1990; Grau & Crespo, 1991; Alcaide *et al.*, 2000; Montero *et al.*, 2004; Mansell *et al.*, 2005; Ohno *et al.*, 2008; Rigos & Katharios, 2010; Miwa *et al.*, 2011; Lu *et al.*, 2012; Minami *et al.*, 2016).

The aim of this review was therefore (i) to describe the major pathogens, which limit the production of greater amberjack in Mediterranean aquaculture and elsewhere (Table 1) and (ii) to highlight possible treatment solutions, by reviewing the existing literature and presenting primary unpublished data generated by our team (Table 2).

Parasites

Copepods

Caligus spp.

Caligus spp. (Copepoda, Caligidae) are universal parasitic copepods, well known as sea lice, that consist of more than 450 species (Morales-Serna *et al.*, 2016). Parasitic copepods feed on host mucous, tissues and blood, while their attachment and feeding activities are responsible for the induced pathology (Johnson *et al.*, 2004). In marine cultured fish, more than 50% of copepod infestations are due to caligids and their impacts range from skin damage to some induced fish mortality (Costello, 2006), while few have been actually devastating to cultured fish (Johnson *et al.*, 2004). *Caligus* copepods identified in farmed *Seriola* spp. included *C. spinosus* (Yamaguti, 1939), recovered from the gills of yellowtail amberjack (*S. lalandi*) (Valenciennes, 1833) and *C. lalandei* (Barnard, 1948), seen in the body surface of Japanese amberjack (*S. quinqueradiata*) (Valenciennes, 1833) (Nagasawa *et al.*, 2011). Their parasitic effects on these hosts were not described. Due to the fact that wild-caught juveniles are often used as aquaculture seeds in Japan, caligid species are considered to be introduced into farming sites with the captured seeds (Ho *et al.*, 2009; Nagasawa *et al.*, 2011). No records have been found yet which could link the presence of copepods in farmed greater amberjack in Mediterranean or elsewhere, but caligids should be considered as potential pathogens for this fish species.

Nematodes

Anisakis spp.

Anisakis spp. (Chromadoria, Anisakidae) are marine zoonotic nematodes with most commercial fish species served as intermediate hosts. Public health risks are attributed to the third-stage larvae of these zoonotic parasites. Fishborne larval nematodes belonging to the family Anisakidae are widespread in wild fish populations worldwide; however, the occurrence of anisakids in farmed fish species is virtually negligible (Fioravanti *et al.*, 2020). Anisakids as fish pathogens are normally associated with little significance, although some reports have shown that can cause inflammation of the lower gut of the fish host (Beck *et al.*, 2008). A preliminary study in greater amberjack revealed that wild-caught imported juveniles that subsequently used as farmed seeds in Japan were heavily infected with anisakid larvae identified as *A. pegreffii* (Yoshinaga *et al.*, 2006). The induced pathology on the host was heavy, including a deformed and shortened stomach accompanied with an obstruction of the fish gastric cavity. As regularly found in wild fish, anisakids have been identified from captured *Seriola* spp. in eastern Atlantic (Cavaleiro *et al.*, 2018). Given that anisakids have been associated with diseased *Seriola* spp. cultured in Asia and diagnosed from wild specimens near to Mediterranean, they should not be neglected from the routine parasitic examination of farmed greater amberjack.

Cestodes

Fishborne zoonotic tapeworms are an emerging problem mainly in relation to consumer welfare. In addition to wild-caught fish, fish produced in aquaculture may present a food safety risk (Clausen *et al.*, 2015). Parasitic cestodes have evolved very complex life cycles, involving an aquatic larval stage followed by one or more larval stages spent in intermediate hosts (Tamaru *et al.*, 2016). The order Trypanorhyncha is a highly diversified parasitic group of cestodes infecting mainly elasmobranches where fish may serve as intermediate hosts (Ogawa *et al.*, 2012). Fish are becoming infected by feeding on copepods or smaller fish, which harboured the cestode larvae. Trypanorhyncha are known to infest the musculature of the teleost fish, and thus, consumer welfare concerns are raised because tapeworms have zoonotic potential if fish or fish products are consumed raw or improperly cooked. The first Trypanorhyncha infection in farmed greater amberjack was described by Ogawa *et al.* (2012) in Japan where the invading larvae were detected in skeletal musculature during filleting with a low prevalence of infection. The possible cestode larvae effects on the host were though not determined. Application of dietary administered praziquantel

Table 1 Pathogens causing disease in farmed greater amberjack

Pathogen	Severity	Fish size	Environment	Season	References
Parasites					
Copepods					
C. spinosus			Cages	Spring, summer	Other *Seriola* spp. Nagasawa *et al.* (2011)
C. lalandei					
Nematodes					
A. pegreffii	High	0^+		Winter, spring	Yoshinaga *et al.* (2006)
Cestodes					
Trypanorhyncha order					Ogawa *et al.,* (2012) and Tamaru *et al.* (2016)
Digenea					
P. grandispinus/ *P. kampachi*	High	0^+	Cages	Summer, fall, winter	Ogawa and Egusa (1986), Ogawa and Fukudome (1994) and Shirakashi and Ogawa (2016)
P. ibericus/ *P. balearicus*	High	0^+, 1^+	Cages	Summer, fall	Crespo *et al.* (1992), Crespo *et al.* (1994), Montero *et al.* (1999), Montero *et al.* (2003a), Repullés-Albelda *et al.* (2008) and Montero *et al.* (2009)
Monogeneans					
Z. seriolae	Severe	0^+ - 3^+	Cages	Spring, summer, fall	Grau *et al.* (2003), Montero *et al.* (2004), Ogawa (2010) and Lu *et al.* (2012)
A. mcintoshi		0^+	Tanks		Montero *et al.* (2003b)
H. heterocerca			Cages		Ogawa and Yokoyama (1998)
B. seriolae			Cages		Whittington *et al.* (2001) and Kinami *et al.* (2005)
N. girellae	Low	0^+	Tanks (challenge)	Fall, winter	Ohno *et al.* (2008), Hirayama *et al.* (2009) and Hirazawa *et al.* (2016a)
Flagellates					
A. ocellatum	High Severe	0^+ Broodstock	Tanks	Fall	Aiello and D'Alba (1986)
Ciliates					
C. irritants	Severe	Broodstock	Tanks	Fall	Rigos *et al.* (2001)
Myxozoans					
K. amamiensis					Sugiyama *et al.* (1999)
U. seriolae					Ohnishi *et al.* (2018)
Microsporidia					
Spraguea sp.	Medium	0^+	Cages	Spring	Miwa *et al.* (2011)
M. seriolae	Medium, severe	1^+	Cages	Summer	Yokoyama *et al.* (2011)
Bacteria					
V. harveyi	Severe	0^+, 1^+	Tanks and cages	Summer, fall	Minami *et al.* (2016) and Kato *et al.* (2019)
P. damselae subsp. *piscicida*					Kawahara *et al.* (1986)
L. garvieae	High	0^+	Cages		Kusuda *et al.* (1991) and Nakajima *et al.* (2014)
S. dysgalactiae	High	1^+, 2^+	Cages	Summer	Nomoto *et al.* (2004), Nomoto *et al.* (2006) and Hagiwara *et al.* (2011)
Mycobacterium marinum	Severe	Adults	Cages	Chronic	Kato *et al.* (2011)
Nocardia seriolae	Severe	All ages	Cages	Chronic	Shimahara *et al.* (2008)
Intracellular bacteria	Extreme	Larvae, 0^+	Tanks	Winter, spring	Crespo *et al.* (1990), Grau and Crespo (1991) and Kobayashi *et al.* (2004)
Viruses					
Red seabream iridovirus	Severe	Juveniles	Cages	Summer	Matsuoka *et al.* (1996)
Yellowtail ascites virus	Medium	Fingerlings	Hatchery		Kusuda *et al.* (1993)

Table 2 Therapeutic regimens against important pathogens of farmed greater amberjack

Pathogen	Compound	Administration	Dosing schedule	Efficacy	References
Parasites					
P. grandispinus *P. kampachi*	Praziquantel	Oral			Shirakashi and Ogawa (2016) and Bader *et al.* (2019)
Z. seriolae	Hydrogen peroxide	Bath	75-100 ppm, 1 h	Extremely high	Hirazawa *et al.* (2016b)
	Praziquantel	Oral	50-75 mg kg^{-1} fish, 6 days	High	Williams *et al.* (2007)
		Bath	2.5 ppm, 24-48 h	High	Sharp *et al.* (2004)
	Formalin plus freshwater	Bath	250-400 ppm, 1-h + 5-min freshwater dip	Moderate–high	Sharp *et al.* (2004)
B. seriolae	Hydrogen peroxide	Bath	75 ppm, 0.5h	High	Hirazawa *et al.* (2016b)
	Praziquantel	Oral	50-75 mg kg^{-1} fish, 6 days	High	Williams *et al.* (2007)
		Bath	2.5 ppm, 24-48 h	High	Sharp *et al.* (2004)
	Formalin plus freshwater	Bath	250–400 ppm, 1-h + 5-min freshwater	Moderate	Sharp *et al.* (2004)
N. girellae	Hydrogen peroxide	Bath	75 ppm, 0.5 h	High	Hirazawa *et al.* (2016b)
	Praziquantel	Oral	40 mg kg^{-1} fish, 11 days	High	Hirazawa *et al.* (2004)
	Freshwater	Bath	2 min	Low	Seng (1997)
A. ocellatum	Copper sulphate	Bath	0.75 ppm, 6 days	High	Aiello and D'Alba (1986)
C. irritants	Formalin	Bath	100 ppm, 1 h	Low	Rigos *et al.* (2001)
	Hyposalinity	Bath	8–10‰, 3 h	High (but not tolerated by fish)	
M. seriolae	Juvenile production using filtered seawater				Ogawa and Yokoyama (1998)
Bacteria					
V. harveyi	Autovaccine	Bath	Formalin killed cells	High	Minami *et al.* (2016), Empirical
	Doxycycline	Oral	100 mg kg^{-1} fish, 5-7 days	Medium/high	Empirical
L. garvieae	Commercial vaccine	Injection		High	Nakajima *et al.* (2014)
	Antibacterials	*In vitro*		Partially high	Furushita *et al.* (2015)
S. dysgalactiae	Antibacterials	*In vitro*		High	Abdelsalam *et al.* (2010)
N. seriolae	Coadministration of N-acetyl-d-glucosamine(NAG) with oxytetracycline	Oral	50 mg kg^{-1}, 5 days (both)	High	Akiyama *et al.* (2018)

(PZQ) has been widely used against fish tapeworms (Bader *et al.*, 2019). Use of artificial diets (extruded or pelleted) and eliminating exposure to the intermediate cestode hosts would easily prevent tapeworm infection in farmed fish. Temporary fish starving, which could force farmed stock to feed on aquatic prey, should be also avoided.

Digenea (Blood flukes)

Paradeontacylix spp.

Paradeontacylix spp. (Digenea, Aporocotylidae) are blood flukes, which have been accused for important pathologies in cultured fish (Bullard & Overstreet, 2002) and considered as serious parasites in marine aquaculture (Shirakashi & Ogawa, 2016). These digeneans have been associated with mortalities in farmed greater amberjack in the Mediterranean region (Crespo *et al.*, 1992; Crespo *et al.*, 1994; Montero *et al.*, 1999; Montero *et al.*, 2009) and Japan (Ogawa & Egusa, 1986; Ogawa *et al.*, 1993; Ogawa & Fukudome, 1994). Particularly, *P. grandispinus* and *P. kampachi* (Ogawa & Egusa 1986) have been described in farmed greater amberjack from Japan (Ogawa & Egusa, 1986), while *P. ibericus* and *P. balearicus* (Repullés-Albelda *et al.*, 2008) in their Mediterranean counterparts (Crespo *et al.*, 1992; Crespo *et al.*, 1994; Montero *et al.*, 1999) (Fig. 1). Blood flukes of greater amberjack induce severe mortalities in 0^+ and 1^+ fish (Crespo *et al.*, 1992; Crespo *et al.*, 1994; Ogawa & Fukudome, 1994). Concurrent infections of *P. grandispinus* and *P. kampachi* have been reported in massive mortalities of caged *Seriola* sp. (Ogawa *et al.* 1989), while *P. ibericus* has been observed also in heavy losses caused by mixed infections with Epitheliocystis in 0+ fish (Crespo *et al.*, 1992).

Sanguinicolids represent an unusual group of digeneans because their life cycles lack a second intermediate host and an encysted or encapsulated metacercaria (Bullard & Overstreet, 2002). Though very little is known about the life cycle of fish blood flukes, it has been suggested that their single intermediate invertebrate host presumably harbours the floating materials in the cage ensuring a habitat overlap of the parasitic stages and the final host (Montero *et al.*, 2009). Considering the migration pattern of *Paradeontacylix* spp., released eggs are transported by the circulatory system of infected fish and accumulate in the capillaries of the gill lamellae (Montero *et al.*, 2003a), where they may cause death due to abnormal blood circulation, haemorrhages and suffocation (Shirakashi & Ogawa, 2016). Interestingly, girdles have been suggested as the main habitat for *Paradeontacylix* spp. worms in Mediterranean greater amberjack (Montero *et al.*, 2003a). Therefore, thoracic and pelvic girdles should be also included in the examination to maximize the efficacy of inspection (Montero *et al.*, 2003a), although gill analysis remains the most practical detection method.

The investigation of a seasonal pattern of *P. kampachi* eggs abundance in greater amberjack gills revealed an increased number of eggs during winter and a decreased pattern when summer was approaching (Ogawa *et al.*, 1993), which should be considered in parasitic management. Supposedly, control of infections of blood flukes in culture systems can be easier than treating parasites with direct life cycles, although their intermediate hosts *Paradeontacylix* spp. still remain unknown. Early detection of blood flukes is essential for elimination of susceptible intermediate hosts from the caged environment. Indeed, increased net hygiene with regular removal of biofouling would perhaps diminish the ideal environment for possible intermediate hosts of blood flukes (Montero *et al.*, 2009). As with most animal pathogens, biosecurity is apparently paramount to prevent outbreaks of blood flukes and quarantine protocols should be implemented especially when imported seeds are used for fattening. Heavy losses due to *Paradeontacylix* spp. were evident in imported Chinese fingerlings in Japan (Ogawa & Fukudome, 1994), reflecting thus the need of health certification and quarantine measures. Oral administration of PZQ seems to be the sole therapeutic measure against *Paradeontacylix* spp. infections in greater amberjack so far (Shirakashi & Ogawa, 2016), a treatment which has been also effective against other digenea infecting farmed fish (Bader *et al.*, 2019).

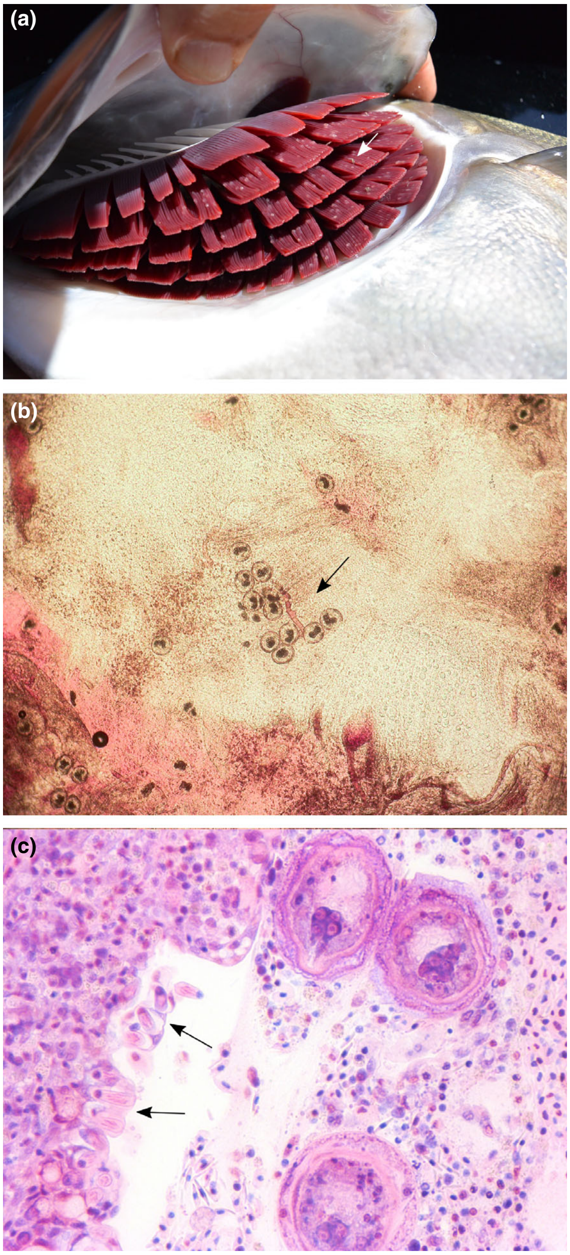

Figure 1 (a) Gills of farmed greater amberjack co-infected by *Zeuxapta seriolae* (arrow) and *Paradeontaxylix* sp., the eggs of which have created occlusions in the gill capillaries visible macroscopically as white spots. (b) Fresh squash preparation of gill biopsies showing numerous eggs of *Paradeontaxylix* sp. (c) Histological section of the affected gills showing the eggs of the parasite but also a marked inflammatory response with infiltration of rodlet cells (arrows). It is not clear whether this immune response is specific for *Paradeontacylix* sp.

Monogeneans (Gill flukes)

Zeuxapta seriolae and Z. japonica

Zeuxapta seriolae (Monogenea, Heteraxinidae) (Meserve, 1938) is a gill monogenean parasite that feeds on blood, causing heavy infestations, which have been associated with anaemia and severe mortalities in farmed greater amberjack in the Mediterranean region (Grau *et al.,* 2003; Montero *et al.,* 2004). Its Asian counterpart Z. *japonica* (Yamaguti, 1961) has been also lethal in cultured greater amberjack in Japan (Ogawa & Yokoyama, 1998) and Taiwan (Lu *et al.,* 2012). The later infects other farmed *Seriola* spp. such as yellowtail amberjack (*S. lalandi*) (Ernst *et al.,* 2002; Sharp *et al.,* 2003; Kolkovski & Sakakura, 2004; Mansell *et al.,* 2005), while *Z. seriolae* has induced outbreaks on both wild greater amberjack (Lia *et al.,* 2007) and yellowtail amberjack (Sepúlveda & González, 2015). Hyperplasia of the gill epithelium with fusion of the gill lamellae and extreme mucus excretion along with diminished haematological condition compromise gas exchange and oxygen transport in infected fish tissues, which inevitably leads to the death of diseased fish (age classes of 0+ to 3+), reaching mortality rates of up to 50% in greater amberjack farmed in the Mediterranean (Grau *et al.,* 2003; Montero *et al.,* 2004) (Fig. 2). High water temperature and fouled nets in the cages accelerate the propagation of *Z. seriolae*, which is able to release extreme numbers of eggs that can easily hook up in the nets and eventually allow hatching oncomiracidia to find a suitable host and invade the gills (Montero, 2001). Cage hygiene is thus crucial for the overall therapeutic strategy against *Z. seriolae*, since regular net replacement removes the entangled eggs along with fouling from the cage environment and, at the same time, copper-based antifouling compounds may display some anthelmintic activity, but this has to be experimentally proved. Older age classes (2^+, 3^+) seem to be less affected or even remain uninfected compared with newly introduced caged greater amberjack in Mediterranean, perhaps due to a acquired protection (personal observations) as previously suggested against *Neobenedenia girellae* (Ohno *et al.,* 2008). However, this assumption has to be scientifically proved, considering that an equal impact of *Z. seriolae* on various sizes of greater amberjack has been observed in previous investigations (Montero *et al.,* 2004).

More importantly, these older fish are usually not geographically separated from the younger fish in the Mediterranean aquaculture, and taking into account that they are less affected and are asymptomatic carriers of the parasite, they serve as a hotspot for the re-infection of the newly introduced fish. Age-class overlap is the most important issue in the management of the infestation and should be considered thoroughly in the frame of integrated pest management programmes that should be employed for the sustainable culture of the species.

Effective treatment plans against *Zeuxapta* spp. infecting both greater amberjack and yellowtail kingfish include mainly baths with hydrogen peroxide (H_2O_2) (75 ppm for 30 min and 300 ppm for 10 min, respectively) (Mansell *et al.,* 2005; Hirazawa *et al.,* 2016b) (Table 2). Caution has to be given when administering a H_2O_2 bath, considering its possible toxicity to treated fish, especially at high water temperatures and during prolonged therapy with increased doses (Hirazawa *et al.,* 2016b). Formalin baths have been generally considered less effective against monogeneans of yellowtail kingfish (Sharp *et al.,* 2004). On the contrary, PZQ baths (2.5 ppm for either 24 or 48 h) appeared highly effective for removing *Z. seriolae* from the gills of yellowtail kingfish, but the parasites continued to deposit viable eggs (Sharp *et al.,* 2004). However, application of PZQ baths is extremely costly and impractical due to the high cost of the compound and to its hydrophobic nature, which necessitates the addition of a solvent in the bath. The antiparasitic efficacy of dietary administered PZQ at dosages of 50–150 mg kg^{-1} for 3–6 days was evaluated in *Z. seriolae*-infected yellowtail kingfish (Williams *et al.,* 2007). Surprisingly, fish fed lower daily doses of PZQ had fewer *Z. seriolae* compared with fish fed higher daily doses for fewer days, a fact which could be attributed to increased palatability issues emerging from the surface-coating of higher PZQ dosages.

Heteraxine heterocerca

Heteraxine heterocerca (Polyopisthocotylea, Heteraxinidae) (Yamaguti, 1938) is also a gill fluke affecting greater amberjack farmed in Japan (Ogawa & Yokoyama, 1998), which is also commonly found in Japanese amberjack (Kearn *et al.,* 1992a; Kearn *et al.,* 1992b; Mooney *et al.,* 2008). The development of *H. heterocerca* along with attachment details to the Japanese amberjack gills has been reported (Ogawa & Egusa, 1981), while its hatching patterns have been described in detail (Kearn *et al.,* 1992a). Information on its related pathology to farmed *Seriola* spp. is not available in the pertinent literature.

Allencotyla mcintoshi

Allencotyla mcintoshi (Polyopisthocotylea, Heteraxinidae) (Price, 1962) is a another gill fluke, which has been identified during a parasitological analysis of greater amberjacks seeds, captured off the Spanish Mediterranean coast and subsequently raised in experimental culture tanks (Montero *et al.,* 2003b). This monogenean was also part of the parasitic fauna of wild greater amberjack in eastern Atlantic (Cavaleiro *et al.,* 2018). The regularity of its presence in wild specimens of greater amberjack reflects the risk of

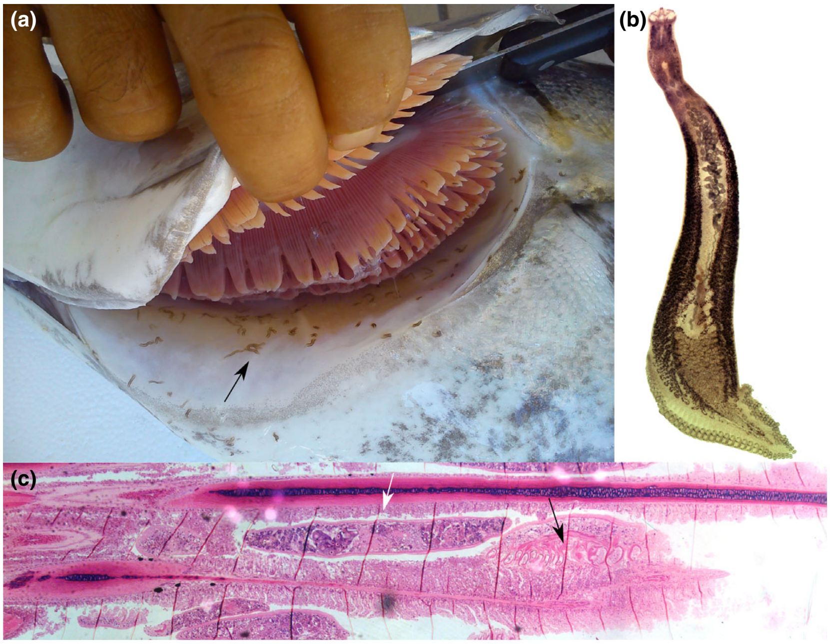

Figure 2 (a) Anaemic gills of farmed greater amberjack parasitized intensively by *Zeuxapta seriolae*. The monogeneans have detached (arrow) since the fish had been kept in ice. (b) Adult *Z. seriolae*. Eggs are visible inside the body cavity of the parasite. (c) Histological section of greater amberjack gills infected by *Z. seriolae*. White arrow points to the body of the parasite and black arrow points to the haptor which is the attachment device of the parasite bearing numerous clams. Note the fusion of the gill lamellae, a host response to the parasitic infection.

introducing a possible novel pathogen in the facilities by using captured juveniles for farming, although its pathological impact on the host has not yet been described.

Monogeneans (Skin flukes)

Benedenia seriolae

Benedenia seriolae (Monogenea, Capsalidae) (Baird, 1853) is a skin monogenean parasite of farmed *Seriola* spp. including greater amberjack, yellowtail amberjack and Japanese amberjack (*S. quinqueradiata*) (Whittington *et al.,* 2001). It has been recorded in farmed *Seriola* spp. from Japan (Whittington *et al.,* 2001), but not so far from the Mediterranean area. This capsalid parasite inhabits the skin and fins and feeds on mucus and epithelial cells (Chambers & Ernst, 2005). Induced severe lesions might be associated with considerable irritation and fish rubbing and occasionally lead to secondary microbial infections and high mortalities (Egusa, 1983), although treatment cost, lost growth and diminished feed conversion are not of less concern (Ernst *et al.,* 2005). Parasitic propagation is environmentally affected and is strongly influenced by increased water temperature (Ernst *et al.,* 2005; Lackenby *et al.,* 2007), considering that temperatures above 28°C appeared to be beyond the physiological tolerance of eggs (Ernst *et al.,* 2005). Indeed, sexual maturity of *B. seriolae* was attained as early as 14 days postinfection in yellowtail amberjack at 26°C, while it was threefold delayed at 14°C (Lackenby *et al.,* 2007), indicating that propagation of the parasite is feasible in a wide range of water temperatures, including winter temperatures, but is clearly favoured by high water temperatures, as those observed in Mediterranean region during spring and summer.

Given the high economic impact of this skin fluke, regular management intervention is advised (Ernst *et al.,* 2002). The principal method of treatment for *B. seriolae* infections is bathing with freshwater when applicable or preferably with H_2O_2 (Ernst *et al.,* 2005). Hydrogen peroxide baths (75 ppm, 0.5 h) are highly effective (Hirazawa *et al.,* 2016b) at killing parasitic adults but re-infection is likely in most occasions due to existence of untreated eggs and free-swimming parasitic larvae in the vicinity around cages and in neighbouring fish (Chambers & Ernst, 2005). Bathing with higher concentrations (300 ppm) for shorter periods (3 min) is also approved against *B. seriolae* in Japan.

Notably, dispersal of *B. seriolae* eggs is possible at very high distances (>8 km), raising the need for specific strategic cage/unit planning (Chambers & Ernst, 2005), which should consider the direction of water currents as well as the distance and orientation of cages within or between farming units of *Seriola* spp. Inevitably, to confront the reappearance of *B. seriolae*, spatial and temporal therapeutic coordination is aimed to break the parasitic cycle (Lackenby *et al.*, 2007).

In addition to H_2O_2 baths, which seem to be the preferable anthelmintic measure against monogeneans of greater amberjack, therapeutic trials with other compounds have been carried out to battle *B. seriolae* (Table 2). The efficacy of bath-administered formalin (250–400 ppm, 1-h plus 5-min freshwater dip) and PZQ (2.5 ppm, 24–48 h) were assessed against *B. seriolae* infecting yellowtail amberjack (Sharp *et al.*, 2004). The PZQ dosing regimens were the most effective for removing the parasite, although viable eggs were seen under the 24-h therapeutic schedule. On the other hand, the combination of formalin baths with freshwater dip was less effective for removing adults, but release of live eggs by the treated parasites was inhibited. Surprisingly, a dose-dependent anthelmintic effect of formalin was not apparent in that study.

Considering alternative dietary therapeutic approaches, the *in vitro* evaluation of caprylic acid at a concentration of 1 mM revealed parasiticidal and contractile effects in oncomiracidia and *B. seriolae* adults, respectively (Hirazawa *et al.*, 2001a) (Table 3). This medium-chain fatty acid has also exhibited some antiparasitic effects when was orally administered alone (Rigos *et al.*, 2013) or in a dietary mixture (Rigos *et al.*, 2016) against the microcotylid monogenean *Sparicotyle chrysophrii* (Monogenea, Microcotylidae) (Van Benedenand Hesse, 1863; Mamaev, 1984) in gilthead sea bream (*Sparus aurata*) (Linnaeus, 1758) and, moreover, showed high anthelmintic efficacy in diclidophorid monogenean *Heterobothrium okamotoi* infecting tiger puffer (*Takifugu rubripes*) (Abe, 1949) (Hirazawa *et al.*, 2000; Hirazawa *et al.*, 2001b). The possible parasiticidal value of caprylic acid against *B. seriolae* in famed *Seriola* spp. remains to be elucidated *in vivo*.

The dietary delivery of surface-coated PZQ has been evaluated at different dosing schedules (50–150 mg kg^{-1}, 3–6 days) in *B. seriolae*-infected yellowtail amberjack (Williams *et al.*, 2007). Paradoxically, fish fed lower daily doses of PZQ for 6 days had fewer parasites than fish given higher daily doses for 3 days. Perhaps the high-dosed PZQ diets affected the palatability of the diet at a greater degree, regardless of the use of fish oil as a masking agent. Surface pellet coating with PZQ is, however, not advisable, as it diminishes the acceptability of the medicated diet. Hirazawa *et al.* (2004) also observed a reduced appetite in spotted halibut (*Verasper variegates*) (Temminck and Schlegel, 1846) fed pellets medicated with PZQ at a dose of 150 mg kg^{-1}. Diminished acceptability due to PZQ-medicated feed has been also seen in gilthead sea bream (Sitjà-Bobadilla *et al.*, 2006); however, this effect was not apparent when greater amberjack was given 75 or 150 mgPZQ kg^{-1} for 5 days by mixing the drug in pelleted diets (Kogiannou *et al.*, 2019). Dietary administration of PZQ could be thus selectively applied as a therapeutic tool against *B. seriolae* parasitizing *Seriola* spp., provided that palatability problems are fully solved. This could be accomplished by mixing the compound with dietary components and possibly avoiding thermal issues associated with specific extrusion stages. Moreover, masking with attractants, such as freshly coated garlic extract, aided overcome the bitterness of PZQ diets in yellowtail amberjack (Pilmer, 2016), while included dietary PZQ microcapsules increased the palatability of the medicated diet but at the same time reduced the bioavailability of the drug in the circulation of the same fish species (Partridge *et al.*, 2014). Intubation with PZQ was proved effective against *B. seriolae* (Williams *et al.*, 2007; Forwood *et al.*, 2016), but this administration route is unfortunately an impractical approach for the treatment of a sick stock containing numerous animals.

Table 3 Non-chemical compounds used against flukes of farmed greater amberjack

Pathogen	Compound	Administration	Dosing schedule	Efficacy	References
B. seriolae	Caprylic acid	*In vitro*	1 mM	High	Hirazawa *et al.* (2001a)
N. girellae	Mannan oligosaccharides	Oral	5 g kg^{-1} MOS or 2 g kg^{-1} cMOS for 90 days	High	Fernández-Montero *et al.* (2019)
	Bovine lactoferrin	Oral	1000 mg kg^{-1} for 2 weeks	High	Yokoyama *et al.* (2019)
	Garlic extract	Oral	50–150 mL L^{-1} for 10–30 days	High (in barramundi)	Militz *et al.* (2013)
	Seaweeds (*Asparagopsis taxiformis*)	Bath	1 mL of extract to 100 mL of seawater	High (in barramundi)	Hutson *et al.* (2012)
	Garlic, ginger, bitter chaparro, onion, papaya (extracts)	*In vitro*		High (ginger, basil and bitter chaparro)	Trasviña-Moreno *et al.* (2019)

Neobenedenia girellae

Neobenedenia girellae (Monogenea, Capsalidae) (Hargis, 1955-Yamaguti, 1963) is a another skin monogenean parasite which, as opposed to *B. seriolae,* exhibits low host specificity invading the fins and skin of several farmed fish species including greater amberjack, yellowtail amberjack, tiger puffer, spotted halibut, red sea bream (*Pagrus major*) (Temminck and Schlegel, 1843), olive flounder (*Paralichthys olivaceus*) (Temminck and Schlegel, 1846) and chub mackerel (*Scomber japonicus*) (Houttuyn, 1782) (Ogawa & Yokoyama, 1998; Hirazawa *et al.,* 2004; Yamamoto *et al.,* 2011). Notably, greater amberjack seems to be one of the most susceptible hosts (Ohno *et al.,* 2008), among numerous *N. girellae*-infected Japanese marine farmed species (Ogawa *et al.,* 1995). Given that *N. girellae* and *B. seriolae* are difficult to distinguish during inspection, Kinami *et al.* (2005) suggested a practical method for the classification of the two skin flukes species, which is based on the different shape at the anterior end in the midline of the helminths. *Neobenedenia melleni* has been detected in greater amberjack raised in the Canaria islands (Sánchez-García *et al.,* 2015), while naturally infected fish with *N. girellae* have been used in experimental trials in the same area (Fernández-Montero *et al.,* 2019). There is great possibility that these *N. girellae* specimens might have been misdiagnosed as *N. melleni* (Brazenor *et al.,* 2018).

The life cycle of *N. girellae* is highly dependent on seasonal temperature (Ernst *et al.,* 2005; Hirazawa *et al.,* 2010). Indeed, eggs of *N. girellae* were observed to hatch from 18 to 30°C but not below 15°C (Bondad-Reantaso *et al.,* 1995), as opposed to *B. seriolae* of which egg hatching may occur, though at relatively slow rates, at 14°C (Ernst *et al.,* 2005). However, both parasitic life cycles and, subsequently, egg hatching process are favoured by high water temperatures, as those characterized in Mediterranean waters during spring and summer.

Neobenedenia girellae feeds primarily on epithelial cells causing haemorrhages, mucus hyperproduction and eventually mortalities (Paperna, 1991; Ogawa & Yokoyama, 1998). During the first period of exposure, *N. girellae* harbour the pelvic and pectoral fins of infected fish and then migrate to the skin surface during parasitic development (Hirayama *et al.,* 2009). Feed utilization and subsequently growth of infected greater amberjack are substantially affected (Hirayama *et al.,* 2009; Hirazawa *et al.,* 2016a), perhaps due to physiological impairment of the host from disruption of the osmotic balance. The resulting ionic disequilibrium provokes liver and kidney dysfunction that ultimately, in severely infected fish, can lead to death (Hirazawa *et al.,* 2016a). Interestingly, a partial acquired protection in greater amberjack was observed by Ohno *et al.* (2008) which could be used in future management against *N. girellae,* although the possible factors involved in this skin immunity remain to be elucidated.

Unregulated importation of greater amberjack fry in Japan has been considered as the source of *N. girellae* outbreaks in Japanese fish during the 90s (Ogawa *et al.,* 1995). In the Mediterranean, a potential infection route could be through imported seeds of greater amberjack or other fish species, although *N. girellae*-induced outbreaks or simple findings have not been recorded yet.

To prevent *N. girellae* infestation, a freshwater dip has been practised to dislodged parasites (Seng, 1997). In contrast, freshwater dip for 2 min significantly increased *N. girellae* infection on both greater amberjack and Japanese amberjack (Ohno *et al.,* 2009). This outcome should be considered for controlling *N. girellae* infections in *Seriola* spp. management. Moreover, prolonged freshwater baths could not be tolerated by Mediterranean greater amberjack and such treatments may eventually damage the fish (Rigos *et al.,* 2001). A 75–100 ppm H_2O_2 bath for 0.5 h was safe and exhibited high anthelmintic efficacy in infected greater amberjack (Hirazawa *et al.,* 2016b). Dietary administration of PZQ was effective against *N. girellae* infestations in spotted halibut, and a long-term, low-dose treatment, such as 40 mg kg^{-1} for 11 days, would be more useful compared with a short-term, high-dose treatment due to the bitterness of the high-dosed diets (Hirazawa *et al.,* 2004). Interestingly, a large amount of research on non-drug supplements has been devoted to battle *N. girellae* infection in farmed *Seriola* spp. and in other fish species (Table 3). For example, increased resistance of greater amberjack against *N. girellae* was obtained when fish were fed with a supplemented diet with mannan oligosaccharides for a prolonged period (Fernández-Montero *et al.,* 2019). Oral delivery of bovine lactoferrin was found to enhance defence factors and antiparasitic effects against the parasite in greater amberjack (Yokoyama *et al.,* 2019). Dietary supplementation of garlic (Militz *et al.,* 2013) and seaweed extracts (Hutson *et al.,* 2012) sealed effectively farmed barramundi, *Lates calcarifer* (Bloch, 1790) against *N. girellae*. Finally, other plant extracts such as ginger, bitter chaparro and basil were proved effective of reducing the hatching success of parasitic eggs *in vitro* (Trasviña-Moreno *et al.,* 2019).

Environmental control methods of *N. girellae* included mainly manipulation of light in the caged environment. Markedly, Japanese flounder (*Paralichthys olivaceus*) (Temminck & Schlegel, 1846) exhibited higher vulnerability to this fluke at brighter conditions, indicating that shading of the cages would help to reduce infection by this fluke (Ishida *et al.,* 2007). Novel biocontrol strategies with the use of cleaner shrimp were recently revealed promising results (Vaughan *et al.,* 2018). The ‘cleaning effect’ of farmed shrimp (*Lysmata vittata*) (Stimpson, 1860) on *N. girellae* eggs was remarkable in infected cultured juvenile grouper (*Epinephelus lanceolatus*) (Bloch, 1790) under simulated recirculating aquaculture conditions in the above study. Cleaner shrimp was able to remove the entangled fluke eggs from the net mesh and significantly reduced *N. girella*e recruitment to fish by as high as 87%.

Flagellates

Amyloodinium ocellatum

Amyloodinium ocellatum (Dinophyceae, Oodiniaceae) (Brown, 1931) is a generalist dinoflagellate ectoparasite, which has been implicated in epizootics of a big number of farmed marine species (Alvarez-Pellitero *et al.,* 1995). It usually infects the gills and less frequently the skin and the buccal cavity of fish. Due to its specific propagation pattern, which requires a substrate/bottom to complete the life cycle and immediately initiate infection (Paperna, 1996), it is normally found parasitizing fish raised in land-based facilities, although rare infestations in Mediterranean fish farmed in shallow cage installations have been also recorded (Rigos *et al.,* 1998). This flagellate can readily infect greater amberjack broodstock (Fig. 3).

During the first farming attempts of greater amberjack in the 80s, land-raised fish in Italy suffered serious mortalities due to *A. ocellatum* (Aiello & D'Alba, 1986). The parasite harboured the gills and skin and, consequently, infected fish showed anaemic and necrotic gills along with depigmented body and eroded fins. This flagellate has been also associated with severe infestations in California yellowtail (*S. dorsalis*) (Gill, 1863) experimentally exposed to the pathogen (Vivanco-Aranda *et al.,* 2018).

Daily bath treatments with 0.75 ppm of copper sulphate for 6 days successfully eliminated the pathogen in the study of Aiello and D'Alba (1986). Environmental friendly approaches such as hyposalinity manipulations (0–8‰) commonly applied as antiprotozoan measures in euryhaline farmed finfish species are unfortunately intolerable by greater amberjack (Rigos *et al.,* 2001).

Ciliates

Cryptocaryon irritans

Cryptocaryon irritans (Prostomatea, Holophryidae) (Brown, 1951) is a generalist parasitic ciliate with a widely studied biology, which infects marine farmed fish (Colorni, 1987). Normally, it invades the gills and skin of sensitive farmed fish species. As in the case of *A. ocellatum*, it requires a bottom substrate to complete its life cycle and consequently the ciliate induces infections almost exclusively in land-based environment although some incidences on caged fish in Japan are evident (Ogawa & Yokoyama, 1998). Heavy mortalities due to *C. irritans* have been recorded in greater amberjack broodstock with fish displaying the common characteristics of the disease including mucus hyperproduction, pale gills and white skin nodules (Rigos *et al.,* 2001). In this incidence, infected greater amberjack was unable to tolerate hyposalinity application of 8–10‰ for 3 h and within 5 days heavy mortality was observed. Moreover, chemical trials consisting of formalin baths (100 ppm for 1 h) and copper sulphate (0.5–0.7 ppm) immersions failed to confront the pathogen (Rigos *et al.,* 2001). Perhaps due to the fact that free-swimming *C. irritans* theronts infect underneath the fish epidermis and as trophonts feed on skin and gill epithelia (Yoshinaga & Dickerson, 1994) are not exposed to environmental water and, thus, bathing of infected fish with any chemicals would not kill all the parasitic stages. The parasite has caused recurrent problems in our broodstock kept in inland facility in Crete island, Greece, and successful management was based on early diagnosis (infected fish show reduced swimming behaviour and often remain motionless with frayed fins), formalin baths and changing of the tanks every 3–4 days. Maintaining good hygiene and siphoning thoroughly the bottom of the tanks on a daily basis are of imperative importance. Interestingly, it has been demonstrated that greater amberjack, which survived infections by this parasite, developed immunity to later infections (de la Gándara *et al.,* 2005).

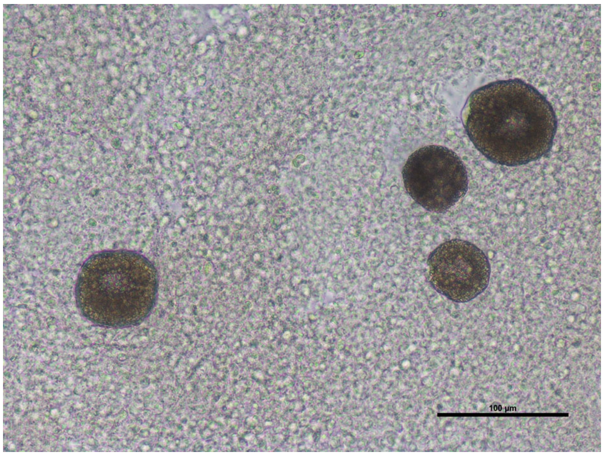

Figure 3 Microphotograph of *Amyloodinium ocelatum* trophonts as observed in a fresh squash preparation from the gills of greater amberjack broodstock.

Myxozoans

Kudoa amamiensis

Kudoa amamiensis (Myxosporea, Kudoidae) (Egusa and Nakajima, 1980) belongs to a group of myxozoans that commonly invade dorsal fish musculature, with infection characterized by a multifocal intracellular infection with associated inflammatory reactions. Infections of *Kudoa* spp. do not usually produce any visible symptoms in fish, but they may induce damage to the end fish products by degrading the muscle causing the myoliquefactive post-mortem condition known as 'milky flesh', with the activation of their potent enzymes (Álvarez-Pellitero & Sitjá-Bobadilla, 1993). The presence of this parasite is mainly of quality concern of the slaughtered fish and does not pose a health risk for consumers, as evidenced in other *Kudoa* spp.-infected fish (Kawai *et al.,* 2012). *Kudoa amamiensis* has been actually identified in greater amberjack farmed in Japan (Sugiyama *et al.,* 1999). The prevalence of infection was low, and it was stated that greater amberjack was less susceptible to the myxozoan than infected Japanese amberjack in the same case. Infected wild fish from neighbouring waters may act as reservoir hosts for cage-cultured fish (Álvarez-Pellitero & Sitjá-Bobadilla, 1993). Effective therapeutic approaches against fish myxozoans are unfortunately scarce or virtually non-existed.

Unicapsula seriolae

Unicapsula seriolae (Myxosporea, Trilosporidae) (Lester, 1982) is another myxozoan that belongs to a genera pathogenic to fish which could, in addition to the negative visual impact on product quality due to postmortem myoliquefaction, cause potential health risks to consumers. It has been suggested that *U. seriolae* is responsible for foodborne disease associated with the ingestion of raw greater amberjack (Ohnishi *et al.,* 2018). Its pathological impact on greater amberjack has not been found in pertinent bibliography.

Microsporidia

Spraguea sp

A microsporidian parasite with a genetic affinity to the genus *Spraguea* sp. has been blamed to cause neural pathology in farmed greater amberjack (Miwa *et al.,* 2011). The disease was named Encephalomyelitis and is characterized by a peculiar spiral swimming behaviour, which has been known for more than a decade in cultured greater amberjack in China and Japan (Miwa *et al.,* 2011). The microsporidian induces severe inflammation in parts of the brain and the spinal cord, which results in considerable cumulative mortalities in infected greater amberjack at relative high temperatures. Microsporidian Encephalomyelitis due to the same aetiological agent has been also described in Japanese amberjack (Yokoyama *et al.,* 2013). Whether greater amberjack is a natural host for this microsporidian or a parasitic transfer from wild fish species is responsible, remains to be elucidated, although importation of Chinese greater amberjack seeds was characterized as the suspected vectors for the transmission to cultured Japanese amberjack (Yokoyama *et al.,* 2013).

Microsporidium seriolae

Microsporidium seriolae (Balbiani, 1884) is an obligate fish microsporidian parasite, which produces visible white cysts in fish trunk muscle (Egusa, 1982). Heavy infection with *M. seriolae* may cause emaciation and eventually death of *Seriola* spp. juveniles (Egusa, 1982). Microsporidiasis due to *M. seriolae* could be linked to consumer rejection of the fish product. Failure of artificial direct transmission has led to the suggestion that an intermediate host is probably required for the life cycle of this microsporidian (Yokoyama *et al.,* 2011). *Microsporidium seriolae* has been detected in greater amberjack at high infestation levels during the summer period (Yokoyama *et al.,* 2011). The disease seemed to decline at lower water temperatures, and no reoccurrence was evident in the following year suggesting an established resistance in survivors. Microsporidiasis is very difficult to control since specific chemotherapeutics are not readily available and the microsporidian life cycle is unknown, although a previous control strategy included the combination of early diagnosis and juvenile production using filtered seawater (Ogawa & Yokoyama, 1998).

Bacteria

Vibrio harveyi

Vibrio harveyi is one of the most important bacterial pathogens of fish with worldwide distribution (Austin & Zhang, 2006). It belongs to the family of Vibrionaceae, and it is ubiquitous in the marine environment. Many different and closely related species form the so-called *Harveyi* clade that includes, in addition to *V. harveyi*, important pathogens of aquatic animals such as *V. alginolyticus*, *V. campbellii* and *V. owensii* (Darshanee Ruwandeepika *et al.,* 2012). *Vibrio harveyi* can be often misdiagnosed as *V. vulnificus* in cases where diagnosis involves only biochemical methods (Del Gigia-Aguirre *et al.,* 2017). However, even with the use of molecular tools, identification of *V. harveyi* can be challenging due to the genetic relatedness with other congeneric species (esp. those of the *Harveyi* clade). *Vibrio harveyi* causes vibriosis in fish, and although septicaemia can be observed at the later stages of the disease, it mostly manifests with cutaneous and ocular lesions in adults, while in young juveniles and larval fish it is mostly related to gastrointestinal infections.

Vibrio harveyi is a component of the greater amberjack microbiota as demonstrated by Alcaide (2003) who studied the bacteria present in cultured greater amberjack in Spain but also in the surrounding waters. There are few reports of *V. harveyi* infections of *Seriola* spp. in the literature.

Minami *et al.* (2016) described an outbreak of *V. harveyi* in farmed greater amberjack, which had been vaccinated against *V. anguillarum*. Affected fish displayed the common lesions of the disease, including dermal lesions in the area of the head and the caudal fins, ascites and ophthalmitis.

In recent epizootics monitored by our laboratory at inland pre-ongrowing tanks and cages in Aegean Sea, *V. harveyi* has caused significant problems in experimentally raised conditions but also in commercial farms. The observed lesions were typical of the disease, with most evident the superficial dermal erosions and the haemorrhages mostly in the abdominal area (Fig. 4). The mortalities were high, persistent and cumulatively could reach 60% of the affected population. The onset of the disease coincides with changes in water temperature, which suggests that it is stress-related. *Vibrio harveyi* is resistant in most antibacterials, although, according to our experience from unpublished experimental trials, dietary administration of doxycycline (100 mg kg^{-1} fish for 5–7 days) is highly effective against the pathogen. The use of autogenous vaccines has moreover shown, again in unpublished work of our group, promise in preventing the disease. To this direction, but also to the comprehension of the virulence of this pathogen, genomic data are extremely important. To date, genomes of the strains VH2, VH5 (Greek isolates) and GAN1807, GAN1709 (Japanese isolates), all isolated from diseased greater amberjack are available in the literature (Castillo *et al.*, 2015; Monno *et al.*, 2018; Kato *et al.*, 2019).

Photobacterium damselae subsp. *piscicida*

Photobacterium damselae subsp. *piscicida* is an important Gram-negative fish pathogen causing Pseudotuberculosis or Photobacteriosis, a severe bacterial septicaemia (Romalde, 2002). The disease has great economic impact both in Japan, where it affects several farmed *Seriola* spp., and in the Mediterranean area, due to the losses in cultured gilthead seabream (*Sparus aurata*) (Linnaeus, 1758) and European seabass (*Dicentrarchus labrax*) (Linnaeus, 1758) farms (Romalde, 2002). Indeed, *P. damselae* subsp. *piscicida* has been mentioned in the past as a significant pathogen of greater amberjack in Japan (Kubota *et al.*, 1970; Kawahara *et al.*, 1986), although it has not been yet isolated from its Mediterranean counterpart. Notably, the pathogen has been experimentally transferred, producing the common characteristics of the disease in challenged greater amberjack farmed in the Mediterranean region (Alcaide *et al.*, 2000). Caution should be given therefore for the possible transmission of the pathogen among different Mediterranean farmed species. Commercially available vaccines against Photobacteriosis have been available for quite some time for farmed gilthead seabream and European seabass (Bakopoulos *et al.*, 2015) and effective chemotherapy exists to confront the bacterium (Rigos & Troisi, 2005).

Figure 4 Juvenile greater amberjack affected by *Vibrio harveyi* showing dermal erosion and ulceration, and redness of the area of the head, typical clinical picture of the disease.

Lactococcus garvieae

Lactococcus garvieae is a Gram-positive bacterial pathogen that causes septicaemia and meningoencephalitis in several species of marine and freshwater farmed fish (Eldar *et al.*, 1996; Vendrell *et al.*, 2006; Meyburgh *et al.*, 2017). Lactococcicosis in particular causes serious economic damage to farmed *Seriola* spp. in Japan (Kusuda *et al.*, 1991; Kusuda & Salati, 1993); however, a widespread use of an effective injection vaccine has considerably reduced disease outbreaks in this area (Nakajima *et al.*, 2014). Moreover, a susceptibility trial of several antibacterials against numerous *L. garvieae* isolates from *Seriola* spp. cultured in Japan revealed that effective chemotherapy is an additional tool to battle the bacterium (Furushita *et al.*, 2015). It should be noted, however, that *L. garvieae* has not yet been isolated from farmed greater amberjack or other marine finfish species in the Mediterranean area. However, it has been described in the Red Sea in wild wrasse (*Coris aygula*) (Lacepède, 1801) (Colorni *et al.*, 2003), and therefore, it can be possibly transferred by lessepsian migrators to the Mediterranean area and finally invade farmed fish including greater amberjack.

Streptococcus dysgalactiae

Streptococcus dysgalactiae belonging to Lancefield group C is a Gram-positive bacterium that is considered to be an emerging fish pathogen with increased clinical significance in Japanese aquaculture as well as in mammalian health

(Abdelsalam *et al.,* 2013). Indeed, many *Seriola* spp. farms including greater amberjack farmed in Japan have suffered huge losses due to *S. dysgalactiae* infection mainly at high water temperatures (Nomoto *et al.,* 2004; Nomoto *et al.,* 2006; Hagiwara *et al.,* 2011). Streptococcosis due to *S. dysgalactiae* has been also noticed, in addition to Japan, in China and Taiwan, with responsible isolates exhibiting high phenotypic homogeneity irrespectively of the sampled countries (Abdelsalam *et al.,* 2010). Therefore, *S. dysgalactiae* outbreaks caused by alien strains could be of great concern for Japanese farmed greater amberjack. The disease is characterized by high mortality and severe muscle necrosis in the caudal peduncle (Abdelsalam *et al.,* 2010), accompanied with severe haemorrhages, inflammatory cell infiltration and necrotizing vasculitis with lesions being extended into the overlying dermis and epidermis of infected greater amberjack (Hagiwara *et al.,* 2011). Pathological lesions have been also observed in the pectoral and dorsal fins as well as in the heart, comprised of severe arterial thrombosis and granulomatous epicarditis (Hagiwara *et al.,* 2011). The same study also described moderate-to-severe non-purulent encephalomyelitis in infected fish. The complete genome sequence and characterization of virulence genes of *S. dysgalactiae* isolated from farmed greater amberjack were recently described (Nishiki *et al.,* 2019). A possible misdetection problem could occur with *L. garvieae*, which exhibits clinical similarities (Nomoto *et al.,* 2004). Domesticated animals have been suspected as potential vectors of *S. dysgalactiae* infection in fish farms (Nomoto *et al.,* 2004), although DNA relatedness between mammalian and fish isolates was unable to fully confirm this hypothesis (Nishiki *et al.,* 2010). An *in vitro* evaluation by disc diffusion method against numerous *S. dysgalactiae* strains isolated from fish collected in Japan and other Asian countries showed that all strains tested were susceptible to erythromycin, florfenicol, lincomycin and ampicillin and resistant to oxytetracycline (Abdelsalam *et al.,* 2010). It should be kept in mind that *S. dysgalactiae* has not yet been detected in greater amberjack or other marine finfish species farmed in the Mediterranean area.

Mycobacterium marinum

Mycobacteriosis is a serious chronic disease of wild and cultured fish species, caused by several species of the *Mycobacterium* genus. The most important species seems *M. marinum*, a Gram-positive, acid-fast bacterium, which is also a human pathogen (Hashish *et al.,* 2018). Following infection, mycobacteria may use this survival ability within the host's macrophage to disseminate in various tissues of the host and establish infection (Clay *et al.,* 2007). Granulomas, which are the chronic host immune response against the infection, provide a niche for the persistence of bacteria (Colorni *et al.,* 1998). These responses are the hallmark of *M. marinum* infection in many animals including fish, and their presence is one of the most important diagnostic signs. More importantly, mycobacteria stain vividly red using acid-fast stains like Ziehl–Neelsen, which makes them easily differentiated from other pathogens.

Greater amberjack has been reported susceptible to *M. marinum* (Kato *et al.,* 2011). Most of the published reports about mycobacteriosis are related to Japanese yellowtail where *M. marinum* has been responsible for high mortalities in farmed fish (Weerakhun *et al.,* 2007). The clinical signs included lethargy, anorexia and emaciation. In the most progressed stages of the disease, fish exhibited dermal lesions, ulceration and haemorrhages. Internally, the disease is characterized by the presence of ascitic fluid in the peritoneal cavity and white nodules, which could be found in almost all internal organs of the affected fish (Weerakhun *et al.,* 2007; Weerakhun *et al.,* 2010).

Until today, there are no published cases of mycobacteriosis in farmed greater amberjack in the Mediterranean. However, the disease is common in this geographical area in other fish species like European seabass (Colorni *et al.,* 1998) and meagre (*Argyrosomus regius*) (Asso, 1801) (Avsever *et al.,* 2014). Therefore, it could present a potential threat to Mediterranean greater amberjack given to its susceptibility to the pathogen, as demonstrated in experimental infections but also in reports from Japan (Weerakhun *et al.,* 2010). Treatment of the disease is extremely difficult and depends on prolonged administration of antibiotics (Hashish *et al.,* 2018), which makes it unpractical for aquaculture. There are no commercially available vaccines, although experimental trials suggest that vaccination could provide partial protection (Kato *et al.,* 2011).

Nocardia seriolae

Nocardia seriolae is a Gram-positive, non-motile, branching bacterium that belongs to the Nocardiaceae family. It is the causative agent of nocardiosis in farmed *Seriola* spp. such as Japanese yellowtail and greater amberjack, and one of the most important bacterial diseases for the Japanese aquaculture (Yasuike *et al.,* 2017). Nocardiosis was observed for the first time in 1967, and ever since, it is responsible for severe economic losses (Kusuda & Nakagawa, 1978). The disease is characterized by abscesses in the skin and tubercles in the gills, while internally there are granulomatous lesions in the kidney and the spleen (Kudo *et al.,* 1988). Heavily polluted waters especially when they are enriched by the nutrients of the uneaten food have been directly connected to the persistence of the bacterium in the affected fish farms (Kusuda & Nakagawa, 1978). Diagnosis is initially based on the clinical signs of the fish and on imprints from lesions where the typical branching filamentous bacteria are evident. *Nocardia seriolae* is acid-fast but this can be demonstrated mostly with Fite–Faraco stain rather than Ziehl–Neelsen. The bacterium can be isolated in routine and selective media, while definitive identification can be achieved with PCR (Labrie *et al.*, 2005).

Nocardia seriolae has been isolated from farmed greater amberjack in Japan (Shimahara *et al.*, 2008) and is currently controlled with antibiotic administration. In Japan, sulphonamides are the drugs of choice prescribed for treating *N. seriolae* (Akiyama *et al.*, 2018). Oxytetracycline is effective *in vitro*; however, its low bioavailability makes it inadequate for controlling the disease in *Seriola* spp, although coadministration with N-acetyl-d-glucosamine (NAG) improved its absorption and efficacy (Akiyama *et al.*, 2018). Today, there are no commercially available vaccines for *N. seriolae* but there are several attempts to develop one using various technologies ranging from inactivated bacterin, live-attenuated (Itano *et al.*, 2006), recombinant subunits (Ho *et al.*, 2018) and DNA vaccines (Kato *et al.*, 2014).

Intracellular bacteria

Epitheliocystis **sp**

Epitheliocystis is one of the oldest infectious diseases described in fish. It is characterized by the presence of intracellular inclusions of bacteria in the epithelial cells of the gills and skin of affected fish. For many years, the disease was considered to be caused by chlamydia; however, recent studies have shown that a great variety of intracellular bacteria belonging to β- and -γ proteobacteria may also cause the disease (Mendoza *et al.*, 2013; Stride *et al.*, 2014; Katharios *et al.*, 2015; Qi *et al.*, 2016; Seth-Smith *et al.*, 2016). All *Seriola* spp. have been reported to be susceptible to Epitheliocystis (Venizelos & Benetti, 1996; Kobayashi *et al.*, 2004; Nowak & LaPatra, 2006), and the list of affected fish includes more than 90 different species both in marine and freshwater environment (Blandford *et al.*, 2018). As in other fish species (Katharios *et al.*, 2008), the disease in greater amberjack is more severe in the early developmental stages and can result in mass mortalities (Crespo *et al.*, 1990; Grau & Crespo, 1991). It is also observed during the first 2–3 months after the transfer of the fish from the hatchery to the open sea. Later, as the fish grow, the disease is benign, and few cysts may occasionally be found in the gills without causing significant pathology. The disease can be diagnosed easily using microscopy; however, at incidents involving fish larvae, it may go undetected due to the rapid deterioration of the delicate specimens. To date, no Epitheliocystis causative agent has been brought to culture, thus making histology the most appropriate method for disease diagnosis. Histologically, densely packed bacterial inclusions are usually found in epithelial cells of the gills but also in the mitochondria-rich cells (chloride cells). In many cases, there is a notable proliferative reaction and cysts are surrounded by concentric layers of tissue giving a granulomatous appearance to the lesion. This is evident in the infections described in greater amberjack from Spain (Crespo *et al.*, 1990) but also in Greece (Fig. 5, unpublished data). Molecular tools have been developed for the detection of Epitheliocystis. However, it should be underlined that co-existing infections by divergent Epitheliocystis-related agents have been reported and this may complicate the identification of the true pathogen (Seth-Smith *et al.*, 2017). Unpublished data from our group suggest that the major Epitheliocystis-causing agent in greater amberjack farmed in Greece belongs to a novel species of the *Ca.* Ichthyocystis genus.

In the majority of the cases, fish infected with Epitheliocystis recover after two to three weeks without treatment. From our experience with farmed greater amberjack in Greece, Epitheliocystis may cause mortality during grow-out if there is a concurrent infection by parasites (usually by the monogenean *Z. seriolae*). Oxytetracycline has been recommended in the past as an effective therapeutic (Goodwin *et al.*, 2005) and UV sterilization at the hatchery as a prevention measure against Epitheliocystis. Azithromycin, an erythromycin derivative, has been recently proposed for the control of some animal chlamydial infections (Bommana & Polkinghorne, 2019), while erythromycin has shown efficacy against Epitheliocystis infections in Japanese farmed fish.

Viruses

Red seabream iridovirus

Red seabream iridovirus (RSIV) belongs to the Megalocytivirus genus of the Iridoviridae family (DNA-templated transcription). It is a highly contagious virus reported from more than 30 different fish species (Kurita & Nakajima, 2012), which has been firstly described in farmed red seabream in Japan, where it was associated with significant economic losses (Matsuoka *et al.*, 1996). The disease was recently listed in the notifiable fish diseases of the World Organization for Animal Health (https://www.oie.int/animal-health-in-the-world/oie-listed-diseases-2020). Affected fish are lethargic and anaemic, while internally the spleen is enlarged. The typical sign of the disease is the presence of hypertrophic cells in various organs when examined with histology.

Both Japanese yellowtail and greater amberjack have been reported to be susceptible to RSIV in Japan (Matsuoka *et al.*, 1996; Kawakami & Nakajima, 2002). Various methods have been developed for the diagnosis of the disease including histopathology, cytology, immunofluorescent antibody tests and PCR (OIE & Red Sea Bream

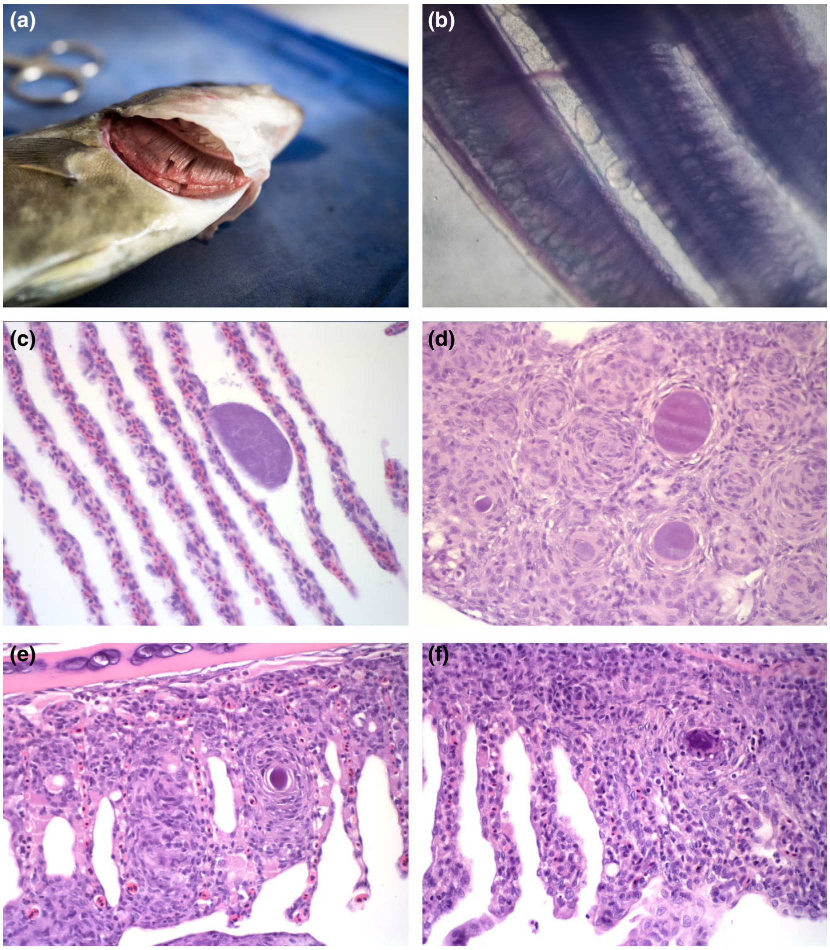

Figure 5 (a) Pale gills with increased mucous in Epitheliocystis-affected greater amberjack farmed in Greece. (b) Epitheliocystis can be visible in fresh squash preparations of gill biopsies when examined under a light microscope. (c) Typical inclusion containing granular material consistent with the description of Epitheliocystis. (d) Two large inclusions containing the bacterial agents and numerous granulomas that are remnants of the host response against the infection. (e, f) Secondary lamellae are fused and massively inflamed following Epitheliocystis infection. (Histological pictures from Dr. Maja Ruetten, Pathovet AG.)

Iridoviral Disease OIE 2019). Prevention can be achieved by a formalin-inactivated vaccine, which is commercially available in Japan. The virus has not been detected in Europe so far.

Yellowtail ascites virus disease

Yellowtail ascites virus (YAV) is a species of Aquabirnavirus and belongs to the family of Birnaviridae (Hirayama *et al.*, 2007). It is an RNA virus that was first isolated from Japanese yellowtail in Japan in the 80s (Sorimachi & Hara, 1985). The disease caused by the virus is associated with mortality in juvenile fish and the characteristic presence of ascitic fluid. In histopathology, affected fish display necrosis of the acinar cells of the pancreas, hepatic parenchymal cell necrosis and hepatic haemorrhages, while some fish may exhibit also lesions in the kidney, stomach and intestine (Egusa & Sorimachi, 1986). The only published report regarding this disease in greater amberjack is from Ehime prefecture in Japan in 1988 when a marine birnavirus showing serological similarity with YAV was isolated from fish with ascites (Kusuda *et al.*, 1993). The disease has not yet been reported in Europe.

Conclusions and recommendations

Disease outbreaks are perhaps the most important obstacles for the further expansion of greater amberjack production in new farming areas like the Mediterranean region. Some of the causative agents like *V. harveyi* and *P. damselae* subsp. *piscicida* are already affecting other cultured species in the area such as European sea bass. Other pathogens are mostly host-specific like some of the monogenean parasites. Finally, completely new or exotic pathogens may emerge as greater amberjack farming intensifies. Fish farmers' previous experience in established farmed fish species can be beneficial, but at the same time it can also create significant problems since greater amberjack farming differs significantly and practices typically employed in the other farmed species may increase the threat of disease outbreaks with catastrophic impact. These concerns include the high fish density in the cages, the age-class overlap at the same sites and the overreliance of the farmers on treatment rather than on prevention. Integrated pest management (IPM) programmes should be the key to success. This type of programmes is being employed for many years in salmon aquaculture in Northern European countries (Jackson *et al.*, 2018) and Canada (BCMAL, 2008; Brooks, 2009), especially for the control of sea lice.

Such programmes include a series of pest assessments/evaluations, controls and decisions. Significant pathogens threatening the viability of the farming of this species should be basically targeted. For greater amberjack raised in the Mediterranean region, the list of potential pathogens is narrower compared with its counterpart farmed in Japan and other Asian countries, and based on the information collected should include the gill fluke *Z. seriolae*, the blood flukes *Paradeontacylix* spp., the bacterium *V. harveyi* and the intercellular Epitheliocystis sp. Caution should be also paid to the protozoan outbreaks in broodstock. Inspections must seriously consider other pathogens as well, which have not been yet discovered or have been detected near to the Mediterranean area (e.g. *Neobenedenia* sp.).

One of the primary concerns in IPM for greater amberjack should be to ensure the quality and the health of the initially used population prior to its introduction in the facilities and especially to the cage environment, where disease management is more complicate. Transfer of greater amberjack seeds is not uncommon among Mediterranean countries or within a country, and consequently, health certificates from the suppliers coupled with sufficient quarantine measures in the recipient enterprises should be paramount to prevent transfer of alien diseases. It should not be neglected that unregulated importation has been blamed as the main aetiology for the emergence/transfer of certain diseases in Japanese farmed greater amberjack. If seeds are produced locally in the farm, maintenance of the broodstock health and hygiene of the land-based facilities should be undoubtedly of primary importance.

Disinfection measures with special reference to ultraviolent application should be enhanced in hatcheries and land-based on-growing facilities to confront outbreaks due to Epitheliocystis and to other microbial pathogens. Advanced mechanical filters, which could prevent the entrance of infectious protozoan stages in land-based facilities, must be mandatory especially for the health of bloodstock, which is highly susceptible. Additionally, tank quality and hygiene must be maintained at the highest levels to aid preventing bacterial and protozoan outbreaks.

Greater amberjack seeds should be vaccinated against *V. harveyi* at the earliest possible (first-stage immunity bath), aiming prolong immunity, which could last at least during the first growing year (second-stage immunity injection) in the cages where fish seem more susceptible. Perhaps, commercial *P. damselae* subsp. *piscicida* vaccines, that are available for other Mediterranean farmed fish suffering from the disease, should be applied, regardless of the fact that the pathogen has not been diagnosed so far in Mediterranean greater amberjack. Possibly, this prevention strategy is already practised in some greater amberjack farmers in the region.

Farming of greater amberjack should be planned with specific strategic cage/unit orientation, considering seawater and tide currents and ensuring a notable distance to avoid the possible contact of potentially common pathogens, as has been stressed for fluke transmission in farmed *Seriola* spp. (Chambers & Ernst, 2005). Greater amberjack cages should be separated from those of meagre, which might harbour Gram-positive bacterial pathogens, as a strategy to eliminate the potential of transferring these novel bacteria. Provided that farming site availability exist, fallowing could be a powerful management measure for the control of flukes in caged *Seriola* spp. (Sitjà-Bobadilla & Oidtmann, 2017). Shading of the conventional cages, which is also a common practice in Mediterranean farming of other fish species, is advised to reduce specific fluke multiplication enhanced by brightness. Net replacement should be applied twice per month, especially during the summer period, to minimize fouling and, thus, reduce the potential egg load of flukes.

Pathogen surveillance and general health monitoring should be continuous, especially during the periods with high water temperatures (spring, summer and fall), where fluke and bacterial outbreaks are favoured. Ideally, fish sampling during these periods for inspection should be carried out at least twice per month. Monthly H_2O_2 (75 ppm for 1 h) baths as a combined preventive/therapeutic approach have been effective for reducing the overall fluke infestations in some Mediterranean greater amberjack farms.

Dietary delivery of effective alternative compounds is strongly recommended to seal the immune defences of fish and/or additionally battle potential pathogens. Practices employed temporary fish starving or feed reduction during the winter period should be always avoided since it could force the fish to feed on aquatic prey and, thus, might acquire pathogenic nematodes or cestodes.

Transfer of pathogens from wild fish aggregated in the vicinity of greater amberjack cages should be also considered, and prophylactic measures are advised with the establishment of perhaps specific net installations in the perimeter of the main cages. This measure could also help the prevention of seasonal attacks from predators as those induced by tunas, dolphins and seals, which can externally damage and stress caged greater amberjack with the potential of the emergence of secondary microbial outbreaks.

Finally, selective breeding programmes have been used with success as prevention tools for a long period of time against important diseases in other domesticated farmed fish species (Henryon *et al.,* 2005). Such strategies, where progeny obtain a genetic architecture sealed with resistant traits against particular disease challenges, are strongly encouraged for greater amberjack.

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