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Schooling properties of an obligate and a facultative fish species

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Schooling fish species are conventionally subdivided into obligate and facultative species, depending on the proportion of the time spent in structured schools, but little is known about the factors affecting the group structure in the absence of external structuring stimuli such as food sources, risk of predators or water flow. Changes in attraction and repulsion indicators, depending on the species and the group size were explored under controlled conditions. Two species, displaying different schooling behaviours in the wild were observed: the bigeye scad *Selar crumenophthalmus* (Bloch) and the barred flagtail *Kuhlia mugil* (Forster). In the bigeye scad, the *Polarity* and *Speed* were high and stable, and the Nearest Neighbour Distance (*NND*) decreased when the group size increased. In contrast, for the barred flagtail, *Polarity* and *Speed* decreased according to the group size, inducing a loss of cohesion and leading to a disorganized school. The *NND* mean was stable whatever the group size and relatively high. This experiment indicated that the ability to polarize is first a species specific trait, rather than a property emerging from the group and led by the circumstances.

Key words: Social interactions, Schooling behaviour, Polarity, Pelagic fish

Running headline: Schooling properties of two fish species

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INTRODUCTION

Pelagic fish schools provide a good example of a social structure that enables individuals to increase their efficiency when foraging and avoiding predators by performing complex and synchronous movements that are beneficial to each individual school member (Pitcher & Parrish, 1993; Parrish & Edelstein-Keshet, 1999; Krause *et al.*, 2000). Previous observations and analyses of swimming fish in aquaria (Breder, 1951; Shaw & Tucker, 1965; Hemmings, 1966; Shaw, 1970; Radakov, 1973; Aoki, 1980) defined sense organs and forces between fish implied in the schooling behaviour. Several of these experiments suggested that fish, like other social animals, had an "exclusive sphere" from which conspecifics were expelled. Moreover, Shaw & Tucker (1965) defined the optomotor reaction as the ability of fishes to synchronize their motions and to adjust their speeds to those of their neighbours. This reaction is one of the most important orientation mechanisms that enable fish to maintain their position and their orientation within a school (reviewed by Warburton, 1997). Consequently, one of the general rules of social behaviour is that schooling fish attempt to maintain a minimum distance between conspecifics (reviewed by Krause & Ruxton, 2002). Polarity measures the tendency of individuals to align with one another and to synchronize their motions. Fish schools under natural condition display a wide range of polarity values over time, from completely non-polarized to perfectly aligned (Shaw,

1978). This characteristic led Breder (1959) to distinguish between obligate schooling fishes which polarized constantly and facultative schooling fishes which only polarized occasionally. This classification was used by Pitcher (1983) to distinguish a shoal (unstructured aggregation) from a school (social structure enabling quick information to be transferred to conspecifics). However, under natural conditions, several external factors such as food source, risk of predators or water flow may have an impact on the cohesion of fish congregation. Differences in hunger (Morgan, 1988), fear (Rehnberg & Smith, 1988), fish size (Parrish & Turchin, 1997), species composition (Allan, 1986) or in group size (Fitzsimmons & Warburton, 1992) may promote individual differences in behaviour that generate variation in the internal organisation of fish schools and ultimately affect the structure and stability of groups. A “real fish school”, defining a fully polarized fish school under natural conditions, could be a temporary and spontaneous response of a shoal to a disturbance or predator. Therefore, until the constraints on fish and the processes enabling them to adjust their positions and synchronize their motions are not fully understood, it seems difficult to deduce from observations in the wild which species are obligate schooling fishes or facultative schooling fishes (Viscido *et al.*, 2004; Wu & David, 2002).

The question then becomes: what governs attraction and repulsion between individuals in the absence of any external structuring stimuli (i.e. when the sources of attraction/repulsion are the fish themselves)? To address this issue,

behavioural interactions among fishes were examined under controlled conditions depending on different group sizes. Polarization is important in minimizing collision between individuals and in allowing the group to transfer information (Radakov, 1973). Therefore, two gregarious species were compared under controlled conditions to check the internal factors influencing this collective behaviour.

MATERIALS AND METHODS

The first studied species was a Carangidae, the bigeye scad *Selar crumenophthalmus* (Bloch). This small circumtropical pelagic fish is an *a priori* obligate schooling fish, travelling in compact groups of hundreds of thousands of fish. In the coastal area around Reunion Island (south-western Indian Ocean), their main natural predators are the giant trevally *Caranx ignobilis* (Forsskål) and the Scombridae Kawakawa *Euthynnus affinis* (Cantor). The second species studied is a Kuhlidae, the barred flagtail *Kuhlia mugil* (Forster). This small pelagic coastal tropical fish is an *a priori* facultative schooling fish living in shoals along the outer slope of the coral reefs.

Barred flagtail were caught in March 2001, bigeye scad in March 2002. Fishes were caught using a small sliding net of 3.5 m in length, 6 m in height and a mesh size of 10 mm. Fishes were gently guided into plastic bags to avoid wounds during extraction from

the net, and transferred into 60 l buckets under hyper-oxygenation and a soft anaesthesia (0.1 ml l⁻¹ of clove oil, Durville & Collet, 2001). For experiments on both species, 80 to 100 fishes were finally conveyed to the marine station and housed in a holding tank of 4 m diameter and 1.2 m high. A preventive treatment with methylene blue (0.2 mg l⁻¹) and formalin (20 mg l⁻¹) was applied in order to avoid parasitism and bacterial or fungal infections. Fishes were fed daily *ad libitum* with a mixture of aquaria flake-food and pieces of fish flesh. Fishes were considered acclimatized when all of them fed on the aquaria flake-food. This weaning period lasted about 15 days. Fork length of studied fishes varied from 19-22 cm for the bigeye scad, and from 22-25 cm for the barred flagtail.

The experiments were performed over six months, in both April to June 2001 and April to June 2002 at the Sea Turtle Survey and Discovery Centre of Reunion Island. A circular tank of 4 m diameter and 1.2 m high similar to the holding tank was used. Opaque curtains were placed around and above the tank to obtain diffuse lighting and to reduce external disturbances from the environment. The tank was supplied with a continuous flow of seawater (Domenici *et al.*, 2000). Since currents may influence fish behaviour, the seawater inlet pipe was placed vertically and the water flow was stopped throughout the observation periods. A digital video camera (Sony model CDR-TRV 900E) was fixed at five meters above the tank and tilted at 45° to observe the totality of the tank. The remotely operated video camera was fitted with a polarizing filter and a wide-angle lens. 80% of the trials were performed in the morning to avoid possible conditions of strong wind that may disturb the fish, and sunshine that may render light inside the tank unsuitable for video recording. Prior to each trial, the fish were deprived of food for 12

hours to standardize the hunger level and were transferred to the experimental tank and acclimatized to their new environment for a period of 20 minutes.

Seventy (70) barred flagtail and 85 bigeye scad were used. For each species, three group sizes were examined: two, four and eight individuals for the bigeye scad and two, five and 10 individuals for the barred flagtail. Five replicates per species and group size were performed. For each replicate, fish behaviour was recorded during five minutes. Three different typical and stable patterns of aggregation (line, column and dense school) were easily but empirically identified during the experiment on four and eight bigeye scad and were post-processed accordingly. Their frequencies were estimated for each replicate by measuring the duration of each pattern over the observation period.

Preliminary trials indicated that, occasionally, one fish might display a fleeting alarm reaction. Because this reaction was undesirable for the purpose of this study, only two minutes without disturbances were retained out of the five recorded. The data processing consisted in sampling one image per second out of the 24 images recorded by the video camera. Then, the coordinates of each fish were recorded using software specially developed for this experiment. In order to convert pixels into distance units and to take into account the parallax error due to the tilt of the video camera and the distortion of the image related to the wide-angle lens, an empirical method was applied. It consisted in recording evenly spaced reference points (every 0.50 m) marked out on the bottom of the tank before the beginning of the experiment. The number of pixels observed between these markers on the image was used to calculate the exact coordinates. Two zones were defined

in the tank: a central zone, where the fish were not affected by the wall, and a peripheral zone, where the fish underwent the edge effect. These zones were defined by measuring the variations of the mean angle between the direction of solitary barred flagtail fish (alone in the tank) and the tangent of the wall *versus* the distance to the wall. The relationship between these two variables displayed a breaking point at 0.3 m from the wall (not shown). In order to test the homogeneity of the spatial distribution, the observed proportion of fish between the peripheral (3.5 m²) and the central zones (9 m²) was compared to the expected proportion under the null hypothesis of a random distribution using a *chi* square test (χ^2). Finally, the third (vertical) dimension of schools was neglected since the shallow water of the tank (1.1 m) precluded serious errors in the horizontal measures and the fish tended to use only the middle part of the water column.

Four variables were analyzed: the *Nearest Neighbour Distance* (*NND*, in m), the *Speed* (*V*, in m s⁻¹), the *Expanse* (ε , dimensionless) and the *Polarity* (Φ , dimensionless). The *NND* for each fish was found by computing the minimum distance from one fish to all the individuals in the area. *V* (in m s⁻¹) was estimated by the linear distance between the positions of the heads of the fish in two successive images (of one-second interval). As far as *V* and *NND* were concerned, for each interval of one second, one value among the values calculated for each individual (for *V*) or for pairwise individuals (for *NND*) was randomly selected. *Expanse* is the mean quadratic distance from each individual to the centre of the group. It gave an accurate estimation of the fish dispersion (Huth & Wissel, 1992). *Expanse* (ε) is expressed as:

$$\varepsilon = \sqrt{\sum_{i=1}^h (|X_i| - |C|)^2} h^{-1} \quad (1)$$

where h is the number of fish in a group, X_i the position vector of individual i and C the position vector of the group.

The group *Polarity* (Φ^*) was estimated by the mean of α_i , the vector angle deviation between the group and the individual courses (Huth & Wissel, 1992). The group *Polarity* (Φ^*) is expressed by the following equation:

$$\Phi^* = \frac{1}{h} \sum_{i=1}^h \alpha_i \quad (2)$$

Because this metric is counter-intuitive, a non-dimensionalized form of polarity was used in order to obtain values ranging from 0 (non-polarized) to 1 (perfectly aligned), as in Viscido *et al.* (2004). This new *Polarity* Φ is defined as:

$$\Phi = (90 - \Phi^*) 90^{-1} \quad (3)$$

Let \mathbf{v}_i represent the unit vector for individual fish i , U the unit vector of the group centre (scaled to preserve direction) and β_i the transformed turning angle θ_i as $\beta_i = 90^\circ - \theta_i$ (θ_i being the difference of course of the fish between two time steps). The vector angle deviation α_i , between group and each individual course is the inverse cosine of the scalar product $\mathbf{v}_i U$:

$$\alpha_i = \arccos \left(\mathbf{v}_i U \cdot |U|^{-1} \right) \quad (4)$$

where:

$$\mathbf{v}_i U = \cos(\beta_i) \left(\sum_{i=1}^h \cos(\beta_i) \right) + \sin(\beta_i) \left(\sum_{i=1}^h \sin(\beta_i) \right) \quad (5)$$

$$|U| = \sqrt{\left(\sum_{i=1}^h \cos(\beta_i) \right)^2 + \left(\sum_{i=1}^h \sin(\beta_i) \right)^2} \quad (6)$$

If the positions were collected too frequently, the data set might be oversampled due to redundant data points. Therefore, to address the issue of the independence of consecutive observations, data were aggregated over an appropriate interval resulting in independent observations. The optimal interval was found by performing autocorrelation and spectral (Fourier) analyses in order to detect positive serial correlations between discrete values and to assess the periodicity in the time series.

Firstly, effect of replicate was tested solely by performing a series of one-way analyses of variance (ANOVA) and secondly by comparing the effect of replicate to other factors (Group Size and *Species*) on the four variables using a multifactor analysis of variance (Multifactor ANOVA). Although Multifactor ANOVA is robust to non-gaussian distribution, for bigeye scad data set, *NND* right-skewed data were log-transformed and a Box-Cox transformation (Box & Cox, 1964) was applied to Φ left-skewed data with an optimal λ value of 8 that removed the skewness: $f(\Phi) = (\Phi^\lambda - 1) \lambda^{-1}$. Other variables did not require transformation. However, bigeye scad's *Speed* had one outlier observation (out of 435), which had to be removed.

In order to detect possible non-linear relationships, General Additive Models (GAMs) were applied using loess smoothing with span value adjusted to optimally remove obvious trends in the residuals. For linear relationships, the correlation coefficient matrices for bivariate relationships were calculated and the relative effects of group size and group-level characteristics on Φ were quantified using a General Linear Model (GLM).

ETHICAL NOTE

Several procedures were used to optimise the welfare of fish. The fishing operation was carried out without fish being directly handled or emerged in order to avoid injuries and losses of scales that are often the first cause of mortality. The mortality rate observed during transfer from the fishing boat to the experimental station was 4%. The continuous seawater flow in both tanks enabled us to maintain a suitable temperature and oxygen content ($T^{\circ} = 28.3 \pm 0.5^{\circ} \text{C}$; $\text{O}^2 = 5.90 \pm 0.02 \text{ mg l}^{-1}$). The maximum density inside the holding tank was less than three fish m^{-3} . During the experiments, low mortality occurred (five fishes in 2001 and five fishes in 2002). These losses resulted from skin wounds and occurred when the fishes rasped against the net during their capture. Three months later, at the end of the experiment, the fish were released at their site of capture. Thus, one can be confident that the experiments had no significant effect on the population and did not cause undue stress to the subjects.

RESULTS

Autocorrelation and Fourier analyses (results not shown) performed on each variable for each factor indicated that a 4-second time-average was appropriate to

avoid biases due to autocorrelated data or periodicity. This time average led us to analyse 29 image samples by replicate. The effect of repeated measurements was significant on most of the variables (ANOVA, $n = 145$, $P < 0.001$), except for the barred flagtail's *NND* and the bigeye scad's *Polarity* and *Expanse* for small and medium groups. However, the Multifactor ANOVAs performed with *Species*, Group Size and replicate as factors on each variable have shown that the percentage of variance due to replicate was lower than 5% of the total variance (results not shown).

Comparison between the ratio of the number of fish observed in central zones to the number in the peripheral zones and the expected ratio that would result from homogeneous spatial distribution have shown contrasted results between the two species. For the bigeye scad, density was higher than expected in the peripheral zone and lower in the central zone for the small and the medium group sizes (χ^2 , $n = 1200$, d.f. = 1, $P < 0.05$; χ^2 , $n = 2400$, d.f. = 1, $P < 0.01$ respectively), whereas fish densities observed in both zones for the large group size were not statistically different (χ^2 , $n = 4800$, d.f. = 1, $P = 0.51$). Therefore, analyses indicated a definite thigmotaxis, *i.e.* a trend to look for contacts and to maintain its body parallel to the tank wall, for bigeye scad, mainly for small and medium groups. In contrast, for the barred flagtail density was always higher in the central zone than in the peripheral zone whatever the Group Size (χ^2 , $n = 1200$, d.f. = 1, $P < 0.001$; χ^2 , $n =$

3000, d.f. = 1, $P < 0.001$; χ^2 , $n = 6000$, d.f. = 1, $P < 0.001$ for small, medium and large group sizes respectively).

Means of *Polarity*, *Expanse*, *Speed*, and *NND* for both species and each group size are summarized in Table I. Since GAMs did not show non-linear relationships between the main group-level characteristics, the product-moment correlation coefficients were analysed and the influence of factors and other variables on *Polarity* were tested using a GLM.

For bigeye scad, the mean *Polarity* was high, regardless of the group size (0.81 to 0.89; Table I). The mean *Expanse* was small and more or less stable (0.22 to 0.28) whatever the group size. These differences (from 5% to 22%) were sometimes statistically significant (Table I) but the relationship between *Expanse* and Group Size was weak ($r = -0.24$, $n = 145$, $P < 0.001$, Table II). *NND* decreased dramatically and significantly with increasing group size ($r = -0.84$, $n = 145$, $P < 0.001$, Fig. 1), indicating that fish adjusted their distances according to the number of individuals in the group. *Expanse* and *NND* were positively correlated ($r = 0.75$, $n = 435$, $P < 0.001$, Table II). This result suggests that, for this species and for the tested Group Size range, *Expanse* was first a group-level expression of *NND* ($r = 0.97$, $n = 145$, $P < 0.001$; $r = 0.95$, $n = 145$, $P < 0.001$; $r =$

0.55, $n = 145$, $P < 0.001$ for small, medium and large groups respectively), but not scaled to Group Size. Mean *Speed* decreased significantly with increasing Group Size ($r = -0.29$, $n = 435$, $P < 0.001$, Tables I and II). *Polarity* was positively correlated with *Speed* ($r = 0.56$, $n = 435$, $P < 0.001$, Table II). Therefore, increasing group size led to an individual speed decrease associated with a decrease in *Polarity*. The GLM showed an expected strong and significant effect of *Speed* on *Polarity*, a weak but significant effect of Group Size, and no significant effect of *NND* and *Expanse*, indicating that schools always tended to display perfect alignment, regardless of these last two variables (Table III).

Detailed observations of medium (four individuals) and large (eight individuals) group sizes have shown that bigeye scad displayed three different and specific spatial patterns. The fishes could follow each other forming a column, swim abreast forming a line or got into small but dense schools (Fig. 2). Analyses have shown that the three patterns were observed in equivalent proportions in the group of four individuals ($32.7 \pm 9.3\%$, $33.8 \pm 7.8\%$, $33.5 \pm 14.2\%$ for line, column and dense school patterns respectively; χ^2 , $n = 584$, d.f. = 2, $P > 0.9$) whereas the group of eight individuals displayed on average the third pattern more often than the other ones ($14.4 \pm 6.3\%$, $10.5 \pm 5.7\%$, $75.0 \pm 9.8\%$ for line, column and dense school patterns respectively; χ^2 , $n = 595$, d.f. = 2, $P < 0.001$). In large Group Size, schooling fish that turned back altogether most often kept the *school*

structure. This behaviour maintained a cohesive pattern and induced small *NND* throughout the observations. Most strikingly, the fish swam along the wall until they reached the opposite part of the tank, turned back and started again in the opposite direction after they had covered more or less half the perimeter of the tank.

For barred flagtail, *Polarity* and *Expanse* were negatively correlated ($r = -0.70$, $n = 435$, $P < 0.001$) and both variables were significantly affected by the size of the group (Tables I and II). *Polarity* decreased with Group Size ($r = -0.73$, $n = 435$, $P < 0.001$) whereas *Expanse* increased ($r = 0.80$, $n = 435$, $P < 0.001$). In other words, increasing group size destroyed the alignment and led to an expansion of the group. The correlation between *Expanse* and *NND* was not significant ($r = 0.09$, $n = 435$, $P = 0.055$). The correlation between Group Size and *NND* was significant but low ($r = -0.26$, $n = 435$, $P < 0.001$), indicating that distance between neighbours is slightly dependent on the group size (Fig. 1). However, the ANOVA has shown that *NND* mean was significantly lower for the large group (0.33 m) compared to the small and medium group sizes (0.41 and 0.42 m respectively, Table I). In other words, the spatial occupation and the heterogeneity of spatial arrangement of fishes increased with group size. *Speed* variability of barred flagtail was similar to that of bigeye scad. *Speed* decreased significantly with increasing Group Size ($r = -0.55$, $n = 435$, $P < 0.001$, Table I and II). *Polarity*

was positively correlated with *Speed* ($r = 0.64$, $n = 435$, $P < 0.001$, Table II). However, mean *Speed* for barred flagtail was significantly lower than for bigeye scad, within each group size (repeated measures ANOVA: $n(\text{barred flagtail}) = 145$ and $n(\text{bigeye scad}) = 145$, d.f. = 4, $P < 0.001$ for the three group sizes). Therefore, increasing group size led to an individual speed decrease associated with a decrease in *Polarity*. Moreover, the standard errors of mean *Speed* for the three group sizes were high but similar (Table I), indicating that the loss of cohesion with increasing group size was not due to a greater difference between individual motions.

DISCUSSION

Cohesion of fish schools is essential to survive in the risky and open pelagic domain. The analysis of the four variables (*NND*, *Speed*, *Expanse* and *Polarity*) linked to the attraction and repulsion forces governing this cohesion for two pelagic species observed in three different group sizes and in the absence of external structuring stimuli have shown contrasted results in terms of the arrangement of individuals inside the school. For the bigeye scad *S. crumenophthalmus*, the fishes were found parallel to each other, with *Polarity* values always greater than 0.81 and displaying little variation when Group Size

varied within the tested range of 2 to 8 individuals. Polarity was unrelated to the dispersion index (*Expanse*) and it was weakly variable depending on *Speed*. This means that most of the time, fish were perfectly polarized and sustained only three stable and regular patterns: line, column and dense school. Mean *NND* decreased dramatically with increasing group size, indicating that the bigger the group, the higher the density. These results suggest that the bigeye scad maintained group cohesion whatever the group size and formed closed ranks when group size increased. In other words, all individuals were mutually influential neighbours to each other and individuals adjusted their speeds and maintained closest contact between them. Most strikingly, high polarization and decreasing *NND* with increasing Group Size appeared in the absence of external factors such as food source, risk of predators or water flow (Hoare *et al.*, 2004). These observations confirm that the bigeye scad forms real fish schools and can be classified as an obligatory gregarious species. This interpretation is reinforced by the observed positive thigmotaxis, particularly for small group sizes, that may be due to a deficiency of conspecifics and then could be attributed to a social taxis, i.e. the search for conspecifics (Grünbaum, 1997). The possible presence of informed school leader(s) (Reebs, 2000) falls beyond the scope of this study. Although this presence cannot be totally excluded, especially when fish move in columns, this factor is not essential here, due to the lack of external stimuli.

Barred flagtail groups were less structured and moved slower than bigeye scad. Only pairs of barred flagtail (small Group Size) maintained a high cohesion ($\Phi = 0.79$ on average) and a medium *Speed* (0.36 m s^{-1}), but both values decreased dramatically with increasing Group Size, inducing both a loss of cohesion and a disorganization inside the shoal. This result was emphasized by a high dispersion index for the medium and large group sizes. The mean *NND* was relatively stable but high with 0.40 m on average (2 body lengths) which is twice as high as the mean *NND* most often quoted in the literature for small schooling pelagic fish (Pitcher & Parrish, 1993; Fréon & Misund, 1999). By pair, a given individual has elected one conspecific by maintaining almost permanently the same swimming direction but in a larger group size, fish was weakly stimulated by the other members. This result is in agreement with Romey (1996) who showed that inter-individual forces alone are enough to characterize the trajectories of simulated groups. Therefore, for this species, social interactions can be considered as tenuous, mainly accomplished via pairwise interactions, and not mainly due to the mutual attraction of individuals. In this way, the barred flagtail can be listed as the facultative gregarious species.

The main difference between the two species was their ability to form polarized group. Since the observations were conducted in the absence of external factors, it was assumed that the observed movement properties of individuals were correlated to species, and deduced that the ability to polarize is first a species specific trait. For obligate schooling fishes like bigeye scad, conspecifics should obtain this pattern by matching the velocity with their neighbours and by decreasing *NND*, leading to a densification of the group that nonetheless retains a high velocity. This pattern regulating the movement of individuals inside the group should result from natural selection at the individual level rather than from a collective and emergent outcome, not directly controlled by any member. In other words, the degree of social motivation (related to species) can be linked to the general attraction/repulsion rules between conspecifics. Moreover, the tendency of individuals to align with one another within the polarized group allows efficient information transfer and fast reaction to predators (e.g. Gerlotto *et al.*, 2006). Therefore, from an ecological and evolutionary point of view, polarity is a species specific trait under low influence of external factors.

The results on barred flagtail, classified as a facultative schooling fish in this study, were similar to those obtained by Parrish & Turchin (1997) on the juvenile blacksmith (*Chromis punctipinnis* (Cooper), family Pomacentridae)

and by Viscido *et al.* (2004, 2005) on the giant danios (*Danio aequipinnatus* (McClelland), family Cyprinidae). However, the experimental results on bigeye scad presented here are different from those obtained on simulated danio by Viscido *et al.* (2004), in two ways. First, *Polarity* was less group size-dependent in the present study than in previous ones: no change in *Polarity* was observed from two to four individuals, and only a decrease of 9% from four to eight individuals was found, compared to a decrease of 28% for danios in Viscido *et al.* (2004). Second, the observed distance between fishes varied in the present study according to Group Size showing that bigeye scads did not have a preferred *NND* linked to their group size. *NND* decreased from 0.54 to 0.12 m when Group Size changed from two to eight individuals, while a non-significant increase was observed for danios (from 0.12 to 0.17 m) by Viscido *et al.* (2004). In the same way, if simulated danios formed large and persistent groups, those groups were never very highly polarized (Viscido *et al.*, 2005). Therefore, the results of the present work imply that like the barred flagtail, the danio is a facultative schooling fish.

Several authors indicated that fish schools observed *in situ* displayed heterogeneous and variable structures at large scale (Fréon & Misund, 1999; Gerlotto & Paramo, 2003). Fréon *et al.* (1992) described the global internal structure of a whole fish school in the wild (made up of hundreds of thousands

of individuals). On a large scale, a fish school was a very heterogeneous 3D structure, with numerous empty sub-volumes (named “vacuoles”), and distant groups of fish displayed different alignments and behaviour. Tensions induced splitting and stretching behaviour and generated a more heterogeneous structure. This was probably due to a higher variability of individual characteristics in the wild and the effect of external factors like a patchy distribution of prey (Pitcher & Parrish, 1993; Parrish & Turchin, 1997). In the same way, the behaviour of facultative schooling fishes in natural conditions could lead individuals to align to each other within a parallel group. Several reasons have been advanced to explain these natural patterns, such as the number of influential neighbours (Warburton & Lazarus, 1991; Huth & Wissel, 1992) or external conditions (risk of predators, food availability, dissolved oxygen, hydrodynamism) which have an effect on fish behaviour by favouring or forcing alignment (Moss & McFarland, 1970; Abrahams & Colgan, 1985; Sogard & Olla, 1997; Hoare *et al.*, 2004). Only obligate schooling fishes should be able to form a real fish school, but in the wild, an aggregation is a dynamic entity exhibiting a range of structures and spacing according to circumstances (Nottestad & Axelson, 1999; Viscido *et al.*, 2005). Therefore, more observational data in natural conditions are needed to better understand how fish groups function and how social behaviours evolve in the wild.

The comparison of this experimental work with the modelling approach allows to have a better understanding of the differences between facultative and obligate schooling fish species. Two different modelling approaches have already been used: a “threshold tendency” approach, used by Viscido *et al.* (2004, 2005), postulating a fixed repulsion zone around each individual in a group (Aoki, 1982; Huth & Wissel, 1992; Couzin *et al.*, 2002) and a “continuous tendency attraction-repulsion” model, where attraction increases and repulsion decreases when inter-individual distance increases (Warburton & Lazarus, 1991; Warburton, 1997). Since bigeye scads seem to be able to adjust their NND according to the number of conspecifics by closing ranks, the increased cohesion between fish with increase in the individual number might be viewed as the decrease of the width of the repulsion zone surrounding each individual. Therefore, the results of this study support the “continuous tendency” model for bigeye scad and the “threshold tendency” approach for barred flagtail. The senses of the facultative schooling fishes like barred flagtail may not be efficient enough to operate an adjustment of the width of the attraction-repulsion and orientation zones, while this should be the case for the obligate schooling fishes like bigeye scad. Therefore, the rules for each model could account for the difference between schooling types described previously by Breder (1959).

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TABLES

Table I. Mean and standard deviation of each variable by species depending on group size and statistical results. P values are the levels of significance of the differences between group sizes according to one factor ANOVAs. *NND* and *Polarity* of the bigeye scad were tested with transformed values.

| | Group size | Small (1) | Medium (2) | Large (3) | P value | | |
|-----------------|-------------|-------------|-------------|-------------|---------|-----|-----|
| | | | | | 1-2 | 2-3 | 1-3 |
| | n | 145 | 145 | 145 | - | - | - |
| | Polarity | 0.89 ± 0.08 | 0.89 ± 0.09 | 0.81 ± 0.12 | NS | *** | *** |
| Bigeye scad | Expanses | 0.27 ± 0.10 | 0.28 ± 0.10 | 0.22 ± 0.07 | NS | *** | *** |
| | Speed (m/s) | 0.47 ± 0.17 | 0.53 ± 0.17 | 0.34 ± 0.22 | *** | *** | *** |
| | NND (m) | 0.54 ± 0.20 | 0.24 ± 0.12 | 0.12 ± 0.04 | *** | *** | *** |
| | n | 145 | 145 | 145 | - | - | - |
| Barred flagtail | Polarity | 0.79 ± 0.16 | 0.51 ± 0.19 | 0.32 ± 0.17 | *** | *** | *** |
| | Expanses | 0.21 ± 0.08 | 0.55 ± 0.17 | 0.74 ± 0.16 | *** | *** | *** |
| | Speed (m/s) | 0.36 ± 0.13 | 0.28 ± 0.13 | 0.16 ± 0.12 | *** | *** | *** |
| | NND (m) | 0.41 ± 0.15 | 0.42 ± 0.15 | 0.33 ± 0.11 | NS | *** | *** |

***: P < 0.001; NS: not significant.

Table II. Product-moment correlation coefficients for variable and for each species, with the significance of correlation (t test). Correlations for *NND* (*nearest neighbour distance*) and *Polarity* of the bigeye scad were calculated on transformed values.

| Species | Variable | Polarity | Expanse | NND | Speed |
|---------------------------------|------------|----------|---------------------|--------------------|---------------------|
| Bigeye scad (n = 435) | Group size | -0.35*** | -0.24*** | -0.84*** | -0.35*** |
| | Polarity | - | -0.02 ^{NS} | 0.18*** | 0.56*** |
| | Expanse | - | - | 0.75*** | -0.02 ^{NS} |
| | NND | - | - | - | 0.17*** |
| Barred flagtail (n = 435) | Group size | -0.71*** | 0.80*** | -0.26*** | -0.56*** |
| | Polarity | - | -0.70*** | 0.02 ^{NS} | 0.64*** |
| | Expanse | - | - | 0.09 ^{NS} | -0.42*** |
| | NND | - | - | - | 0.19*** |

P < 0.01; *P < 0.001; NS: not significant.

Table III. Results of the MANOVA (adjusted R-square = 0.34) on the *Polarity* of the bigeye scad fishes (n = 435).

| | Sum of Square | d.f. | F | p |
|----------------|---------------|------|--------|--------|
| Intercept | 0.0420 | 1 | 77.22 | 0.0001 |
| <i>Speed</i> | 0.0632 | 1 | 116.08 | 0.0001 |
| Group Size | 0.0081 | 2 | 7.41 | 0.0007 |
| <i>NND</i> | 0.0014 | 1 | 2.48 | 0.1158 |
| <i>Expanse</i> | 0.0001 | 1 | 0.16 | 0.6881 |
| Error | 0.2330 | 428 | | |

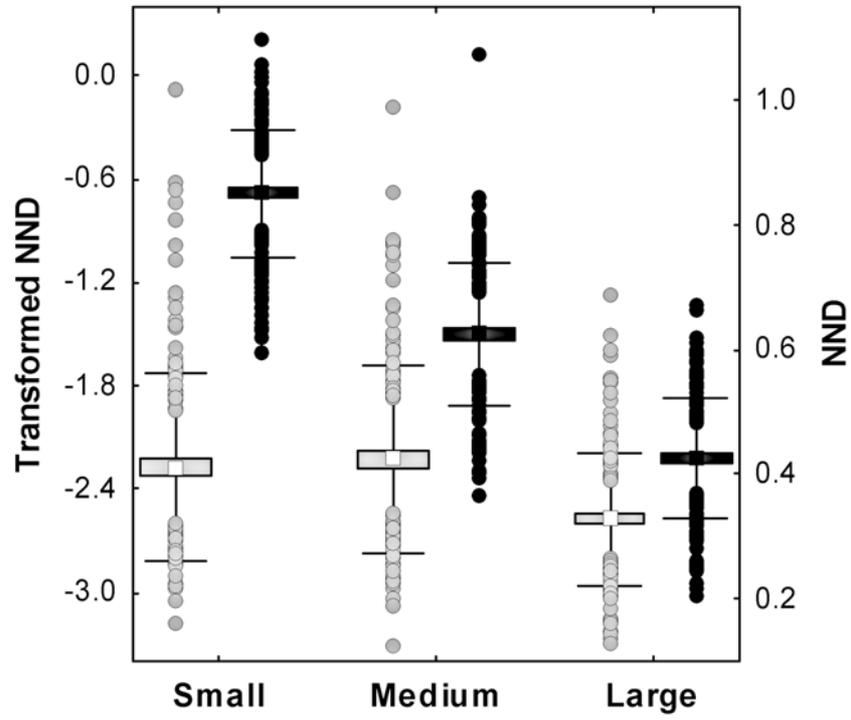


Figure 1. Categorized box plot of the nearest neighbour distance (*NND*) vs. the group size for the bigeye scad. (■ : Mean, ■ : \pm SE, ▤ : \pm 0.95*SD, ● : Extreme) and the barred flagtail □ : Mean, □ : \pm SE, ▤ : \pm 0.95*SD, ○ : Extreme). *NND* of the bigeye scad were calculated on transformed values.

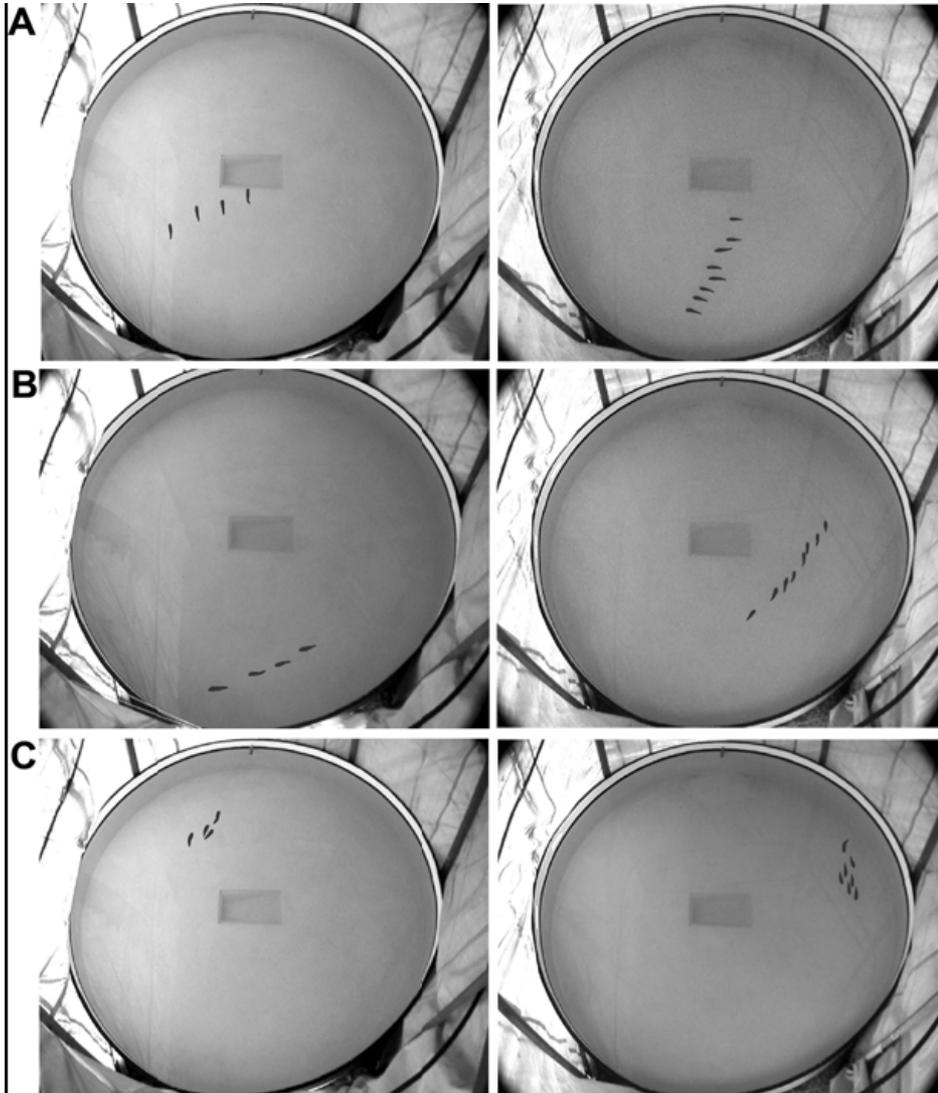


Figure 2. Images resulting from the observations carried out on groups of four (left) and eight (right) bigeye scads, illustrating the three patterns displayed by the fish (A: line, B: column, C: dense school).