

Schooling in fishes

Valentina Di Santo, Division of Functional Morphology, Department of Zoology, Stockholm University, Stockholm, Sweden

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Key points

- Fish in school formations display remarkable swimming synchronization and polarization.
- Fish may take advantage of vortices shed within a school to save energy.
- School formation is a fundamentally 3-D dynamic system and, as such, we need to quantify volume and 3-D kinematics to understand the rules of this locomotor behavior.
- It is still unclear how to quantitatively discern shoaling and schooling behaviors, and how disturbances may affect the stability of the formation.
- Schooling requires integration of sensory systems and swimming performance that might be affected negatively by climate change stressors.

Glossary

Aggregation Process or behavior of species coming together and forming groups. It is commonly observed in fishes wherein individuals gather benefits such as improved foraging, protection, and mating opportunities.

Lateralization Specialization and differentiation of functions between the left and right hemispheres of the brain. It is the tendency for certain cognitive processes or behaviors to be more dominant or localized in one hemisphere compared to the other. This phenomenon is commonly observed in animals, including fishes.

Polarization Phenomenon where individuals of a group tend to align themselves along a particular axis or direction. This behavior is usually observed in animals such as fishes and birds for various reasons such as improved navigation or group protection.

Rheotaxis It is the behavior of an aquatic organism to move against or along the flow.

Schooling This refers to cooperative behavior observed in fishes, where individuals of the same species swim together closely in a synchronized manner. This behavior is often observed in forage fishes, where the benefits of schooling include predator avoidance and improved foraging and locomotor efficiency.

Shoaling It is the behavior of fish coming together and swimming closely in a group. Shoaling is more loosely organized than schooling and it is commonly observed in fishes that live in shallow waters, such as rivers and ponds.

Vortex trail It is a series of vortices formed behind a moving object in a fluid medium, such as air or water. This phenomenon is commonly observed in birds, fishes, and insects, as well as aircrafts.

Von Kármán vortex street Phenomenon observed in fluid dynamics, where an array of vortices form in the wake of a solid object placed in a flowing fluid. When a fluid flows past a solid object, such as a cylinder or an airfoil, it separates into two streams, one on each side. The flow on the side facing the incoming fluid is faster, while the flow on the opposite side is slower. As the faster-moving fluid flows past the object, it creates regions of low pressure, causing the fluid to curve around and behind the object. This curved flow generates vortices that alternate in a regular pattern, known as the von Kármán vortex street. The vortices form in pairs, with each vortex rotating in an opposite direction to its neighbor. The alternating vortices shed by the object result in a series of swirling patterns that trail downstream. These vortices form a distinctive pattern of alternating eddies, resembling a row of spiral-shaped whirlpools. This pattern persists as long as the fluid continues to flow past the object. Von Kármán vortex streets can be observed in various natural phenomena, such as the flow of water around rocks in rivers or the movement of air around mountains. They are also encountered in engineering applications, such as the wake turbulence behind tall buildings or the flow around bridge piers. The phenomenon is named after Hungarian-American physicist Theodor von Kármán, who first described it in 1912.

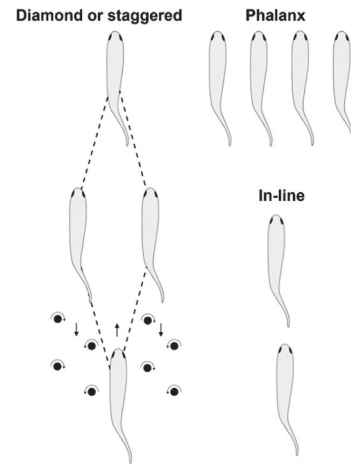
Abstract

Schooling is the collective movement of fishes characterized by high polarization and swimming synchronization of individuals within the group. This locomotor behavior is fundamental to the survival of many species of fish that exhibit schooling during some stage of their life. While collective motion has been a topic of extensive research, this article provides an overview of the mechanics and energetics of locomotion during schooling behavior, including the potential effects of climate change on this movement, and suggests future research directions.

Teaching slide

Schooling in Fishes

- What makes a fish a 'schooler'?
- Fish in school formations display remarkable swimming synchronization and polarization
- Fish may take advantage of vortices shed within a school to save energy by maintaining particular positions in the formation
- Schooling requires integration of sensory system and swimming performance that might be affected negatively by climate change stressors



Di Santo V Schooling in Fishes. In *Fish Physiology, Muscles and Movement*. (EM Standen and D Fudge, eds.). New York: Academic Press.

Introduction

Fishes display remarkable diversity in collective motion, sometimes forming large groups and undertaking large-scale migrations, other times forming loosely associated aggregations and shoals with dynamics that shift rapidly (within seconds), or on daily and seasonal scales. Schooling behavior, where individuals within a species swim in a coordinated fashion in the same direction, is exhibited by the majority of fish species during at least one stage of their life. School formations may include a few to millions of individuals swimming together, and large aggregations of forage fishes are often associated with areas of great marine productivity. The main characteristic of fish schools is the ubiquitous presence of interindividual interactions by which individuals affect the locomotor behavior of the rest of the group members (Couzin and Krause, 2003). School formations can be explained using self-organization theory which suggests that form and function of collective movement are guided by behavioral traits and interactions among individuals using local information from the nearest neighbors but can also be influenced by environmental cues. Individuals within these aggregations display attraction towards neighboring conspecifics and they tend to swim in the same direction and geometrically precise positions. The collective movement dynamics seem to be the result of the emergence of multiple local interactions among neighbors in a formation (Tunström et al., 2013). Moving in school formations may have several advantages, including spending more time foraging instead of being vigilant for predator attacks (Seghers, 1981), migrating during favorable periods (Ryer and Olla, 1995), locating food more efficiently, and reducing the costs of finding a mate. Perhaps one of the most interesting aspects of collective behavior is the potential for individual fish in a school to save energy. The energetic savings could reflect a "calming effect" in shoaling or aggregating fishes (Nadler et al., 2016), or an increase in locomotor efficiency in "proper schools" where fish maintain precise positions within the group to take advantage of vortices shed by swimming conspecifics (Liao, 2022; Weihs, 1975). To take advantage of this locomotor behavior, schooling fishes possess an array of physiological and morphological adaptations that allow them to sense the flow and movement of conspecifics and translate this information into an appropriate response that maximizes stability and efficiency or triggers a coordinated change in swimming direction. Although schooling and collective motions have been addressed extensively in a number of interesting papers and reviews, especially as social behaviors (Couzin and Krause, 2003; Jolles et al., 2017; Katz et al., 2011; Kotschal et al., 2020; Tunström et al., 2013), in this article I will emphasize the locomotor aspects of schooling, including some new data on schooling dynamics, and provide some insight on the consequences of environmental changes on the energetics and biomechanics of this behavior.

Collective and coordinated swimming in fishes

Fishes display an astonishing diversity of collective motion and use a variety of anatomical systems to execute some stunning maneuvers during synchronized movement. From a biomechanical perspective, it is useful to define and quantify collective movement based on the degree of cohesiveness and interactions of individuals within the group, particularly if the goal is to compare across populations or species. However, this is a daunting task as different species exhibit a large degree of variability in schooling mechanisms. One of the hallmarks of schooling behavior is the ability to swim in the same direction (i.e., polarization). Nevertheless, individuals may swim in the same direction but so distantly that interactions may not be significant. In laboratory settings, fishes are often placed in a flow tank where direction and speed of movement are dictated by the researcher. This is necessary to challenge fish and quantify specific locomotor patterns, but even fishes that are solitary swimmers and are placed against an incoming flow and within the boundaries of a tank will exhibit polarization as a result of rheotaxis and spatial limitations. Therefore, the question remains whether a group of fish placed in a flow tank and forced to swim in the same direction are schooling or not. While it is qualitatively simple to observe fish in a flow tank and determine which fishes are schooling (i.e., interacting with each other) or not, it may be harder to define thresholds to classify a species as shoaling or schooling (Berio et al., 2023). In other instances, the natural environment can favor the aggregation of solitary swimmers, like sharks, but it is still unclear if these individuals reduce locomotor costs by taking advantage of interactions with each other and the flow (Papastamatiou et al., 2021). Sharks are an interesting example because, unlike forage fishes, they are not generally known to properly school. However, they can undertake migrations together and are known to aggregate and swim in the same direction to exploit environmental characteristics, such as favorable temperatures or high-flow environments (Hight and Lowe, 2007; Kajiura and Tellman, 2016; Speed et al., 2011). In one field study, reef sharks were observed to swim against currents in “schools” and individuals swimming behind others were found to have a lower tail beat frequency than sharks swimming in leading positions (Papastamatiou et al., 2021). An analysis of the bathymetry and the currents in the area revealed that one factor that may have favored these aggregations was the formation of current updrafts which sharks could exploit to lower the costs of locomotion during parts of the day (Papastamatiou et al., 2021). Similarly, fishes swimming upstream may be oriented in the same direction but not schooling (Delcourt and Poncin, 2012; Pitcher, 1983). It is possible therefore that fishes that are otherwise solitary and are placed in flow and spatial limitation, might aggregate and swim together. What sets apart schooling and aggregations, then, is the degree of synchronization and interaction between individuals of a group.

There have been significant attempts to categorize and quantitatively define the differences between fish aggregations, shoals, and schools (Hemelrijk et al., 2015; Pitcher, 1983; Shaw, 1962; Weihs, 1973). The fundamental measurement that is necessary to determine whether a group of fish is schooling or not is the relative position of fish in a formation, as it can help quantify cohesion. Group cohesion can be measured as a function of the distance of each fish to the nearest neighbor, and this is the most commonly reported parameter (Parrish et al., 2002; Tunström et al., 2013; Warburton and Lazarus, 1991) because it is possible to compare across species and studies relatively easily. The shape of the school may change with swimming speed and environmental parameters (Di Santo, 2022; Di Santo and Lauder, 2021; Miller et al., 2016). In this case, group cohesion may be measured as the mean distance to the center of the school (average center distance) or the mean separation distance, considering the average distance of every individual in the school to one another (Delcourt and Poncin, 2012; Hunter, 1966; Katz et al., 2011; Miller and Gerlai, 2007). Clearly, the number of individuals within a school will affect these parameters and will render comparisons across studies more difficult. However, the shape of school is important to understand the dynamics of collective behavior when the formation is challenged or perturbed by environmental factors. Quantification of the distance between individuals and the shape of the school is also important in studies of ontogenetic shifts and onset of schooling behavior.

In natural settings, schooling behavior is characterized by a high degree of polarization, a measure of how aligned fish are within a group. To quantify polarization, it is necessary to measure the differences in body angle to the direction of swimming in each individual within the school. Measuring polarization in the laboratory is useful in fishes that are tested in still water rather than in a flow. However, in most biomechanics and energetic studies of locomotor behavior, fishes are typically placed in a variable speed swim tunnel. Under these settings, speed is controlled, and fishes show a high degree of polarization because of rheotaxis. Therefore, this parameter is less useful to discern schools from shoals as the angles between fishes tend to be less significant if fish are holding position against the flow within the tank (Castro-Santos et al., 2022; Lauder, 2015; Miller and Gerlai, 2007). However, at low speeds the geometric formations of schools tend to break down (Di Santo and Lauder, 2019), and quantifying the critical speeds at which fish are no longer polarized is important to understand shifts in dynamics of collective behavior and the energetic costs of locomotion at different velocities.

Another parameter to describe a fish school is speed. Synchronization of speed is an important factor that describes collective swimming, as it provides information on individual swimming performance as well as group stability and coordination. Individuals in a school may move at the same velocity over time (perfect synchronization of speed) which suggests either that the average position within a formation is stable, or that individuals in a school show variation in velocity (i.e., acceleration and deceleration mostly accompanied by changes in position) but that overall, the mean speed is maintained. This measurement can be paired with quantification of fin beat frequency to understand if some positions are more energetically advantageous than others (Bainbridge, 1958). If some individuals in the school can match the average speed of the school while reducing their fin beat frequency, they are likely saving energy by interacting with vortices of the school (Thandiackal and Lauder, 2022). Schooling fishes can maintain extraordinarily stable formations and individuals within the group do not change position often (i.e., within seconds) (Weihs, 1973). However, there is a continuum in swimming kinematics across shoalers and schoolers, making it difficult to assign the

parameters describing these collective behaviors within either category. Perhaps more useful than classifying fishes into “true” schoolers or shoalers is to provide a quantification of the portion of the total time that an individual has maintained a given position during the experiment.

Collective behavior typically originates in fishes very early in life during the larval stage when the larvae are just 10–12 mm in length, or post-flexion (Buske and Gerlai, 2011; Miller and Gerlai, 2007; Shaw, 1960, 1961). When larvae reach the post-flexion stage, they typically become active and increase swimming (Hunter and Coyne, 1982). Schooling at an early age provides protection to young fish, which increases their chance of surviving a predator attack by up to 30% (Hunter and Coyne, 1982; Shaw, 1962). The onset of schooling behavior is reported as an increase in interactions between larvae, a decrease in nearest neighbor distance and a decrease in the angle between individuals, meaning that larvae are orienting parallel to each other (Buske and Gerlai, 2011; Hunter, 1966) (Fig. 1). As larvae respond to social cues and learn to orient themselves in relation to other conspecifics near them, it is likely that any environmental stressor (e.g., pollution, climate change, etc.) that affects this learning process, acquisition of visual cues, or the lateral line of fishes may significantly impair this vital behavior. Fishes use multiple sensory systems, including visual, odor, and flow pressure cues (i.e., lateral line) to orient themselves in the flow, maintain position, and synchronize speed within a school (Hemmings, 1966; Humston et al., 2000; Katz et al., 2011; Lopes et al., 2016; Mekdara et al., 2018). Several studies have now shown that the elimination of one of these systems rarely eliminates schooling behavior, as fishes can rely on any of these sensory mechanisms to maintain schooling. However, the lateral line seems to play a more important role in maintaining cohesiveness, geometric formations, synchronization of speed, and direction in schooling fishes (Partridge, 1981; Partridge and Pitcher, 1980). In an experiment with saithe (*Pollachius virens*), schooling was maintained even when fish were temporarily blindfolded or when their lateral line was ablated (Partridge and Pitcher, 1980). In fact, blindfolded saithe showed little change in their schooling behavior, with fish in some instances making fewer mistakes. When the lateral line was ablated, saithe showed a decrease in the nearest neighbor distance, and an inability to correctly respond to lateral shifts and changes in direction after the sudden introduction of a perturbation (Partridge and Pitcher, 1980).

Energetics and mechanics of schooling

Fish in schools display polarized and highly coordinated swimming, where individuals maintain relatively stable parallel positions (Ashraf et al., 2017; Shaw, 1962; Weihs, 1973). Hydrodynamic models expect that fish may gain a hydrodynamic advantage by positioning themselves in a diamond or staggered configuration within the aggregation due to the pattern of vortex trails formed by neighboring swimming fish (Breder, 1926; Weihs, 1973). In fact, individuals may take advantage of the reversed von Kármán vortex street produced by conspecifics swimming ahead in the group to reduce the energetic costs of locomotion (Fig. 2). Directly behind a swimming fish, the vortex trail has increased water velocity opposite to the swimming direction but with the slight lateral shift; thus, fish in trailing positions can benefit from vortices shed by upstream individuals to increase locomotor efficiency. Remarkably, fish swimming directly in front of other individuals might also gain an advantage because they benefit from a “push” coming from the trailing fish. Fish trailing behind others (in-line) may also interact with vortices shed by the fish swimming ahead and show reduced tail beat frequency when compared to solitary swimmers (Thandiackal and Lauder, 2022). Recent work showed that a phalanx configuration, where fish swim side by side and synchronize their tail movement may correlate with reduced tail beat

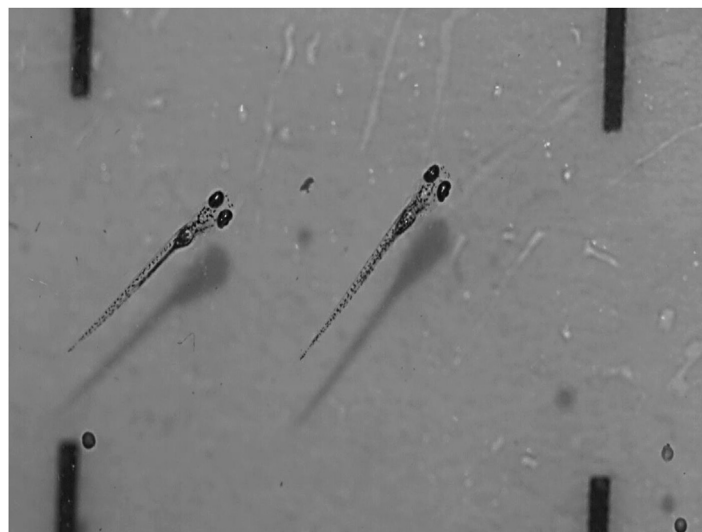


Fig. 1 Wild-type zebrafish (*Danio rerio*) exhibiting parallel behavior as early as 8 days post fertilization. The onset of shoaling behavior however seems to occur later in the larval stage, closer to metamorphosis into juveniles.

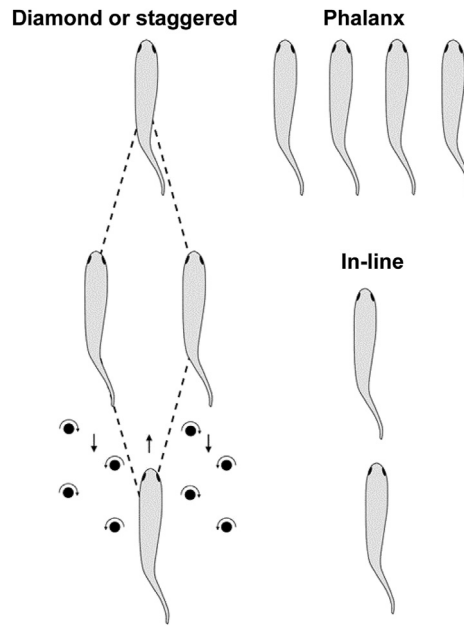


Fig. 2 Fish within a school can gain hydrodynamic benefits by positioning themselves between two leading fish (diamond or staggered configuration), by swimming in a row to take advantage of a channeling effect (phalanx), or by swimming directly behind other fish to take advantage of negative pressure created by vortices shed by the fish swimming ahead (in-line). Figure adapted from Ashraf et al. (2017), Thandiackal and Lauder (2022), Weihs (1973).

frequency, a proxy for energetic expenditure (Ashraf et al., 2017; Saadat et al., 2021). Consequently, swimming in a school formation can be beneficial to reduce the energetic costs of movement, regardless of the position (Marras et al., 2015). Fish may take turns to maximize their energetic benefits, however inter-individual differences in metabolic capacity could influence the position of individuals within schools (Killen et al., 2012).

Very few studies to date have attempted to measure the energetic costs of swimming in a school (Burgerhout et al., 2013; Currier et al., 2021; Berio et al., 2023) which reduces our capacity to understand the possible energy-savings mechanisms underlying collective behavior (Di Santo, 2022). The main hurdle when measuring the costs of collective behavior is the task of discerning between “collective” and individual costs of locomotion. In fact, there is a variation in metabolic rates across individuals, the individuals may have slightly different body sizes, and they may occupy different positions across the time the measurement is taken. Additionally, the collective metabolic rate may change as well because the shape and positioning of fish in a formation will affect their oxygen consumption at any given environmental condition. Oxygen availability may also vary depending on the size and number of individuals in a school. As oxygen concentration affects both metabolic rates and locomotor activity in fishes (Di Santo et al., 2016; Müller et al., 2016; Svendsen et al., 2011), it is likely to affect locomotor performance during schooling. Additionally, it is currently impossible to discern the partial oxygen consumption contributions of the fish swimming in peripheral or central positions to the collective metabolic rate with standard energetics techniques. For this reason, studies so far have opted to use fin beat frequency as a biomechanical proxy for the energetic costs of locomotion (Bainbridge, 1958). Additionally, metabolic rates may significantly differ if individuals within a school occupy more (or fewer) central positions, behind other fish. A direct assessment of the effect of positioning and shifts on the energetics of schooling is missing. Precise estimation of metabolic rates requires that individuals hold their position for a relatively long period of time. This rarely happens, at least in laboratory settings. Such measurements may be improved by choosing species that show relatively small variation in position within a short period of time (5–15 min), in other words, fish species where individuals maintain stable positions in a school. For example, obligate schoolers (most forage fishes) maintain a relatively stable position (at least a few minutes), when no perturbation such as food is introduced (Di Santo and Lauder, 2021; McLean et al., 2018).

The energetics of locomotion, measured as oxygen consumption rates, in individual fishes have been investigated in several species under different environmental and flow conditions (Bale et al., 2014; Boisclair and Tang, 1993; Bone, 1975; Brett, 1967; Schmidt-Nielsen, 1972, 1997; Webb, 1984, 1994). Understanding the consequences of speed, flow, and environmental conditions on the energetics of swimming is important, but there are still just a few studies on “schooling metabolic rates” (Currier et al., 2021; Di Santo, 2022; Berio et al., 2023). Previous work on fishes that are not obligate schoolers found that when rainbow trout (*Oncorhynchus mykiss*) and bluegill sunfish (*Lepomis macrochirus*) are placed in a flow and swum in groups at different speeds, only bluegill sunfish benefit energetically from shoaling (Currier et al., 2021). In fact, trout increase metabolic rates and tail beat frequency when swimming with other conspecifics (Currier et al., 2021). This is somewhat surprising as trout are known to undertake spawning migrations as groups, so they are expected to take advantage of group formations to save energy (Steinhausen et al., 2008). More studies should focus on the costs of group swimming across different species of fish.

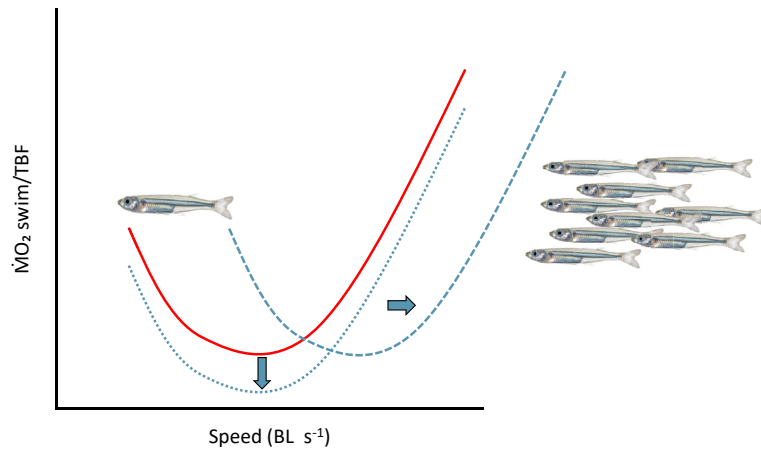


Fig. 3 Metabolic or tail beat frequency (TBF) – speed curve can shift for fish swimming in a school formation. Fish during schooling can reduce the costs of swimming (curve shifts down) or swim faster using the same amount of energy (curve shifts right) when taking advantage of vortices in a school formation. Figure adapted from Di Santo (2022).

Whether a fish is a solitary, shoaling, or schooling swimmer, it is important to understand if they could take advantage of structures in the environment, including other fish, to reduce energetic costs of locomotion. This advantage could be represented, for example, by a higher optimal speed or overall reduced metabolic rates at each tested speed, as suggested previously (Di Santo, 2022) (Fig. 3). School formations seem to break down when the speed is too low (~ 1 body length per second, BL/s) as observed in Inland silverside (*Menidia beryllina*) and Barents Sea capelins (*Mallotus villosus*), possibly due to postural problems and lack of rheotaxis behavior at extremely low flow speeds (Behrens et al., 2006; Di Santo et al., 2017; Di Santo and Lauder, 2019). As speed increases, the volume of the school decreases in Inland silverside, suggesting that fish may reduce the nearest neighbor distance to save energy, thus changing the overall shape of the formation (Di Santo and Lauder, 2019). Fish, in fact, may move to place themselves behind another fish to save energy. Even though social fishes reduce metabolic rates by just being in a school (Marras et al., 2015), the position within this formation matters. In particular, swimming behind another fish reduces tail beat frequency and metabolic rates (Berio et al., 2023). Speed, therefore, has a significant effect on the shape of the school formation. It has been suggested that at high speeds, schooling fishes may swim closer to each other to take advantage of the vortex patterns in the formation. By swimming closer to each other and by maintaining a more precise formation, fishes swimming at intermediate to high speeds create more stable formations.

Yet, it is unclear how perturbations can affect the stability of formations at different speeds. One important perturbation for fishes is the introduction (or discovery) of food. When food is introduced to the flow tank, the school formation is disrupted but reforms after feeding (Fig. 4). It is unclear to what extent individual spatial position within the school is resumed post-feeding. For example, when schools of Inland silverside are fed while swimming at high flow speeds (>3 BL/s), they tend to re-occupy the same spatial position as pre-feeding (Fig. 5). In comparison, silversides swimming at low to intermediate speeds (~ 1 BL/s) tend to switch position after a feeding event. Fish swimming in leader positions tend to return to the same functional position (albeit not the same spatial position) while fish swimming in trailing positions tend to move toward the periphery and front of the school. However, at high speeds all fish in a school tend to re-occupy their pre-feeding position (Di Santo and Lauder, 2021). These results may suggest that at high speeds fish try to maintain stable positions even after a perturbation that disrupts the school formation.

Climate change and schooling

In the past 200 years, anthropogenic activities have increased the concentration of carbon dioxide ($p\text{CO}_2$) in the atmosphere to about $417 \mu\text{atm}$ (in 2023) from $280 \mu\text{atm}$, a change that has not been experienced by most organisms for the past 65 million years (Intergovernmental Panel on Climate Change, 2018). As $p\text{CO}_2$ levels grow, the average temperature increases, causing global heating. The oceans act like a sink for a large portion of the CO_2 emitted in the atmosphere and store this carbon for a long period in deep, cold, acidified waters. However, marine animals are faced with a multi-faceted challenge as the oceans are becoming increasingly warmer and more acidic (Belkin, 2009; Dupont and Pörtner, 2013). The effects of ocean acidification and warming have been investigated extensively across many aspects of fish biology (Byrne and Przeslawski, 2013; Cattano et al., 2018; Clark et al., 2020; Di Santo, 2022; Doney et al., 2009). These environmental stressors have profound effects on fish physiology at the individual level (Angilletta, 2009; Angilletta et al., 2004; Baumann, 2019; Byrne and Przeslawski, 2013). Temperature is broadly considered the “abiotic master factor” as it has both direct and indirect effects on nearly every physiological process in fishes (Brett, 1971). It is not surprising therefore, that many studies have looked at the intricate relationship between thermal physiology and ecology of

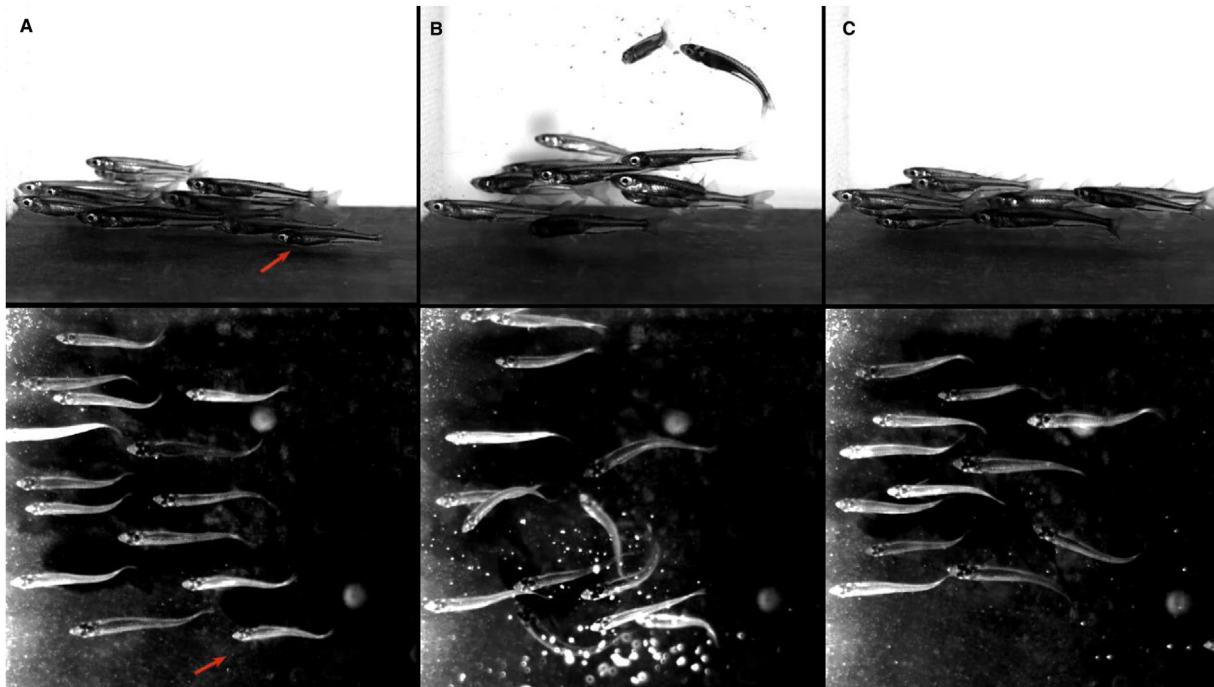


Fig. 4 Fish school (A) of Inland silverside (*Menidia beryllina*) is disrupted after the introduction of food (B) and returns to its apparent original shape after the perturbation is no longer present (C). Individual (indicated with a red arrow) and the entire formation can be tracked over time to quantify shifts in relative and absolute positions within a school.

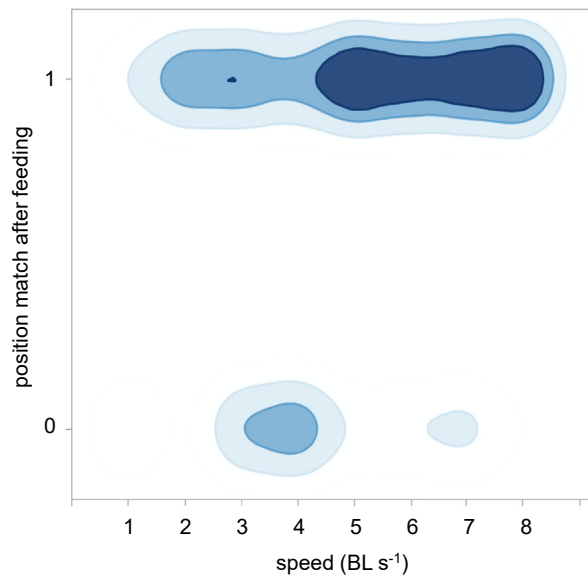


Fig. 5 Fish schools might change shape and individuals may temporarily change position during a perturbation such as a predator attack or the localization of food. Here, food was introduced as a perturbation while a school of Inland silverside (*Menidia beryllina*) swam at different speeds. Following the feeding event, the school reformed and individual fish were tracked from pre- to post-feeding positions (Di Santo and Lauder, 2021). Most fish returned to the same row within the school even though not the exact position. At higher speeds there was a tendency to match the pre-feeding row within the school, suggesting higher stability of school formation at higher rather than low speeds.

fishes at multiple levels of organization (Andreassen et al., 2022; Angilletta, 2009; Di Santo et al., 2018; Eliason et al., 2011; Johnson and Bennett, 1995; Pörtner et al., 2007).

Fish schools undertake seasonal and daily migrations in response to local abiotic or biotic conditions. The movement of schools of large pelagic fishes is often associated with sea surface temperature gradients (Olson et al., 1994). In fact, thermotaxis in schooling fishes is fairly common. Even in large pelagic species such as swordfish (*Xiphias gladius*) (Podesta et al., 1993) and tunas (*Thunnus alalunga*, *T. thynnus*) (Humston et al., 2000; Kimura et al., 1997), migrations seem to correlate with temperature gradients. This is not surprising in fishes, as they are known to select thermal environments to enhance physiological processes (Di Santo and Bennett, 2011; Fry, 1967; Meese and Lowe, 2019). Unlike most fish species, however, bluefin tuna are not poikilothermic and can maintain significantly higher internal temperatures compared to the surrounding environment (Blake, 2004; Fudge et al., 1997; Katz, 2002). Thus, heterothermic fishes have less dependence on environmental temperature than most fish species, and even when tunas concentrate in areas of preferred temperature (Humston et al., 2000), they might just be responding to prey distribution. Indeed, forage fishes are known to be strongly affected by daily and seasonal changes in temperature (Abookire et al., 2000; Gobler et al., 2018; Kuruvilla et al., 2022). In addition to distribution, social behaviors are also affected by temperature. For example, the nearest neighbor distance may increase with temperature in school formations, which consequently expand in volume with warming (Bartolini et al., 2015; Colchen et al., 2017). The response though, is species specific as some fish may swim closer to each other as temperature increases, as observed in female guppies (*Poecilia reticulata*) (Weetman et al., 1999) and the zebrafish (*Danio rerio*). Warming affects shoaling behavior across ontogenetic stages in zebrafish swimming at different speeds (Berio et al., 2023). The mean separation distance across individuals decreases from larvae to juvenile to adults, suggesting that shoals become more cohesive, and shoaling improves across the life of zebrafish (Berio et al., 2023). Under warming conditions, only adult zebrafish increase the rate at which the position of individuals in the school changes across speeds (Berio et al., 2023). It is possible that adult zebrafish may have “learned” to select positions in the shoal that are energetically advantageous, and that therefore may compete to swim behind other fish. This would explain why the adult formations may be more volatile under warming conditions. There are quite a few differences across acclimation regimes, laboratory set-ups, and populations of fish sampled, so it is not surprising that different responses are observed across species. Regardless, when a school is less compact, it is likely that fishes are less able to exploit the vortices shed by other swimming individuals in the formation, but this needs to be tested in experiments and simulations under different speeds and turbulence (Di Santo, 2022; Lauer et al., 2022; Zhang et al., 2023). Temperature can increase locomotor performance in schools by affecting individual swimming performance (Brett, 1967; Di Santo, 2016). Furthermore, schooling fishes often possess some degree of brain asymmetry and cognitive function (Katz et al., 2011; Kotrschal et al., 2020; Tunstrøm et al., 2013), with a tendency to turn either right or left in response to stimuli (Lopes et al., 2016; Mitchell et al., 2022). During collective movement, behavioral lateralization can help fish reduce predation risk through dilution and confusion effects (Turner and Pitcher, 1986). Lateralization and cohesiveness might be altered at elevated temperatures (Colchen et al., 2017; Mitchell et al., 2022; Vila Pouca et al., 2018). However, the effect of temperature on lateralization is often not repeatable (Mitchell et al., 2022).

The effect of ocean acidification on school performance has been evaluated to a much lesser degree (Di Santo, 2022). Often studies on sociality, lateralization and patterns of cohesiveness and polarization show contrasting results (Clark et al., 2020; Kwan et al., 2017; Lopes et al., 2016; Mitchell et al., 2022). Behavioral traits might show higher variability compared to morphological and physiological traits. Ocean acidification is known to have a detrimental effect on morphology and tissue development in forage fishes, especially when exposed to low pH conditions during early life stages (Baumann et al., 2012; Chambers et al., 2014; DePasquale et al., 2015; Pimentel et al., 2016). Ocean acidification is known to increase skeletal mineralization in fishes (Di Santo, 2019; Mirasole et al., 2020). Mineralization has a direct effect on the stiffness of bone and cartilage and shapes the mechanical properties and physiological performance of fishes. Denser skeletal elements are stiffer and allow fishes to transfer energy more effectively and swim faster (Di Santo, 2019; Porter et al., 2007; Porter and Long, 2010). At the same time, fishes may benefit from more flexible fins especially at low speeds, and while treading the water (Lauder and Di Santo, 2015; Mignano et al., 2019; Videler, 1993). Denser skeletons are heavier, and swimming performance might decrease because of the higher costs of lifting and controlling posture (Blake, 1979; Di Santo et al., 2017; Webb, 2005). Perhaps one of the most significant effects of ocean acidification on fish schooling mechanics may relate to the change in growth of otoliths. In fact, pCO₂ levels expected by the end of the century (~1000 µatm) can cause an increase in pCO₂ in the endolymph of the ear of fishes that may produce abnormalities in otolith growth (Bignami et al., 2013a,b; Kwan and Tresguerres, 2022). Otoliths are mineralized structures made of aragonite-protein bilayers and are used by fishes to sense orientation, acceleration and to maintain postural equilibrium (Popper and Fay, 2011). Otoliths and associated hair cells serve as an inertial system whereby the movement of the head relative to an external pressure wave causes movement of the body relative to the otoliths which stimulate hair cells (Popper and Fay, 2011; Popper and Lu, 2000). The shape and size of otoliths correlate to sensitivity to angular acceleration, and fast swimming fishes engaging in rapid turns have small otolith-to-body size ratios to avoid overly sensitive detection of changes in angular motions (Popper et al., 2005). Ocean acidification can trigger accumulation of buffers such as bicarbonate and calcium carbonate, accelerating the formation of otolith aragonite (Anken, 2006; Beier et al., 2004; Ibsch et al., 2004; Kwan and Tresguerres, 2022). Large otoliths and asymmetry between left and right ears have been documented in larval fishes maintained at high pCO₂ regimes (~1000 µatm) (Popper and Fay, 2011). The inability to control body orientation and maneuvering in fish with affected sensory systems can significantly alter locomotor kinematics. Even small changes in the capacity to control body and fin movement could disrupt the school formation, and this requires further investigation.

More work needs to clarify the cascading effects of climate change stressors on individual and collective locomotor performance. The vast majority of schooling fishes are forage fishes that undertake daily, seasonal, or annual migrations between foraging and mating grounds. Migratory and dispersal capacities might be impaired in forage fishes because of a limited locomotor capacity under climate-related stressors (Bonanomi et al., 2015). Because the effect of warming and acidification tends to be stronger early life stages, we might expect a shift in forage fish recruitment. Local extirpations or declines of forage fishes can alter marine ecosystem composition and functioning. Plastic responses to environmental change, such as developmental and transgenerational acclimation, can provide relief to fish populations. Forage fishes have relatively fast generation times among vertebrates, so they might be able to respond rapidly to changes in the environment through transgenerational acclimation, adaptation, and shifts in geographic ranges (Somero, 2010). More studies should focus on such transgenerational effects (Agrawal et al., 1999; Donelson et al., 2012; Munday, 2014; Ryu et al., 2018; Schade et al., 2014) beyond the individual level, by looking at effects on group swimming behavior.

To improve projections of future consequences of climate change on collective locomotor performance, it is also necessary to implement multistressor studies on groups of fishes collected at different locations and across life stages (Byrne and Przeslawski, 2013; Lauder and Di Santo, 2015). This will help identify vulnerable stages and populations, and whether locally adapted populations may be more resilient to changes in the environment expected by the end of the century. Such efforts are already underway to identify populations of marine organisms that can be transplanted to new sites to avoid local extirpation of species (Jensen et al., 2008; Morikawa and Palumbi, 2019; Palumbi et al., 2014; Ziegler et al., 2017). Such studies also reveal characteristics that allow some populations (or phenotypes) to be resilient under rapidly changing ocean conditions (Somero, 2010). However, we should take a balanced approach where number of stressors and statistical power are both considered in laboratory settings. Single-stressor studies are still very useful to pinpoint specific responses of individual and collective locomotor behaviors to changes in the environment. There is a need to construct a theoretical framework that takes into account the consequences of single stressors on locomotor performance but also the possibility that the effect of multiple stressors may not be additive, but rather antagonistic or synergistic, as often observed in climate change physiology studies (Byrne and Przeslawski, 2013; Cattano et al., 2018; Di Santo, 2016; Lefevre, 2016; Murray et al., 2019; Murray and Baumann, 2018). Moreover, the effect of stressors can impact different aspects of fish locomotor performance at different rates (including positive effects), even within systems.

Conclusions

Schooling behavior has been studied extensively in the past 60 years; however, important knowledge gaps remain. For example, very little is known of the 3-dimensional mechanics of fish schooling. Most measurements of schooling are reduced to 2 dimensions, likely missing relationships among individuals and configurations of 3-dimensional dynamics over time. Additionally, most of the studies on schooling behavior and dynamics have been done in still water, with no control over the speed or the direction of the school. Metabolic rates of schools as “units” are also largely missing. Some studies have quantified metabolic rates of groups of fish, but often the species selected are not obligate schoolers, thereby showing large variation in their response to the flow and movement of swimming mates. Other proxies for energy expenditure such as tail beat frequency are important but do not provide a complete picture of the costs of locomotion for fish schools. Measurements of fin beat frequency are yet very useful to infer the consequences of positions and locomotor behavior on efficiency of swimming from a biomechanical point of view. Additionally, it is unclear what minimum number of fish is needed for a school to obtain an energetic benefit during swimming. It has been suggested that even two fish swimming next to each other use less energy than a solitary fish (Ashraf et al., 2016). Is there an increase in energy efficiency with the number of fish in a school? Is there a minimum number of fish that maximize the energetic advantage during schooling? Fundamental kinematics and energetic analyses of the variation in swimming performance in fish schooling and shoaling under different conditions of flow, temperature, and CO₂ are limited. How does collective movement of schoolers and shoalers respond to changes in the environment? The remarkable diversity in kinematics of schooling locomotor behavior is affected by fish behavioral characteristics, learning, sociality, and physiology; however, studies so far have focused on a few species and a limited set of conditions. Future work on schooling locomotion will benefit greatly from the integration of behavioral, energetics, biomechanical, engineering, and computational work to understand the rules and diversity of collective movement in fishes.

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