Influence of fish aggregating devices (FADs) on anti-predator behaviour within experimental mesocosms

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ABSTRACT

Commercial fishers have used fish aggregating devices throughout the Mediterranean Sea for over 40 years. These devices attract numerous predatory and forage species in both coastal and offshore environments. This study examined the influence of fish aggregating devices on schooling and aggregating behaviour by small forage fish in quasi-natural mesocosms. Anti-predator behaviour was evaluated for juvenile *Caranx crysos* under a variety of treatment conditions. Results suggest that, in the absence of physical structure, *C. crysos* first respond to a predatory threat by forming a school. When a physical structure is present, however, *C. crysos* show an occasional tendency to aggregate near the structure. These results suggest that a threatened prey species can change their defensive strategy against predatory behaviour. Further examination is required to explain if fish aggregating devices can increase survival rates of post-larval and juvenile prey species in the southern Mediterranean Sea. Management agencies should consider the relationship between the use of fish aggregating devices by commercial fisheries and the potential influence such devices possess on population dynamics of aggregating fish species.

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1. Introduction

In open ocean environments, many pelagic species are attracted to physical structures such as drifting algal mats (Ida et al., 1967; Casazza and Ross, 2008), animal carcasses (Castro et al., 2002), jellyfish (Masuda et al., 2008; Masuda, 2009), pillars (Hunter and Mitchell, 1967; Kingsford, 1993; Fréon and Dagorn, 2000), petroleum platforms (Hastings et al., 1976; Franks, 2000), discarded fishing gear (Carr, 1987), rafts (Shomura and Matsumoto, 1982), and trash (Riera et al., 1999). These structures, commonly referred to as fish aggregating devices (FADs), facilitate spatially heterogenetic aggregations of marine species in otherwise oligotrophic waters. Such aggregations have been well documented for hundreds of fish

species throughout the world's oceans (Castro et al., 2002).

It is commonly believed that aggregative behaviour in fish, either obligatory or facultative, likely evolved to reduce individual predation risk (Hamilton, 1971), enhance food detection (Stephens and Krebs, 1987), or increase mating success (Pitcher and Parrish, 1993). Schooling behaviour is defined by further organization of the aggregate into synchronized groups whereby swimming speed and direction uniformly change to increase hydrodynamic efficiency (Weihs, 1973) or reduce predation risk (Brock and Riffenburgh, 1960). For small aggregative fish, FADs provide either direct protection from predation (Hunter and Mitchell, 1967; Rountree, 1989; Castro et al.,2002) or they facilitate the implementation of mimicry or camouflage techniques that reduce a predator's ability to detect and capture its prey (Hunter and Mitchell, 1967; Kingsford, 1993; Fréon and Dagorn, 2000).

In the southern Mediterranean Sea, the number of permanently moored offshore FADs has consistently increased in recent decades (Morales-Nin et al., 2000). Moored FADs are often placed at great depths (800—1000 m) by commercial fishers, and, despite their

obvious differences, possess a similar function and attractive capacity compared to man-made drifting FADs employed by purse seine fisheries in tropical waters (Dempster and Taquet, 2004; Dagorn et al., 2013). In general, FADs exploit aggregative behaviour of both demersal juvenile and adult pelagic species (Andaloro et al., 2007; Sinopoli et al., 2011). Of these, greater amberjack *Seriola dumerili* (Risso, 1810) and blue runner *Caranx crysos* (Mitchill, 1815) are two of the most common FAD-aggregated species in the Mediterranean Sea during their juvenile and semi-adult stages (Andaloro et al., 2007; Sinopoli et al., 2011). In these early life stages, both species are considered opportunistic predators that consume a variety of crustacean and teleost prey (Badalamenti et al., 1995; Sley et al., 2009), including the consumption of *C. crysos* by *S. dumerili* (Stergiou and Karpouzi, 2002; Auster et al., 2009). As adults, however, both species establish themselves as demersal reef-associated piscivores (Cervigón et al., 1992; Riede, 2004) with little direct predatory interaction (Andaloro and Pipitone, 1997).

Often, large-scale quasi-natural experimentation is hindered because of physical constraints such as the inaccessibility (i.e. depth) to offshore FADs (Andaloro et al., 2007). As a result, predator-prey experiments that observed the defensive strategies of prey in relation to physical structure have largely been carried out in laboratory reconstruction systems that try to mirror the environment of natural habitats (Masuda and Tsukamoto, 2000; Shoji et al., 2007; Masuda, 2009). Similar to large-scale experiments, predator-prey interactions observed under laboratory settings are also subject to limitations such as the size of the prey, the size of the predator, and physical structure implemented in the mesocosm (Masuda, 2009). Consequently, the functional basis of aggregative behaviour in fish is currently based upon empirical observations and unsubstantiated hypotheses (Capello et al., 2012; Dagorn et al., 2013; Robert et al., 2013). Among these, the "shelter from predator (SfP)" hypothesis (Hunter and Mitchell, 1967; Castro et al., 2002) attempts to disentangle the function of these behaviours in small aggregative fish.

The SfP hypothesis describes anti-predator behaviour of small fish when they are aggregated near FADs in open ocean environments (Fréon and Dagorn, 2000). Castro et al. (2002) proposed that post-larval and juvenile fish might aggregate with FADs in order to increase their dispersal capabilities and likelihood of survival during phases when they are most vulnerable to predation. Despite the importance of understanding the behavioural aspects implicated in SfP, studies that examined predator-prey interactions in relation to physical structure *in situ* are limited. Furthermore, if one considers the escapement potential by smaller fish from the gear commonly used in the commercial FAD purse seine fishery (Sinopoli et al., 2012), the SfP hypothesis could play an important role affecting the mechanisms that underlie fish population structure and dynamics. Therefore, additional predator-prey experiments using large-scale mesocosms under quasi-natural conditions are required to examine the role of SfP on aggregative behaviour in fish.

This study examined the two primary traits implicated in SfP behaviour (i.e. schooling vs. aggregative) during predator-prey interactions between *S. dumerili* (predator) and *C. crysos* (prey) held within offshore mesocosms. Three hypotheses related to SfP behaviour were examined using a variety of treatments (e.g., the presence of physical structure and/or predators). First, *C. crysos* would display a greater tendency to form schools as a main defensive strategy in the absence of FADs when predators were present. Second, *C. crysos* would show a significant tendency to aggregate if provided with available structure when predators were present. Finally, *C. crysos* would display randomized swimming behaviour similar to fish associated with FADs under natural conditions when predators were not present. The results of this study

are necessary for implementing proper management strategies under conditions of increasing FAD use in the southern Mediterranean Sea.

2. Material and methods

2.1. Study area

This study was conducted from August–October, 2010 in the Gulf of Castellammare, on the northern coast of Sicily (LAT 38°02′31″ N; LONG 12°55′28″ E). Experimental treatments were performed in both quasi-natural mesocosms (i.e. large aquaculture cages; 3000 m³, diameter 12 m, depth 6 m, mesh size of 12 mm) and open-sea environments. Mesocosms were positioned approximately 1.2 km off the coastline in the eastern Gulf of Castellammare, moored to the bottom at a depth of 32 m. Open-sea treatments were performed in an area approximately 4 km off the coastline at depths between 40 and 100 m.

2.2. Sample collection

Juvenile *C. crysos* (n = 389; mean TL ± S.D. = 8.0 ± 0.9 cm) and semi-adult *S. dumerili* (n = 247; mean TL ± S.D. = 37.0 ± 2.8 cm) were collected during August 2010 in the Gulf of Castellammare using a purse seine beneath commercially implemented FADs. Within 1 h of collection, specimens were transported to separate (*C. crysos* versus *S. dumerili*) offshore aquaculture holding cages. Fish were allowed to acclimate to the holding cages for two weeks prior to selection for experimental treatments; only non-debilitated individuals were selected for use in the study.

2.3. Experimental design

Experimental FADs were constructed by tying three *Phoenix canariensis* palm leaves together with six 2.5 L plastic bottles anchored to either the centre (base) of the mesocosm (i.e. mesocosm treatments) or to the substrate by a 30–40 kg boulder (i.e. open-sea treatments) (Fig. 1A). Polypropylene anchor lines (0.5 mm diameter) were long enough to allow the FADs to float at the surface of the water. With the exception of the mooring point (i.e. the anchor was connected to the centre of the mesocosm instead of the sea floor), all FADs were similarly constructed to those used by the commercial purse seine fishery.

Experimental treatments at both mesocosms and open-sea sites were sequentially conducted for 10 consecutive days between 0900 and 1400 h. Treatments were classified into one of the following three categories:

1) Prey + FAD − Predators (hereinafter FNP; Fig. 2A);
2) Prey + FAD + Predators (hereinafter FP; Fig. 2B); or
3) Prey − FAD + Predators (hereinafter NFP; Fig. 2C).

To assess the effect of captivity (i.e. presence of the mesocosm) on *C. crysos* behavioural responses, additional experiments were performed at FADs in open-sea environments (i.e. Prey + FAD − Predators − Mesocosm, hereinafter WFNP treatment; Fig. 2D). Open-sea experimentation allowed for the observation of aggregative behaviour by *C. crysos* near FADs in the absence of predators.

All treatments included 21 individuals of *C. crysos*; three specimens of *S. dumerili* were used in treatments that incorporated predators (e.g., FP and NFP). The number of individuals of *C. crysos* and *S. dumerili* used per treatment was based on the average number of fish present under FADs within the same season and geographic area as the experimental treatments (Sinopoli et al.,
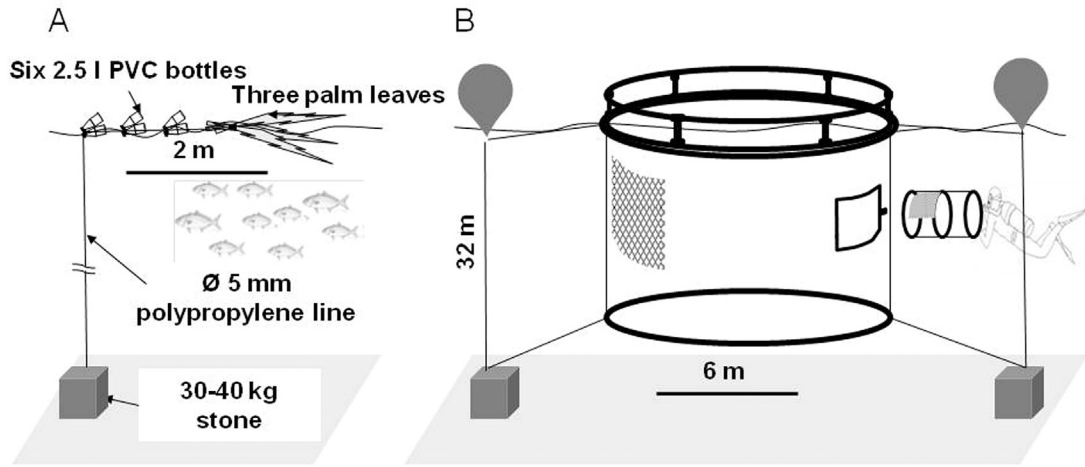
Fig. 1. Technical schematics of A) Fish Aggregating Devices (FADs) and B) the transfer cage and mesocosm used during experimental treatments.
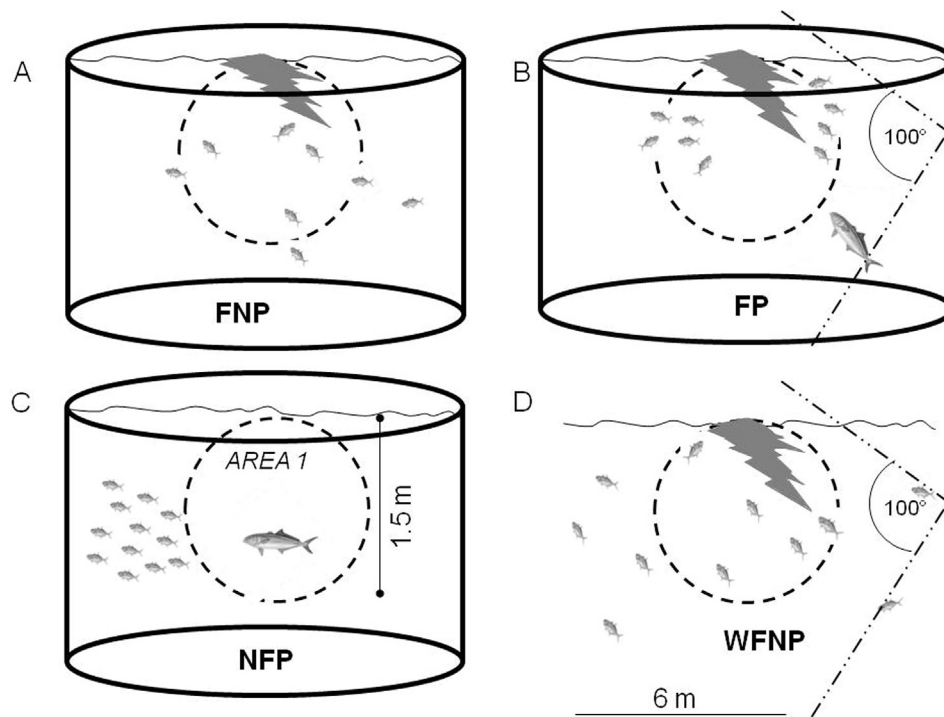

Fig. 2. Experimental treatments for A) FNP = FAD without Predator, B) FP = FAD with Predator, C) NFP = No FAD with Predator, and D) WFNP = Wild FAD without Predator. Dark shaded regions (e.g. A, B, and D) represent a FAD. Large fish depict *S. dumerili* (predator); small fish depict *C. crysos* (prey). The 100° angle (Fig. 2B) identifies the field-of-view for cameras mounted inside the mesocosm arms. Area 1 (identified by the dashed circle) is the distance at which *Ag-Deg* is defined (Fig. 2C).

Table 1
Summary of the total number of treatments used to investigate anti-predator behavioural responses of *C. crysos*. FP = FAD with Predator; FNP = FAD without Predator; NFP = No FAD with Predator; WFNP = Wild FAD without Predator. *Sc-Deg* = schooling behaviour; *Ag-Deg* = fish-FAD aggregation behaviour.

Time period	Treatment				Response variables		
	Mesocosm			Wild	Replicates	*Sc-Deg*	*Ag-Deg*
	FP	FNP	NFP	WFNP			
T1 (0–40 min)	0–40	0–40	0–40	0–40	3	12	12
T2 (40–80 min)	40–80	40–80	40–80	40–80	3	12	12
T3 (80–120 min)	80–120	80–120	80–120	80–120	3	12	12
					Total videos	36	36

2003; Andaloro et al., 2007; Sinopoli et al., 2007). The average number of *C. crysos* was also reflective of natural (i.e. wild) conditions where it is frequently the only species present under FADs. To examine the hypothesis that exposure time to *S. dumerili* affects behavioural responses in *C. crysos*, all treatments (mesocosm and open-sea) were triplicated with increased exposure time during subsequent sessions (Table 1).

2.4. Introduction of fish into experimental mesocosms

C. crysos and *S. dumerili* were transferred separately from holding cages into the mesocosms via small transfer cages (500 L; Fig. 1B) designed to reduce transport stress (Mazzola et al., 2000). For treatments that utilised predators (e.g., FP and NFP), *C. crysos* were introduced into the mesocosm first. *S. dumerili* were held in the transfer cage for a 5-min acclimation period prior to release into the mesocosm. During the acclimation period, the transfer cage was covered with a white tarpaulin so predator and prey were unable to see each other. Experimental time periods began upon release of the predators into the mesocosm (t0).

2.5. Behavioural observations and response variables

Underwater video observations were recorded using Klarstein Fishfinder 20 m Hi-8 waterproof cameras mounted inside the mesocosm. For each treatment, one video camera was hidden inside a pipe that was part of the exterior frame of the mesocosm structure at a depth of 1.5 m beneath the water's surface. Video probes were equipped with an ultra-wide lens, allowing for an approximate 80% field-of-view within the mesocosm (Fig. 2B). Thus, only fish near the extreme perimeters of the top and/or bottom of the mesocosm (i.e. directly above or below the camera) were out of view from the camera angles at any moment in time. During WFNP treatments, video cameras were camouflaged as FAD components and mounted on the FADs at the same distance as in the mesocosm arms.

Predation events and predator avoidance were observed by analysing zoomed single-frame images recorded during individual treatments. Response variables examined in the present study were 1) features of schooling behaviour (i.e. a group of at least five *C. crysos* individuals with polarized and coordinated swimming), hereinafter referred to as *Sc-Deg* and 2) fish-FAD aggregation behaviour (i.e. the percentage of time spent by at least five *C. crysos* at a distance <1.5 m from the FAD), hereinafter referred to as *Ag-Deg* or when the FAD was removed in the NFP treatment when fish were recorded in an area previously occupied by a floating object, we refer to "area 1" (Fig. 2C). The *Ag-Deg* distance of 1.5 m was chosen because *C. crysos* are known to display sheltering behaviour at distances <2 m from FADs (Sinopoli et al., 2011). In order to standardise the distance between the aggregation and the FAD, metric benchmarks were tied onto the palm leaves to provide a scale for distance.

During each 120 min experimental treatment, video recordings were proportioned into three 40 min time periods (Table 1) and independently examined for *Sc-Deg* and *Ag-Deg* Both response variables were expressed as the percentage of time that *C. crysos* schooled or aggregated near FADs during each 40 min observational time period (Martin and Bateson, 2007; Sinopoli et al., 2011). In order to meet the assumption of sample independence (Underwood, 1997), individual fish were replaced between replications within an experimental treatment. For each of the treatments in which both predator and prey were present, the number of unsuccessful and successful attacks (i.e. the consumption of a prey by a predator) were recorded.

2.6. Data analyses

Two-way analyses of variance (ANOVA) were performed on the behavioural variables *Sc-Deg* and *Ag-Deg*. Homogeneity of variances was checked through Cochran's C test (Winer, 1971). The Student-Newman-Keuls (SNK) test was used to examine significant differences ($\alpha = 0.05$) in predator-prey response variables (Underwood, 1997). The GMAV 5.0 software (University of Sydney) was used to perform statistics.

3. Results

3.1. Schooling formation (Sc-Deg)

In the presence of predators, *C. crysos* displayed an immediate schooling behavioural response. Significant differences in *Sc-Deg* were observed between the treatments, time periods, and interaction of the two factors. The SNK test analysing treatments within periods showed a fast response by *C. crysos* to predator presence. During T1, prey in the NFP treatment showed a significantly higher *Sc-Deg* than prey confined within a mesocosm with available structure (i.e. FP; Table 2; Fig. 3). However, *C. crysos* in both NFP and FP treatments showed a significantly higher *Sc-Deg* than prey in treatments without predators during all time periods. For both FP and NFP treatments, longer exposure to predators led to significant increases in prey *Sc-Deg*. No significant differences were observed in *Sc-Deg* between FNP and WFNP treatments (Table 2; Fig. 3).

3.2. Fish-FAD aggregation behaviour (Ag-Deg)

The addition of FADs into the mesocosm played a significant role in observed *Ag-Deg* when both *S. dumerili* and *C. crysos* were present. Significant differences in *Ag-Deg* were observed between the treatments, time periods, and interactive effects of the two factors (Table 3). During the FP treatment, *C. crysos* significantly aggregated at a higher rate to the FAD during later time periods (e.g., T2 and T3) than all other treatments (Table 3; Fig. 4). A significant difference in *Ag-Deg* was observed during the FP treatment compared to all other treatments (Table 3).

3.3. Prey capture success

Although schooling behaviour was similar between FP and NFP treatments (Table 2), *S. dumerili* initiated fewer attacks and experienced less predation success when *C. crysos* were sheltered by FADs. During the cumulative experimental period (i.e. the sum of T1, T2 and T3; ~21 h) of the NFP treatment, a mean of 3.6 ($\pm$0.7 S E) unsuccessful attacks and 2.1 ($\pm$0.6 S.E.) successful attacks were recorded. During the same number of hours of exposure in the FP treatment, however, *S. dumerili* experienced a mean of 2.0 ($\pm$0.6 S.E.) unsuccessful attacks and 0.6 ($\pm$0.3 S.E.) successful attacks. The low number of *C. crysos* predated (26 of 378 used in the two treatments with predators) led us to exclude an implication of a reduction in the number of available prey on group behaviour.

4. Discussion

### 4.1. Disentangling behavioural effects

Compared with natural conditions, *C. crysos* displayed similar *Sc-Deg* and *Ag-Deg* in our experimental mesocosms. Although differences in environmental conditions between coastal and offshore systems can influence fish behaviour, for the purposes of the present study, we assumed that behaviour and abundance of *C. crysos* and *S. dumerili* were not dependent upon the distance between the

Table 2
Results of the ANOVA performed on *Sc-Deg* (schooling behaviour) data for the four treatment levels (FNP, FP, NFP, and WFNP) and the three time periods (T1, T2, and T3). SNK test results are reported. FNP = FAD without Predator; FP = FAD with Predator; NFP = No FAD with Predator; WFNP = Wild FAD without Predator. T1 = 0–40 min; T2 = 40–80 min; T3 = 80–120 min.

Source	DF	MS	F
Treatment	3	14,445	816.9**
Time	2	706.1	39.9**
Tr × Ti	6	194.1	11.0**
RES	24	17.7	
TOT	35		

SNK test			
T1	T2	T3	
NFP > FP > WFNP = FNP	NFP = FP > WFNP = FNP	NFP = FP > WFNP = FNP	

FNP	FP	WFNP	NFP
T1 = T2 = T3	T3 > T2 > T1	T1 = T2 = T3	T3 > T2 > T1

** = P < 0.01.
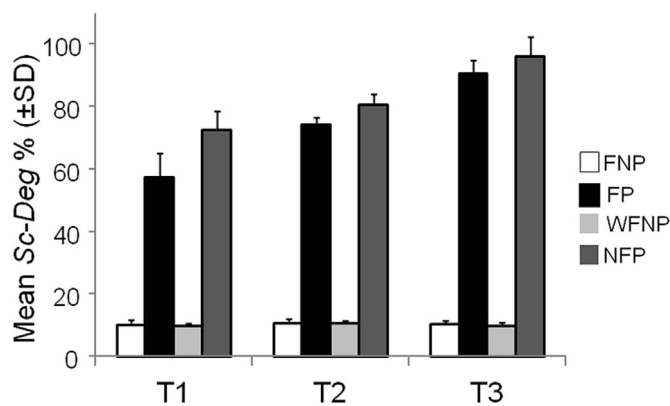
Fig. 3. Mean time (% ± S.D.) in which *C. crysos* displayed schooling behaviour (*Sc-Deg*) for each treatment (FNP, FP, NFP, or WNFP) by time period (T1, T2, or T3). FNP = FAD without Predator; FP = FAD with Predator; NFP = No FAD + Predator; WFNP = Wild FAD without Predator. T1 = 0–40 min; T2 = 40–80 min; T3 = 80–120 min.
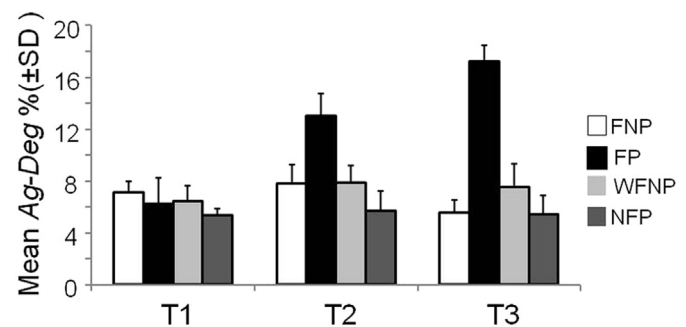

Fig. 4. Mean time (% ± S.D.) in which *C. crysos* displayed aggregation behaviour (*Ag-Deg*) for each treatment (FNP, FP, NFP, or WNFP) by time period (T1, T2, or T3). FNP = FAD without Predator; FP = FAD with Predator; NFP = No FAD + Predator; WFNP = Wild FAD without Predator. T1 = 0–40 min; T2 = 40–80 min; T3 = 80–120 min.

FADs and the coastline (Sinopoli et al., 2010, 2011). This allowed us to exclude potential interference due to placement of the mesocosms on *C. crysos* behaviour (e.g., similar use of FADs in both experimental and wild conditions). Furthermore, we recognize that the spatial heterogeneity afforded by mesocosms may influence prey aggregative behaviour (e.g., aggregation to shade produced by the mesocosm structure). However, we did not observe any form of attraction towards the mesocosm structure by our experimental prey groups and we assumed that our observations were not influenced by this behaviour.

The response variables examined in our study yielded similar results with prior analogous research (Masuda et al., 2008; Masuda, 2009). Masuda et al. (2008) and Masuda (2009) observed that another carangid species, jack mackerel *Trachurus japonicus* (Ayers, 1855), avoided predation by increasing their associative behaviour (corresponding to our aggregation behaviour) with available shelter (i.e. natural and artificial jellyfish). Masuda (2009) also noted that predation avoidance due to increased association degree, however, did not result in increased prey survival rates. Although survival rate was not a focal point of the current study, the decline

Table 3
Results of the ANOVA performed on *Ag-Deg* (aggregation behaviour) data for the four treatment levels (FNP, FP, NFP, and WFNP) and the three time periods (T1, T2, and T3). SNK test results are reported. FNP = FAD without Predator; FP = FAD with Predator; NFP = No FAD with Predator; WFNP = Wild FAD without Predator. T1 = 0–40 min; T2 = 40–80 min; T3 = 80–120 min.

Source	DF	MS	F
Treatment	3	74.4	36.6**
Time	2	24.4	12.0**
Tr × Ti	6	23.4	11.5**
RES	24	2	
TOT	35		

SNK test			
T1	T2	T3	
FNP = FP = WFNP = NFP	FP > FNP = WFNP = NFP	FP > FNP = WFNP = NFP	

FNP	FP	WFNP	NFP
T1 = T2 = T3	T3 > T2 > T1	T1 = T2 = T3	T1 = T2 = T3

** = P < 0.01.

of successful attacks by *S. dumerili* when *C. crysos* were sheltered by FADs suggests that FADs may increase prey survival. Observed differences in predation success between our study and prior works may be related to the amount of shelter offered by the FAD (i.e. the size ratio between the prey and the FAD), the size ratio of the predator to the prey, or the ability of the prey to shelter itself within the physical structure to avoid predation. Future studies should examine the role of these effects as related to potential increased survival rates of prey species near FADs.

4.2. The role of FADs in schooling and aggregation behaviour

In the absence of a physical structure, small forage fish frequently form schools as a natural defensive strategy to predators (Pitcher and Parrish, 1993). Results from our study suggest that *C. crysos* similarly display schooling behaviour when not provided with shelter. In contrast, when both predators and physical structure were in the mesocosm, *C. crysos* showed an increased tendency to aggregate with the FAD. In addition, the dynamics of the aggregative behaviour adopted by *C. crysos* were dependent upon the duration of predator exposure.

Many papers have argued that both schooling behaviour (Pitcher and Parrish, 1993) and the use of physical structures are defensive strategies employed by fish when they become threatened by predators (Rangley and Kramer, 1995; Eklöv and Persson, 1996; Scharf et al., 2006; Shoji et al., 2007). The choice of implementing either strategy seems dependent upon several factors that are likely linked to morphological, developmental, or evaluative characteristics of the species (Masuda and Tsukamoto, 1998, 1999; Masuda et al., 2008; Masuda, 2009; Sinopoli et al., 2011). For example, Masuda (2009) reported that small (<20 mm) *T. japonicus* were unable to school because they lacked of a completely developed lateral line. As a result, these fish compensated by using physical structures as a defensive strategy. In contrast, the increased tendency of *Sc-Deg* by *C. crysos* may be the product of a well-defined lateral line system (Masuda and Tsukamoto, 1999; Sinopoli et al., 2011). Given that *C. crysos* often associate with FADs regardless of the presence of a predator, the significant increases in *Sc-Deg* and *Ag-Deg* support the use of FADs as a defensive strategy by *C. crysos* and falls within the "occasional" category of the defensive behavioural model proposed by Fréon and Dagorn (2000). In contrast, Sinopoli et al. (2011) reported that *C. crysos* <3 cm TL exploited the shadow created by FADs and used them as a "preventative" shelter to reduce the risk of predation. Although this difference may imply that behavioural response may be sensitive to the presence of predators, it does not necessarily indicate that the role of FADs is exclusively related to predator-prey interactions. However, the significant increase in *Ag-Deg* to FADs with increased exposure to a predator highlights a learnt defensive strategy. This antipredator behaviour is well documented in many fish species that are capable of improving their predation response through experience (Kieffer and Colgan, 1992; Kelly and Magurran, 2003). Additionally, learnt individual predation responses are capable of affecting schooling behaviour whereby the school changes movement behaviour in response to an individual's level of perceived threat (Pitcher et al., 1986). Therefore, socially learnt (Brown and Laland, 2003) behaviours related to predation responses likely explain why *C. crysos* rapidly form schools and synchronously aggregated near FADs in the presence of *S. dumerili*.

4.3. Support for SfP and implications for management

Several studies have corroborated the hypothesis that fish use FADs as a shelter from predators (Soemarto, 1960; Gooding and Magnuson, 1967; Hunter and Mitchell, 1967; Rountree, 1989). Fish

aggregating devices can offer direct protection through two mechanisms: (1) by means of interference with a predator's ability to capture prey or (2) via camouflage and mimicry (Castro et al., 2002). During our experimental treatments, we observed direct attacks by *S. dumerili* on *C. crysos*. This led to several observations regarding predatory avoidance dynamics by *C. crysos*. For example, when a predator threatens *C. crysos*, they rapidly formed a group and swam towards the FAD. As the group approached the FAD, it showed a strategy similar to that described as the "fountain effect", where it would divide into two subgroups that swam in opposite directions (Pitcher and Parrish, 1993). This strategy increases prey survivability by inducing a reduction in the predator's attack velocity. While further quantitative studies are necessary to explain the dynamics of predator-prey interactions (e.g., number, direction, and speed of attacks, variability in prey response, etc.), similar predatory avoidance behaviour is frequently observed throughout nature (Davies et al., 2012).

Although not directly supported by this study, the SfP strategy likely increases the survival rate of post-larval and juvenile fish species. In our study, prey groups experienced increased attack rates and higher predation risks when FADs were not present. In southern Italy, the most recent estimate reported over 19,000 permanently moored FADs (Morales-Nin et al., 2000) implanted by the commercial purse seine fishery. However, FADs have been widely used for over 40 years in Spain, Greece, and Malta and it remains uncertain as to how many cumulative FADs exist throughout this region. As FADs become more prevalent, potential increases in survival rates of fish due to FAD association could lead to increased abundance estimates of some species. Alternatively, Masuda (2009) did not find a correlation between increased FAD association and increased survival rate in *T. japonicus*. Furthermore, other factors, such as the deployment distance of FADs from the coast, can impose ecological traps that result in declining indices of growth, condition, and survivability for highly aggregative fish species (Marsac et al., 2000; Schlaepfer et al., 2002). Despite this, *C. crysos* populations off the Sicilian coasts have increased in the last 10–20 years (M. Sinopoli, personal observation). Therefore, further studies are required to investigate the potential long-term effects of increased FAD usage on the population dynamics of small aggregative fish.

In conclusion, the current study utilized a large-scale experimental system to examine predator-prey interactions within quasi-natural mesocosms. Underwater cameras proved to be useful tools to evaluate the influence of FADs with regard to behavioural mechanisms utilised by small forage fish in response to a predation threat. Other methods, however, such as passive acoustic telemetry, have also proven effective as observational tools under similar experimental designs (Forget et al., 2015) and could enhance our understanding of these behaviours when examined concurrently. It is important to understand the relationship between the use of FADs for protection from predators and potential increased survival rates of prey species (Dempster and Taquet, 2004). These relationships have important management implications as fluctuations in fishery stocks will likely influence the number of permitted FADs implemented by commercial fisheries throughout the Mediterranean Sea. The information from this study may also be useful when considering the relationship of physical changes in coastal and marine environments (e.g., coastal development, marine renewable energy developments, etc.) as they relate to fluctuations in fish populations (Wilhelmsson et al., 2006; Fayram and de Risi, 2007).

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