Article

New Classification of Collective Animal Behaviour as an Autonomous System

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Abstract: Integrated information theory (IIT) was initially proposed to describe human consciousness in terms of intrinsic, causal brain-network structures. This theory has the potential to be useful for conceptualising complex living systems. In a previous study, we analysed collective behaviour in Plecoglossus altivelis and found that IIT 3.0 exhibits qualitative discontinuity between three and four fish. Other measures like mutual information did not have such characteristics. In this study, we followed up on our previous findings and examined timescale effects on integrated information of collective behaviour. We found that a long timescale (1 s) causes Boid-like local interactions to dominate over interactions with the whole, but only when the group size is five at a given time scale (i.e. around 0.2 s). Interestingly, the most suitable time scale is roughly equal to fish reaction time. We used these data to propose a new classification for fish schools, with each size group being a unique and autonomous system, despite small group sizes.

Keywords: Integrated Information Theory; Collective Behaviour, Self-Organization; Cause and Effect Structure

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1. Introduction

Collective behaviours in nature are emergent properties produced through local interactions of self-organising individuals. Such behaviours include swarming [1–6], fish schooling [7–11], bird flocking [12–17], or high-level cognitive functions arising from 'bottom-up' neural networks. These systems of many interacting elements can achieve optimal information processing capabilities when poised at the critical boundary separating chaos from order. Several analyses have demonstrated individuals responding swiftly as a collective to changing environments [14–16] and that a group can achieve relatively good decision-making [18–20]. Conflicts among individuals do not necessarily lead to group disruption and can instead provide valuable insight into what collective responses are effective [21,22]. The unity of collective behaviours remains a natural mystery of nature [23], because interactions are hidden, while the resultant actions are observable.

Self-organised criticality (SOC) is a valuable concept for interpreting complex collective behaviours. Flexibility and robustness can be achieved collectively when the group is in the intermediate state between order and disorder [24–29]. For instance, external perturbations of collective systems in SOC models optimise the effective correlation range of each individual to accomplish efficient information transfer [13–16]. However, the SOC models are unreliable with small groups, because individual interactions are less likely to be homogeneous [30,31]. In fish, for example, groups of two and three appear to exhibit differential between-individual interactions [32,33]. Therefore, many researchers have examined information transfer (or causal relationships) among individuals in small groups [34–36], often employing local transfer entropy [37–42]. For example, transfer of misinformation happens in schools with five fish when the whole group changes direction [36]. Animals could potentially use active information storage to predict the timing of nontrivial information transfer [43,44]. Despite capturing some aspects of collective behaviour systems, however, SOC models provide little insight on the causal structures within groups [45].

In contrast, integrated information theory (IIT) may be a good metric for group interactions [46] because it has the potential to model intrinsic causal structures. Proposed by Balduzzi and Tononi [47] in 2009, IIT was originally developed to quantify consciousness from brain activity [47,48]. In principle, the core concept of IIT is to define integrated information (Φ) as degree of information loss (or increase in uncertainty [49]) caused by a given partition of the system [48,50]. The versatility of this concept has led to widespread application in multiple fields [48–53]. Recent studies have indicated that IIT can discriminate between various states of lost consciousness, such as dreamless sleep [54], general anaesthesia [55], or vegetative states [56]. Some studies have suggested that integrated information could act as an order parameter of complex systems, similar to the generalised Ising model [57], coupled oscillators [58], and coupled mapping [59]. In these order parameters, Φ peaks indicate critical points. Assuming that biological systems such as schools of fish evolved to reside in a critical state for advantages such as fast information transfer, having high Φ values may provide meaningful insight into collective animal behaviour, especially if we understand the universal features of Φ near critical points.

Integrated information theory is also resonant with complex systems because it posits that the whole cannot be reduced into its parts; the components produce synergetic information that would be lost upon separation [60,61]. Complex biological systems are also irreducible owing to their intrinsic causal structures [62]. When applying IIT to these systems, Φ can be a measure of an autonomous system's wholeness [60], capturing intrinsic causal structures [63] while also acting as its order parameter. As an initial step to modelling collective animal behaviour, some researchers have applied IIT to interpret classifications of cellular automatons [45], animats [64] and Boolean networks [65]. For instance, average Φ values for five to six automata cells correlated well with their complexity (e.g. class III and IV rules), despite the small cell-set number [45]. This finding suggests that Φ can be used to distinguish between even groups of small sizes.

Existing studies applying IIT as an order parameter employed IIT 2.0, among the different variants of this theory [66]. In the present work, we instead chose to use IIT 3.0 because its modelling of integrated-information variance (or susceptibility) is more similar to an order parameter. In our previous study [67], we applied IIT 3.0 to schools of two to five fish (Plecoglossus altivelis) and found that Phi was discontinuity between three- and four-fish schools in Phi. In the present work, we extended our approach further to examine how integrated information changed under different timescales. We aimed to determine whether group size could distinguish between fish schools as distinct autonomous systems.

2. Results

2.1. Definition of the local and the global parameter settings

Because collective behaviours do not have specific ON/OFF firing states, we first defined binary states among fish schools so that IIT 3.0 could be applicable. We followed our proposal in the previous study of using local and global parameters as a threshold for ON states.

First, local parameters comprise three interaction categories: distance (contact with other individuals), field of view (seeing other individuals), and turning rate (being affected by other individual's movements). These three parameters are often present in flocking models and reflect local Boid-like interactions [11,67,68]. Next, global parameters comprised two interaction categories: distance from the centre of mass and deviation from the group's average direction.

There are clear conceptual differences between local and global parameters. The latter assumes that each individual knows the state of the entire group and thus can refer to the global state for determining subsequent behaviour. This assumption allows us compare individual state with average group values. In contrast, local parameters do not have such an assumption.

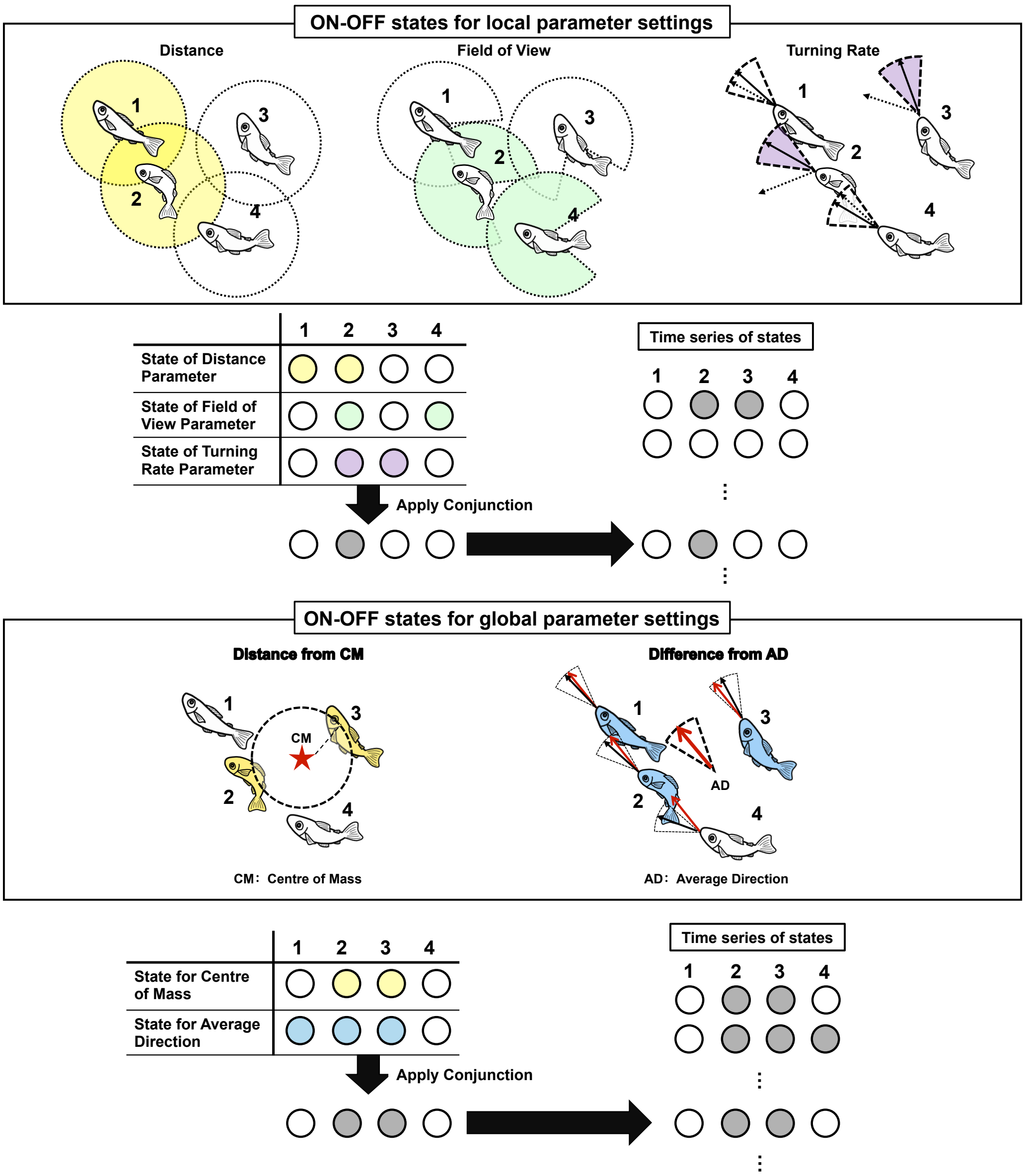


Figure 1. (a) ON and OFF states for local parameter settings. Three parameters determine a school's state (yellow: distance, blue: field of view, purple: turning rate). Coloured fish are in the ON state. (b) ON and OFF states for global parameter settings. Two parameters determine a school's state (yellow: centre of mass, blue: average direction). Coloured fish are in the ON state. For both local and global parameters, we applied a conjunction of all school states to obtain the final school state at time t. We then computed Φ from a time series of these states in PyPhi.

After obtaining binary states of local and global parameter settings per fish, we took a conjunction of three (local) or two (global) bits of information to produce individual fish states at time t. For example, if we have Distance: ON, Visual field: OFF and Turning rate: OFF for fish i, that yields OFF (i.e. $s_i^t = 0$) for the fish i. This procedure applies to all fishes in the group at time t, or N-bit state $\boldsymbol{s}^t$. When these procedures are applied to all time steps, we obtained s, a sequence of n bit states $(\boldsymbol{s}^0, \boldsymbol{s}^1, ..., \boldsymbol{s}^T)$ for n fish school (T is the maximal time step for each data set). These bit sequences are not sensitive to parameter or timescale (length of time step) selection. In contrast to our previous study, we examined a timescale range: $\Delta = 5/120$ s, $\Delta = 10/120$ s, $\Delta = 20/120$ s, $\Delta = 40/120$ s, $\Delta = 80/120$ s, and $\Delta = 120/120$ s.

To clarify our definitions of local and global parameters, consider a situation where each parameter is given as $\zeta = 200$ mm, $\eta = 3/2\pi$ rad, and $\delta = 0.1$ rad. The first two parameters are metric distance (i.e. ζ) with blind sight (i.e. η), variables that have been used in other flocking models. Combined, they determine a fish's interaction radius in the group, a necessary condition for agent interactions. Specifically, the outside of this radius generates immediate interactions. The third parameter (δ) is turning rate. If the value is >0.1 rad, some environmental factors are involved in generating individual movement. In flocking models, this environmental effect always stems from neighbours (after excluding noise).

In summary, the combination of these three parameters models a situation where information transfer occurs only when the individual changes direction within their interaction radius, similar to existing flocking models [69,70]. Notably, using 'OR' to connect the parameters is illogical. For example, if distance and field of view are connected by 'AND', while turning rate is connected to them by 'OR', that essentially signifies information transfer occurring irrespective of interaction status when some agents change direction. The same logic applies to other connective relations. Therefore, combining the three parameters with 'AND' is the most reasonable setting to capture information transfer in collective behaviour.

Conceptualisation of the global parameters differs from the local parameters. For example, if a fish's distance from the centre of mass is always above its threshold, this fish never reaches the core of the school. If a fish's direction almost always differs from the average group direction, this fish changes its direction irrespective of group direction. Overall, global parameter settings depict feedback information from the whole school. Such feedback is often observed in complex systems because they contain several nested scale events [6]. All parameter settings include one parameter dependence: (effect of distance parameter alone. The latter can be obtained with $\delta = 0$ and $\eta = 2\pi$, resulting in an always 'ON' conjunction between the two variables. The setting of these two parameters does not influence 'ON' and 'OFF' states generated by the distance parameter alone. Such parametric tuning allows for separating the effects of any parameter settings. As in our previous study, we set the network structure of fish schools to be entirely connected, without self-loops. This assumption stemmed from the observation that the minimum distance between any pair of fishes was <5 mm in our experiments. Such a distance suggests that some interactions must happen among all fishes after about 10-15 min of free swimming.

2.2. *Φ values for local parameter settings across timescales*

We found that the general tendency across all groups is for Φ to increase as timescales increased (Fig. 2). Notably, when N = 5 s (out of 120 s), mean Φ reached 5.0, approximately two times greater than mean Φ for short timescales in five-fish schools. Furthermore, mean Φ for all group size decreased after passing the peak, at around 20/120 s. The timescales that corresponded to peak Φ approximately match fish reaction times. Our brief overview suggests that the effect of timescales on Φ may generate qualitatively different information.

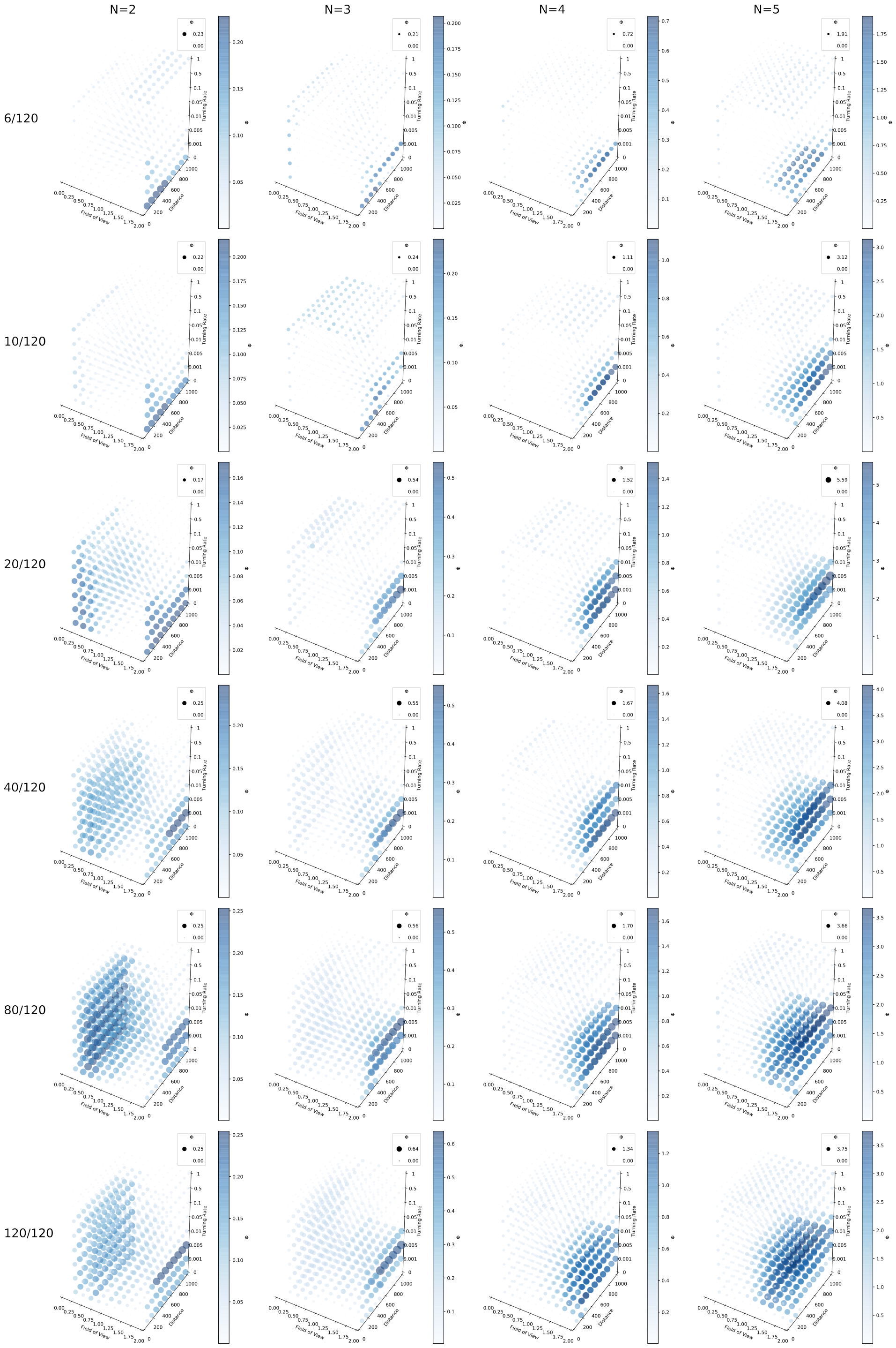


Figure 2. The heat map shows mean Φ values, represented by circle colour and size. Each axis corresponds to a different parameter (Field of View (π rad), Distance (mm) and Turning Rate (π rad)). Mean Φ values peak around 20/120 and 40/120 s. After passing peak values, Φ gradually decreases. Standard deviation of Φ highly correlates with the mean (see SI.1).

Turning rates rarely affected Φ in short timescales. However, their impact on Φ increased considerably with long timescales (>0.2 s). These outcomes suggest that under a long timescale, changing direction contributes to fish collective behaviour as an autonomous system. The importance of changing direction in animal flocks is often examined with simple agent models, such as the self-propelled particle model or the Boid model [11,67,68]. The 'agent' generally transfers information to its neighbours through changing direction. Our results thus reflect the tendency of long timescales to become increasingly important for direction changing in a group. However, our analysis has some major differences from simple flocking models. In our parameter settings, OFF states of fish are rare compared with ON states. These differences imply that changing directions is not informative or does not have much causal power for fish schools, a possibility that might provide new insight into the collective behaviour as autonomous systems.

Variance of Φ values (SI.1) reveal completely different information from mean values. Because IIT 3.0 computes Φ for every group state (2^n states for n fish schools), we can calculate standard deviations (SD) of Φ from all states in addition to mean Φ. In IIT 3.0, Φ refers to the causal structure's degree of irreducibility to specific parts (i.e. minimum information partition) [45,51,65]. The irreducible system will lose much cause-effect power if removing a group member results in two different systems.

A highly integrated information group means each fish uniquely contributes to establishing densely connected autonomous systems. In our study, all fish schools experienced a cut of only one fish from the remaining group members. The lack of that single element results in loss of intrinsic causal power among a highly integrated group. In contrast, a less integrated information group has two situations upon the loss of a group member. One is that the original conceptual information (before cutting) is low. The other is that the original conceptual information (before-cutting intrinsic causal structure) is high, but post-cutting information loss is low. Both cases indicate that removing one element does not strongly affect the system. Lowly integrated systems contain relatively independent small clusters because remaining fish can cover the loss of information.

Fish schools can have with high SD in both highly integrated and lowly integrated systems, the former exhibiting well-coordinated group activities and the latter having relatively independent elements. Compared with the distribution of SD of Φ values in SI.1, SD is strongly correlated with mean Φ. This observation suggests that raising mean Φ also increases SD of Φ values. Having both highly integrated and lowly integrated groups may contribute to boosting fitness.

2.3. Peak shifting across each parametric space

Based on our hypothesis that living systems evolve to increase Φ, we selected the top five Φ values from each data series and averaged them (Fig. 3). All groups tended to increase Φ with increasing timescales, with the most values around 20/120 or 40/120 s.

Notably, Φ values of $N = 2$ exhibits the most change all over the parameter space along with timescale. This movement is generated by followership characteristics observed mainly in the two-fish school. Specifically, Φ increases in the two-fish group when either fish traces the other's trajectory (i.e. the narrow threshold of the visual field). In contrast, three- and four-fish schools never radically changed parametric values except turning rate. However, followership and not leadership explains a one point decrease on the field of view axis at 10/120 s in $N = 3$. In contrast, the field of view axis drops slightly for short timescales below 10/120 s in $N = 4$. This drop is due to leadership, which was more conspicuous in the five-fish group. These differences suggest that the four- and five-fish schools are fundamentally different autonomous systems in terms of timescales.

We applied the same method to global parameter settings and observed shifts in $N = 2, 4, 5$ (Fig. 4). For long timescales in $N = 4$ and 5, distance from average values becomes increasingly restricted. This tendency suggests that relatively large groups form distinct boundaries that are more distinct when aggregating.

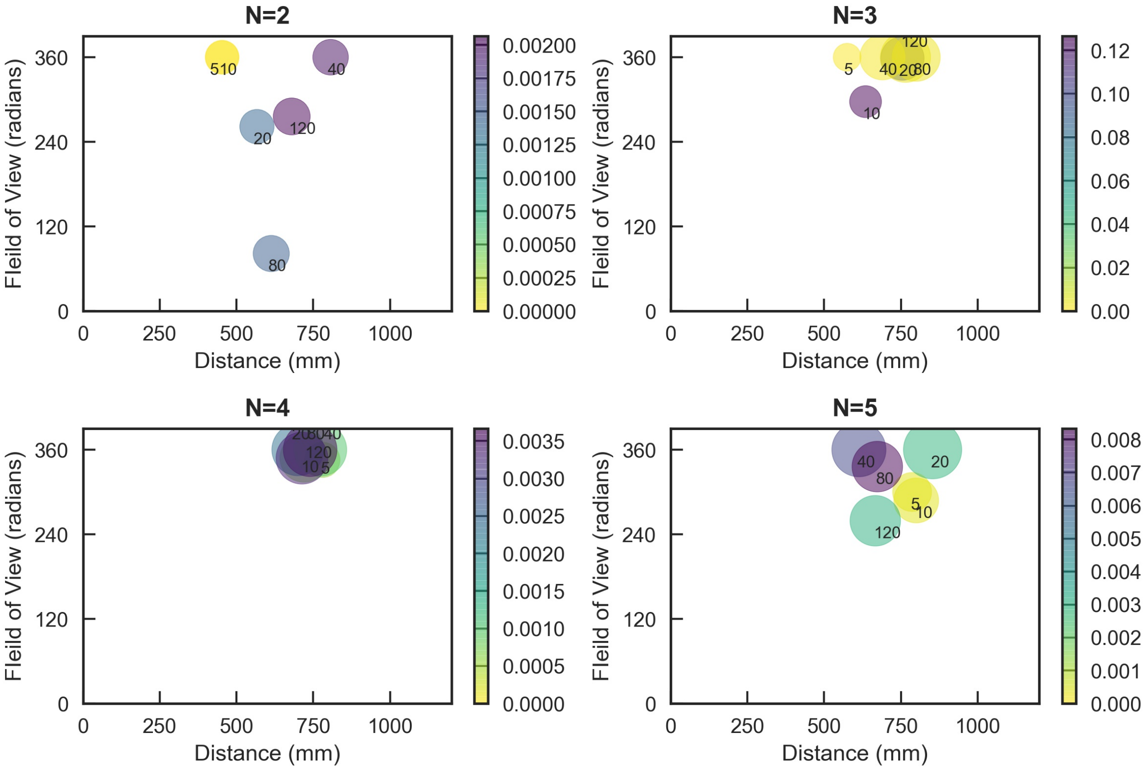


Figure 3. Transition of averaged top five Φ values and other parameters per group size. Each colour corresponds to turning rate. Two- and five-fish schools move drastically in the parametric space. Changes in the two-fish school are due to followership, while changes in the five-fish school are due to leadership.

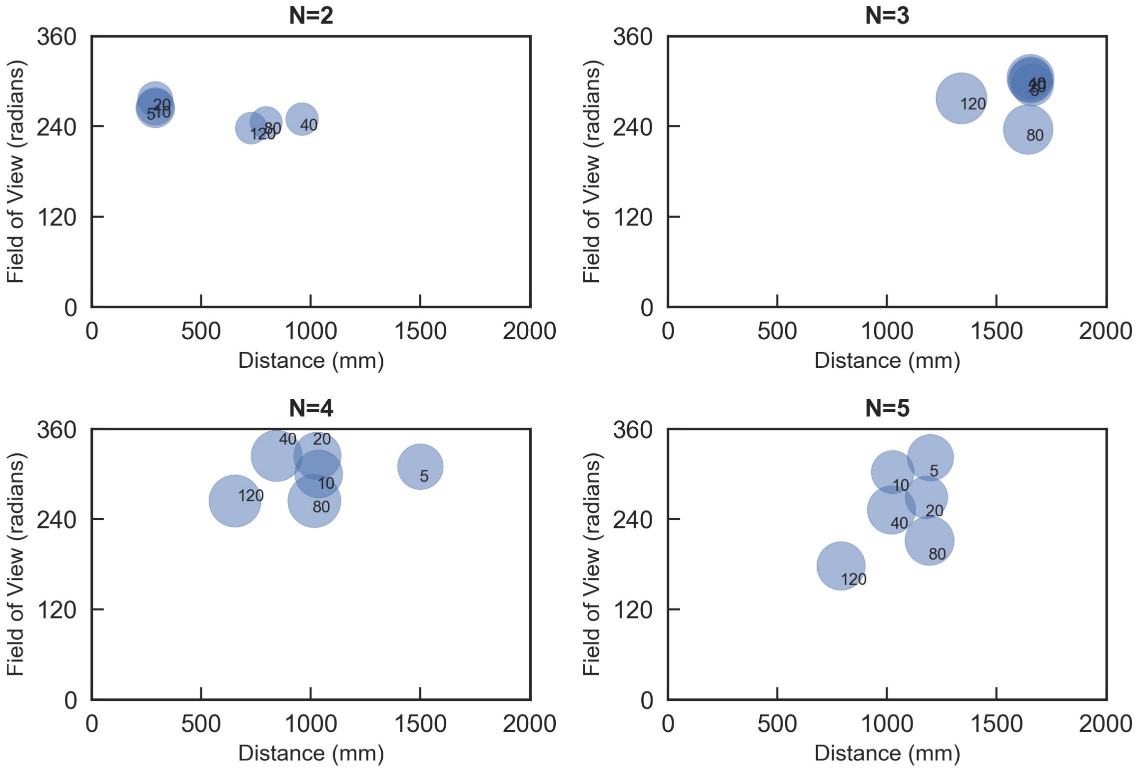


Figure 4. Transition of averaged top five Φ values and other parameters per group size. There is a general tendency to move leftward and downward in the parametric space. More distribution data can be seen in SI.2.

2.4. Φ_{local} *versus* Φ_{global}

Local parameter settings and global parameter settings yield qualitatively different Φ values. We therefore denoted Φ_{local} for the local parameters and Φ_{global} for global parameters. Φ_{local} is an intrinsic causal power generated by Boid-like local interactions, while Φ_{global} is generated by interactions with the global reference. For a longer timescale, we have already confirmed that Φ for both parameter settings generally increase but eventually saturate above a specific timescale.

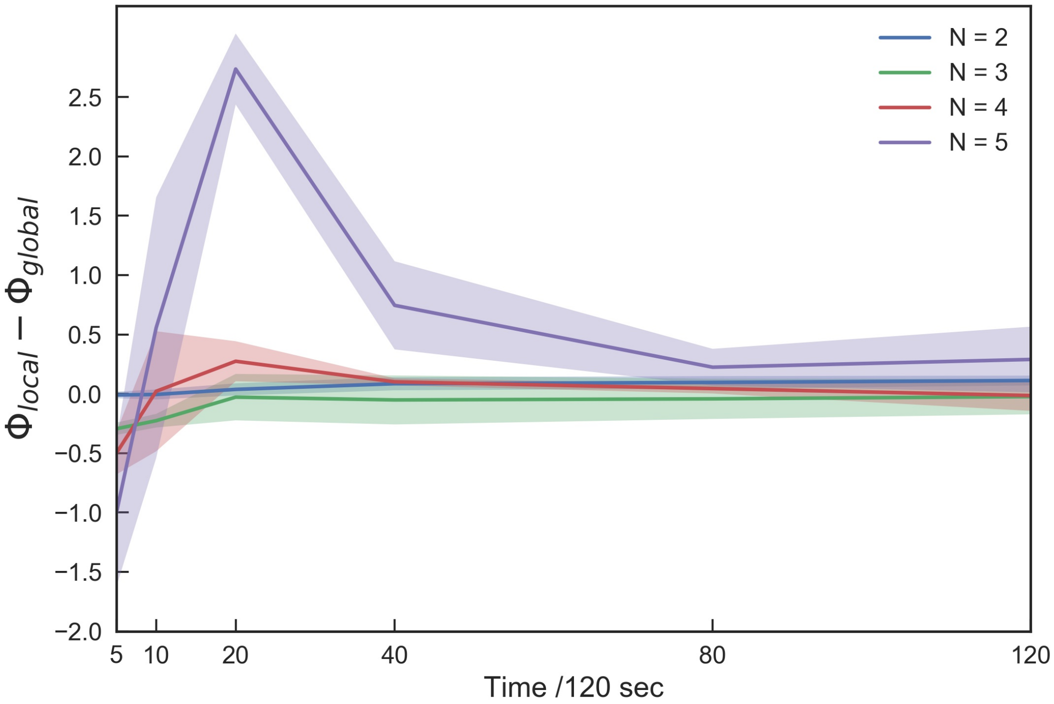


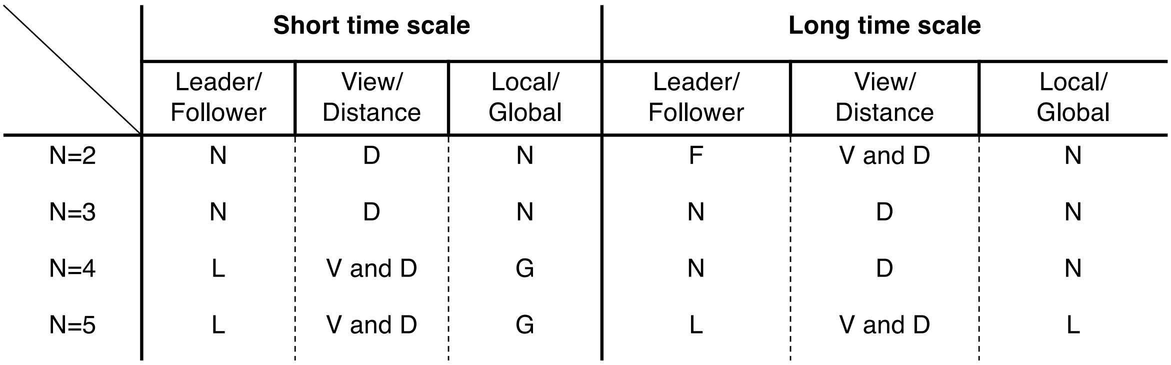
Figure 5. The difference in Φ_{local} and Φ_{global} along timescales per group size. Positive values indicate that causal power generated by local interactions is greater than its global reference. The difference increases over a long timescale when the group size is five. Under a short timescale (<0.10 s), causal power generated by the global reference tends to be higher than what is generated by local references except in the two-fish school.

The difference between Φ_{local} and Φ_{global} indicates which is the dominant process for a group at a given timescale. The dominant process in a short timescale (5/120 s) is high Φ_{global}, or interaction with the global reference (Fig. 5). However, in relatively long timescales above 20/120 s, the apparent high peak emerges in N = 5. This positive peak at 20/120 s suggests that the dominant process at this timescale is the Boid-like local interaction. Interestingly, this timescale approximately corresponds to fish reaction times [36].

Our data, therefore, suggest that local interactions dominate in schools with over five fish. Thus, four and five-fish schools appear to be clearly distinct.

2.5. New classification of fish schools as a different autonomous systems

As explained earlier, the aim of this study was to discriminate the qualitative different autonomous systems in terms of several parameter settings. Most research on collective behaviour rarely focuses on small groups as different systems from each other, with much of the interest being targeted at information processing inside groups ([45]). Using the hypothesis that living systems evolves to inflate Φ, we inferred optimal parameter values for each fish school. We succeeded in classifying all fish schools from two to five and described four distinct autonomous systems (Fig. 6). (I) Two fish: the group shows fission-fusion dynamics on short timescales and followership relations in long timescales. (II) Three fish: the group also shows fission-fusion dynamics on short timescales like two-fish groups. This group has no notable characteristics compared with other groups and is a borderline between two and four-fish school. (III) Four fish: this group has leadership that can be confirmed using transfer entropy. Our analysis suggests that this autonomous system would have high intrinsic causal power due to the presence of leadership. (IV) Five fish: in addition to leadership, Boid-like local interactions dominate this group for long timescales. The intrinsic causal power of local interactions overwhelms global interactions.



	Short time scale			Long time scale		
	Leader/ Follower	View/ Distance	Local/ Global	Leader/ Follower	View/ Distance	Local/ Global
N=2	N	D	N	F	V and D	N
N=3	N	D	N	N	D	N
N=4	L	V and D	G	N	D	N
N=5	L	V and D	G	L	V and D	L

Figure 6. Classification of fish schools. The first column classifies the existence of leader (L), follower (F), or neither (N). The second column classifies the most influential parameter pair of distance (D) or field of view (V). The third column classifies the dominant interaction mode: local interaction (L), global interaction (G), or neither (N). The same classification applies for short and long timescales.

3. Discussion

Studies on collective behaviour have long focused solely on within-group interactions, such as transfer entropy among individuals and collective information transfer seen in scale-free correlations or shock-waves[13,69]. In this study, we shed light on an overlooked aspect of collective behaviour through our focus on how group size affects collective behaviour.

Continuous small changes make a qualitative difference, but it can be difficult to determine the tipping point or the one change that triggers the difference. This sorites paradox (adding individual grains eventually becomes a heap) can be observed all over the domain of complex systems (ex. neurons build consciousness, individuals build group behaviour). From this perspective, the emergence of collective behaviour is about identifying the number of individuals that trigger collective behaviour. Therefore, the distinction for a small number of groups as an autonomous system does not seem crucial for understanding collective behaviour.

In terms of applying the sorites paradox to actual living systems, consider the following. If we construct a heap for a given environment, we need to keep the area around the heap clean and indicate the correct place to place grains. The former refers to environmental factors that may destroy the heap, while the latter suggests that disorganisation results in the complete lack of a heap. To build the heap, the external observer must intervene in each process since the heap image exists in his head.

This ceaseless intervention to the system is vital for the sorites paradox. However, what are the relations of this argument and collective behaviour?

Forming groups is not an easy task for individuals because no one has a rigorous blueprint of aggregations. Each individual attempts to maintain tight relations with each other and sometimes may deviate from the group for individual needs. Most collective behaviour in nature is unstable, with group fission being just as essential for improving fitness as group fusion. Thus, individual animals are constantly intervening in the process of forming aggregations, similar to the external observer in the sorites paradox.

The manipulativist view [70] helps explain why IIT 3.0 is the best candidate for analysing those requirements. The causal-effect structure of an autonomous system represents 'what causes what', considering all counterfactual states [63]. Lombardi et al. correctly pointed out that the central idea of 'differences that make differences' represents intervention in the cause-effect structure of a system [70]. Note that this manipulation in the system does not need to be an actual one. This potential cause-effect structure makes the system autonomous.

We can also apply this argument to collective behaviour. The intrinsic causal structure in fish schools represents how each fish effects each other to maintain an aggregation. Since the cause-effect structure in fish schools represents virtual interventions inside the group, the sorites tipping point becomes invalid in IIT 3.0. Instead, we can confirm the existence of various tipping points in collective behaviour, supporting our hypothesis of living systems evolving to raise Φ. We have already seen one of tipping points as discontinuity between schools of different sizes in this and previous studies [29].

Furthermore, high mean Φ strongly correlated with high SD of Φ. This pattern indicates that the group forms a well-organised causal structure as an autonomous system and contains relatively independent groups in the same system. Plecoglossus altivelis may solve the paradox of balancing between forming a grain heap (high Φ values) while also containing independent grains (low Φ values). This is possible because ceaseless intervention from the outside (extrinsic perspective) turns into ceaseless intervention inside the group (intrinsic perspective).

We provide a new list of classifications as a different autonomous system for a small number of fish schools. The list is not decisive, as other suitable parameter settings are, of course, possible. However, we believe that our parameter settings fit well with present theories of collective behaviour. The local parameter setting is based on a Boid-like interaction model, and the global parameter setting is based on the feedback from the whole system. Using our parameter settings, IIT 3.0 can discriminate between two- to five-fish school as distinct systems.

IIT 3.0 showed that local interactions dominate in five-fish schools. The difference between Φ_{local} and $\Phi_{global;}$ becomes a positive maximum near fish reaction times. This finding suggests that Φ generated by the local interaction scheme defeats global interaction when group size is over five. Two- and three-fish schools show little difference between local and global interactions. Even if the global dominance emerges above the four-fish school, this difference soon disappears for long timescales. Only the five-fish school retains their difference for long timescales. This outcome strictly distinguishes the five-fish school from schools with fewer fish.

4. Materials and Methods

4.1. Ethics statement

This study was carried out in strict accordance with the recommendations in the Guide for the Care and Use of Laboratory Animals of the National Institutes of Health. The protocol was approved by the Committee on the Ethics of Animal Experiments of the University of Tsukuba (Permit Number: 14-386). All efforts were made to minimise suffering.

4.2. Φ computation

All computations, in this paper, were performed using the PyPhi software package with the CUT_ONE_APPROXIMATION to Φ.

4.3. Experimental Settings

We studied *ayus* (*Plecoglossus altivelis*), also known as sweetfish, which live throughout Japan and are widely farmed in Japan. Juvenile *ayus* (approximately 7-14 *cm* in body length) display typical schooling behaviour, though adult *ayus* tend to show territorial behaviour in environments where fish density is low. We purchased juveniles from Tarumiyoushoku (Kasumigaura, Ibaraki, Japan) and housed them in a controlled laboratory. Approximately 150 fish lived in a 0.8 m^3 tank of continuously filtered and recycled fresh water with a temperature maintained at 16.4°C, and were fed commercial food pellets. Immediately before each experiment was conducted, randomly chosen fish were separated to form a school of each size and were moved to an experimental arena without pre-training. The experimental arena consisted of a $3 \times 3 m^2$ shallow white tank. The water depth was approximately 15 *cm* so that schools would be approximately 2D. The fish were recorded with an overhead grey-scale video camera (Library GE 60; Library Co. Ltd., Tokyo, Japan) at a spatial resolution of 640 × 480 pixels and a temporal resolution of 120 frames per second.

4.4. Data Summary

Table 1. Data Summary. N: Number of individuals (Unit: None), x: Average distance (Unit: (mm)), v: Average veolocity (Unit: (mm) per second), Error (S.D.) (Unit: Degrees (rad)), d_{min}: Minimum distance (Unit: (mm)), Total Time Steps (steps)

N	**Average distance (mm)**	**Average veolocity (mm/s)**	**Error (S.D.)**	**Minimum distance (mm)**	**Total Time Steps**
2	166.3	268.8	0.18	1.90	106961
	90.67	271.68	0.23	0.10	99431
	122.0	256.08	0.18	1.60	107206
3	170.8	301.2	0.23	1.80	90051
	159.1	343.2	0.14	1.83	83654
	173.1	300.0	0.13	2.82	97446
	132.0	240.0	0.19	1.67	93931
4	164.3	270.72	0.14	1.18	106327
	141.5	190.8	0.12	1.38	103226
	114.9	148.56	0.38	1.83	98126
5	143.8	259.92	0.28	0.79	102895
	146.0	213.12	0.12	1.16	97346
	143.7	259.2	0.28	1.44	92116

4.5. Timescales

We prepared the trajectory data in different time intervals (In Python $\boldsymbol{X}[:;\delta t]$) and applied smoothing by convolving three data points to reduce noise. δt is a timescale in $\delta t/120$.

4.6. The definition of ON and OFF state for each parameter

We define a function for each parameter that returns either 0 (OFF) or 1 (ON) for given input values. Generally, we denote a function as $F_i^t(\cdot)$, where F is the name of the function, i is the index of the individual and t is the time. The arguments of the function can be either in the position vectors $\boldsymbol{x}_i(t)$ or the velocity vectors $\boldsymbol{v}_i(t)$ of each individual at time t. In general, the dimensions of these vectors are $d \leq 3$; the experimental setup used here gives $d = 2$. The number of individuals is N.

4.6.1. Local parameters

- Distance function $D_i^t(\boldsymbol{x}_1(t), \boldsymbol{x}_2(t), \cdots, \boldsymbol{x}_n(t))$: $\mathbb{R}^d \times \mathbb{R}^d \times \cdots \times \mathbb{R}^d \to \{0,1\}$

  For each individual i we obtain a set $S_i^t = \{j | d(\boldsymbol{x}_i(t), \boldsymbol{x}_j(t)) < \zeta, j \neq i\}$ of all other individuals within a specified distance ζ. Here $d(\boldsymbol{x}, \boldsymbol{y})$ gives the Euclidean distance between $\boldsymbol{x}$ and $\boldsymbol{y}$. Then, $D_i^t(\boldsymbol{x}_1(t), \boldsymbol{x}_2(t), \ldots, \boldsymbol{x}_n(t)) = 1$ when $|S_i^t| > 0$ and is 0 otherwise, where $|S|$ denotes the number of elements of a set S.
- Blind sight function $B_i^t(\boldsymbol{v}_1(t), \boldsymbol{v}_2(t), \cdots, \boldsymbol{v}_n(t)) : \mathbb{R}^d \times \mathbb{R}^d \times \cdots \times \mathbb{R}^d \to \{0,1\}$

  For each individual we form the set $O_i^t = \{j|\ \arg(\boldsymbol{v}_i(t),\ \boldsymbol{v}_j(t)) < \eta,\ j \neq i\}$ of all other individuals whose velocity vectors point in a direction within an angle η of that of the focal individual. The function $\arg(\boldsymbol{v}_1(t),\ \boldsymbol{v}_2(t))$ gives the angle between two vectors. Then, $B_i^t(\boldsymbol{v}_1(t), \boldsymbol{v}_2(t), \cdots, \boldsymbol{v}_n(t)) = 1$ when $|O_i^t| > 0$ and is 0 otherwise.
- Turning rate function $T_i^t(\boldsymbol{v}_i(t), \boldsymbol{v}_i(t - \Delta t)) : \mathbb{R}^d \times \mathbb{R}^d \to \{0,1\}$

  The turning rate function returns 1 when an individual's turning rate exceeds a specified thresholdδ. That is, $T_i^t(\boldsymbol{v}_i(t), \boldsymbol{v}_i(t - \Delta t)) = 1$ when $\arg(\boldsymbol{v}_i(t), \boldsymbol{v}_i(t - \Delta t)) \geq \delta$ and is 0 otherwise. The time step used in this paper is $\Delta t = 0.05$, $\Delta t = 0.1$ or $\Delta t = 0.2$ s.

To obtain the states of the fish school, we take a conjunction of these result, that is, $D_i^t(\boldsymbol{x}_1(t), \boldsymbol{x}_2(t), \cdots, \boldsymbol{x}_n(t)) \wedge B_i^t(\boldsymbol{v}_1(t), \boldsymbol{v}_2(t), \cdots, \boldsymbol{v}_n(t)) \wedge T_i^t(\boldsymbol{v}_i(t), \boldsymbol{v}_i(t-\Delta t))$ for each individual i. The conjunction is given as $\wedge : \{0,1\}^2 \rightarrow \{0,1\}$ where $1 \wedge 1 = 1$ and is 0 otherwise. Thus the state of each individual i at time t is $s_i(t; \zeta, \eta, \delta) \in \{0,1\}$ which depends on the triplet of parameter values (ζ, η, δ). The state of the school at time t is then a vector $\boldsymbol{s}(t) = (s_1(t), s_2(t), \ldots, s_n(t)) \in \{0,1\}^n$, where the parameter dependence has been omitted for simplicity.

4.6.2. Global parameters

- Average direction function $Avd_i^t(\boldsymbol{V}(t), \boldsymbol{v}_i(t)) : \mathbb{R}^d \times \mathbb{R}^d \rightarrow \{0,1\}$

  $\boldsymbol{V}(t)$ is the average of $\{\boldsymbol{v}_1(t), \boldsymbol{v}_2(t), ..., \boldsymbol{v}_n(t)\}$. If an individual's direction of motion deviates from the average by more than a threshold amount Θ then the individual is in the OFF state: that is, $Avd_i^t(\boldsymbol{V}(t), \boldsymbol{v}_i(t)) = 1$ when $\arg(\boldsymbol{V}(t), \boldsymbol{v}_i(t)) \leq \Theta$, and is 0 otherwise.
- Centre of mass function $Com_i^t(\boldsymbol{X}(t), \boldsymbol{x}_i(t)) : \mathbb{R}^d \times \mathbb{R}^d \rightarrow \{0,1\}$

  $\boldsymbol{X}(t)$ is the average of $\{\boldsymbol{x}_1(t), \boldsymbol{x}_2(t), \cdots, \boldsymbol{x}_n(t)\}$. If an individual is further from $\boldsymbol{X}(t)$ than a specified threshold Ω then the individual is in the OFF state: that is, $Com_i^t(\boldsymbol{X}(t), \boldsymbol{x}_i(t)) = 1$ when $d(\boldsymbol{X}(t), \boldsymbol{x}_i(t)) \leq \Omega$ and is 0 otherwise.

  To obtain the state of the fish school, we take a conjunction of these results to obtain a state for each individual which depends on the pair (Θ, Ω):, $s_i(t; \Theta, \Omega) = Avd_i^t(\boldsymbol{V}(t), \boldsymbol{v}_i(t)) \wedge Com_i^t(\boldsymbol{X}(t), \boldsymbol{x}_i(t)) \in \{0,1\}$. The state of the school at time t is then a vector $\boldsymbol{s}(t) = (s_1(t), s_2(t), \ldots, s_n(t)) \in \{0,1\}^n$, where the parameter dependence has been omitted for simplicity.

Supplementary Materials: Figure S1: Susceptibility of Φ, Figure S2: Mean values of Φ with global parameter settings, Figure S3: Susceptibility of Φ with global parameter settings.

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Abbreviations

The following abbreviations are used in this manuscript:

IIT	Integrated Information Theory
SOC	Self-organising Criticality

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