

Towards of a firmer explanation of large shoal formation, maintenance and collective reactions in marine fish

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Abstract Avoiding predation is generally seen as the most common explanation for why animals aggregate. However, it remains questionable whether the existing theory provides a complete explanation of the functions of large shoals formation in marine fishes. Here, we consider how well the mechanisms commonly proposed to explain enhanced safety of group living prey explain fish shoals reaching very large sizes. By conceptually re-examining these mechanisms for large marine shoals, we find little support from either empirical studies or classical models. We address first the importance of reassessing the functional theory with predator-dependent models and the need to consider factors other than predation to explain massive fish shoals. Second, we argue that taking into account the interplay between ultimate benefits and proximate perspectives is a key step in understanding large fish shoals in marine ecosystems. Third, we present the growing body of evidence from field studies that identify shoal internal structure as an

important feature for how large shoals can form, maintain and react as a coordinated unit to external stimuli. In particular, we consider a mechanistic basis of local rules of interaction for group formation and collective dynamic properties that can account for groups reaching very large sizes. Recent research in collective animal behaviour has shifted focus from the importance of global properties (group size) to local properties (local density and information transfer). In contrast to studies of fish shoals in the laboratory, the difficulty in measuring behaviour in large shoals in marine systems remains a major constraint to further work. Advances in acoustical observation have shown the greatest potential to provide data that can link proximate mechanisms in, and ultimate functions of, large marine fish shoals.

Keywords Large marine fish aggregations · Shoaling behaviour · Collective behaviour functional explanations · Local properties · Shoal internal structure

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Introduction

Aquatic ecosystems can host spectacular massive aggregations of micro- and macro-organisms where, for instance, some pelagic fish species are able to reach shoal sizes up to several million individuals (Misund 1993; Makris et al. 2006). By its complexity and

taxonomically widespread nature, animal aggregations have fascinated and challenged scientists for decades. Unraveling the mechanisms and functions of aggregations has been one of the main foci of the study of animal behaviour (Krause and Ruxton 2002). In general, reducing predation risk is presented as the most widely-applicable explanation for why animals aggregate (Hamilton 1971; Pulliam 1973; McNamara and Houston 1992; Lima 1995b; Krause and Ruxton 2002; Caro 2005) and is regularly used to explain the formation of large aggregations observed in marine fishes (Pitcher and Parrish 1993). However, one important limitation to a better understanding of *why* and *how* some fish species form large aggregations remains the challenging task of obtaining accurate behavioural data in natural conditions. It thus remains questionable whether the existing ultimate explanations are suitable to ascertain the functions of large marine fish shoals.

The main objective of our article is not to review the literature related to group-living behaviour in fishes. Instead we aim to build a better understanding of how large shoals form, are maintained, and behave. Firstly, we revisit the classical ultimate explanations of large marine shoals; secondly, we integrate results from in situ research on large shoals of pelagic fish with recent considerations from research in collective behaviour. Before starting this exercise, it is necessary to define the terminology employed throughout our article such as shoals, schools and, especially what we mean by ‘massive shoals’. The term ‘aggregation’ will be used to define any collection of fish that is clumped in space; this could be due to either active attraction between individuals or aggregation around a resource. In contrast, we employ the term ‘shoal’ to refer specifically to an aggregation of fish presenting a level of social cohesion (Pitcher 1983). The term ‘school’ will be employed as a specific subset of a fish shoal where fish present polarized, synchronous swimming patterns and are equally spaced with between-individual distances typically not greater than one body size (Pitcher et al. 1976; Pitcher 1983; Pitcher and Parrish 1993). Yet, it is noteworthy that these well-accepted heuristic definitions have received recent critics as they “...lack precision in terms of quantification” (Delcourt and Poncin 2012). If the minimal shoal size is obviously 2 fish, attempting to clearly define the concept of “massive shoal” remains a difficult task and, to date, we are not aware of any published

definition in the scientific literature. Here and thereafter, we will use the expression ‘massive shoals’ or ‘massive schools’ to refer to large-scale shoals or schools of such a size that any given individual cannot interact directly with *all* shoal/school members simultaneously due to sensory limitations.

By re-examining the classical mechanisms explaining prey group security and challenging them beyond the group sizes that they were originally designed to apply to, we consider how well the ultimate benefits explain very large marine fish shoals. In particular, we highlight the current knowledge gap between the conclusions made by experiments on relative small fish groups in controlled environments (e.g., tanks) and information from field studies on large-scale aggregations of marine fishes. We address the importance of reassessing the functional theory with predator-dependent models as well as taking into account factors other than predation such as foraging or abiotic factors. A better understanding of massive fish shoals requires considering the interplay between proximate mechanisms and ultimate benefits. In particular, we argue that by combining knowledge from in situ studies on large pelagic schools that identify the importance of structural and morphological school features (Fréon et al. 1992, 1996; Gerlotto and Paramo 2003; Gerlotto et al. 2004, 2006; Paramo et al. 2007) and developments in the field of collective behaviour will help identify the *whys* and *hows* of massive shoal formation in marine fishes. There is now a wealth of evidence from field studies on pelagic fishes that aspects of shoal structure, such as inter-individual distance, packing density, internal density heterogeneity (e.g., vacuoles and nuclei) and fish polarization and alignment, are more important in the functioning of large shoals than simple group size, for example in how fish collectively and synchronously respond to external stimuli (e.g., environmental factors and predation). Recent research in collective animal behaviour focuses on local inter-individual interactions to give a mechanistic basis for how animal groups are formed, maintained and move. This framework can account for groups reaching sizes far beyond the perceptual limit of any group member, i.e., a ‘massive school’. As group size increases over orders of magnitude, a conceptual shift from the importance of global properties (e.g., group size) to local properties (e.g., local density or information transfer) in explaining both the behaviour of

individuals within groups and their risk of predation can be identified.

Risk protection in group-living prey: is the traditional view applicable to massive shoals?

Many authors have identified shoaling behaviour as an adaptation to avoid predation (Magurran 1986; Pitcher and Parrish 1993). Over the years, various theoretical models have been developed to formulate predictions on the security advantages of animal grouping (Hamilton 1971; Pulliam 1973; Bertram 1978; Turner and Pitcher 1986; Dehn 1990; Bednekoff and Lima 1998). It has been often argued that grouping offers a combination of several anti-predatory mechanisms to social prey such as a greater power of predator detection through collective vigilance (Lima and Dill 1990; Magurran 1990; Lima 1995a, b), a numerical dilution of risk (Foster and Treherne 1981; Ioannou et al. 2011a) and reduced predator's efficiency due to a confusion effect (Miller 1922; Landeau and Terborgh 1986; Krakauer 1995; Ioannou et al. 2008) and/or coordinated evasion (Magurran and Pitcher 1987). An increase in an individual prey's safety as group size increases is commonly reported in various taxa; the classical group size effect (Lima 1995a; Krause and Ruxton 2002; Caro 2005). As group size increases, prey benefit from an enhanced safety allowing them to reduce their individual effort in anti-predator behaviour (e.g., individual level of vigilance) without increasing their vulnerability. As they experience a reduced predation risk, group-living prey can reinvest time and effort saved in anti-predator behaviour into other fitness enhancing activities as foraging, parental caring or searching for reproductive partners.

Despite this research, there are still important gaps in our basic knowledge of the functions of massive groups. This shortcoming mostly arises because the predictions of the classical theoretical models have only been empirically validated for small to medium prey group sizes, mainly in controlled laboratory settings. As a consequence, when applying these theoretical frameworks to massive marine fish aggregations only extrapolation is possible. In this section, we examine how well the different mechanisms proposed to explain enhanced safety of group-living prey are likely to apply to large-scale fish shoals.

The dilution of risk

Once a prey group has been detected by a predator, prey benefit from a reduced risk of predation from the direct presence of their congeners. This numerical dilution of risk (Bertram 1978) is generally considered an important anti-predator mechanism that provides safety benefits to group-living prey. The concept (Cresswell 1994; Bednekoff and Lima 1998) is based on the simple assumption that, at a given time, only one group member is preyed upon during a solitary predator's attack. In this specific situation, an individual's probability to survive an attack can be numerically expressed by $(N - 1)/N$ where N represents the size of the group threatened. However, we see some issues with arguing unswervingly that risk dilution confers security improvement to prey when transposed to large size aggregations.

When parameterized for large group sizes, the risk dilution model predicts that an individual's survival probability would rapidly pass 95 % (corresponding to a group of 97 individuals) but any further increases of group size would not provide supplemental advantages in the absolute level of security. It is important to note that the maximal group size parameterized, 10,000, is still several orders of magnitude lower than, for example, aggregations size of Atlantic herring (*Clupea harengus*) during winter periods (Misund 1993). Therefore, above a certain shoal size the dilution effect is unlikely to solely explain these observed large shoals.

When shoaling, fish may not *only* face predation pressure from solitary predators killing *only* one individual per attack, but may also be preyed upon by predators in social groups employing cooperative hunting strategies or large predators able to catch several prey during a strike. For instance, some whale species are able to engulf a large number of prey at once and sometimes even the entire prey shoal (Goldbogen et al. 2006, 2008). When parameterized for large group sizes and accounting for different predators' hunting strategies (number of prey caught per attack), the risk dilution model predicts that the survival probability of an individual attacked by a predator taking several prey during an attack would not pass 95 % until a higher number of individuals were caught. In addition, it appears that a very large group size would still not provide supplemental benefits in security (Fig. 1).

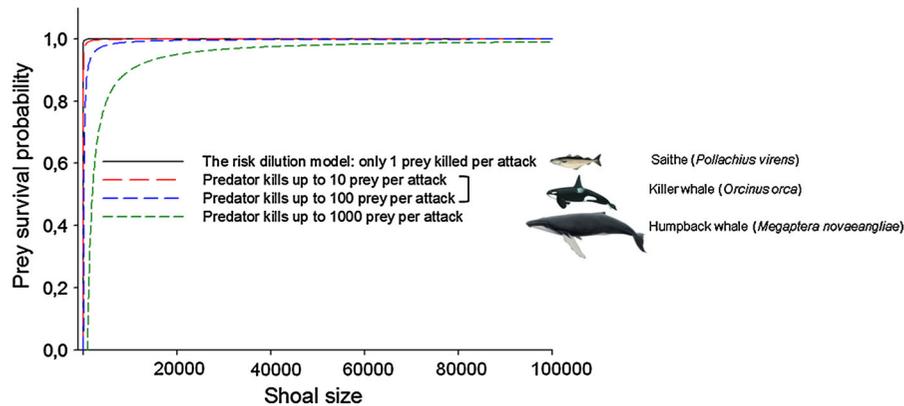


Fig. 1 The Norwegian Spring Spawning herring (*C. harengus*) example: the “predator-dependent risk dilution model” parameterized for large size aggregations (up to 100,000 fish) and accounting for different predators’ hunting strategies

Furthermore, many marine predators use hunting strategies that take advantage of the aggregative behaviour of their prey (Pitcher and Parrish 1993) by forcing shoals to become denser to ensure a better catch efficiency during a single attack (Jonsgård 1966; Nøttestad et al. 2002) or multiple successive attacks. In this case, large shoals become great foraging opportunities for these predators where the high density of prey located in a particular place reduces the search effort or time required to locate the next foraging item. Whilst aggregating in large groups is a successful anti-predator strategy to relax prey from the predation pressure exerted by solitary predators, it may also be a deadly trap for high density fish aggregations when facing large predators that can capture a part (e.g., killer whales) of or the entire shoal during an attack (e.g., baleen whales and human fishing fleets using trawls and purse seine technology).

Surprisingly, general knowledge about the survival patterns of aggregated prey when the predator(s) can consume more than one individual is very limited. Connell (2000) experimentally varied group size in juvenile *Acanthochromis polyacanthus* (Pomacentridae) while manipulating predator exposure in a lagoon environment using a two-treatment design: in one treatment prey were threatened by large predatory fish able to eat several prey during a single attack, and in a second treatment those predators were removed using exclusion cages. This tested the hypothesis that predation pressure from large fish predators on *A. polyacanthus* increases with shoal size inducing a decline in survival in larger shoals. Connell (2000) found a greater per capita mortality in large prey

groups compared to small ones, challenging the traditional “safety in number” principle. Shoaling may not enhance safety at all times, particularly when more than one prey are killed during a single strike.

When facing large predators able to consume prey in large numbers, a safer strategy could be to disperse rather than to aggregate, but to date empirical evidence supporting this idea is lacking. In marine ecosystems, shoaling fish may experience predation pressure from a large spectrum of predator species using different hunting modes, and shoaling could enhance security in most cases. It has been proposed that benefits of group size depend both on predator types and hunting modes (Cresswell and Quinn 2010). The development of a predator-dependent theoretical framework that incorporates predators’ attack efficiency (e.g., number of prey killed during a strike), hunting strategy (e.g., solitary or in cooperating groups) (Lima 2002; Cresswell and Quinn 2010) and is informed by the results of direct experiments on large fish aggregations in natural conditions is therefore warranted.

Risk abatement and predator avoidance

Safety of aggregated prey may be related to the interplay of predator avoidance and the numerical dilution of risk (Turner and Pitcher 1986; Inman and Krebs 1987). Massive fish shoals generally occupy an important volume in the environment making them more conspicuous for predators against the open marine background (Pitcher and Parrish 1993), especially for predators detecting prey items visually or by echo-location. The absence of sensory barriers in the

oceanic pelagic zone (as well as refuge for prey) can make it easier to localize prey aggregations than solitary prey. Turner and Pitcher (1986) presented the attack abatement model that shows that despite an animal group being more likely to be detected by a predator than a solitary prey individual (Pitcher and Parrish 1993), aggregated individuals may nevertheless reach the security benefits of grouping from a decrease in the individual risk of being captured, assuming a fixed number of prey is taken per detection (Ioannou and Krause 2008).

To date, most studies addressing this question have focused on solitary foragers, and the general pattern emerges that prey evolve towards clumped distributions, a response that reduces the overall efficiency of predator searching (Ioannou et al. 2011a). However, predators in large groups have been reported to locate food patches more quickly than fish in smaller groups (Pitcher et al. 1982). Cooperative social hunters are expected to be more efficient locating prey as they can combine their search efforts. However, social foraging may not always improve search efficiency (Giraldeau and Beauchamp 1999; Giraldeau and Caraco 2000). This is especially true if some individuals use the search effort of their companions at their advantage; a situation akin to the game theoretic producer/scrounger scenario (Barnard and Sibly 1981; Parker 1984; Barta et al. 1997; Giraldeau and Caraco 2000). Using simulations based on genetic algorithms, Hamblin et al. (2010) explored the evolution of a prey clumping strategy when preyed upon by non-social or social predators (which include producers searching for prey by themselves and scroungers joining the discoveries of others). The study demonstrated a strong selection for high “clumpiness” (sensus Hamblin et al. 2010) for prey under the pressure of non-social predators and conversely low “clumpiness” for individuals preyed upon by social predators. In both cases, prey survival was improved by inducing higher rates of scrounging and reducing predator search efficiency. Consequently, these results call for a firmer re-examination of the predator avoidance effect while accounting for the various hunting strategies employed by social predators.

Position within a shoal and the selfish herd

An individual’s position within a group affects its risk of predation. A great deal of work on differential

predation risk within prey aggregations in various taxa shows that individuals at the periphery of a group suffer greater predation risk compared to individuals at the group center (Rayor and Uetz 1990; Colagross and Cockburn 1993; Krause 1994; Krause and Tegeuder 1994; Barber and Huntingford 1996; Bumann et al. 1997; Stankowich 2003; Morrell and Romey 2008). However, even though the majority of empirical studies exploring differential predation risk within prey groups reported a positive gradient of risk from the group center to its edge, several studies on fish aggregations nevertheless challenged this result (Parrish 1989; Parrish et al. 1989). Parrish (1989) found an opposite gradient of risk in shoals of Atlantic silversides (*Menidia menidia*), with fish that occupied more central positions suffering greater predation risk from predatory black sea bass (*Centropristis striata*) whereas silversides located at the periphery of the shoal were targeted less often by predators. Therefore, it seems important to consider predator hunting strategies (e.g., original position of the attack, prey preference) during predator–prey interactions (Lima 2002) for a better understanding of the centre-edge effect within animal aggregations.

Within an aggregation, prey should attempt to seek positions that minimize their chance of being the victims of an attack. Gregarious animals can enjoy a reduced predation risk by minimizing the space around them that is closer to them than any other prey, their “domain of danger”, assuming that predators can appear anywhere and attack the nearest prey. This “selfish herd” model, formulated by Hamilton (1971), allows individuals to reduce their risk of being killed by a predator by simply moving toward their neighbours, selfishly interposing neighbours between the predator and themselves. This results in group formation and a compaction of groups (Hamilton 1971; Vine 1971; Viscido et al. 2002). Although the movement rules leading to the group compaction predicted by Hamilton (1971)’s model have been theoretically challenged over the years (Viscido et al. 2002; Reluga and Viscido 2005; Morrell et al. 2011), in nature animal groups becoming denser once alarmed is a widespread observed phenomenon across many animal species including fish (Parrish 1989), supporting the predictions of the selfish herd model (Hamilton 1971).

However, this common view of differential safety related to the spatial distribution of individuals within

an aggregation can be undermined when transposed to large fish shoal systems. In the wild, a common response to increased predation risk exhibited by schooling pelagic fish is a reduction of inter-fish distances and greater fish polarization levels (Fréon et al. 1992; Gerlotto et al. 2006). This particular anti-predatory strategy, increasing school cohesion and density, nevertheless favours the foraging success of large marine mammal predators (Jonsgård 1966; Nøttestad et al. 2002). Again, predator foraging strategies can alter the relationship between social behaviour and risk. A recent study on the manipulation of the aggregative behaviour of hosts (*Artemia* sp.) by parasites (*Flamingolepis liguloides*, *Anostracospora rigaudi* and *Enterocytozpora artemia*) showed that the parasites induce host swarms to become denser, increasing the catch efficiency of filter-feeding avian predators (Greater Flamingos, *Phoenicopterus roseus*), and therefore their transmission to their final hosts (Rode et al. 2013). It appears then that in some cases an increase in group size may not necessarily translate to an increase in security for aggregated individuals. This suggests that a reduction of the “domain of danger” through group compaction may not always enhance prey safety but on the contrary favor predators foraging success.

Collective detection and information transfer

Sharing information about approaching predators among group members is a critical component of safety in fish shoals. Individuals may reduce the risk of predation as group size increases through a greater detection power of the group provided by the increased number of individuals available to detect approaching predators: the “many-eyes hypothesis” (Elgar 1989; Lima and Dill 1990; Lima 1995b). The collective vigilance models generally assume that a whole group will be unambiguously risk aware as soon as one individual detects a threat (Pulliam 1973; Dehn 1990; Lima and Dill 1990; McNamara and Houston 1992). Even if supported by empirical evidence from small animal aggregations, the “one aware, all aware” principle behind collective detection remains to be explored empirically for large-scale animal aggregations.

Dehn (1990) developed a series of models predicting survival probability of group-living prey with the aim of investigating the specific contribution of risk dilution and collective detection with an increase of the animals’

group sizes. Amongst these models, the “security model” predicts that animals gain security benefits with increasing group size through the combination of risk dilution and collective detection. Later, several studies employed the security model to explore vigilance behaviour of free-ranging gregarious species showing its ability to adequately explain the observed vigilance patterns (Rieucan and Martin 2008; Rieucan et al. 2012). However, the size of the groups under investigation was relatively low (never exceeding 50 individuals). When challenged by large group sizes, the “security model”, when considering one predator catching only one prey, predicts that above a moderate group size, approximately 95 individuals, prey survival probability passes over 95 % with only limited security enhancement for groups beyond this size.

It is becoming increasingly clear that rapid information transfer is vital for many group-living animals. The process of information transmission in shoals is thought to affect the dynamics and behaviour of shoals in natural conditions (Gerlotto et al. 2006; Handegard et al. 2012). For instance, Handegard et al. (2012) demonstrated that coordinated predatory sea trouts (*Cynoscion nebulosus*) use an attack strategy that forces prey shoals (juvenile Gulf menhaden, *Brevoortia patronus*) to split, reducing the shoals’ cohesion and thus disrupting information transfer within the shoal and thereby increasing predators’ catch success. The principal requirement for an efficient transmission of information is that the information is conveyed rapidly among all group members before the attack regardless of their positions in the group. The speed of transmission through the group can exceed the speed of an approaching predator: the “Trafalgar effect” as demonstrated by Treherne and Foster (1981). Sudden changes in swimming speed or direction from risk-aware fish can inform other individuals of the threat. Then, the speed at which information spreads through the shoal can outpace the swimming speed of fish ensuring a rapid propagation of predator cues improving the safety of all group members (e.g. “waves of agitation” Radakov 1973, Treherne and Foster 1981). The transmission of detection information through a group can be affected by the structure of the aggregation (Lima and Zollner 1996; Proctor et al. 2003), warning signals specificities (Beauchamp and Ruxton 2007), or characteristics of the environment such as water turbidity (Abrahams and Kattenfeld 1997) or water flow (Chicoli et al. 2014). For instance, water

turbidity can alter the transmission of visual information in fish shoals (Abrahams and Kattenfeld 1997), with fish not directly responding to the threat being less likely to observe the anti-predatory behaviours of risk-aware companions, reducing their probability to survive an attack.

Although there is evidence that anti-predator reactions of fish can propagate rapidly across large shoals, understanding how information spreads in shoals remains a central challenge. Numerous studies have examined the mechanisms of long-range information transfer in animal groups (Radakov 1973; Gerlotto et al. 2006; Ballerini et al. 2008; Makris et al. 2009; Cavagna et al. 2010; Bialek et al. 2012; Strandburg-Peshkin et al. 2013). Waves of agitation have been proposed as a possible mechanism for how massive shoals can react collectively to external stimuli (Radakov 1973). Radakov (1973) first experimentally demonstrated the process of waves of agitation in laboratory settings on relatively small shoals (300 individuals), and recent field studies have observed and quantified such waves of agitation directly in free-ranging shoals (Axelsen et al. 2001; Gerlotto et al. 2006; Makris et al. 2009). For instance, Gerlotto et al. (2006) found, using multibeam sonar, that the average speed at which waves of agitation crossed schools of anchovies (*Engraulis ringens*) was 24 times faster than the average schools speed. A key result from these in situ studies is that information can be conveyed rapidly and effectively, with no loss of informative content (Axelsen et al. 2001), over great distance size, and importantly regardless of the shoal size.

Several field studies have highlighted the importance of shoal internal organization on the transmission of information among fish (Fréon et al. 1992; Freon et al. 1993; Fréon et al. 1996; Axelsen et al. 2001; Gerlotto and Paramo 2003; Soria et al. 2003; Gerlotto et al. 2004; Makris et al. 2009; Paramo et al. 2010). Variations in shoal internal structure (e.g., inter-fish distances, polarization and alignment levels between neighbouring fish) are common in pelagic fish exposed to the risk of predation or changes in environmental factors (Fréon et al. 1992; Misund 1993; Fernö et al. 1998; Axelsen et al. 2000). Shoal structural flexibility is considered as an adaptation improving information transfer among school members (Axelsen et al. 2001; Gerlotto and Paramo 2003; Gerlotto et al. 2006; Makris et al. 2009). The internal structure of massive Peruvian anchovy schools

changed after the passage of a first wave of agitation in response to an attack from sea lions (*Arctocephalus australis* and *Otaria byronia*), with fish becoming more homogeneously distributed (Gerlotto et al. 2006). This indicates that anchovies adopted spatial organization that would enhance the propagation of information during subsequent waves of agitation, and ultimately the efficiency of their collective evasive reactions towards predators. In particular, high degrees of polarization and alignment between neighbours fish are thought to enhance shoal cohesive structure and facilitate an effective information propagation (Viscido et al. 2005, 2007; Herbert-Read et al. 2011; Ioannou et al. 2011b). Atlantic herring can regain their pre-exposure level of alignment extremely rapidly (<1 s) after being exposed to an artificial stimulus, demonstrating the importance of aligned swimming in schooling fish (Marras et al. 2012). Shoal internal structure appears to be a key component that needs to be considered to better understand the reactions of shoals' to external stimuli and predators, as the security benefits from collective detection cannot be fully explained by simply looking at the number of individuals shoaling together.

Confusion effect, coordinated escapes and shoal maneuvers

Cognitive constraints on information processing can reduce the targeting efficiency of predators as they attack multiple prey, reducing risk for prey in groups (Tosh et al. 2006; Ioannou et al. 2008). To overcome the increased difficulty of selecting and successfully targeting an individual prey item from many, predators can reduce vigilance for their own predators (Milinski 1984), increase the time taken to make an attack (Milinski 1977a), and/or shift attacks to prey in smaller groups or on the edge of the group (Milinski 1977b). The result is an increased safety for prey that join and stay with large groups. However, as was discussed previously with regards to the dilution effect, predators that do not rely on targeting single individuals, such as Great Flamingos which filter feed (Rode et al. 2013) or baleen whales, are unlikely to suffer from a confusion effect and instead increase their feeding efficiency when prey aggregate. A predators' experience with large prey groups can reduce the strength of the confusion effect (Tosh 2011), suggesting a frequency-dependent effect. Prey movement is generally thought

to be required for the confusion effect, but the coordinated movements seen in fish aggregations and other prey groups such as European starlings (*Sturnus vulgaris*) (Cavagna et al. 2010) are not necessary to induce the effect (Ruxton et al. 2007; Ioannou et al. 2012). Thus, the confusion effect is likely to apply to most fish shoals irrespective of the degree of coordinated motion. It is likely, however, that the coordinated responses seen in fish shoals as directed responses to predators' attacks, e.g., splitting and joining behind the predator or the "fountain effect" (Major 1978; Magurran and Pitcher 1987; Handegard et al. 2012), increases predatory confusion as well as social information transfer and a selfish herd effect. There will of course be a minimum number of fish in a school required to perform these coordinated responses, suggesting that the relationship between group size and the degree of confusion will not be simple (e.g., increasingly sharply at a threshold number of prey before saturating at large group sizes).

The confusion effect is produced by a cognitive overload of the predator's sensory system (Tosh et al. 2006). As prey group size increases, it becomes increasingly likely that only a subset of the group is visible to the predator, especially when the predator is close to prey (Ioannou et al. 2009). In aquatic systems where water turbidity can substantially reduce visual range, this could occur at relatively small group sizes. The degree of confusion would thus be related to the number of prey visible in the predator's visual field (i.e., the local density of prey), and not the total group size. In support of this hypothesis, Ioannou et al. (2009) demonstrated that targeting accuracy of three-spined sticklebacks (*Gasterosteus aculeatus*) was related to the density of other prey close to the target individual, rather than a larger-scale measure of density that included all prey individuals in the group. To date, no study has explicitly tested whether the confusion effect is affected more by local density than overall group size in large groups of prey, and it is highly unlikely that individual predators can see all prey in groups that can exceed many kilometers in size (Makris et al. 2006).

The need to consider factors other than predation

Apart from anti-predatory behaviour, fish are also engaged in other fitness enhancing activities where

group size may influence performance. Within the same species, variability in both shoal size and external shape are regularly observed in marine systems and generally explained by the actions of several abiotic and biotic factors. For example, in the North Sea, a great variability in intra-specific shoal size of herring, saithe (*Pollachius virens*), and sprat (*Sprattus sprattus*) has been reported (Misund 1993). Although predation is seen as the main driver for the evolution of group behaviour, factors other than predation can be identified to explain the formation of massive shoals in marine fishes (Parrish 1991; Pitcher and Parrish 1993), and the intra-specific differences in shoal shape and structure (e.g., diffuse layers or dense schools). Among these factors, the most commonly cited are geographic differences (Misund 1993), vertical distribution and migration in the water column (Axelsen et al. 2000), seasonality (Nøttestad et al. 1996), diel cycle and light intensity (Skaret et al. 2003), reproduction (synchronous spawning) (Axelsen et al. 2000), reduced oxygen levels inside dense shoals (Dommasnes et al. 1994; Brierley and Cox 2010), and energetic requirements or motivational state (Langård et al. 2014).

Locating resources is critical for fish undertaking long distance migrations (Makris et al. 2009) where navigating to a suitable habitat in an energetically efficient way is crucial. There is evidence that schooling fish and other migrating animals can orient more accurately in larger groups (Quinn and Fresh 1984) because different individual migration tendencies or errors in gradient following are averaged resulting in a more accurate estimate of the correct destination (the "many wrongs" principle: Simons 2004, see also Grünbaum 1998; Torney et al. 2009). Such a positive effect of collective behaviour would, however, be expected to saturate above a certain number of individuals. In a recent laboratory study using golden shiners (*Notemigonus crysoleucas*), Berdahl et al. (2013) demonstrated that shoals were increasingly able to track gradients of darkness as group size increased within a range of 1–256 fish and that individuals have only a poor ability to track the gradient when solitary. Both of these results suggest that the advantage of grouping is more robust and general than the "many wrongs" principle as this is expected to saturate at relatively small group sizes. Fish also seem to rely on experienced group members during group movements (Corten 1999), and in a large

group there is a greater probability that at least some individuals know the way. A certain number (Couzin et al. 2005) or proportion (Huse et al. 2002) of experienced fish seem to be required to navigate or maintain traditional migration routes.

Foraging is a particularly important activity to be considered in a thorough examination of large shoal sizes. Empirical evidence suggests that a group of fish (up to 20 individuals) locates food faster than solitary foragers, and a larger group is more effective than a small group (Pitcher et al. 1982). However, the benefit of reduced search time is expected to reach an asymptote fairly quickly as group size increases (Pulliam and Caraco 1984). Competition for food appears as the major cost of shoal membership (Pitcher and Parrish 1993), and for large groups the ratio between the benefit and cost is rapidly reduced by increasing group size since the benefit stays the same while competition is assumed to increase continually. Smaller, less cohesive shoals have a reduced overlap of perceptive field resulting in less competition and less interference of individual feeding acts (Blaxter 1985).

Fish also have to overcome the hydrodynamic drag from the water. Schooling may offer hydrodynamic advantages as it may reduce energy costs as the fish can stay in the slipstream of another (Weihs 1973; Sfakiotakis et al. 1999; Hemelrijk et al. 2014). For instance, rainbow trout utilize vortices when swimming in strong water currents (Liao et al. 2003). However, the hydrodynamic advantages of schooling are debated with some species not swimming in the optimal spatial positions to minimize drag (Partridge and Pitcher 1979). While testing empirically the hydrodynamic effects in schooling fish remains a difficult task, the recent development of computer models considering complex hydrodynamic effects of fish swimming, such as viscosity or interactions among wakes and individuals (Hemelrijk et al. 2014), allows researchers to better grasp the energetic benefits of swimming in schools. Additionally, although the fish can divide the costs by changing position in the school over time, it remains untested whether potential positive hydrodynamic effects will increase above a moderate shoal size.

Parasites are believed to constitute a very serious threat for group-living fish (Barber and Rushbrook 2008). An increased group size gives, under some conditions, protection from parasites by a dilution of

risk and by an increased chance of the parasites being eaten by the predatory fish (Poulin and FitzGerald 1989). However, here again this has only been clearly demonstrated for small to moderate group sizes (up to 20 fish).

In conclusion, with regard to factors other than predation it is unlikely than fish benefit significantly by staying in shoals above a certain size. The positive effects of an increase in group size has generally been demonstrated for a relatively small number of fish in captivity and strong evidence suggesting that an increase above a moderate shoal size would provide any benefits is still lacking.

Constraints in available information and mechanisms

Traditionally, it has been questioned if an optimal group size exists under realistic conditions (Sibly 1983; Pulliam and Caraco 1984). However, even if we assume that there is an optimal shoal size, it is still a formidable task for fish to stay in a shoal of that size (Fernö et al. 1998). Due to variations in abundance and type of predators and resources, the theoretically optimal shoal size would be expected to show large fluctuations, often over short time intervals. A dynamic interplay between the threat constituted by different predators with various hunting strategies together with variations in abundance and patchiness of resources at different scales should make it practically impossible for an individual fish to be, at all times, in a shoal with the optimal number of conspecifics. To be in a shoal of the optimal size averaged over longer time periods is a challenge that would demand advanced perceptive and cognitive skills. Nevertheless, we can attempt to depict the set of decisions that fish in shoals would take to accomplish such adjustments. First, fish would have to monitor the average situation they experience to determine their mean preferred shoal size. Further, to adjust to this set value, fish would need to estimate their present shoal size. In theory, it would be possible that fish could get a rough estimate of current shoal size based on, for instance, the number of times they are in contact with the edge of the aggregation. Finally, between-individual differences must be accounted for. What constitutes the optimal shoal size for one individual is not necessary the right one for another individual in a

different state, for example, an individual with higher energetic demands.

Given these constraints in the perceptive, cognitive and group size-adjusting mechanisms, it is not realistic to expect fish to stay in groups of the theoretically optimal size. It becomes conceptually difficult to identify mechanisms that would permit shoal size to be reasonably well adjusted to the prevailing conditions. However, this does not rule out that some variations in shoal size seem clearly adaptive. Several studies with small numbers of fish have shown that hungrier fish spend less time with larger groups of conspecifics than do well-fed individuals (Barber and Huntingford 1995; Reeb and Saulnier 1997), and non-feeding pelagic fish shoals have been observed to be larger than feeding shoals (Nøttestad et al. 1996). We will now consider how fish could accomplish such structural adjustments in shoals.

Local rules explaining the existence and behaviour of massive fish shoals

In contrast to the functional discussion above on the reasons why fish form shoals of a particular size, research on collective behaviour has shifted focus to the individual local rules of interaction that generate groups and collective properties (Aoki 1982; Giardina 2008). In this section we advocate that by combining the results from collective behaviour research and acoustic observations of oceanic shoals, a more accurate explanation for the formation, maintenance and structural and morphological variations of massive shoals in marine fishes can be provided.

An individual fish does not need an overview of the composition and behaviour of the shoal it is within at a particular moment; information that may be costly or impossible to acquire when shoals are large. Instead the properties of a shoal are the product of local rules between neighbouring fish that, via self-organization, generate behaviour at the group level as an emergent consequence of individuals' interactions (Parrish et al. 2002; Vabø and Skaret 2008). Models of collective behaviour generally make the assumption that individuals repel one another when they get too close and otherwise are attracted toward, and/or align their direction of travel with their neighbours. Despite seeming over-simplified, these models have been successful in recreating both distributions of local

properties such as inter-individual spacing (Lukeman et al. 2010) and global properties (Hemelrijk and Hildenbrandt 2012). For example, by simply changing the distance over which individuals align with their neighbours, Couzin et al. (2002) simulated disordered swarms, groups milling around an empty core (as often observed in several pelagic fish species), and highly aligned, mobile groups (see also Nøttestad et al. (2004)). Increasingly realistic models based on attraction-alignment-repulsion in shoals of fish are also able to recreate empirical observations of shoal shape and internal structure (Hemelrijk and Hildenbrandt 2012).

In the past few years, detailed examination of shoaling behaviour based on large datasets collected in controlled settings has been possible with advances in computer tracking and analysis (Katz et al. 2011; Gautrais et al. 2012). This has been facilitated greatly by the extensive modeling that has established a conceptual framework for interactions in groups, allowing empirical tests of both the models' assumptions and predictions. One important finding from these studies is that the rules fish use to interact with one another appear to be qualitatively similar across group sizes (Katz et al. 2011; Gautrais et al. 2012). In the study of Tunstrøm et al. (2013), local and global group properties were examined across a range of group sizes from 30 to 300 fish in a shallow tank. Although global properties such as the degree of rotation and time spent in a disorganized, swarm-like state changed with increasing group size, local properties (fish speed and local density) were constant across group sizes and only affected by the type of shoal formation (swarm, polarized and milling). This suggests that grouping behaviour is not directly affected by the total group size and instead fish regulate local properties that are within their immediate perceptual range.

Variations in shoal size can thus be explained by simple individual behavioural rules based on attraction and repulsion towards near-by fish (Katz et al. 2011) in combination with attraction to external stimuli like food (Nøttestad et al. 2004). In particular, Katz et al. (2011) found attraction between individuals until they have reached a certain inter-fish distance after which they repel each other. In non-feeding fish with no other force influencing them, this could result in larger and larger shoals, as shoals that encounter each other would have a certain probability to join because of attraction between near-by fish in different

shoals that come into contact. If, however, the fish are engaged in feeding activities or are strongly motivated to feed, the relative attraction to conspecifics will then decrease, resulting in more individualistic behaviour with increasing inter-fish distances as food level decreases (Robinson and Pitcher 1989; Sogard and Olla 1997; Hensor et al. 2003). This should increase the probability for individuals and groups to come apart, and the resulting splitting of shoals will reduce the shoal size. Banded killifish (*Fundulus diaphanous*) freely form shoals where size is adjusted in a context-dependent fashion, forming smaller shoals when presented with food odour and aggregating in larger shoals when exposed to chemical alarm cues (Hoare et al. 2004). Modeling work has demonstrated that a range of shoal sizes and characteristics can occur by changing the strength and range of the attraction and repelling forces between the individual fish (Vabø and Nøttestad 1997). Hence, by assuming interplay between these tendencies, it is then possible to develop a better understanding of how shoal size can be roughly adjusted to the relative importance of predation and food.

Individual fish not only have the option to join, stay or leave a shoal based on the prevailing conditions but may also influence the shoal density by changing their inter-fish distances. Variations in shoals density, which are often observed in pelagic fish (Nøttestad et al. 1996), are usually explained by changes in the parameter values of the forces between nearby fish influencing the local interactions. Such changes in density would enable individuals within a shoal to rapidly adjust to various situations without adjusting the number of fish in the shoal. For instance, although increasing prey density may increase conspicuousness to a predator (Ioannou et al. 2009), a more compact shoal should decrease risk via a stronger confusion effect and more effective escape maneuvers. Likewise, a shoal can decrease competition for food or avoid oxygen depletion that arises at the center of dense aggregations (Dommasnes et al. 1994; Brierley and Cox 2010) by spreading out without splitting into smaller groups or by distributing at depth with more dissolved oxygen. Such behavioural and structural changes would reduce possible negative effects associated with massive shoals.

Acoustics surveys, conducted in oceanic systems, showed that large shoals of sardines, herrings and anchovies can display a great range of shape and internal organizations, for example shoal density, fish

positioning or intra-shoal density distribution (Fréon et al. 1992; Gerlotto and Paramo 2003; Gerlotto et al. 2006; Paramo et al. 2007, 2010). Several mechanisms have been identified, such as the “moving mass dynamic” (Misund 1990) or “compressing-stretching-tearing” (Fréon et al. 1992), to explain variations in internal organization of a shoal, and in particular its internal density distribution (Fréon et al. 1992; Misund 1993). The compressing-stretching-tearing (CST) hypothesis (Fréon et al. 1992) predicts that inter-fish distances and polarization level depend on the state of the environment (e.g., stressed vs. unstressed situations). Under low stress, shoaling fish should exhibit more individualist/exploratory behaviour resulting in greater inter-fish distances and lower polarization until the shoal would reach its lowest cohesive limit; the “maximal stretching distance” (Fréon et al. 1992). This “stretching” mechanism is used to explain how vacuoles, i.e., zone with few or no fish, can form in a shoal as the results of a set of decisions made by each fish to join or leave their closest neighbours. Conversely, when exposed to higher risk, schools should become denser, with fish getting closer to each other, exhibiting greater polarization, and closing the vacuoles until reaching a “minimal compressing distance” (Fréon et al. 1992). An expected result of the compressing mechanism is the formation of zones of high fish density inside a shoal, i.e., nuclei (Gerlotto and Paramo 2003). Nuclei are presented as the maximal self-organized units of interaction responsible of shoal cohesion, efficient information flow and emergence of collective reactions (Gerlotto and Paramo 2003; Viscido et al. 2005; Gerlotto et al. 2006). In wild sardines (*Sardinella aurita*), shoals are comprised of several nuclei of which the diameter can reach 10 m (Gerlotto et al. 2006).

In conclusion, there are obvious parallels between the attraction–repulsion rule of interaction and the proposed mechanisms of variation in pelagic shoal internal organization, reinforcing the idea that formation of massive shoals in natural conditions can be mechanistically understood without referring to the specific shoal size.

Does shoal size still matter?

Evidence accumulating from in situ observations and experimentation in controlled settings allow us to now

tease apart the mechanisms directly involved in large-scale collective behaviours and formation of massive shoals. The joint achievements of these two axes of research have demonstrated the importance of considering internal organization in the formation of very large marine shoals and their reactions to external stimuli such as predators, vessels or other environmental factors.

Strengthening the idea that a shoal's internal structure is critically important compared to shoal size in the case of massive shoals will require the development of experiments in which internal organization could be manipulated and collective responses quantified. Recently, Rieucau et al. (2014) and (Rieucau et al. in press) explored the collective evasive reactions of wild caught Norwegian herring by conducting a series of simulated-predator encounter experiments in sea cages on schools which matched the sizes of natural aggregations (~60,000 fish). In particular, school density, perception of risk and predator characteristics were manipulated. Using echosounders and high-resolution imaging sonar, they demonstrated that the strength of herring collective avoidance depends on the sensory signature of the simulated predator and on the school density. For instance, weaker collective avoidance reactions were observed in a low density school compared to a denser school, suggesting that the magnitude of collective reactions and how efficiently predator-related information spreads across a school strongly depend on a shoal's internal organisation.

Finally, fish can combine the advantages of being in a small and large group. As mentioned earlier, shoal clustering could provide shoals with the option of rapid size adjustments through splitting and joining and thus permit flexibility of responses to a dynamic environment (Mackinson et al. 1999). This may enable shoals to have effective predator defense whilst simultaneously receiving foraging benefits associated with smaller schools. Hence, both changes in density and keeping close distance to neighbouring shoals could be alternative mechanisms that in a given situation could reduce the negative fitness consequences of deviations from the theoretically optimal shoal size. However, can these simple mechanisms really explain the existence of massive aggregations of several millions of fish? In non-feeding shoals there is, with increasing shoal size, initially an increasing ratio between benefits and costs resulting in an increased

individual fitness up to a certain shoal size. If the fitness to stay in shoals above that size remains relatively constant, then very large shoals will not be more beneficial than shoals of a moderate size but neither do they incur any significant disadvantages. The availability of other shoals in the vicinity may be restricted. Hence, it could be an advantage to stay in a somewhat larger shoal that provides a buffer against such unforeseen events. In addition, splitting can take place relatively easily when the presence of resources decreases the cohesion between the fish.

Conclusion

By re-examining the classical functional theory and the commonly proposed mechanisms that underlie improved safety of group-living prey (dilution of risk, predator avoidance, enhanced predator detection, confusion effect, coordinated evasive maneuvers) for large group sizes, we advocate that the functional framework, in its current state, does not adequately account for the formation of fish shoals reaching very large sizes. Reassessing the functional theory requires the development of predator-dependent theoretical models combined with direct observations and experimentations on large fish shoals to better understand the ultimate benefits and costs of massive fish aggregations. In particular, more explicit attention should be devoted to integrating the large range of predator types, hunting strategies (e.g., solitary vs. social, prey preference, original position of the attack) and attack efficiency (e.g., number of prey catch per strike) that aggregated prey may encounter.

The collective behaviour framework provides a mechanistic basis focusing on local rules of interaction for group formation and collective dynamic properties that can explain how marine fish form massive aggregations. Recent research in collective animal behaviour suggests that the rules of individuals' interactions are constant across group sizes, explaining the occurrence of very large aggregations beyond the perceptual limit of any group member (Kunz and Hemelrijk 2012). Thus, the further development of a framework that integrates ultimate and proximate perspectives would allow the generation of precise functional and mechanistic predictions to build a firmer explanation of large shoals in marine fish. In addition, field studies on pelagic social fishes have accumulated

supporting evidence that identify the important role of internal organization (e.g., packing density, density heterogeneity, fish position and polarization) to explain why marine fishes aggregate in massive shoals and how they collectively react to environmental (e.g., abiotic factors and predation) and anthropogenic (e.g., fishery gear, vessels) perturbations.

Advances in acoustical and optical observation technology provide efficient means to precisely quantify large-scale collective behaviours in shoaling fish in situ. These techniques can be used to address several of the challenges we face when validating and refining the behavioural models and to link proximate mechanisms and ultimate benefits. In particular, simulation frameworks where different behavioural patterns are simulated and the corresponding acoustic signals are predicted (Holmin et al. 2012) provide a powerful tool to aid the interpretation of the observations. Fine-scaled prey-predator interactions can be observed, and changes in anti-predator behaviours as a function of predator strategy and shoal size could be assessed. To our knowledge, no other biological system can be observed across these scales, and the marine systems are thus well suited to challenge the existing theoretical models.

We believe that collectively we possess most of the puzzle's pieces to explain the evolutionary basis of the formation of massive shoals. The missing pieces of knowledge will certainly be found in experimental studies conducted on wild massive shoals directly in the open ocean.

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