



## Review article

# Energy saving mechanisms, collective behavior and the variation range hypothesis in biological systems: A review

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## ABSTRACT

Energy saving mechanisms are ubiquitous in nature. Aerodynamic and hydrodynamic drafting, vortice uplift, Bernoulli suction, thermoregulatory coupling, path following, physical hooks, synchronization, and cooperation are only some of the better-known examples. While drafting mechanisms also appear in non-biological systems such as sedimentation and particle vortices, the broad spectrum of these mechanisms appears more diversely in biological systems that include bacteria, spermatozoa, various aquatic species, birds, land animals, semi-fluid dwellers like turtle hatchlings, as well as human systems. We present the thermodynamic framework for energy saving mechanisms, and we review evidence in favor of the variation range hypothesis. This hypothesis posits that, as an evolutionary process, the variation range between strongest and weakest group members converges on the equivalent energy saving quantity that is generated by the energy saving mechanism. We also review self-organized structures that emerge due to energy saving mechanisms, including convective processes that can be observed in many systems over both short and long time scales, as well as high collective output processes in which a form of collective position locking occurs.

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## 1. Introduction

For living organisms, the simple processes of living and moving to overcome gravitational and drag forces are energetically costly. Where possible organisms seek to reduce those costs, and in a purely physical sense, organisms seek to reduce those costs by remaining physically close to one another. In this way, nearby organisms couple their energy systems and facilitate energy saving mechanisms, and reduce their individual metabolic costs and/or travel faster in groups than in isolation. Examples of such mechanisms include air or hydrodynamic drafting, whereby drag forces are reduced in specific regions around massive bodies; vortice uplift whereby fluid motion effectively pushes organisms in their active trajectory; or the synchronization of body kinetics. In human systems, for example, drafting is a commonly observed energy saving mechanism among cyclists that occurs when cyclists follow behind others in zones of reduced air-resistance. Power requirements when drafting a single rider are reduced by approximately 18% at 32 km h<sup>-1</sup>, 27% at 40 km h<sup>-1</sup>; and, when drafting in a group of eight riders, power requirements are reduced by as much as 39% at 40 km h<sup>-1</sup> (McCole et al., 1990). See Alexander (2004) for an earlier review of drafting mechanisms.

Energy saving mechanisms have a fundamental role in evolutionary processes, and necessarily involve thermodynamic considerations. Thermodynamic approaches to evolutionary processes may be traced to Lotka (1922), who proposed that evolution and biological systems are mass and energy dependent, in flux and driven to increase. Schrodinger (1944) recognized that a highly organized biological system draws energy from its environment to generate within itself a lower entropy state, and suggested that the study of living systems must involve reconciling the self-organizing principles of biology with the laws of thermodynamics.

Prigogine and Lefever (1973) proposed that living systems are dissipative structures that maintain stable far-from-equilibrium states wherein the flow of energy and entropy fluctuate across system boundaries. Kaila and Anilla (2008) developed equations to describe how evolution is a process of diminishing energy gradient and dissipation that show up as overall decreases in mass. Similar processes include allometric scaling whereby body size correlates to energetic demands and energy dissipation is minimized (West et al., 1997; Brown et al., 1993). Further, thermodynamics are increasingly recognized as a framework for understanding ecosystem dynamics (Jorgensen and Svirezhev, 2004).

Apparently less studied or understood are the mechanisms that drive evolutionary systems toward their energy minima, and how these mechanisms propagate and affect the general process of evolution. Here we argue that energy saving mechanisms in biological systems have a fundamental role in evolutionary processes as they propagate and attract to lowest energy states, while conserving

entropy. Further, we propose that energy saving mechanisms permit self-organizing structures at lower collective energy states and a broader range of heterogeneity among system organisms than might otherwise evolve without the energy saving mechanisms.

Our analysis begins with a general discussion of how energy saving mechanisms fit within far-from equilibrium entropy physics. We evaluate the broad thermodynamic role of energy saving mechanisms in evolutionary processes. Then we identify a variety of energy saving mechanisms in coupled natural systems, and summarize research regarding these mechanisms. Further, we develop the variation range hypothesis, which Trenchard (2015) proposed as a general theory, having observed the close correspondence between the ~36% range of the maximum power outputs of 14 cyclists in a mass-start race, the ~38% energy saving implied by Olds' (1998) drafting coefficient, and the 39% energy saving achieved by drafting at 40 km h<sup>-1</sup> within a group of 8 found by McCole et al. (1990).

In this review we are concerned with coupling dynamics that involve some energy saving for one or both members of the coupled system, generalized globally to multi-agent systems. We do not consider kinetic or morphological efficiencies that have evolved in individual animals, such as the streamlined body shapes of fishes, or the wing apparatus' of birds.

## 2. Energy saving mechanisms and the second law of thermodynamics

Prigogine and Stengers (1997) described far-from-equilibrium stable living systems and their entropy production as:

$$\Delta S_1 + \Delta S_e = 0, \text{ or } \Delta S_e = -\Delta S_1 < 0 \quad (1)$$

where  $\Delta S_1$  is the change of entropy within a given system, and  $\Delta S_e$  is the change of entropy across system boundaries.

Further, in far-from-equilibrium dissipative structures, the distance from equilibrium is a critical parameter in which probabilistic energy and entropy fluctuations of both internal and external origin cause the system to bifurcate within a critical regime (Prigogine and Stengers, 1997).

Thus in any far-from-equilibrium system like evolution or other more narrowly bounded biological systems, we might expect the presence of some entropy conservation mechanism, such as an energy saving mechanism. This mechanism allows the system to descend periodically to lower collective energy states, and reduces the energy required for the emergence of self-organized structures within the system. The entire system therefore retains a shorter distance from equilibrium than expressed in a higher energy system, and thus conserves entropy within the system, as illustrated in Fig. 1.

The proposition that far-from equilibrium systems “fight” to conserve entropy was proposed by [Schneider and Kay \(1994\)](#), whose analysis of the second law of thermodynamics followed from a proof derived by [Kestin \(1966\)](#), whereby energetic systems,

“...as they are moved away from equilibrium they will utilize all avenues available to counter the applied gradients. As the applied gradients increase, so does the system’s ability to oppose further movement from equilibrium” ([Schneider and Kay, 1994, p. 29](#)).

[Schneider and Kay \(1994\)](#) identified Rayleigh-Bénard cell convection dynamics as an example of this entropic tension, a system that we shall explore further in this article. Rayleigh-Bénard convection cells self-organize in fluids at a critical temperature gradient, while additional increases in temperature gradient result in exponential heat dissipation, meaning that increasingly greater work is required to increase the temperature gradient ([Schneider and Kay, 1994](#)). The authors proposed that the second law implies that self-organizing structures, such as the general process of evolution, will emerge as systems “attempt to resist and dissipate the external gradients that are moving them away from equilibrium” (p.45).

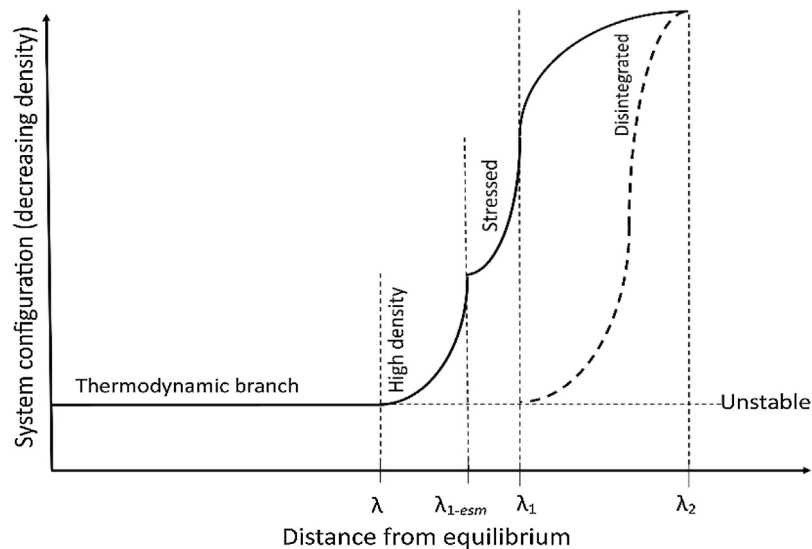
Consistent with this proposition, we propose that biological systems are driven to exploit energy saving mechanisms as a means of resisting or narrowing system temperature gradients that would otherwise decrease entropy by increasing the energetic requirements of the system and dissipating entropy into the environment. In living systems, the temperature gradients are a function of the individual and collective metabolic processes of organisms within these systems. Individual temperature differentials change as environmental stressors drive organisms to increase or change their speed of movement (e.g. to run, swim, or fly faster) at higher or changing metabolic outputs. Energy saving mechanisms therefore serve to reduce heterogeneous individual energy expenditures, which, without the presence of the energy saving mechanism, would be substantially higher.

Thus for many living systems, the energy required for the emergence of self-organized structures may in fact be *too high* without the presence of an energy saving mechanism; or, from an entropic standpoint, the system may never attain the necessary balance of energy inflow and entropy dissipation for self-organized structures to emerge without an energy saving mechanism. The range of possible biological differences is therefore narrower without the energy saving mechanism, and such energy saving mechanisms may ultimately permit for a greater diversity of life to evolve than without the energy saving mechanisms.

### 3. The variation range hypothesis

That energy saving mechanisms are critical to the diversity of life is particularly evident if the maximal energetic capacities among coupled organisms are heterogeneous, spanning some relatively broad range of variation in individual maximal capacities. Obviously no species exhibits perfect homogeneity among its members, and we naturally expect some range of variation in physiological or metabolic capacities. Central to this concept, however, is the proposition that the range (percent difference) of heterogeneous metabolic variation within species tends to converge on the equivalent magnitude of the energy saving (percent difference) afforded by the energy saving mechanism. Makoto was an early proponent of this hypothesis, who suggested that hydrodynamic effects might determine a size range among fish schools of up to 50% ([Makoto, 1970](#); as cited in [Weihs \(1973\)](#)). [Trenchard \(2015\)](#) developed the hypothesis independently on the basis of group sorting principles demonstrated among simulated bicycle pelotons, which he demonstrated as self-organized effects that are independent of top-down anthropocentric tactical or strategic motivations.

This convergence in variation range occurs as organisms within a given system are driven by stressors to their individual near maximal physiological or metabolic outputs. At these near maximum outputs, groups divide into sub-groups (shown as transition  $\lambda_1$  in [Fig. 1](#)), the memberships of which are determined by the capacity of the weakest within each group to retain proximity to



**Fig. 1.** A far-from-equilibrium system with an energy saving mechanism. External energy crosses the boundaries of the system, driving it away from equilibrium and reducing entropy within the system. The system is susceptible to fluctuations from which different phases may emerge. Between  $\lambda$  and  $\lambda_1$  is the energy saving regime which permits phase changes at energy (temperature) gradients closer to equilibrium, thus conserving entropy within the system. Without the energy saving mechanism, the system transitions at higher energy gradients and farther from equilibrium, indicated by the dashed curve. Depending on the range of heterogeneity among system members, transitions beginning at  $\lambda_1$  develop across a smaller energy gradient than within the energy saving regime; these transitions are driven from the high density phase to disintegrated phase while bypassing the stressed phase, which is dependent on the energy saving mechanism.  $\lambda_{1-esm}$ , where the value 1-*esm* represents the percent energy saving generated by the energy saving mechanism, indicates a transition to a stressed phase. The energy saving mechanism permits a lower overall energy state for the system and maximizes entropy within the system. Figure inspired by analysis in [Prigogine and Stengers \(1997\)](#).

stronger members by exploiting the energy saving mechanism. In this way the energy saving mechanism facilitates group cohesion, and obviously biological reproduction can occur only when group members stay within sufficient proximity to others. Without this cohesion mechanism, group divisions are likely to result in dispersion effects that are too great to permit reproduction and long-term cross-generational survival. This of course does not exclude other mechanisms for group cohesion, but we suggest energy saving is a fundamental and primitive mechanism that is likely a precursor to other cohesion mechanisms that have evolved over geologic time. We refer to this as the **variation range hypothesis**.

The basic coupling equation describing group divergence and convergence and the variation range is

$$GCR = \frac{P_{\text{pacesetter}} * d}{MSO_{\text{follow}}} \quad (2)$$

where  $GCR$  is “group convergence ratio”;  $P_{\text{pacesetter}}$  is the power output, speed or metabolic output, of the pacesetter;  $d$  is the coefficient of the output of the follower, or beneficiary of energy saving, to the output of the pacesetter due to the energy saving mechanism;  $MSO_{\text{follow}}$  is the maximal sustainable output of the follower, or beneficiary of the energy saving mechanism.

Here  $(1-d) * 100$  is the percent energy saving conferred by the energy saving mechanism, and the value that we propose is equivalent to the variation range of  $MSO$  among group members. When  $GCR > 1$ , coupled organisms diverge. Thus we see that among a collective of heterogeneous organisms with diverse  $MSOs$ , all those whose  $MSOs$  are within the range equivalent of  $(1-d) * 100$  will remain within a cohesive collective, whereas any organisms for which the range of their  $MSOs >$  range equivalent of  $(1-d) * 100$ , will decouple and form separate groups ( $GCR > 1$ ), as shown in Fig. 2, and shown as the threshold  $\lambda_1$  in Fig. 1.

Since there are many reasons why organisms within living systems may be stressed to near maximal outputs, even if temporarily, it is apparent that Eq. (2) well describes a general group sorting mechanism, and that the energy saving in terms of percent,  $(1-d) * 100$ , is a critical system attractor.

In this paper we will refer in some cases to speeds as representing  $P_{\text{pacesetter}}$  and  $MSO_{\text{follow}}$  values and energy saving percentages. Generally, power output, or metabolic parameters like maximum oxygen consumption, or body movement frequencies are preferable since speeds are not a good indicator of power requirements. This is because the power required to overcome fluid drag is proportional to the cube of the velocity, according to standard equations:

$$F_D = C_D \frac{1}{2} \rho A V^2 \quad (3)$$

where  $F_D$  is the drag force,  $C_D$  is the drag coefficient for the given fluid medium,  $\rho$  is the fluid density,  $A$  is the surface area facing direction of movement, and  $V$  is the velocity of the object relative to the velocity flow of the medium. The power required to overcome the drag force is given by

$$P_D = F_D * V = \frac{1}{2} \rho V^3 A C_D \quad (4)$$

However, in some cases, metabolic parameters are not available, and where necessary we will approximate  $P_{\text{pacesetter}}$  and  $MSO_{\text{follow}}$  and energy saving values using speeds independently of the other factors that determine power.

To summarize, we propose this sorting mechanism, the basis of which is the energy saving parameter and the relative outputs of pacesetters and followers, is a fundamental evolutionary mechanism that determines certain boundaries for the diversity of life as groups divide and speciate over geologic time.

Our objectives now are to outline many of these energy saving mechanisms in nature, to examine the structures in which these

mechanisms reveal themselves, and to identify the principles of and the evidence for the variation range hypothesis.

#### 4. Energy saving mechanisms in non-biological systems

It is instructive to begin by identifying energy saving mechanisms in non-biological systems, the presence of which is evidence of their universal importance among dynamical systems generally. Indeed, given their presence in non-biological systems as a basin of attraction and mechanism for self-organized complex behavior, it is easy to speculate that they play a critical role in the primordial origins of life itself, although further analysis is beyond the scope of this paper.

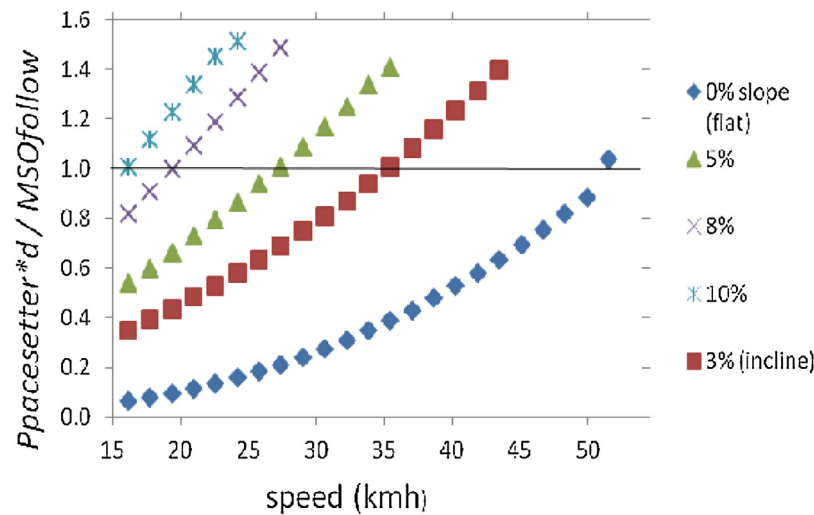
Recheirt and Stark (2004) demonstrated that in a system of circling particles suspended in an optical vortice, two particles in close contact move faster than a single particle because the friction per particle is reduced, a form of drafting. Increasing the ring radius of the vortices increases particle alignment, which therefore move faster than in smaller radius vortices (Recheirt and Stark, 2004). Further, the collective motion of four particles in a chain self-organize positional exchanges between first and third particles (Recheirt and Stark, 2004). While the authors did not extend their study of positional exchange beyond four particles, we may extrapolate that larger aggregates will tend to exhibit self-organized positional exchanges involving more particles, and hence the emergence of dynamic collective patterns.

Recheirt and Stark (2004) did not report the percentage increase in speeds for the faster travelling particles. In a similar study, however, Grujic and Helleso (2007) reported a pair of particles moving 15% faster than a single particle; this increase in speed can be explained by hydrodynamic coupling of particles within the cohesive no-slip zone where the leading particle displaces fluid for the following particle and entrains its motion (Grujic and Helleso, 2007). Šiler et al. (2012) studied polystyrene beads (520 nm diameter) in water. In Šiler's (2012) study, the beads were aligned in linear chains up to 18 beads long; particles in the centre of the chain caught up with leading particles and distanced themselves from tail particles. The authors reported increases in speed among faster moving chains of up to 50%.

Similarly, Wang and Guo (2015) reported the effects of “drafting, kissing, tumbling” (DKT) between two particles of equal size in a fluid medium. “Experiment A” featured two particles of equal size; “Experiment B” featured two particles of size ratio 2, with the smaller particle below the larger one; and “Experiment C” in which the smaller particle was located above the larger. Wang and Guo (2015) found that particles attract due to the wake and reduced drag generated by the leading particle. The authors found that speed of attraction was greatest for experiment B and slowest for experiment C, but there was a clear process of the small particle accelerating to catch up and contact (“kiss”) the leading particle. Wang and Guo (2015) reported that where particles were equal in size, the DKT process would repeat more than once, whereas the process occurred only once for particles of unequal size.

These dynamics indicate that not only does a leading particle in non-biological systems generate a low drag wake in which a following particle may accelerate, but that ongoing coupled interactive processes can emerge from the energy saving mechanism. This supports the proposition that energy saving mechanisms are a fundamental and primitive process that precedes other cohesive principles in evolutionary dynamics, and that dynamical processes emerge from these mechanisms.

For the purpose of demonstrating the ubiquity of energy saving mechanisms in coupled systems, we refer again to a non-biological system involving deformable bodies: flags. Zhu (2009) found that the relative drag forces of a leading and following flag in a down-



**Fig. 2.** The group convergence ratio ( $GCR$ ). The example shows the effect of the energy saving mechanism (drafting) on coupled cyclists. On a flat course, the equalizing effect of drafting allows a weaker cyclist with a maximum sustainable output (MSO) of 379 W to maintain the pace of a stronger cyclist with MSO 525 W up to  $\sim 50$  km  $h^{-1}$ , when  $GCR = 1$ . On steeper terrain when equivalent power is required at speeds providing smaller drafting benefit, decoupling ( $GCR > 1$ ) occurs sooner. On very steep hills when drafting is negligible, decoupling occurs immediately (this occurs in the regime  $\lambda_1$  to  $\lambda_2$  in Fig. 1) unless riders are nearly equal in strength. In any coupled system involving an energy saving mechanism, decoupling occurs similarly: a smaller energy saving mechanism means coupled organisms must be closer in strength to maintain coupling; greater energy saving means organisms with greater strength differential, within the variation range equivalent of  $(1-d) \cdot 100$  (given as percent), can stay coupled (reproduced with permission, from Trenchard (2013b)).

stream fluid flow depends on the Reynolds number ( $Re$ ) of the viscous fluid. When  $Re$  is sufficiently high, Zhu (2009) found that the leading flag has less drag than the following flag, which Ristroph and Zhang (2008) referred to as “inverted drafting”; at sufficiently low  $Re$ , the intuitively expected case of drafting is observed, i.e. the following flag has lower drag. Zhu (2009) found that the transitional value depends on the bending rigidity of the flags and the distance between flags. Ristroph and Zhang (2008) found that inverted drafting may be observed among flags which deform in response to the altered flow of neighboring bodies, while rigid bodies like birds or fishes do not.

## 5. Convective processes

Having referred to Schneider and Kay’s (1994) application of Rayleigh–Bénard convection to entropic principles, now we examine convection patterns that emerge from collective interactions. This is distinct from convection in terms of ambient heat or rising heat from body surfaces, which comprise a different field of study (Chappell et al., 1989). In Fig. 1, convective processes occur in the high density regime.

Rayleigh–Bénard convection involves a rolling cycle of fluid particles vertically across a temperature gradient  $\Delta T = T_2 - T_1$  whereby heated particles rise and cooling particles fall; the cyclical process involves gravity and buoyant forces and occurs at critical values of fluid density, temperature, and viscosity (Bergé and Dubois, 1984). In pans with large aspect ratio (cylinder diameter to height  $> 1$ ), two dimensional cellular patterns emerge (Rivier, 1992). In cylindrical containers with aspect ratio approaching 1, Rayleigh–Bénard convection can generate a large scale circulation loop with upflow and downflow appearing on opposite sides of the cylinder (Brown and Ahlers, 2009). Convection processes have also been demonstrated in granular flows whereby grains in a container under vibration generate central upward flow, and downward flow along container walls (Jaeger et al., 1996).

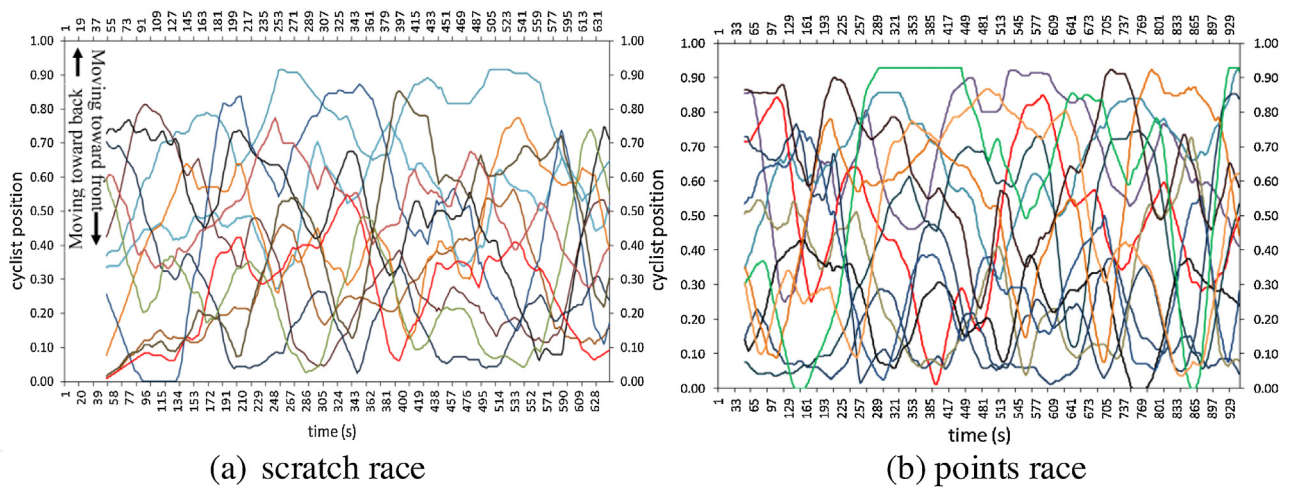
Although Rayleigh–Bernard and granular convection involve externally applied energy gradients in terms of heat or vibration, we propose that large scale bioconvection emerges from internally generated temperature differentials between system organisms.

Here we distinguish between large scale macroscopic bioconvection and small scale microscopic bioconvection.

The initial condition from which large scale bioconvection emerges is the inherent temperature differential between high energy positions and low energy positions that exist in the presence of an energy saving mechanism. In a system of coupled self-propelled agents, this temperature differential is unstable, and the broader convective process begins when organisms alternate positions across the temperature gradient, similar to the positional exchanges among four particles in an optical ring vortice studied by Reichert and Stark (2004). In this way, dyadic, or locally coupled positional alternations may be considered low-degree convection. In multi-agent collectives, large scale convection emerges as multiple “energetic” organisms move uni-directionally along lower density peripheral regions, and pass fatiguing organisms that move effectively backward within the system. This generates the internal rotational dynamics characteristic of convection. We propose that convection dynamics are a natural outcome of systems involving energy saving mechanisms and represent one phase or property of elementary evolutionary processes.

Mathematically, Rayleigh–Bernard convection generates vertically oscillated sinusoidal patterns,  $\delta' \cos \omega t$ , described by Rayleigh and Prandtl numbers and two dimensionless parametrically driven equations (Rogers et al., 2002). Such sinusoidal movement patterns have, for example, been observed in the collective movements of cyclists in pelotons, as shown in Fig. 3, and throughout this paper we will identify examples of low-degree (dyadic or locally coupled) convection and high degree convection (globally coupled) both in terms of large-scale macroscopic bioconvection and small-scale microscopic bioconvection.

Toner and Tu (1998) and Toner et al. (2005) developed a fluid dynamical framework for flocks and referred to the “convective transport” of information and fluctuations in local velocities within flocks, but they do not appear to have examined the specific rotational effects we identify here, and not in the context of an energy saving mechanism. Alberts (1978) referred to rotational movements of huddling rat pups as a convective current, but did not model the behavior. Bacteria have been shown to exhibit bioconvection, as we discuss subsequently; but it appears that these



**Fig. 3.** Cyclists' positional profiles in two races. Moving averages (period 20) reveal approximately sinusoidal trajectories of cyclists in two directions moving from back to front, and moving from front to back. Rotations are approximately elliptical. In (a) 12 female cyclists in mass-start race on velodrome (circular track), fastest time wins; in (b) 14 (identical cyclists for scratch race +2), points accumulated every 5 laps by finishing order, most points wins (reproduced with permission, from Trenchard et al., 2014).

processes have not been extrapolated to macroscopic biological systems.

Macroscopic biological systems may exhibit fluid-like properties akin to granular flows which do not require consideration of the surrounding medium if the grains are dry (Jaeger et al., 1996). In this way, macroscopic self-propelled agents (e.g. birds, fishes, cyclists) may be modeled as the fluid particles that generate their own intrinsic viscosity and density independently of any fluid medium in which they thrive, as shown in Fig. 5. However, the factors determining bacterial bioconvection appear to be more complex (Wolgemuth, 2008).

## 6. Packing and phyllotaxy

We consider the role of Rayleigh-Bénard type convection as an energetically minimal and optimal packing state in long timescale phyllotactic formations. We distinguish convection processes over long time scales from those of shorter or rapid timescales, such as cyclists, birds, or fishes. These processes may be considered two sub-categories of a broader class of energetic systems, and that flocking systems and phyllotactic systems are fundamentally related by the presence of convective processes and energy saving mechanisms, differentiated largely in terms of timescale, as shown in Fig. 5.

Hexagonal phyllotactic structures are typically observed in a variety of flora (Pennybacker et al., 2015). Lee and Levitov (1991a,b, 1998) proposed that such structures represent the lowest energetic condition (the ground state) toward which mutually repulsive particles attract. Levitov (1991a,b) further proposed that the phyllotactic ground state is the two-dimensional Bravais lattice (Bravais and Bravais, 1837) that matches the cylindrical optimal spiral packing formation in which lines connecting central nodes form triangles. Nisoli et al. (2010) reproduced the energetic ground state experimentally using a magnetic “cactus” in which magnets stacked cylindrically self-organized to the collective lowest energy state in a Bravais lattice. Douady and Couder (1996) also demonstrated that ferromagnetic drops in a dome-shaped magnetic field form phyllotactic patterns, indicative of a minimal energy state.

Pennybacker and Newell (2013) observed that energetic minima and optimized packing in phyllotactic arrangements are a dynamic process involving the physical motion and velocity of a moving annulus front which forms over the course of a few days — a much slower process than that seen in pelotons (e.g. Fig. 5a and b). Identifying

sunflowers as an example, the authors noted that sunflowers form in two stages: first, flowers are initiated in an annulus, which moves farther out as the plant grows and configures in spiral patterns. At a certain point, central cells shift in phase such that they propagate florets or seeds from the outside in, ring by ring. There is a defined velocity at the front of this propagating inward dynamic (Pennybacker and Newell, 2013).

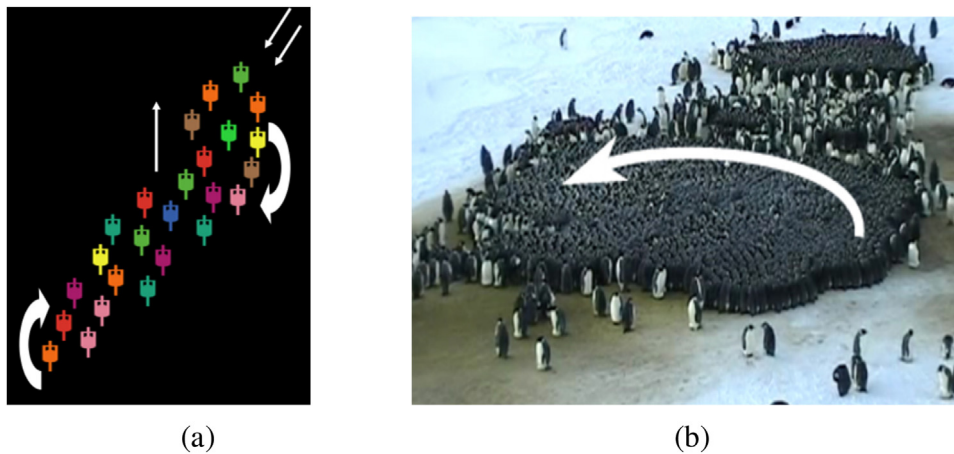
These fronts comprise two kinds: pulled fronts and pushed fronts (Pennybacker and Newell, 2013). The first is determined by conditions ahead of the front; the second is determined by conditions behind the front and involve speeds greater than pulled fronts. For both fronts, the authors observed that the emerging pattern is a manifestation of the lowest possible energetic landscape. The authors thus described the floret generative process, a process of constant but comparatively slow motion, as one that inherently involves energetic minima. They suggested that hexagonal formations involve low local energy and high packing efficiency, for example as shown in the skunk cabbage spadix, Fig. 5a. Huddling penguins are also observed to pack in a hexagonal pattern (Zitterbart et al., 2011); indeed, Waters et al. (2012) used the hexagonal pattern as a modeling parameter, as shown in Fig. 12. Cyclists in pelotons pack similarly, albeit in faster continuous motion and at lower density than penguin huddles, and are positioned at angles to each other to avoid collision and to accommodate positional relocations ahead or behind neighboring riders, as shown in Figs. 4a and 5b.

In summary, the hexagonal floret pattern formation is an attractive low energy state, indicative of an energy saving mechanism that emerges over a lengthy temporal scale involving semi-permanent, quasi-static configurations. By contrast, systems like flocks or herds are temporally compressed (faster) versions of similar processes that, in terms of their relatively high speed movement, oscillate around their optimal collective configurations.

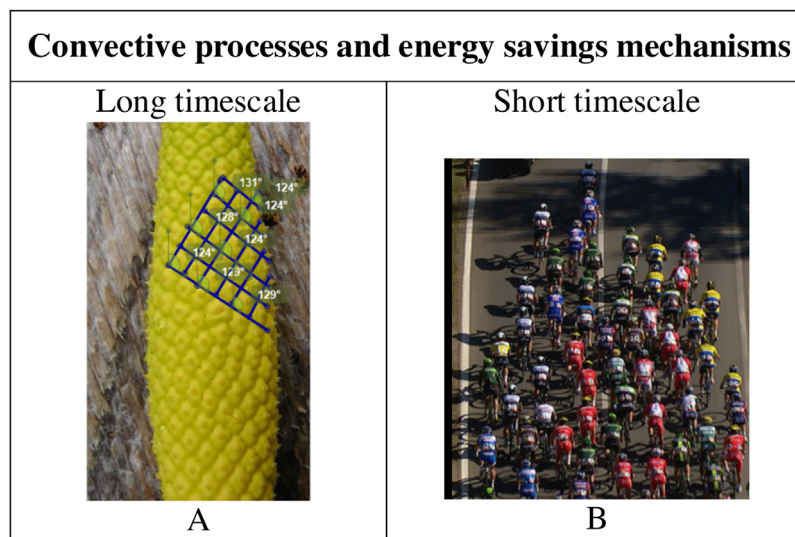
## 7. Bird flocks

We build our analysis by turning first to systems that are frequently observed in the ordinary course of human experience, birds and fish. We then review the evidence for energy saving mechanisms in a number of other systems.

Lissaman and Schlossenberger (1970) were perhaps the first to develop a robust quantitative power output model, based on a fixed-wing analog of the same geometry as birds; although they did



**Fig. 4.** (a) Simulated echelon formation (simulation by H. Trenchard, using Netlogo) (Wilensky, 1999). Cyclists proceeding north into a northeast wind begin a clockwise rotation; (b) Penguin rotations (reproduced with permission from from A. Ancel, M. Beaulieu, and Creative Commons licence, Gerum et al., (2013)). The cyclists and penguins are the particles of the fluid system, and the rotational dynamics are a form of convection.



**Fig. 5.** A broad class of convective systems with energy saving mechanisms. (a) Skunk cabbage spadix with two-dimensional Bravais lattice and approximate angles to the vertical, involving long timescale convective processes and inferred energy saving mechanism (angles may be distorted; image by Trenchard). (b) Peloton involving short timescale convective dynamics and energy saving mechanism of drafting. While avoiding collision and maintaining drafting positions, cyclists optimize packing formation in collective lowest energy state (reproduced with permission from race organizers Volta ao Algarve, Portugal 2014).

not say what kind of bird was analyzed for their unstated dimensions. They reported a maximum possible energy saving of about 70% for a flock of 25. They further observed that V formations permit an even distribution of drag, while birds in central positions among an in-line abreast formation (wing-tip to wing-tip) obtain greater energy saving than birds in peripheral positions, since central birds obtain the upwash advantage of two birds; in a group of 10, central birds obtain twice the energy saving of peripherally located birds.

By applying the aerodynamic model of Lissaman and Schlossenberger (1970), Hainsworth (1987) reported induced power (power to sustain sufficient lift to overcome gravity) reduction of 36% for a total of 55 Canada geese (*Branta canadensis*) based on a median wing tip spacing of 19.8 cm—a critical parameter in determining vorticity since closer wingtip spacing means greater upwash effect and energy saving (Lissaman and Schlossenberger, 1970). Lift forces that facilitate energy saving are also observed in locusts, in which a 16% lift advantage occurs at up to 15 cm behind others (Camhi et al., 1995).

Cutts and Speakman (1994) reported that, based on measurements of wing-tip spacing among 54 skeins, Pink-footed geese

(*Anser brachyrhynchus*) achieved mean power output reductions of 14%; this is less than one third of the maximum 51% for 9 birds, as deduced by Badgerow and Hainsworth (1981) by applying a modification of the Lissaman and Schlossenberger (1970) model. The substantial inconsistency with the predicted values of Lissaman and Shollenberger was thought to be due largely to geese constantly adjusting positions resulting in relatively large variation in wing-tip spacing, and corresponding flight time in non-optimal positions (Cutts and Speakman, 1994).

In addition to energy saving through formation flight, when flocks fly closer to smooth ground surfaces like water, they obtain energy saving through ground effect where wind speeds, wingtip vortices and downwash drag are reduced, allowing for increased lift and gliding times (Finn et al., 2012). For flocks of brown pelicans (*Pelcanus occidentalis*) exploiting ground effect, Hainsworth (1988) estimated energy saving between 49% for gliding altitudes (mean ~33 cm), applying the aerodynamic model of Lissaman and Shollenberger.

Although the energetic costs of birds can be predicted from aerodynamic models, such models predict only mechanical power

requirements, which represent 10–23% of total metabolic costs (Ward et al., 2002). This suggests more accurate models will be derived from empirical data that reflects aerobic costs, such as volume of oxygen consumption, or heart-rate. Ward et al. (2002) noted, however, that the correct relationship between heart rate and energy consumption is not established, although new methods to determine the energetic consumption of free-ranging animals are being developed (Nathan et al., 2012; Bairlein et al., 2015).

Weimerskirch et al. (2001) obtained heart rate data for a group of eight white pelicans (*Pelcanus onocrotalus*) which exhibited heart rate reductions corresponding to 11.4–14.0% energy saving due to increased gliding time. Somewhat contrary to the findings of Hainsworth (1988), Weimerskirch et al. (2001) found no significant difference between heart rates of pelicans at 1.0 m above water versus those at 50 m above water. Hainsworth's (1988) findings were, however, in relation to altitudes closer to the water surface (0.2 to 1.0 m) where ground effects are greatest. (Finn et al., 2012). It should be noted that Hainsworth's (1988) findings were based on Lissamen and Shollenberger's (1970) aerodynamic model and not actual data.

Using a computational fluid dynamical model, Maeng et al. (2013) found that Canada geese (*Branta canadensis*) can save 15% energy by changing their wing morphology, and 16% by taking advantage of upwash vortices between 0 and 0.4 m wing tip separation. This is closer in agreement to the values reported by Cutts and Speakman (1994) for Pink-footed geese (*Anser brachyrhynchus*) whose mean wing-tip spacings were observed to be 16.9 cm.

Based on these various values, if we consider an approximate mean energy saving of 15% for migratory birds, then according to the variation range hypothesis, if weaker fledglings are to sustain faster speeds of stronger adults, adults cannot fly at speeds greater than ~15% faster than the maximum sustainable speeds of the younger birds, as averaged approximately over migration duration. However, in this analysis it is important to consider the effects of higher speeds set by stronger birds which could force weaker birds to decouple from the skein. This suggests that the mean energy saving of 15% may not be the appropriate quantity by which to model flock cohesion whereby cohesion is defined as birds that maintain proximity sufficiently close to obtain an energy saving benefit.

Conversely, the variability in energy saving during flight may provide better information than the mean energy saving in understanding the nature of flock cohesion. Consider that at one instant, a weak bird may slip outside the optimal energy saving position and, if it is approaching its maximum output, it will be forced to decelerate relative to faster birds. However, if it adjusts to a near optimal position, it will resume equal pace to a stronger bird, albeit perhaps in a different relative position within the flock. In this way, the dimensions of the flock are important because they indicate how long a weaker bird can afford to decelerate before it must resume an optimal position, or risk being decoupled from the flock. This can be shown according to the relation, as adapted from Trenchard et al. (2014):

$$T_{gap} = D_{last} / (V_p - V_{GCR > 1}), \quad (5)$$

where  $T_{gap}$  is the time (s) for a bird that is decelerating relative to its flock mates to decouple from the flock; i.e. when it drops beyond the last possible energy saving zone in the flock. We may refer to this as global de-coupling, versus local de-coupling when a bird suffers a temporary deceleration and falls outside the optimal energy saving zone of its nearest neighbors, but is sufficiently within flock boundaries to resume matching speeds with other nearby birds before it decouples from all possible energy saving zones within the group.

$D_{last}$  is the distance between the decelerating bird's position when it begins to decelerate, and the last energy saving zone in the flock, at which point it globally decouples;  $V_p$  is the mean flock velocity determined by the pacesetter at the apex;  $V_{gcr > 1}$  is the

velocity of the decelerating bird when it decouples locally as shown in Fig. 6.

It is clear therefore that the larger the flock, the more time a bird has to find an optimal position before it globally decouples. Similarly, the larger the flock, the more time there is for a skein to reduce its mean speed, which at sufficiently reduced speed will allow a locally decoupled bird to resume its coupled condition ( $GCR < 1$ ). Eqs. (6) and (7) and the discussion in the following section on fish schools, models this further.

Eq. (5) implies that smaller flocks will tend to consist of birds within a narrower variation range, while larger ones will contain birds within a larger variation range. This permits predictions that: 1) when high speeds are sustained for  $> T_{gap}$ , groups will tend to sort into sub-groups whose variation range, as a percentage, converges on the energy saving benefit, as a percentage; 2) weaker birds will tend to be found in larger flocks whose variations in speed tend not to be of durations  $\geq T_{gap}$ .

This also predicts that flocks will tend to divide into sub-groups early in the migratory period when heart rates are high, after which flock size will stabilize as speeds or relative power requirements diminish. For example, Svalbard Barnacle Geese (*Branta leucopsis*) exhibit a relatively high heart rate at earlier stages of migration flights (mean 317 beats  $\text{min}^{-1}$ ) compared to the landing stage (mean 226 beats  $\text{min}^{-1}$ ) (Butler et al., 1998), which suggests early stage group sorting. The reduction in heart-rates over the migratory period is likely caused by the fact that stronger birds will have fatigued after setting a faster pace earlier in the migration, while fledglings and weaker birds will have saved energy from remaining in the energy saving positions; thus overall there has been an equalization of maximal sustainable power outputs among group members.

Among formations in which some positions offer greater benefits than others, we might expect some rotation between higher cost and lower cost positions; or, we might expect weaker birds to spend longer periods in more advantageous positions, such as couched within the V formation where birds effectively assume an in-line abreast formation. In fact Lissaman and Schlossenberger (1970) suggested this possibility, noting that young or weak birds may tend to spend more time in positions of greatest energy saving. Bill and Herrkind (1976) also recognized this possibility in the context of the queue formations of spiny lobsters, as we will discuss subsequently, as did Makoto (1970) in the context of fishes.

Consistent with the Lissaman and Schlossenberger (1970) proposition, Voelkl et al. (2015) reported that Northern bald ibis' (*Geronticus eremita*) swap in-wake positions (dyadic reciprocity) where in-wake positions permit lower metabolic output. The authors argued that this dyadic reciprocity is a cooperative mechanism, and that such positional reciprocity is especially beneficial for juvenile birds for which there are high mortality rates. We also observe that these dyadic positional rotations are consistent with a convection process, in which the shift from a higher metabolic position to a lower one is a small-scale convective roll from a higher temperature position to a lower one.

In terms of juvenile mortality rates, Menu et al. (2005) reported a pair of pertinent observations: that snow geese (*Chen caerulescens atlantica*) goslings fledge (develop flying feathers) when their body mass rises to 76% of its adult maximum; and migratory departure occurs within a few days of fledging (citing Blouin, 1996). Menu et al. (2005) noted that fledglings "too weak or too light" (presumably lighter than 76% body mass of adults) will not survive. To the extent that mass correlates with strength, the authors did not explain why fledglings that are approximately 24% weaker than adults can, in fact, survive, since the expectation is that without some mechanism to permit speed equalization, weaker birds would simply be dropped from the group if pacesetter speeds exceed the maximum sustainable by the fledglings, even by a



small margin. Even when adults relax their own pace by 24% to accommodate fledglings, the absence of an energy saving mechanism would necessitate fledglings travelling at their maximum pace while adults are flying comfortably. We would expect fledglings to fatigue faster than adults in such a case, resulting in even larger differentials in maximal sustainable outputs between adults and fledglings. The fact this differential does not arise since fledglings frequently arrive at their target destinations together with adults, can be explained by the energy saving mechanism. We suggest that, according to the variation range hypothesis, the value 24% (in the specific case of the data from Menu et al. (2005)) approximates the energy saving afforded by maintaining optimal energy saving positions, which are likely to be exploited largely by weaker fledglings.

This 24% difference between adult and fledgling metabolic capacity obviously exceeds the mean energy saving value of approximately 15%, as earlier identified. However, survival rates among young geese are determined by a combination of factors, including body mass, fledging date, and air temperature (Menu et al., 2005). Therefore, a more complicated analysis of the effect of fatigue rates and energy consumption factors on current maximal sustainable outputs is required to accurately evaluate the relationship between variation range and energy saving, and to establish their precise proportions. Nonetheless, the absence of this precision does not undermine the logic of the variation range hypothesis and the basic relationship it establishes between maximal sustainable outputs as modulated by the energy saving benefit, and the variation range of individuals' maximal outputs within a given group.

It is important to state that not all flocking behavior involves energy saving. The energy costs of turning motions are high (Wilson et al., 2013; Amélineau et al., 2014); indeed pigeon flocks, which exhibit frequent turning behavior, have been shown to incur higher energetic costs due to the increased g-forces of banking (Usherwood et al., 2011). Also, Baldaccini et al. (2000) surmised that flocks of wild rock doves (*Columba livia*) engaging in direct “commuting” flights up to 18.9 km flying in three-dimensional clusters (as opposed to flat V formations) of up to 40 or more did not entail an aerodynamic advantage because of the lack of precise spacing between individuals. However, we suggest that in a rotating three-dimensional cluster, birds are likely to pass frequently in and out of advantageous upwash vortices, while avoiding high turbulence positions that are directly behind others, thereby avoiding collisions and aligning trajectories for continuous passing motion. We have not seen studies that sum the costs and benefits of passing in and out of upwash positions in clustering flocks; hence, where a cluster flock flies in point-to-point trajectories without a high degree of banking behavior, the aerodynamic advantages of cluster flight remain unknown.

Flack et al. (2013) have, however, proposed that clusters provide navigational efficiencies, which is yet another kind of energy saving mechanism that permits for reduced flight distances. This is similar to the leader/follower energy saving dynamic due to attentional efficiencies, as shown by Piyapong et al. (2007). This kind of navigational efficiency is also similar to Wilensky's (1997) ant following algorithm in which following ants wait a short time before advancing across the secant of the path taken by leaders, a strategy that eventually leads to the shortest distance between travel points.

## 8. Fish schools

Hydrodynamic drafting and Karman gait (kinematic synchronization with vortices) (Liao, 2007), are now well-established as energy saving mechanisms among schooling fishes, although the extent of their effect on schooling behavior has been a matter of

controversy (Pitcher and Parrish, 1993; Lopez et al., 2012). Breder (1965) was perhaps the first to identify energy saving mechanisms in fish schools. Weihs (1973) predicted energy saving of 40–50% for fishes in optimal positions, while earlier Zuyev and Belyayev (1970) reported tail beat frequency (TBF) reductions of 15–29% for trailing horse mackerel (*Tracurus mediterraneus*) compared to leading fishes.

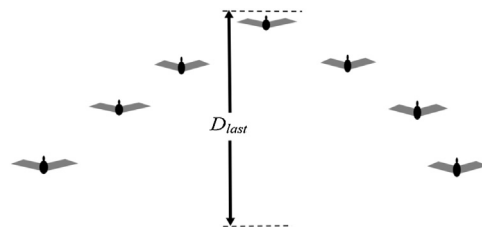
More recently, Herskin and Steffensen (1998) reported that sea bass (*Dicentrarchus labrax*) in trailing positions during natural swimming activity showed 9–14% reductions in TBF, and a 9–23% reduction in oxygen consumption. Marras et al. (2015) reported that Grey mullets (*Liza aurata*) swimming within sufficiently close proximity to others generated reductions in and TBF up to 28.5% at  $10 \text{ cm s}^{-1}$ , relative to TBF when swimming in isolation. Rates of oxygen consumption for fishes benefiting from energy saving by swimming in optimal positions were lower by between 8.8% and 19.4% relative to swimming alone (Marras et al., 2015).

Svendsen et al. (2003) studied groups of eight roach (*Rutilus rutilus*) with length variations between 7 and 14% (which is within the body-length variation of natural schools) and mass variations between 17 and 41%. The authors increased flume current speeds from  $1_{LTM} \text{ s}^{-1}$  (mean body-length per second) to  $4_{LTM} \text{ s}^{-1}$ , and observed that between 2 and  $4_{LTM} \text{ s}^{-1}$  fishes positioning within the group of eight stabilized while trailing fishes obtained TBF reductions of 7.3, 11.9, and 11.6% for 2, 3 and  $4_{LTM} \text{ s}^{-1}$  respectively.

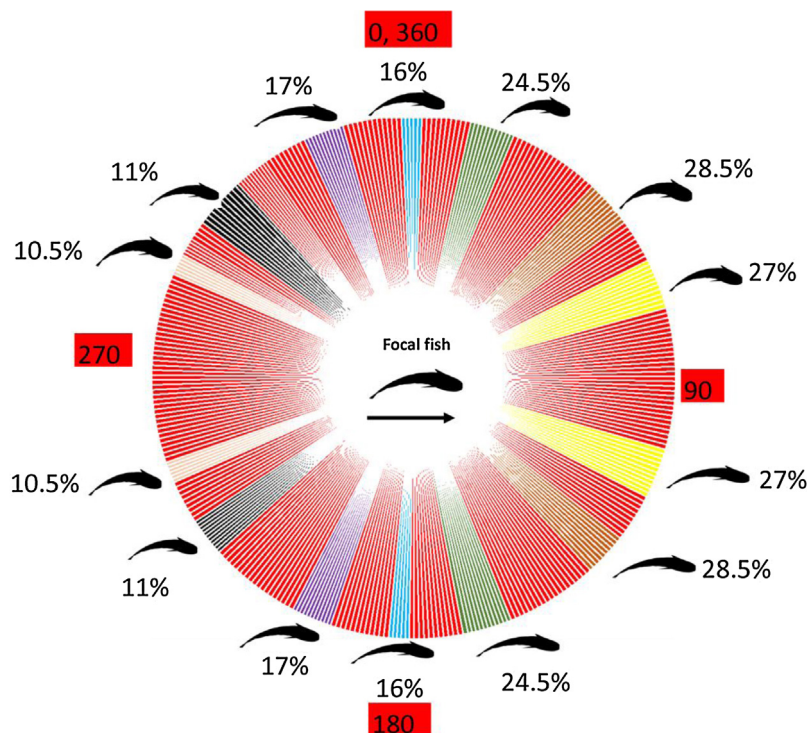
Pitcher and Parrish (1993) were critical of arguments for hydrodynamic advantages generally, arguing that the evidence did not bear out some of Weihs (1973, 1975) pioneering wake theory predictions, including: precise distances between fishes, tail-beat anti-phase, and the existence of the “scramble for good positions”. Pitcher and Parrish (1993) considered competition for best positions to be evolutionarily unstable, and further considered that any alternations between costly and optimal positions required altruistic behavior. Their criticism, however, ignores the self-organized nature of fish positioning which naturally emerges, without altruism, from metabolic stresses that necessitate adjustments in speeds according to drag and other physical forces.

Liao (2007) cautioned that a reduction in TBF could arise from a combination of wall effects (Webb, 1993), flow refuging, and vortex effects, and not from vortex effects alone. Further, the hydrodynamical benefits of three-dimensional positioning has not been well-studied (Liao, 2007). Weihs (1973) suggested that, in addition to horizontal two-dimensional energy saving, vertical stacking and vortice upwash from fin tips may provide additional energy saving. Blake (1983) noted that downwash forces may neutralize the beneficial effects of vertical stacking.

Nevertheless, in a subsequent study Marras et al. (2015) found that, except for an approximate  $30^\circ$  cone directly behind others where turbulence increases energy requirements, some energy saving was present in all planar regions around individual fishes, even directly ahead of others, as shown in Fig. 7. Using computa-



**Fig. 6.** Illustrating  $T_{gap}$ . In this example, the skein travels vertically to the page. If the leading bird decelerates relative to the group, it has  $T_{gap}$  (s) to find an energy saving position and resume the speed of the pacesetter, or it will decouple globally. While the bird will need to move at an angle to the vertical,  $T_{gap}$  is still determined by  $D_{last}$  as shown by the arrows.



**Fig. 7.** Overhead view showing energy saving zones in terms of tail-beat frequency (values from Marras et al. (2015)). Energy saving quantities within red (color online) zones are the averages of the zone quantities on either side, except for the zone in the  $30^\circ$  region on either side of  $90^\circ$  where there may be negative energy saving because of turbulence. Using computer simulations of fluid dynamics, Hemelrijk et al. (2015) found that even in this zone, if fishes bend their heads sideways, they may capture energy from vortices.

tional fluid dynamics simulations, Hemelrijk et al. (2015) found that fishes can save energy even directly behind others if followers bend their heads sideways and capture energy from the vortex flows. Becker et al. (2015) similarly simulated the fluid dynamics of flapping fishes, and found energy saved in groups of flapping fishes would enhance speed and reduce power output.

In this paper, we describe pacesetters as those generally at the front of a group in the direction of travel and, in this position, incur higher costs than individuals in energy saving positions. Although for fishes, the front position costs may be somewhat lower than the position directly behind others, this does not weaken our argument. When proceeding in the direction of travel, fishes will likely avoid the position directly behind in favor positions to the sides; furthermore, the higher cost rear position merely suggests that group de-coupling may occur in different configurations and at different spatial positions for different animals.

The Marras et al. (2015) findings expand earlier findings by Killen et al. (2011), who reported that trailing fishes within a school required fewer tail beats to swim at the same speed as fishes at the front of schools. Due to energy saving in the entire circumference around nearby fishes, the authors proposed that such reduction in locomotion costs is one of the primary drivers of fish schooling behaviors in general.

### 8.1. Convective and proto-cooperative dynamics

We have proposed that an energy saving mechanism is likely to generate a convective phase for organisms when collective outputs enter a critical range. Among schools, convective behavior is likely observed when fishes alternate between high cost and less costly positions. This behavior also describes a form of cooperation.

In their phase transition model, Becco et al. (2006) observed that the cross-sectional distance between fishes at school boundaries (schooling width) describes the degree of fish cooperativeness,

but they did not state what factors define cooperativeness. Their model does permit analysis of school structure based on relative fish velocities and, by extension, durations spent by fishes in particular positions within schools. This kind of analysis may assist in more precisely defining cooperativeness and ‘proto-cooperative behavior’ (Trenchard, 2015) within schools because it will show the extent to which fishes share the most costly positions.

Proto-cooperative behavior is defined by two collective behavioral phases: first, a comparatively low collective metabolic or power output phase in which biological agents are capable of sharing highest-cost positions (usually at the front of the group), which we may describe as the ‘cooperative phase’ (the high density regime shown in Fig. 1); secondly, a high collective output phase in which agents can sustain the speeds of stronger agents by exploiting an energy saving mechanism, but cannot pass the stronger agents in order to share highest-cost front positions - we may describe this as the ‘position-locking phase’ (the stressed regime shown in Fig. 1); the threshold between these phases is the proto-cooperative threshold (Trenchard, 2015) shown as  $\lambda_{1-esm}$ , in Fig. 1.

With respect to the cooperative phase, Domenici et al. (2002) quantified the nature of herring (*Clupea harengus*) positional shuffling behavior and O-turns, while controlling for the water oxygen concentration necessary to induce fish hypoxia. O-turns occur when fishes in front or near-front positions turn  $180^\circ$ , proceed in the opposite direction, then turn  $180^\circ$  again at the rear of the school; shuffling involves adjustments in relative positions uni-directionally (Domenici et al., 2002). Svendsen et al. (2003) observed similar O-turn behavior among roach (*R.utilus*).

Pitcher and Parrish (1993) might argue that altruism is required to explain the presence of O-turn shuffling behavior. To the contrary, O-turn and shuffling behavior are evidence of the cooperative phase of proto-cooperative behavior (Trenchard, 2015), as well as of convective behavior similar to, for example, Northern bald ibis dyadic rotations (Voelkl et al., 2015), Emperor penguins huddle

rotations (Le Maho, 1977), or spiny lobster (Bill and Herrnkind, 1976) lead position rotations.

We suggest O-turns and shuffling in which fishes alternate between high drag front positions and lower drag following positions, represent low degree convective behavior because they appear to involve power output fluctuations in which energy expended is greater in high cost front positions, and lower in positions of reduced drag, corresponding to a temperature gradient. These positional alternations are also a form of proto-cooperative behavior in which we may predict that fishes, at lower outputs, are capable of sharing these positions, but at a critical speed or output threshold are unable to share high cost positions and will maintain their relative positions by exploiting the energy saving mechanism; i.e. the position-locking phase (Trenchard 2015).

Domenici et al. (2002) found that in conditions of higher oxygen saturation, the herring engaged in O-turns more frequently, but reduced O-turn frequency as oxygen saturation decreased (increased hypoxia). Thus at oxygen saturation below 25%, O-turn frequency occurred at less than 1/3 of reposition manoeuvres, compared to more than 1/2 in conditions of normal oxygen saturation (Domenici et al., 2002). The authors suggested this may be due to a pair of factors: the high cost of relatively swift O-turn manoeuvres, and the fact that, in larger schools, rear positions are further reduced in available oxygen.

We propose an alternative hypothesis, consistent with proto-cooperative behavior (Trenchard, 2015): the threshold at which O-turn frequency drops is a function of individual fish hypoxia relative to maximal individual oxygen uptake capacity, modulated by the output required for the position whether it is a high cost front position, or a lower cost energy saving position. This alternative hypothesis is supported theoretically by Killen et al.'s (2011) results which demonstrated that grey mullet (*L. aurata*) with the highest aerobic and metabolic capacities tended to shift toward the front as current speeds were increased, while the converse was true for weaker fishes.

Increase in hypoxia in rear positions can be discounted for the moment in rear positions because this effect was unlikely in the small schools of 19–22 fishes studied by Domenici et al. (2002). Thus, fishes in optimal energy saving positions will experience effectively reduced hypoxia because oxygen uptake requirements are lower. The front positions therefore represent the highest costs in terms of combined highest drag and hypoxia. At sufficiently high oxygen saturation, fishes of all aerobic capacities may trade-off between the highest cost front positions; as hypoxia increases, only the fishes with highest aerobic capacities will be capable of sustaining the highest cost front positions, while weaker fishes can maintain their positions in lower cost energy saving positions (the position-locking phase), a determination consistent with the observations of Killen et al. (2011). This condition is unstable if the strongest fishes accelerate beyond their sustainable maximums, or when current speeds are too high for even the strongest fishes. In this case, if the strongest fishes choose to O-turn, then the entire formation collapses; and indeed Domenici et al. (2002) appear to have described such a breakdown in formation between very low oxygen saturations between 12 and 25%, the range at which fishes began swimming in different directions.

Domenici et al. (2002) found that fishes tended to shuffle at relatively constant rates over different oxygen saturation levels. Svendsen et al. (2003) reported continuous positional movement over three speeds (lowest, intermediate, highest), with greatest positional movement rates at the intermediate speed, and somewhat lower movement at the lowest and highest speeds. Domenici et al.'s (2002) findings are somewhat inconsistent with proto-cooperative theory (Trenchard 2015), which suggests that the rate of positional change falls at or near the higher speed proto-cooperative threshold, at which organisms can sustain pacesetters' speeds

by exploiting the energy saving mechanism, but cannot pass them (the stressed regime, as shown in Fig. 1).

On the other hand, Svendsen et al.'s (2003) findings are not inconsistent with proto-cooperative theory, since we would expect higher positional movement at intermediate speeds (the cooperative or convective phase), and reduced movement at higher speeds (the position-locking phase). Furthermore, the position-locking phase is comparatively unstable and determined in part by the fatigue rates of pacesetters and, at sufficiently high speeds, even the strongest fishes are forced to decelerate. This may result in the strongest fishes reducing speed to shift positions backward to lower cost positions, which potentially leaves weaker fishes exposed to the highest cost positions. In this state, the overall effect is collective deceleration and a breakdown of the higher speed formation, similar to the noted collapse of the fish formation between 12 and 25% oxygen saturation in the Domenici et al. (2002) study.

## 8.2. Evidence for the variation range hypothesis

It is well known that fishes often school with others of similar size (Hoare et al., 2000). Fish speeds tend to increase in correspondence with fish size (Krause et al., 2005), and so a natural explanation for fish school sorting is that faster, larger, fishes tend to aggregate together and likewise will slower, smaller, fishes. Pitcher and Parrish (1993) were critical of this hypothesis because, as they reasoned, groups are more likely to separate completely according to speed groupings, and this is observed where there are very large size and age differences among fishes, as opposed to size sorting within larger cohesive groups but without group separation. Foraging competition, individual decisions to swim next to neighbors of similar size (Pitcher and Parrish, 1993) and chemical cues (Ward and Currie, 2013) are among the explanations for school sorting by size.

Pitcher and Parrish (1993) did observe that among schools there may be body-length differences in the range of 30% within the same shoal or school. According to the variation range hypothesis, to the extent that body-length or size variation correlates with fishes' maximal metabolic capacities (Weihs, 2003), this 30% variation in body-length leads to the prediction that the energy saving quantity is ~30%. Similarly, strictly based on the energy saving quantity, the variation range hypothesis predicts that for the Grey mullet (*L. aurata*) schools studied by Marras et al. (2015) in which there is approximately mean 20% reduction in oxygen consumption, the variation in individual maximal metabolic capacities (correlated to body-length) among school members is approximately 20% – remarkably near the 30% variation described by Pitcher and Parrish (1993) in this context.

These variation quantities are suggestive of sorting processes among existing schools, particularly during migration periods, when speeds may be expected periodically to be driven sufficiently high by stronger fishes to cause group sorting as proposed; these quantities also suggest that fishes' body-lengths converge to within this range over geologic timescales. If groups, sufficiently large for viable reproduction, separate permanently as a result of these sorting processes, speciation is a natural consequence.

The work of Koutrakis et al. (1994) included extensive measurements of the body-lengths of different mullet species. The authors collected specimens intermittently in two-day periods over two years. Given that samples were taken over the course of two days and therefore not all sample sets were composed of fishes from the same schools, the reliability of the data as evidence for the variation range hypothesis is limited, although it does reflect long term adaptation. Also, school sizes from which samples were collected were not given. Nonetheless, we excerpt size data from the Koutrakis et al. (1994) study and include percent variation ranges, as shown in Table 1 below.

**Table 1**

Body-length ranges for five species of mullet. Table modified from Koutrakis et al. (1994) (any missing data also missing in the original).

months	Liza aurata (157)			Liza ramada (550)			Chelon labrosus (745)			Liza saliens (641)			Mugil cephalus (24)		
	min	max	range%	min	max	range%	min	max	range%	min	max	range%	min	max	range%
4/89	32.0	46.0	30.4	16.7	29.3	43.0	13.6	22.3	39.0	21.8	126.0	82.7	32.0	46.0	30.4
5/89				32.7	43.9	25.5	14.8	38.3	61.4	99.0	99.0	0.0			
6/89				53.0	75.0	29.3	19.7	58.0	66.0	102.0	124.0	17.7			
7/89							38.5	64.7	40.5	30.7	30.7	0.0			
8/89							58.0	83.0	30.1	15.6	59.5	73.8			
9/89							66.0	107.0	38.3	17.2	53.0	67.5			
10/89							74.0	117.0	36.8	19.2	56.8	66.2	20.4	20.4	0.0
11/89	16.9	24.3	30.5							19.0	45.5	58.2	19.9	22.9	13.1
12/89										18.3	54.5	66.4	20.3	25.5	20.4
1/90				14.6	18.3	20.2%				17.7	24.2	26.9			
2/90															
3/90	22.5	35.5	36.6							41.8	41.8	0.0			
4/90	28.0	35.5	21.1	24.1	29.7	18.9	19.2	22.7	15.4	24.6	53.6	54.1			
5/90				28.5	44.4	35.8	13.0	29.0	55.2	29.4	33.1	11.2			
6/90				49.0	60.8	19.4	25.1	52.0	51.7	67.5	99.0	31.8			
7/90							43.8	62.0	29.4	11.6	99.0	88.3			
8/90				107.0	108.0	0.9	79.0	95.8	17.5	9.3	102.0	90.9			
mean			29.7			24.1			40.1			46.0			16.0

We also note that finding an exact correspondence between the variation range and the energy saving quantity is unlikely due to imprecise measurements of the energy saving quantity; imprecision in this quantity likely arises from both the lack of exact correlation between body-length and strength, and the prediction that very large schools are likely to increase the variation range (Eq. (7)). However, the basic mechanism of size sorting occurs when speeds are driven high enough to separate weak fishes from the group, and the actual reasons for high schooling speeds, whether because of migration, predator avoidance, hunger, or something else, are irrelevant to the production of sorting as a consequence of school speeds that are driven to a decoupling threshold.

In a study of the oddity effect, a phenomenon in which different species will intermingle when their body-lengths are similar, Ward and Krause (2001) reported fish body-lengths among 13 complete shoals composed of between 5 and 78 European minnow (*Phoxinus phoxinus*). From the authors' data and statistics, we estimated body-length ranges as percent differences using the range rule: range = s.d. \* 4; max = mean + (range/2), as shown in Table 2.

DeBlois and Rose (1996) reported the sorting of very large shoals into sub-groups by size. For a shoal of migrating Atlantic cod (*G. morhua*) that spanned 22 km and tracked for 36 days, the authors reported the presence of sub-groups for which the mean body-length of fishes in the leading group was 47.2 cm, and the mean body-length of fishes in the hindmost group was 43.6 cm, as shown in Fig. 8. DeBlois and Rose (1996) did not report maximums and minimums, but using their data and statistics, we estimated length ranges of 36–53% for the five categories reported.

The sorting reported by DeBlois and Rose (1996) supports the predictions of the variation range hypothesis. In Fig. 8, we summarize the observations of DeBlois and Rose (1996), and show its similarity in structure to the peloton simulation results of Trenchard et al. (2015), whereby groups of 100 simulated cyclists with a 36% variation range of maximal sustainable power outputs (MSO) were driven to near maximums for periods that corresponded to actual race results. By the end of each simulated test trial, the original groups had divided and sorted according to relative strength, with new groups containing riders whose MSOs spanned a narrower range.

In contrast to this mechanism by which fishes sort according to size and/or strength, Ward and Currie (2013) proposed that fishes are able to locate others of similar size through a chemical cue mechanism. We suggest that although chemical cues may have evolved to become a component of school sorting and are not mutu-

**Table 2**European minnow (*P. phoxinus*) body-length of ranges (percent difference), estimated from Table 1 in Ward and Krause (2001). Mean range = 39.54%.

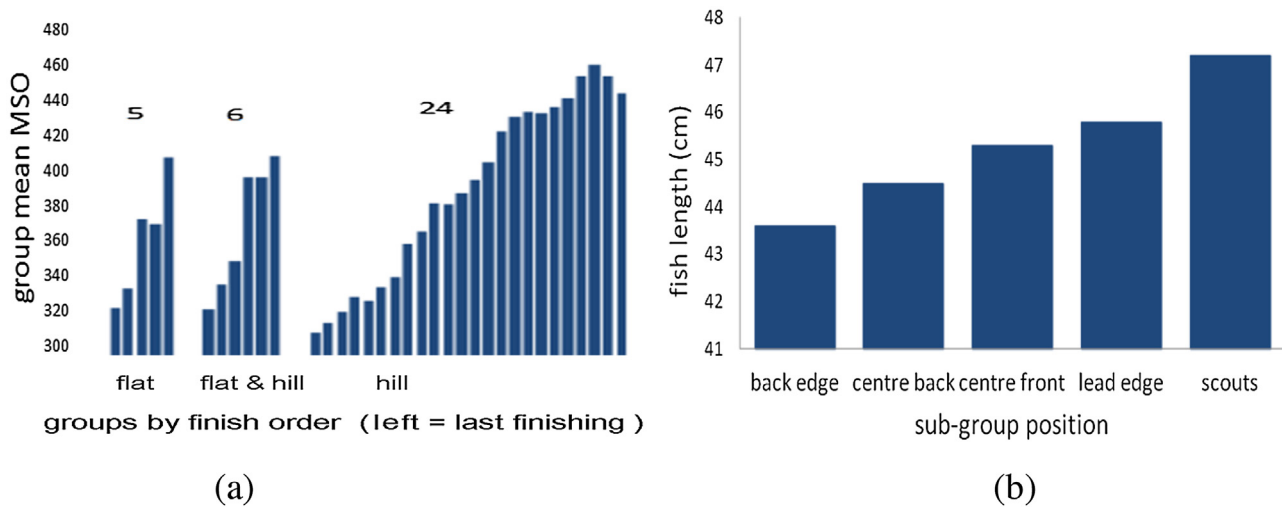
shoal	shoal number	mean body-length (mm)	s.d.	range	range%
1	10	44.35	3.38	13.52	26.45
2	7	40.71	3.9	15.6	32.16
3	67	12.81	1.26	5.04	32.88
4	8	46.25	5.5	22	38.43
5	10	44.3	7.04	28.16	48.24
6	5	42	2.92	11.68	24.41
7	22	51.36	5.8	23.2	36.85
8	8	50.25	4.71	18.84	31.57
9	54	18.5	3.85	15.4	58.78
10	78	48.8	4.92	19.68	33.56
11	72	15.81	3.35	13.4	59.53
12	10	53.5	6.92	27.68	41.10
13	14	17.29	2.89	11.56	50.11
mean					39.54

ally exclusive of sorting by strength, the sorting principle proposed by Trenchard et al. (2015) in the context of pelotons, and as a consequence of the variation range hypothesis, is a simpler and more intuitive explanation. Since we expect that individual fish size will correspond to metabolic capacity, we argue that when schools are driven to speeds corresponding to the maximal output of weaker fishes, even for relatively short periods, the schools will sort into sub-groups defined by a specific, narrow range of maximal outputs and size, such as shown in Fig. 8. As the variation hypothesis range predicts, this narrow range will approximately correspond to the energy saving quantity, modulated by the school size.

The inferred ranges from both Koutrakis et al. (1994), Ward and Krause (2001), and DeBlois and Rose (1996) all indicate variation ranges higher than predicted by a one-to-one correspondence between the energy saving quantities as determined for certain species, and the variation range. We should not, however, generalize the energy saving quantities of certain species to those of others. For species in which energy saving quantities co-exist with body-length variation range data, the correspondence between these parameters appears closer, as shown in Table 3.

While the paucity of data presented in Table 3 cannot be conclusively relied upon, it indicates evidence of a relationship between the variation range of fish lengths and the energy saving quantity in terms of tail-beat frequency.

Notwithstanding the apparent relationship shown in Table 3, we argue that even taking into account the effects of other schooling behaviors and some imprecision among measures of the energy



**Fig. 8.** (a) Peloton sorting. Simulated cyclists were randomly assigned maximum sustainable power outputs (MSO) between 305 W and 479 W (range 36%), power outputs converted from cyclists' 200 m times. For each trial, groups of initial size 100 were run for simulation time ~16 min. Trial speeds were based on speed profile from an actual mass-start flat race, varying for (1) a flat course (2) the presence of a single hill (4%) for 19 s and otherwise flat, and (3) the entire trial on a hill (3%). At trial completion, for a flat course and flat & hill, the original group of 100 divided into a small number of groups, with weaker groups finishing last and each group with narrow MSO range (i.e. <36%). Due to the continuous high output required on the 3% hill and reduced drafting benefit, the original group of 100 sorted into 24 groups (c.f. Fig. 2) (reproduced with permission, from Trenchard et al., 2015). (b) Sub-group positioning of large shoal of Atlantic cod, from data in DeBlois and Rose (1996).

**Table 3**  
Summary of energy saving quantities, here tail-beat frequency vs. length ( $VO_2$  vs. length data obtained is insufficient for meaningful statistics). Here the first 6 quantities for *D. labrax*, *L. aurata*, and *R. rutilus* yield  $R^2 = 0.8218$ , P-value = 0.7048; Pearson correlation = 0.9065.

	Energy saving TBF	Length range%	Comments	Reference
<i>D. labrax</i>	14	2	juveniles chosen from rearing tanks	Herskin and Steffensen (1998)
<i>L. aurata</i>	28.5	29.7*	from Koutrakis et al. (1994); captured from wild	Marras et al. (2015)
<i>R. rutilus</i>	11.6	10.5	here length% is mean of 7–14%; captured from wild	Svendsen et al. (2003)
<i>T. mediterraneus</i>	29			Zuyev and Belyayev (1970)
<i>Gadus morhua</i>		44.91		DeBlois and Rose (1996)
<i>P. phoxinus</i>		39.54		Ward and Krause (2001)
<i>L. aurata</i>		29.7*		Koutrakis et al. (1994)
<i>L. ramada</i>		24.1		Koutrakis et al. (1994)
<i>C. labrosus</i>		40.1		Koutrakis et al. (1994)
<i>L. saliens</i>		46		Koutrakis et al. (1994)
<i>M. cephalus</i>		16		Koutrakis et al. (1994)

saving quantities, the variation range hypothesis is not strictly a function of the energy saving quantity, but is partly also a function of school size.

So, for very large schools such as reported by Koutrakis et al. (1994) and DeBlois and Rose (1996), we may predict higher variation ranges as described by Eqs. (6) and (7). This is because the permissible power differential between strong and weak fishes increases according to the size of the school due to the fact weaker fishes have more time to fall back within the school, yet maintain proximity to energy saving zones of other fishes.

By adapting Eq. (5), we can model the process in which weaker fishes drift to the back of groups and lose contact with those groups. Under this model, fishes will drift backwards by physiological necessity only if group speeds are increased such that the inequality in Eq. (2) is satisfied ( $GCR > 1$ ). If this condition is satisfied ( $GCR > 1$ ), a fish ("Fish A") will decelerate within the school as long as the pacesetter speed in that condition is maintained, or if the pacesetter's speed increases. However, if the pacesetter decelerates sufficiently such that  $GCR < 1$ , Fish A can remain within school boundaries, albeit having shifted its position farther toward the rear.

Thus by adding a school size parameter, we can modify the argument that fishes' maximal sustainable outputs will, over time, tend to converge to a range percentage that is within the range of  $(1-d) * 100$  (as a percent) where  $d$  is the output coefficient of a follow-

ing fish in an energy saving position relative to a stronger fish in a non-energy-saving position, and  $1-d$  is the energy saving quantity.

As noted, if at any time the pacesetter's speed falls such that a following fish's output relative to the pacesetter's output is  $GCR < 1$  before time (s) exceeds  $T_{gap}$  (Eq. (5)), the following fish will stay within the boundaries of an existing school. The following equation (Eq. (6)) describes the opposite condition, the formation of sub-schools:

$$Sf \Leftrightarrow T_{GCR>1} > T_{gap} \quad (6)$$

where  $Sf$  is the formation of sub-schools;  $T_{GCR>1}$  is the duration at which a following fish's output is insufficient to sustain the pacesetter's speed, even by swimming in optimal energy saving positions.

Thus for large schools or groups, we may modify the variation range such that:

$$VR = ESB + \left[ ESB * \left( \frac{T_{gap}}{T_{gt}} \right) \right] \quad (7)$$

where  $VR$  is variation range;  $ESB$  is the energy saving benefit as a fraction, i.e.  $(1-d)$  in Eq. (2);  $T_{gt}$  is the total time required for a fish at  $GCR > 1$  (Eq. (2)) to drift from the front of the group to the back before decoupling (i.e.  $T_{gt}$  corresponds to the total length of the school). For example, given an  $ESB$  of 0.25 (25%) a fish that takes 30 s to decouple relative a total time of 60 s required for a fish positioned at the front to decelerate through the entire group and decouple,

where  $\frac{T_{gap}}{T_{gt}} = 0.50$ , VR is 0.375. Thus in this example fishes within a school that shift backward relative to school-mates, may be 37.5% weaker than pacesetter fishes and remain within the boundaries of the group as long as  $Sf$  (Eq. (6)) is not satisfied. This implies that high speeds set by strong pacesetters must be sustained for considerable durations before weak fishes will decouple from the group; should the pace slow for any period, weaker fishes have an opportunity to shift forward within the group.

Eq. (7) will hold true only for large groups, the critical minimal size for which is unknown, but is likely to correspond to some extent to fatigue rates and the time that leading fishes sustain maximal speeds before a relaxation in pace occurs such that decelerating weaker fishes stabilize their positions within the school. Thus the exact relationship between the variation range and school size is unknown, and Eq. (7) may require the inclusion of additional parameters.

Nonetheless, the literature and data reviewed in this paper indicates that the sum of any increase in variation range due to school size and the energy saving quantity, generally does not exceed a total variation range (i.e. VR (Eq. (7)) of 50–60% (Table 6).

In the case of small schools for which VR (Eq. (7)) is unlikely to apply, like those reported by Herskin and Steffensen (1998) where the length range was ~2% for juveniles, it is not clear why the variation range would be substantially smaller than the proportionate energy saving quantity. Nevertheless, it is consistent with the variation range hypothesis that the range be smaller, but not greater than the proportionate energy saving quantity (except for the increases that account for school length), since organisms within this smaller range in terms of strength will be capable of sustaining the speeds or outputs of pacesetters. Such a narrow variation range of ~2% for juveniles implies either or both a correspondingly low energy saving quantity and frequent periods of high speed that produce sorting within this narrow range. A low variation range for juveniles may also be related to the egg size variation. The implications of this for the variation range hypothesis bear further study.

The question also arises why for small schools (or any given small biological collective), the body-size variation range might be significantly higher than the proportionate energy saving quantity. Indeed, we expect that many animal collectives will contain infants and juveniles whose maximal sustainable outputs are well below the hypothesized variation range. This problem does not undermine the logic of the variation range hypothesis, but rather points to two evolutionary solutions or a combination thereof: some form of parental energetic investment in which infants and juveniles are carried (often, quite literally) by parents or stronger group members during migratory movement until the maximal outputs of these young, weaker, members increase sufficiently to attain the proportionate lower boundary of the energy saving quantity  $(1-d) * 100$ ; secondly, that animal collectives maintain a period of comparatively sedentary or slow moving mobility during which young members grow in strength prior to migration. In this way, parental investment compensates for the difference between the maximal sustainable outputs of the young members and the lower boundary of the hypothesized variation range, while a sedentary or slow moving growth period simply allows the young time to grow before migration. We explore this compensatory parental investment further in the case of dolphins and have discussed previously the sedentary juvenile growth period prior to migration in the case of geese (Menu et al., 2005). In the section that follows, we explore this further in the case of eels, which remain in a growth stage for years before migrating (DeLeo and Gatto, 1996).

From this we may also predict that when groups begin their migration, their variation ranges may be broader than the equivalent energy saving quantity because the group will contain weaker juveniles which begin their journey too soon. Over the course of

their migration, however, the group variation range will tend to converge toward the energy saving quantity as weaker animals are filtered from the group, thus narrowing the adaptive range.

## 9. Eels

In contrast to schools of caudal fishes (fin swimmers) which swim in rhomboid or diamond patterns, anguilliform (undulatory) swimmers like eels swim in close contact and parallel to each other, temporarily synchronizing undulations (Burgerhout et al., 2013).

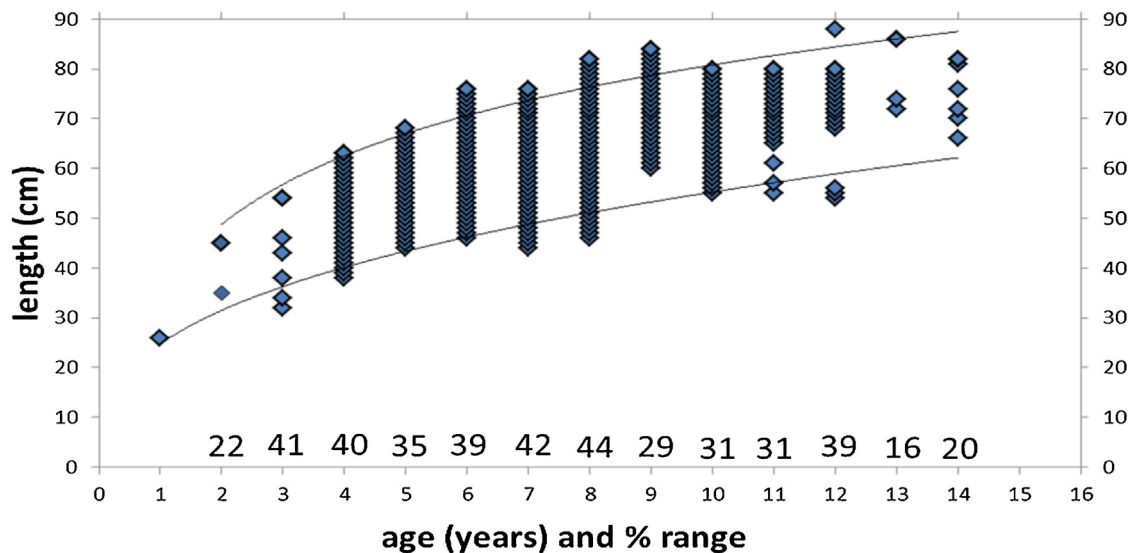
Burgerhout et al. (2013) studied European eels (*Anguilla anguilla*) which are capable of migrating distances up to 6000 km. In their study, the authors first determined that  $0.9 \text{ m s}^{-1}$  was approximately the eels' maximum sustainable speed. The authors then increased swim tunnel currents from 0.4 to  $0.9 \text{ m s}^{-1}$  for solitary eels and in groups of seven, and found a ~30% reduction in oxygen consumption by eels in a group compared to those swimming in isolation.

There is reasonable proportionate correspondence between this ~30% reduction and eel size ranges. DeLeo and Gatto (1995) reported a curvilinear increase in length with age among male and female yellow and silver eels, as shown in Fig. 9. In Fig. 9 we also show the approximate percent body-length ranges for each age (not shown in the original).

DeLeo and Gatto (1995) obtained data from eels as they exited a large (10,000 ha) fishery (which they entered from the ocean in the spring) in autumn after metamorphosing into silver eels. The eel samples were taken from a population well-mixed both in age and length; however, the authors' reported that each year eels arrive at the fishery from the ocean as elvers (young eels), where they remain for a varying number of years as yellow eels before metamorphosing into silver eels (usually by 8–9 years old for females, and between 4 and 7 years for males); then they return to the ocean for spawning. In natural conditions, elvers remain in freshwater regions for years before they migrate to spawn (Ellerby et al., 2001).

From the data in DeLeo and Gatto (1995) we derived a total body-length range of ~76% (Fig. 9) among all the eels sampled as they exited the freshwater region. However, the critical migratory ages are 4–7 years for males, and 8–9 years for females, and the body-length ranges of 44% to 29% for females in these age groups, as shown in Fig. 9 are considerably closer to the indicated 30% energy saving quantity (Burgerhout et al., 2013). In principle, the potential is high for group divisions to occur if the variation range exceeds this proportionate 30% energy saving quantity in the case of such long migrations. Because eels do not feed during this migration period (Vøllestad, 1992), their energetic levels diminish constantly; thus differentials in energy levels are more closely related to eels' relative sizes, as opposed to being a result of differential feeding opportunities that arguably have a significant independent influence on how groups divide.

Vøllestad (1992) observed that at metamorphosis, which occurred at mean ages of 5.99 years for males and 8.73 years for females, mean male length was 405.6 mm, compared to 623.2 mm for females. Vøllestad (1992) found this 35% range between males and females difficult to explain particularly without knowledge of eel reproductive behavior, for which there is little or none because eel spawning in nature has not been observed. Vøllestad (1992), however, acknowledged that a male must be of a minimum size to withstand migration stress. We suggest that it is not necessary to observe eel spawning to explain the 35% difference in size between males and females; indeed, this range is expected from the variation range hypothesis and the actual 30% energy saving quantity determined by Burgerhout et al. (2013); this saving enables the weaker males in that range to sustain the speeds of the larger, stronger, females.



**Fig. 9.** Female yellow and silver eel size ranges by age (not distinguished in this reproduction). Data approximated from Fig. 3 in DeLeo and Gatto (1995) and adapted to show approximate size ranges. Ranges within age groups show reasonable correspondence to the  $\sim 30\%$  reductions in oxygen consumption (Burgerhout et al., 2013) during group travel. The total size range from the smallest shown to the largest is  $\sim 76\%$ .

## 10. Spiny lobsters queues

Bill and Herrnkind (1976) reported single-file queuing behavior among spiny lobsters (*Panulirus argus*) which the authors argued is a drag reduction mechanism. Single-file behavior that involves some recognized or hypothesized energy saving mechanism is also observed, for example, in caribou migrations (Miller et al., 2005), American coots on water (Trenchard, 2013a,b), ducklings (Fish, 1994), and bicycle pelotons (Trenchard et al., 2014).

Bill and Herrnkind (1976) reported lobster single-file queues of between 2 and 65 individuals migrating at average speeds of  $28 \text{ cm s}^{-1}$  for periods of over half a day. Larger queues of 40 or more were observed only over level unobstructed sand substrate. The authors reported that following lobsters in a group of 19 at  $35 \text{ cm s}^{-1}$ , the maximum speed observed, enjoyed a 65% drag reduction (a form of hydrodynamic drafting), relative to lobsters travelling in isolation. The authors noted that drag reduction implies a faster sustainable collective speed, and identified the advantage of drag reduction to weaker lobsters as the facilitation of increased walking speed.

From data in Kanciruk and Herrnkind (1978) of four migration groups adopting single-file formations, we have approximated the carapace length variation ranges for these groups as 45.3%, 56.7%, 53.6% and 52.2% (from Fig. 4, Kanciruk and Herrnkind (1978)). These ranges are in reasonable correspondence with the maximum drag reduction of 65%. This again supports the variation range hypothesis, assuming a correlation between lobster size and their maximum sustainable power outputs (MSO) and bearing in mind the caveats regarding the relationship between drag reduction, speed and power output implied by Eqs. (3) and (4).

Bill and Herrnkind (1976) also reported that lobsters will spontaneously trade leading positions, and observed that among groups of 4–7 lobsters contained in circular pools, all of them shared the leading position. Again this indicates a convective pattern characteristic of energy saving mechanisms in biological systems, including for example: cyclists (Trenchard et al., 2015), the dyadic exchanges of ibis (Voelkl et al., 2015), penguin huddle rotations (Waters et al. 2012; Le Maho, 1977), fish O-turns (Domenici et al., 2002) and rat pup huddle rotations (Alberts, 1978).

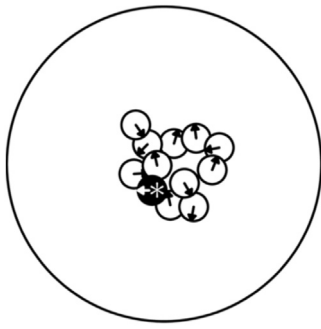
Leader position sharing among spiny lobsters is both a good example of proto-cooperative behavior (Trenchard, 2015), and a

simple example of the reasonability of the variation range hypothesis. Under the proto-cooperative framework, we hypothesize that sharing of the most costly front position can only occur when the speed of the pacesetter leads to the result  $GCR < d$  (Eq. (2)) where  $d$  is the ratio of the maximum sustainable output (MSO) of the follower to the output set by the pacesetter, and  $1 - d$  is equal to the energy saving quantity (0.65 for spiny lobsters, and  $d = 0.35$ ).

To illustrate, assuming that a lobster's MSO approximately corresponds to its size (i.e. larger lobsters are stronger and have higher MSOs), we first develop the situation in which following lobsters can sustain speeds of the pacesetter by drafting but are unable to pass the pacesetter (the position-locking phase of proto-cooperative behavior). Thus given an energy saving of 0.65 (65%) and a pacesetter lobster travelling at the MSO of the strongest lobster at  $35 \text{ cm s}^{-1}$ , the minimum MSO of a weaker lobster required to maintain the pace of the faster lobster by drafting is  $12.25 \text{ cm s}^{-1} = 35 \text{ cm s}^{-1} - (35 \text{ cm s}^{-1} * 0.65)$ , and whose MSO is thus 35% of the strongest lobster ( $12.25 \text{ cm s}^{-1} / 35 \text{ cm s}^{-1}$ ).

If  $12.25 \text{ cm s}^{-1}$  is in fact the MSO of the weaker lobster, then  $GCR = 1$  and any subsequent increase in speed by the pacesetter means  $GCR > 1$ , and the lobsters decouple. When the speed is sustained at  $35 \text{ cm s}^{-1}$  no lobster can have  $MSO < 12.25 \text{ cm s}^{-1}$  and remain coupled with the group. Moreover, passing can occur only if the MSO of followers exceeds the pace set by the leader. For passing to occur, either the leader must decelerate, or the follower must be stronger: in both cases,  $GCR < 1$ . This illustrates the decoupling threshold and how it occurs, leading to the hypothesis that the MSO variation range of any biological collective enjoying an energy saving benefit is proportionately equivalent to that same energy saving benefit, because any individual whose MSO is less than a value within this range will decouple from the group. Thus, in this example, the 65% drag reduction found by Kanciruk and Herrnkind (1978), is equivalent to an MSO range variation of 65%.

In circumstances in which speeds fluctuate between maximum and lower speeds, lobsters with  $MSO < 12.25 \text{ cm s}^{-1}$  may reintegrate after decoupling from the group when the pace decelerates sufficiently; however this will be highly fatiguing if speeds oscillate and decoupled individuals are forced continuously to catch up to the group ahead and eventually they will decouple permanently, especially over long migration periods and in relatively small groups, as indicated by Eq. (6). If groups decouple permanently



**Fig. 10.** Huddling rat pups in a convective process; arrows indicate direction of movement relative to the focal pup, black circle (Image 2a reproduced with permission, from Glancy et al., 2015; Creative Commons Attribution Licence).

such that sub-groups form and reproduce among themselves in isolated geographical locales, the potential for speciation occurs. When this process is repeated continuously over geologic time, the entire diversity of species emerges in which each species exhibits its own unique maximal metabolic output variation range, usually in the form of size variation, that corresponds proportionately to the available energy saving quantity.

As discussed, in large schools of fishes, a greater variation range may exist because of the longer period experienced by weaker fishes to drift to the back of the group (Eq. (7)). However, lobster queues are typically less than 40 individuals long (Bill and Herinkind, 1978), forming a group length that is probably too small to permit lobsters who are significantly weaker than 35% of the strongest lobsters to remain within the group through an entire migration.

## 11. Penguin and other huddles

Alberts (1978) was perhaps one of the first to liken collective animal behavior to a “convection current” in describing the rotational behavior of huddling rat pups (*Rattus norvegicus*), or “pup flow”. He described the process as one of cooler pups in a huddle burrowing downward into the insulated region of the group, which displaces other pups to peripheries; by contrast, warm pups ascend to the surface, shifting the direction of collective movement, as shown in Fig. 10 (from Glancy et al., 2015).

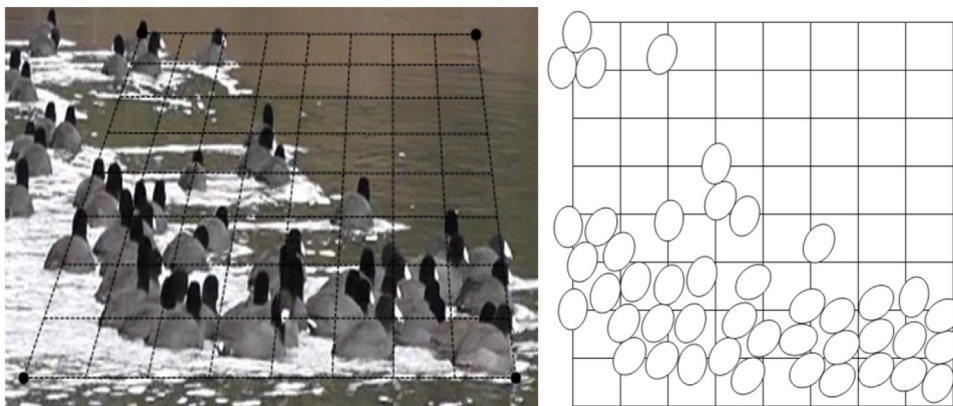
Glancy et al. (2015) reported an equation for the rate of pup flow (rate of positional exchange) in terms of the time derivative of proportions of exposed surface area. Their equation describes a form of convective flow, yielding a positive value when a pup moves

from the centre to the periphery and a negative value when a pup moves from periphery to the centre (Glancy et al., 2015).

Similar descriptions of penguin huddling rotations (Waters et al. 2012; Le Maho, 1977) are consistent with convective behavior. This occurs when huddling penguins shift positions by advancing from windward positions up huddle peripheries, thus sharing the coldest exposed windward positions where heat loss is greatest (Le Maho, 1977). This behavior can be observed in publicly available video (Emperor Penguin, 2016). Stead (2003) applied Le Maho’s (1977) description to a computer simulation of this behavior. For a review of huddling behavior and its reductions in metabolic costs see Gilbert et al. (2010), which identifies metabolic reductions by huddling of between 6% and 53% for 28 different species. In terms of timescale, rotational flow is in the order of hours, longer than other convective motion among animals we have discussed, but vastly shorter than any convective motion that generates phyllotactic arrangements, discussed previously.

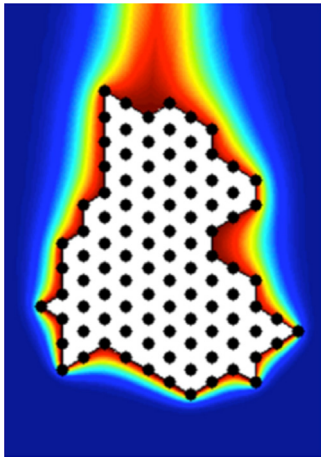
A different description of huddling rotations is from Zitterbart et al. (2011) who described standing wave motion and “treadmilling” behavior in which penguins join the huddle at the trailing edge and leave it at the leading edge. Similar rotational spiral movement as an element of wave-front motion was simulated by Gerum et al. (2013) (c.f. Fig. 4b). Nonetheless, Le Maho’s (1977) description and Zitterbart’s (2011) treadmilling description and Gerum et al. (2013) spiral motion, appear to be similar convective processes in different directions, generated according to different initial conditions that may induce preferential rotational flow in one direction or another.

Trenchard (2013a) observed similar collective rotations and sharing of the anterior (lead) position among American coots (*Fulica americana*) in broad planar formations, as shown in Fig. 11, and single-file on-water formations. Due to near proximity surface swimming and similar hydrodynamic forces as experienced by mallard ducklings (*Anas platyrhynchos*) on water (Fish, 1994; Trenchard, 2013a), Trenchard (2013a) inferred that American coots on water are likely to experience similar metabolic reductions to those of ducklings on water. Fish (1994) examined on-water duckling formations and found that compared to solitary ducklings, those in single file behind a decoy “mother” experienced 7.8–43.5% reduction in metabolic output, and a maximum of 64% energy saving for ducklings in larger groups. In high density American coot formations, such as those shown in Fig. 11, in which convective patterns occur, we would expect a similar thermographic profile as that shown in Fig. 12, albeit with smaller temperature differentials than that of penguins.



**Fig. 11.** American coots in high density formation (reproduced with permission, from Trenchard, 2013a). Grid approximates overhead perspective. Coots show collective rotational patterns, and given their positional similarity to those of ducks on water which experience substantial energy saving (Fish, 1994), coots are likely to experience similar energy saving by high density on-water formations.





**Fig. 12.** Computed temperature distribution around penguin huddle: blue corresponds to cold temperatures; red to warm; individual penguins are black; white indicates polygonal huddle structure (reproduced with permission, from Waters et al., 2012; Fig. 1: Creative Commons license). Though not stated in Waters et al. (2012), we infer wind direction from the image bottom, with the warmest temperature in the sheltered zone at the top of the image. Note the similarity to Fig. 5(b), whereby the temperature distribution here roughly corresponds to what we would expect in Fig. 5(b), except the wind direction is reversed as the cyclists' highest outputs, and corresponding temperatures, are among those at the front in zones of highest drag.

We have not reviewed studies of the flight energy costs and saving of mallards or coots in flight, which may have greater effect on group divisions during longer distance migration than on-water energy costs and saving when birds may be comparatively sedentary or remain within relatively small geographic regions, thus reducing the probability of long term group separations. Mallards migrate in groups up to thousands of kilometres (Krementz et al., 2011), and coots follow similar migratory patterns to mallards and other waterfowl (Eddleman et al., 1985).

With respect to body size variation ranges, by analyzing data from Owen and Montgomery (1978), we derived ranges of wing measurements for adult and juvenile mallards, male and female: 16.5% (mean) for the four groups; body-lengths differed by 9.3% (mean) for the four groups. Compared with on-water energy saving of ducklings as measured by Fish (1994), these wing size variation ranges are closer to the proportionate in-flight energy saving of 16% for geese reported by Maeng et al. (2013), and the 14% energy saving reported by Cutts and Speakman (1994). Nonetheless, further study is required of the combined effects of on-water and in-flight energy saving on variations in size and strength for species that experience both kinds of energy saving.

## 12. Dolphins

Weihhs (2004) showed that a dolphin newborn (neonate), born at approximately 0.4 the body-length of its mother, exploits Bernoulli suction when it is separated by a few centimeters from the mother's upper body surface and near to its mother's nose; in this position neonates reduce by 90% the thrust required to travel at speeds up to  $2.4 \text{ m s}^{-1}$ . For dolphins, Bernoulli suction occurs when the water flow between mother and calf increases in correspondence to increases in dolphin speed, producing a drop in pressure between mother and neonate, while pressure above the neonate increases (Weihhs, 2004).

Dolphin mothers incur a high energetic cost by high speed swimming and increased drag to induce the Bernoulli effect for the neonate, which move to this position immediately following birth and might otherwise “pop like a cork” from the water surface (Weihhs, 2004). Shoele and Zhu (2015) show the optimal suction

force position between mother and calf is about 0.2 of the body-length of the mother.

When dolphin mothers “carry” their neonates in this way, they experience increased drag and turbulent flow; and, when carrying their neonate, mothers are capable of sustaining only 76% of their ordinary speeds when swimming in isolation (Noren, 2008). Noren (2008) posited that it is unlikely that mothers decelerate in order to accommodate the slower speeds of neonates; rather, mothers decelerate by necessity as a result of increased drag and turbulent flow when carrying the neonate, as evidenced by a 17% increase in the mother's tail-beat frequency at slower speeds. This is an example of the predicted initial parental investment required to nurture the young up to the lower boundary of the variation range.

Within a few hours of birth, the calf shifts position to the “echelon position”, down to a more lateral position within 10 cm of the mother's flank, where energy saving induced by hydrodynamic drafting is about 62%; at separations of 30 cm is about 25% and, for older infant calves, energy saving is about 20% (Weihhs, 2004). Noren et al. (2008) reported an average 28% increase in speed for calves in the echelon position.

The variation range hypothesis predicts that once juveniles reach the lower boundary of the variation range, little or no further parental investment is required. In the case of dolphins, the mother's initial energetic investment to overcome increased drag and to swim faster while the neonate is drawn in close by Bernoulli suction, is followed soon after by a reduced energetic investment by the mother as the calf orientates itself to the echelon position where it can sustain the higher speeds of the mother (Weihhs, 2004). This transition from “carrying” to drafting is consistent with the variation range hypothesis, although there may remain some parental investment in terms suckling or protective vigilance. It is noteworthy that the calf is born relatively large: 0.4 BL of the mother; and within hours is capable of sustaining the relatively high speeds of the mother by drafting (Weihhs, 2004).

While research has established the energy saving mechanisms of drafting and Bernoulli suction between mothers and calves, there appears to be little or no published research that quantifies energy saving mechanisms among adults or larger dolphin collectives. Connor et al. (2006) suggested that, as an alternative hypothesis to cooperating alliances among bottlenose dolphins staying within 0–5 to 1 m of each other, such close proximity behavior could be an adaptive trait due to drafting. This would be particularly advantageous to pregnant dolphins whose increased frontal surface area and corresponding drag forces result in high reductions in speed when they can achieve only 56% of their speeds when not pregnant (Noren et al., 2011).

Williams et al. (1992) demonstrated that dolphins and porpoises preferentially seek out bow and stern waves for durations up to hours, exploiting energy saving advantages in these “wave-riding” positions. However, the authors did not present evidence that coupled adult dolphins exploit similar advantages. Similarly, while interactions between dolphins and other cetaceans like right whales have been observed, the research is inconclusive as to whether the purpose of these interactions is to exploit the energy saving mechanisms between dolphins and other cetaceans (Wursig and Wursig, 1979).

In a somewhat unique context, Fish et al. (2013) reported that Bowhead whales (*Balaena mysticetus*) displayed V formation echelons and vortice patterns during coordinated surface feeding behaviors; and from these behaviors Fish et al. (2013) inferred hydrodynamic drafting and energy saving benefits. These behaviors do not appear to have been observed, however, among dolphins.

## 13. Caribou

Miller et al. (2005) observed that caribou (*Rangifer tarandus*) tend to migrate in single-file, with followers stepping in exactly

the same spot as those ahead. Fancy and White (1987) suggested this is a behavioral adaptation, although they did not expand upon how this is so, while Miller et al. (2005) suggested this behavior permitted trail marking with scent glands. Mattfeld (1973) (as cited in Boertje (1985)), found that energy requirements for white tailed deer (*Odocoileus virginianus*) walking in snow were 40% greater than walking on barren ground, and so we may expect caribou to reduce energy costs by following in the footsteps of those ahead in a similar quantity as the white tailed deer reductions described.

Particularly in view that caribou will tend to place their feet where snow has already been compacted by those ahead, the energy saving benefits of single-file walking are strongly indicated. Single-file walking and trail creation are therefore a form of drafting in that leading animals expend greater energy in breaking the snow relative to followers. This is similar to spiny lobsters queue formations, for which Bill and Herrkind (1976) reported drag reduction benefits. Similarly, Couzin and Krause (2003) modeled pedestrian lane formation behavior in which following pedestrians reduce the energy costs of lateral motion by following in the paths of others.

Fancy and White (1987) reported that the locomotion cost for caribou moving through snow increased exponentially with sinking depth, and that dense snow or crust further increases drag and requires animals to lift their legs higher. The authors noted that for caribou 1 year or older, leg length is a better predictor of net locomotion costs than body weight, and that calves would achieve maximum leg lengths in their second year, despite increasing mass. Fancy and White (1987) noted that the locomotion costs relative to sinking depths are similar for caribou, elk, white-tailed deer, and mule deer.

Duquette (1988) observed that in deep snow conditions, lead caribou appear reluctant to break the trail, and that caribou are often observed to walk routes that have previously been travelled by upwards of thousands of caribou. Presumably, caribou must break trails relatively frequently, although the presence of pre-existing trails distributes the energy saving advantages in a complex fashion that may be difficult to model. While there is some indication that leg length is an adaptation to snow depth (Fancy and White, 1987), and a relationship is indicated between the energy saving of followers relative to trail-breaking caribou, further research is required to establish the appropriate parameters to establish a link between caribou size or leg length, and their path creation and drafting behavior. In terms of aerodynamic drafting between caribou, quantities may be similar to those determined by Spence et al. (2012) for race-horses.

#### 14. Turtle hatchlings and semi-fluid dwellers

An emerging area of study involves the motion of animals through semi-fluids like sand or wet soil (Dorgan, 2015). Rusli and Booth (2016) studied the upward digging of Brisbane river turtle hatchlings (*Emydura macquarii signata*) through moist sand. Using respirometers to measure hatchling CO<sub>2</sub> production, the authors found that larger clutches produced lower total CO<sub>2</sub> when ascending to the sand surface. In a clutch of 4, the slowest turtle took 162.77 h to emerge from the sand, while the fastest took 112.25 h to emerge. In a clutch of 14, the slowest turtle took 49.94 h and the fastest took 39.94 h to emerge. The authors reported that a hatchling digging on its own would consume ~2.05 kJ compared to 0.59 kJ in a clutch of 14: a ~71% energy saving for *E. signata* hatchlings.

Larger groups required less resting time between bouts of digging, which the authors suggested was probably due to lower blood lactate accumulated during digging periods. The authors reported the formation of discreet groups that engaged in synchronous digging activity, which could be triggered by any member of the group. The cue used to trigger the digging activity is unknown, but the

authors proposed that it may be related to the fall of blood lactate levels below a critical threshold. The actual energy saving mechanism was not identified, but the movement of multiple turtles through the sand in synchronous motion is consistent with shear and friction force reductions in vibrated sand (Jaeger and Nagel, 1992), which may be the source of an energy saving mechanism.

Rusli and Booth (2016) did not report the size variation among the *E. signata* hatchlings they studied. However, Janzen (1993) showed a correlation between *Chelydra serpentina* hatchling size and survival success in moving from nest site to water, supporting the “bigger is better” hypothesis. Similarly, Janzen et al. (2000) made findings for red-eared slider turtles (*Trachemys scripta elegans*), in which smaller hatchlings had lower survival rates than larger ones. In their test procedure, Janzen et al. (2000) did not observe survival rates from the point at which turtles emerged from the sand, but rather the authors released hatchlings systematically on the sand surface. Thus for *T. elegans* we cannot infer a relationship between an energy saving quantity and hatchling sizes or the group structure that may have formed during their vigorous ascent to the sand surface after hatching.

Nevertheless, Janzen et al.'s (2000) data does assist our analysis because it shows *T. elegans* hatchling adaptive size ranges: 34.3% carapace length range (23–35 mm), and 64.2% (3.18–8.89 g) mass range. Kolbe and Janzen (2002) reported a somewhat smaller mass range of 54.5% for 463 snapping turtle (*C. serpentina*) hatchlings upon release. Congdon and van Loben Sels (1990) reported carapace length range of 22.6% (30.0–38.8 mm) and a similar mass range of 53.8% (6–13 g) for Blanding's turtle hatchlings (*Emydoidea blandingii*).

In analyzing these results, we see the carapace length variation for two turtle species (*T. elegans* and *E. blandingii*) is not in close agreement with the proportionate energy saving quantity of ~71% found by Rusli and Booth (2016) for *E. signata*. However, the mass variations of 64.2%, 54.5% and 53.8% for *T. scripta*, *C. serpentina*, and *E. blandingii*, respectively, are considerably closer to the proportionate energy saving quantity for *E. signata* as reported by Rusli and Booth (2016). Although the mass variation data is drawn from species other than *E. signata* – the only species for which we know the approximate energy saving quantity – there is reasonable consistency among the three mass ranges identified. This increases our confidence that similar mass ranges may be present among *E. signata* and therefore that these ranges reasonably correspond to the approximate energy saving quantity of 71%, as predicted by the variation range hypothesis.

It is important to reiterate that the relationship between body-length, mass, and the energy saving quantity is uncertain. In our review of the fish schooling literature, for example, the fishes' body-length ranges appeared to be in closer agreement to the energy saving quantity than their masses, which may be reasonable because fishes body-length correlates to tail beat stride length and swim speed (Weihs, 1973) better than body mass does. For turtles, however, their masses may be a better indication of the oxygen consumption capacity in the unique sand-fluid dynamics of vibrating sand (Jaeger and Nagel, 1992). Generally, whatever parameter(s) that best correspond to organisms' maximal sustainable power will be the appropriate one(s) by which to determine a correspondence between the variation range and the proportionate energy saving quantity.

#### 15. Bacteria

Bacterial collective dynamics involve complex considerations like dipole forces; and, at small separations certain factors dominate hydrodynamic factors, including, noise factors, repulsion

forces that reduce adhesion, flagellar and lubrication forces (Drescher et al., 2011). In the specific case of *Bacillus subtilis* high bacterial concentrations are shown to involve counterintuitive fluid behavior, and hydrodynamic feedback between the fluid and the bacteria (Wolgemuth, 2008). Further physical dynamics specific to micro-organisms like bacteria and not observed among larger animals include Brownian motion, wall effects, and unique morphological adaptations like rotors, flagella and spontaneous reverse directional capabilities without inertial forces (Condat and Sibona, 2002; Condat et al., 2005).

### 15.1. High collective bacteria speed compared to speed in isolation

The presence of an energy saving mechanism implies that coupled organisms exploiting such a mechanism will probably travel at higher speeds than individuals moving singly in isolation. Indeed this is true among a number of systems where there is a well understood energy saving mechanism, such as cyclist pelotons (Olds, 1998), inorganic circulating particles (Grugic and Helleso, 2007), and bull spermatozoa (Woolley et al., 2009).

Because bacteria have been shown to travel faster as a group than when alone in isolation (Cisneros et al., 2007), we may infer an energy saving mechanism, despite that a clear energy saving mechanism does not appear to be revealed in the literature. Cisneros et al. (2007) reported certain speed-density correlations in *B. subtilis*, and observed that aggregates of *B. subtilis* bacteria move faster than isolated individuals.

When individually isolated, *B. subtilis* tend to move at variable speeds, whereas when forming co-directional phalanxes, all members of the phalanx proceed at the same velocity, more than double the speed of individuals: individuals typically swim between  $15\text{--}30\ \mu\text{m s}^{-1}$ , whereas phalanxes typically swim  $\sim 60\ \mu\text{m s}^{-1}$  (max  $150\ \mu\text{m s}^{-1}$ ) (Cisneros et al., 2007). Cisneros et al. (2007) indicated that the mechanism for increased collective speeds is the transverse flows between the body of a follower and the tail of a leader; and such flow speeds increase as organisms approach walls and each other.

Mitchell et al. (1995) reported even greater collective bacteria swimming speeds compared to isolated individuals: marine bacteria inside a micro-swarm sustained a speed of  $230\ \mu\text{m s}^{-1}$ , about five times the mean speed of  $45\ \mu\text{m s}^{-1}$  shown for a bacterium outside the micro-swarm. Subsequently, Mitchell et al. (1996) showed that when isolated outside a micro-swarm, individual *Shewanella putrefaciens* bacteria achieved mean fastest speeds of  $97\ \mu\text{m s}^{-1}$ , whereas inside a micro-swarm, the mean fastest speeds were  $187\ \mu\text{m s}^{-1}$ , approximately twice the individual maximums.

Indeed, Mitchell et al. (1995) identified the unresolved extraordinary efficiencies in energy consumption by which micro-swarming bacteria move in speeds at multiples of the predicted 100 % energetic consumption. These efficiencies imply a set of energy saving mechanisms that are not yet well understood.

### 15.2. Bioconvective behavior

In addition to faster collective bacterial speeds relative to the speeds of isolated bacteria, we have argued that an energy saving mechanism is likely to generate convective behavior as a collective manifestation of dyadic rotations between low and high energy positions, as discussed earlier.

Although known since 1848 (Plesset and Winet, 1974), Platt (1961) appears to have been the first to identify polygonal structures similar to Rayleigh-Bénard cells in micro-organism aggregations due to external stimuli like gravity, light or chemical sources, but not as a thermal convection process (Plesset and Winet, 1974).

For example, *B. subtilis* form three-dimensional bioconvection patterns (Janosi et al., 1998; Kessler et al., 1994), in which critical aggregate densities and fluid Reynolds numbers (Yanaoka et al., 2009) determine a transition to bioconvection. In this state, bacteria swimming vertically to water surfaces for oxygen do so in lower concentrations than plume regions that descend centrally (Yanaoka et al., 2009). Janosi et al. (1998) did not report the ascent speeds of bacterial concentrations relative to descent speeds, although they suggested that swimming speeds are correlated with bacterial cell concentrations. Wolgemuth (2008) described *B. subtilis* roll-like patterns involving collective density fluctuations that precede turbulence, which are similarly reminiscent of convective behavior.

Although not explicitly identified as convective behavior, Mitchell et al. (1996) provided data indicating periods of relatively high bacterial speeds on the edges of micro-swarms relative to speeds inside swarms. This appears to describe horizontal two-dimensional bioconvection as opposed to vertical three-dimensional convection, similar to the collective uni-directional rotational effects observed in penguin huddles (Fig. 4b) and bicycle peloton echelon formations (Fig. 4a).

### 15.3. Consistent with the variation range hypothesis

A prediction that follows from the variation range hypothesis is that when collective speeds are five times maximal individual speeds, as indicated by Mitchell et al. (1995), some bacteria among the collective will be smaller in size or maximal metabolic capacity than their larger or stronger counterparts by a corresponding factor of five, bearing in mind appropriate adjustments for the unique fluid dynamics of bacteria, as discussed.

These approximate size variations are in fact observed. From data in Trueba and Woldringh (1980), 1253 *B. subtilis* cells ranged in length between  $\sim 0.5\ \mu\text{m}$  and  $\sim 4.8\ \mu\text{m}$ , although within a narrow diameter range of  $\sim 0.75\ \mu\text{m}$  and  $0.9\ \mu\text{m}$ , grown with a doubling time of 65 min. Similarly, Trueba and Woldringh, (1980) reported 3000 *E. coli* ranged in length between  $\sim 1\ \mu\text{m}$  and  $3.3\ \mu\text{m}$ , and diameter ranges between  $0.4\ \mu\text{m}$  and  $0.72\ \mu\text{m}$ . Donachie and Begg (1989) reported similar size ranges for *E. coli* (range  $\sim 1\ \mu\text{m}$  to  $\sim 7\ \mu\text{m}$ ). It is known, however, that under steady state conditions, bacterial sizes are fairly constant but are more variable in the face of environmental challenges (Chien et al., 2012).

Overall, a direct correspondence between bacterial cell size and magnitude of energy saving oversimplifies the complexities of the physical dynamics that drive bacterial metabolic output, as well as oversimplifying the lifecycles and nutrient availabilities of bacteria and their effects on cell growth and size. Nonetheless, increases in collective speeds relative to the speeds of individuals, in addition to the presence of bioconvective behavior, implies an energy saving mechanism. Further, there is some evidence of a correlation between the energy saving mechanism and the size variation ranges of bacteria, as predicted by the variation range hypothesis. Further analysis of existing research and new research is required to determine the extent of this correlation.

## 16. Spermatozoa

The mechanisms by which sperm aggregate, and the evolutionary advantages of these aggregations, are not well understood (Higginson and Pitnick, 2011). Pizzari and Foster (2008) argued that these agglomeration behaviors are examples of sperm cooperation, altruism, and spite. We propose that sperm aggregation behaviors are driven by their underlying energy saving mechanisms, and these mechanisms likely precede such factors as cooperation, altruism and spite in the evolutionary lineage because they emerge from basic physical forces, drag and fluid principles. This proposition

is supported to some extent by the statistical finding that head conjugating (connecting) among diving beetle sperm is ancestral (Higginson et al., 2012), and that head conjugation is therefore a basic and primordial manifestation of sperm behavior.

Energy saving mechanisms have been reported for a number of sperm aggregates. Woolley et al. (2009) observed that flagella synchronization magnifies beat frequencies and swimming velocities, (see also, Yang et al. (2008)) similar to that observed for eels (Burgerhout et al., 2013). Moore and Taggart (1995) found that, by conjugating their heads, opossum sperm (*Monodelphis domestica*) improve collective speeds relative to solitary individuals. Moore et al. (2002) found wood mouse sperm (*Apodemus sylvaticus*) link together with apical hooks, forming trains of multiple individuals that travel faster together than alone. For a review of sperm aggregation properties, see Pizzari and Foster (2008); Higginson and Pitnick (2011).

Hayashi (1998) reported that fishfly spermatozoa (*Parachauliodes japonicas*) form bundles, and as bundle sizes increase, so do bundle speeds; whereas bundle speeds tend to decrease as the medium viscosity increases. Hayashi (1998) noted that it was impossible to count the number of individual sperm within each bundle; thus it is not possible to compare the maximal speeds of individual fishfly sperm in isolation from their bundle speeds. Nonetheless, the correlation between bundle size and speed indicates that bundle formation involves an energy saving mechanism that permits higher collective speeds relative to individual spermatozoa swimming in isolation.

### 16.1. Determining the energy saving quantity

Woolley et al. (2009) noted that sperm synchronize their motion when their heads are in contact and, when synchronized in this way, sperm swim at higher speeds than when each swim alone. As in the case of other biological collectives discussed in this article, we suggest these higher collective speeds indicate the presence of an underlying energy saving mechanism. Thus, in order to determine the energy saving quantity, using data from Woolley et al. (2009) (their Fig. 4), we noted sperm speeds while synchronized, and compared these speeds to sperm swim speeds for individual sperm in isolation.

Thus, for two sperm identified in Fig. 4 from Woolley et al. (2009) as sperm A and sperm B, we approximated the following for 22 data points: connected sperm A and B were 39% faster than sperm A in isolation; connected sperm A and B were 25% faster than sperm B in isolation; for the two sets, the connected sperm were on average 32% faster than isolated sperm.

### 16.2. Do sperm size variation ranges correspond to the energy saving quantities?

Sperm velocity and size are positively correlated (Mossman et al., 2009; Gomendio and Roldan, 2008), although it should be noted that there is a trade-off between the number of sperm on course to egg fertilization, and their size (Gomendio and Roldan, 2008); and this may affect the degree of correlation between sperm velocity and size. Nonetheless, the variation in sperm sizes within a given spermatophore (single mass ejaculate), appears to correlate reasonably with their swimming strength. Sperm velocity is usually presented as both curvilinear, which accounts for head yawing motion, and as straight-line velocity (e.g. Woolley et al. 2009).

What then are the sperm size variation ranges? Here we seek evidence of variations among individuals within distinct spermatophores so as to compare that variations with the energy saving quantity, and not variations between spermatophores of different males or between species. Although we did not undertake an exhaustive search of the literature, size measurements of sperm

from individual spermatophores were components of a number of papers (e.g. Morrow and Gage, 2001; Hettley and Roberts, 2006; Miller and Pitnick, 2002; Hayashi, 1998), but of those we reviewed, only Birkhead and Fletcher (1995) provided sufficient information to determine sperm size range (for Zebra finch sperm (*Taeniopygia guttata*)), as shown in Table 4.

The values in Table 4 show that the size variation range for Zebra finch sperm (*T. guttata*) reasonably corresponds to the energy saving quantities of four other species' sperm. Although we do not have an energy saving quantity for Zebra finch sperm (*T. guttata*), the general consistency among the energy saving quantity for the others provided suggests a similar energy saving quantity for Zebra finch sperm (*T. guttata*). In turn, the values in Table 4 provide some evidence of a correspondence between sperm size variation ranges and the proportionate energy saving quantity

### 16.3. Sperm proto cooperative behavior

We further propose that sperm aggregation is an example of the position-locking phase (high output) of proto cooperative behavior. In this phase, individuals exploit the energy saving to sustain the speeds of pacesetters, but are unable to pass them (see discussion on fish schools) (Trenchard, 2015). For cyclists, this phase emerges at the threshold  $GCR=d$  (drafting coefficient) when, above this threshold, collective behavior self-organizes as single-file formations; below this threshold, collective behavior manifests in higher density and as high frequency and magnitude passing behavior (Trenchard, 2015).

Because sperm are driven competitively toward egg fertilization and tend to swim at maximal sustainable speeds (Gomendio and Roldan, 2008), a lower output convective phase in which abundant passing occurs is less likely. However, when swimming near maximum speeds, we may expect sperm to operate at a higher output phase in which passing frequency and magnitude are diminished.

Thus sperm travelling near their maximal sustainable outputs will naturally form aggregates and bundles, thus evolving to link and swim together, locked in position, without passing one another. In this way, the bundling phenomenon may be the sperm equivalent of single-file behavior in cyclists when cycling in a high output, low passing frequency phase, as shown in Fig. 13. In Fig. 1, these high output processes occur in the stressed regime. Furthermore, we suggest that sperm aggregations represent an intermediate evolutionary stage in which bundles begin to act as unified individuals (superorganisms) and develop coupled relationships in which additional energy saving may occur between bundles.

## 17. Krill

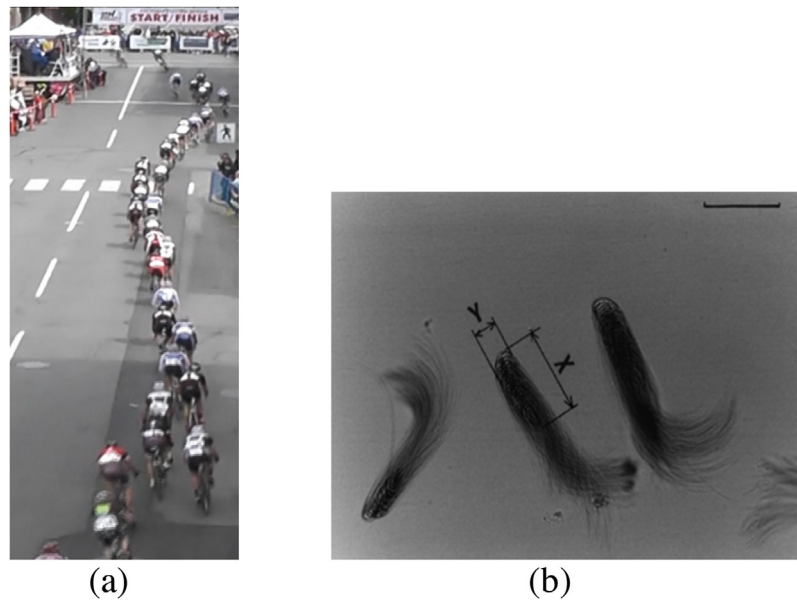
Antarctic krill (*Euphausia superba*) aggregate in high density schools up to 20,000–30,000 individuals/m<sup>3</sup> in which krill orient in

**Table 4**  
Energy saving among given animal spermatozoa, and size ranges where given or implied.

Species	Energy saving (%) <sup>a</sup> $\mu\text{m s}^{-1}$	Size range (%)	Reference
Opossum	28.0		Moore and Taggart (1995)
Zebra finch		27.1	Birkhead and Fletcher (1995)
Bull	32.0		Woolley et al. (2009)
Norway rat (lab)	12.9		Immler et al. (2007)
Norway rat (wild)	25.2		Immler et al. (2007)
House mouse	–33.0 <sup>b</sup>		Immler et al. (2007)
Wood mouse	34.1		Moore et al. (2002)

<sup>a</sup> straight line or curvilinear trajectories.

<sup>b</sup> groups were slower than individuals, but the authors suggested that the groups may still exhibit greater thrusting power than individuals.



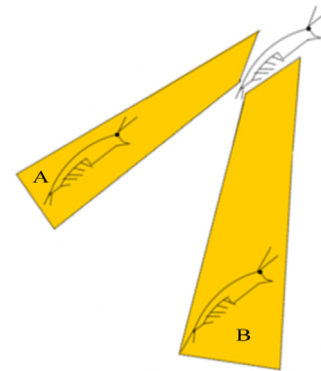
**Fig. 13.** (a) Cyclists in high-output (position-locking) phase in which passing frequency and magnitude are diminished (image by H. Trenchard); (b). Sperm bundle in apparently similar high-output phase in which passing frequencies and magnitudes are diminished; when sperm sustain speeds of pacesetters by exploiting energy saving mechanisms that arise in close-proximity regions, such bundling may be a natural evolutionary consequence. Bundles may become superorganisms in which higher order group coupling behaviors occur, and drafting between bundles is possible (image from Hayashi (1998) with licence to reproduce from John Wiley and Sons.).

parallel (Ritz, 2000); or krill may pack loosely and non-uniformly in swarms up to 1000 m long by 30 m thick (vertical depth), in areas of more than 9000 m<sup>2</sup> (Tarling and Thorpe, 2014; Tarling et al., 2009). Krill can swim horizontally at 20 cm s<sup>-1</sup> (Hamner, 1984) and migrate hundreds of kilometres in a few days (Kanda et al., 1982). Adult Antarctic krill average about 4 cm in length (Patria and Wiese, 2004), and tend to swim at 45° above and below nearest neighbors (O'Brien, 1989).

Ritz (2000) studied energy saving in mysids (*Paramesopodopsis rufa*), which have similarly shrimp-shaped bodies to *E. superba*, between 9 and 13 mm. He found that swarm aggregations up to 50 or 100 mysids consumed on average 7.2 times less oxygen per milligram than non-aggregating individuals. High density schooling can result in reduced oxygen supply (Catton et al., 2011), and so one advantage of the reduced consumption capacity that Ritz (2000) reported may be to compensate for the reduced oxygen supply associated with high-density schooling.

Ritz (2000) observed that when swimming at high speeds, euphausiids and mysids orient more horizontally in the water, and the aggregations may themselves be a source of updraft that minimizes individuals' efforts to keep from sinking. Unlike pelagic fishes, euphausiids and mysids have no buoyant swim bladder and so the energetic costs to sustain swimming to oppose gravity are high, and Ritz (2000) suggested saving energy by schooling is a necessary selection mechanism.

Ritz (2000) identified the lift-generating vortex rings of neighbors as the energy saving mechanism. Patria and Wiese (2004) studied the field flow of North Atlantic Krill (*Meganycitphanes norvegica*), a species related to *E. superba*. *M. norvegica* use their 5 pairs of pleopods (swimming legs) to produce a propulsion jet in a circular cross-section, extending 8–10 cm from jet origin, relative to approximate body-lengths of 45 mm, as shown in Fig. 14. The authors observed that a leader and follower tend to synchronize pleopod beat frequencies, and that upward and forward directed water flow within the vortex represent lift and propulsion which assist following krill to maintain positions relative to the leading krill. While this strongly indicates an energy saving benefit for followers, Patria and Wiese (2004) identified both the ener-



**Fig. 14.** Krill energy saving zones. Adapted from images from Patria and Wiese (2004), colored cones (color online) represent approximate zones of upwash vortices for the vertically ascending leader. The unmarked region between the cones is a jet flow, where following costs are increased. Vertically directed krill A is likely to accelerate in the vortex uplift over the top of the leading krill, while krill B accelerates beneath the leading krill. Collective rotation may be predicted in the direction of body orientation, consistent with findings of Ritz (2000) for mysids.

getic advantage of these vortices and their utility in short range communication.

Yen et al. (2003) examined similar flow fields of *Euphasia pacifica* and hypothesised the presence of both the energy saving benefit of drafting in the flow induced by neighbors as well as the signalling effect in revealing the locations of potential mates.

#### 17.1. Does the size or output variation range correspond to the energy saving quantity?

If we apply the findings of Ritz (2000) for mysids and hypothesize that the reduction in aerobic requirement by a factor of 7 corresponds to an energy saving mechanism, we would predict mysids with a seven-fold range of oxygen capacity and, therefore, size to be present within the same school, exploiting the corresponding energy saving. In our review of the literature, krill size ranges do not span such a large range (i.e. by a factor of 7) (Table 5). Thus, there is no correlation between the energy saving quantity

determined by Ritz (2000) and krill size ranges, and so these findings do not support the variation range hypothesis.

On the other hand, the lack of a correspondence between krill size ranges and the energy saving quantity reported by Ritz (2000) permits us to question the validity of the energy saving quantity he found. For instance, Ritz (2000) seven-fold reduction in aerobic requirements or even similar values do not appear to be replicated in the literature, despite the evidence for some undefined energy saving indicated by Patria and Wiese (2004) and Yen et al. (2003). It should be noted that Ritz' (2000) values are similar to those found for bacteria. Bacteria, as we discussed, however appear to represent a special case because they involve unique fluid dynamics and, in any case, we did observe some correspondence between the energy saving quantities and the size range variation for bacteria.

Consequently, despite the findings of Ritz (2000), we suggest the question remains open: what is the evidence of an equivalence between ranges of krill metabolic capacities and any energy saving benefit from their collective coupling? Conversely, can we look at the size variation ranges, and predict the energy saving quantity? We suggest, based on the circumstantial evidence that we show among other animal collectives for this relationship, it is possible to predict the energy saving quantities from variation ranges, as percentages.

Watkins et al. (1992) studied the size and composition variation among 38 *E. superba* swarms. While the authors did not report the maximum and minimum body-lengths (BL) in each swarm, they did report the mean BL in each swarm and the BL range. The mean BLs per swarm do not allow an accurate computation of the percentage variation, but we used ( $\% \text{ variation} = \text{BL}_{\text{range}}/\text{BL}_{\text{mean}}$ ) to obtain an approximation, returning a mean variation range for 38 swarms of 34.2%, which will be somewhat lower than the more accurate evaluation ( $\% \text{ variation} = \text{BL}_{\text{range}}/\text{BL}_{\text{max}}$ ). This in turn predicts an approximate energy saving benefit of >34%. This of course implies a correlation between body size and capacity to generate swimming power, which is reasonable but other factors that we do not consider here may also affect power capacity.

Nicol (1984) studied size variation among swarms of *M. norvegica*. He reported sizes ranged between 25 mm and 35 mm, a variation of 28.6%. Nicol also presented two tables summarizing size ranges found in several studies involving *M. norvegica* and other species, which we consolidate to include variation percentages and the findings of Watkins et al. (1992) (Table 5). Thus we predict that the percent variations in Table 5 correspond approximately to the percent energy saving coupling benefit. From these values we therefore predict energy saving quantities among krill to be between ~10 and 58%.

### 17.2. Travelling faster as a group

As discussed, an energy saving mechanism will tend to increase the travel speeds of groups over isolated individuals. Kawaguchi et al. (2010) studied krill behavior in holding tanks, and reported a school of eight krill swam on average  $\sim 20 \text{ cm s}^{-1}$  compared to  $\sim 10 \text{ cm s}^{-1}$  for a non-schooling group of nine. The authors did not report the speeds of individuals, however, and did not specify whether the individual speeds achieved were maximal sustainable speeds.

Catton et al. (2011), studied small groups between 3 and 6 krill of two types, *E. pacifica*, and *E. superba* in still-water tanks of diameter 600 mm and height 400 mm. The authors reported slightly slower mean speeds for the groups than individuals: means for solitary *E. superba*  $\sim 7.7 \text{ cm s}^{-1}$ ; group *E. superba*  $\sim 6.9 \text{ cm s}^{-1}$ . The authors noted that inter-individual variation in speed was large enough that mean values were not significantly different. Further, the authors noted that in their study, typically *E. superba* exited the access pipe and swam in a straight line to the other side of the tank before drop-

ping to the tank bottom, limiting data acquisition. Additionally, the results of Catton et al. (2011) were based on small krill sample sizes in relatively small tanks, and their results do not permit conclusions as to differences between group swim speeds and solitary swim speeds, nor do they provide insight into saving in collective hovering costs which Ritz (2000) demonstrated to be substantial relative to non-swarming *P. Rufa*. In general, the literature appears inconclusive as to whether krill swarms are capable of faster swimming than isolated individuals.

Within schools, individuals in leading positions generally incur a higher energy cost than followers which exploit available energy saving mechanisms, as we have discussed in previous sections. For North Atlantic krill (*M. Norvegica*), a close relative of *E. superba* (Patria and Wiese, 2004), the energetically beneficial vortice zones are approximately  $30\text{--}60^\circ$  below and  $0\text{--}30^\circ$  above the krill body horizontal axis and where the propulsive jet flows between this region, as shown in Fig. 14. This suggests that at speeds approaching krill maximal sustainable outputs, following krill will gravitate toward vortice uplifts, generating a phase change in collective behavior analogous to phase changes observed in bicycle pelotons as speeds increase toward collective power output thresholds (Trenchard et al., 2015).

### 17.3. Spatial relationships and collective rotations

In studying spatial relationships between various krill species, O'Brien (1989) observed that at relatively low speeds, *E. superba* showed a strong preference for being positioned in the same plane as neighbours, at  $0^\circ$  elevation along the horizontal body axis, as illustrated in Fig. 14. O'Brien's (1989) study did not include incrementally increased current (swimming) speeds for *E. superba*, although he did induce higher swimming speeds for *Tasmanomysis oculata*, *Nictyphanes australis*, and *Teganymysis*, and observed that as speeds increased there was a tendency for each of these to shift preferred positions to  $\sim 30\text{--}60^\circ$  above and below neighbors, while *Teganymysis* also showed increased preference toward even axis positioning. Such a shift in position when swimming speeds rise, is similarly consistent with animals moving to optimal energy saving zones, preceding a phase change in collective dynamics.

### 17.4. Direction of collective flow

Although there appears to be no existing literature that describes krill formations specifically as convective processes, there are results within the literature that are consistent with convective processes. Using a dye plume to trace mysid directional movement in a holding tank, Ritz (2000) observed a collective clockwise rotation among the currents generated by the krill. Tarling and Thorpe (2014) modeled clockwise and counter-clockwise krill swarm rotations, relative to the background ocean water flow. These rotations produce approximate convection sinusoidal trajectories, an example of which is shown in Fig. 3. As discussed, we suggest these are signatures of energy saving mechanisms, representing large-scale or multi-agent versions of dyadic oscillations, similar to those observed in Northern Bald ibis flocks that exhibit dyadic oscillations (Voelkl et al., 2015), or to "two-up" positional alternations that are well known in the sport of cycling.

Tarling and Thorpe (2014) discussed the effects of hydrodynamic drag on krill speeds moving with background water flow and moving against background flow, and referred to the standard drag Eq. (3). The authors observed that when working against the background flow, krill speeds decreased with increasing background flow velocity. The authors suggested this means the krill are acting in some way either to reduce the drag force, or to work harder to maintain speeds.

**Table 5**  
Consolidation of Tables 1 and 2 from Nicol (1984), with the addition of variation percentages, and the result derived from data in Watkins (1994). We predict that the variation percentages approximately correspond to the percent energy saving obtained from the coupled energy saving mechanism. [Except for \*, citations are as found in Nicol (1984)].

Species	Size range (mm)	Range (%) (max-min/max; unless stated)	Source
<i>M. norvegica</i>	12–20	40	Patience (1909)
<i>M. norvegica</i>	21–29	27.5	McDonald (1927)
<i>M. norvegica</i>	28–31	9.67	Fish and Johnson (1937)
<i>M. norvegica</i>	11–22	40.9	Einarsson (1945)
<i>M. norvegica</i>	25–34	26.5	Cassanova-Soulier (1970)
<i>M. norvegica</i>	15–36	58.3	Aitken (1960)
<i>M. norvegica</i>	15–28	46.4	Cox (1975)
<i>M. norvegica</i>	25–35	28.6	Nicol (1984)*
<i>E. superba</i>		34.2 (range/mean)	Watkins (1994)*
<i>E. pacifica</i>	17–19	10.5	Odate (1979)
<i>E. pacifica</i>	12–22	13.6	Terazaki (1980)
<i>E. pacifica</i>	12–32	31.3	Endo (1981)
<i>E. kronii</i>	9–16	41.2	Baker (1970)
<i>T. raschii</i>	24–32	25.0	Zelickman (1961)
<i>Thysanoessa longicaudata</i>	11–16	31.3	Forsyth and Jones (1986)

In terms of increased energetic costs to krill at school leading edges where drag is higher relative to zones of reduced drag, there is some evidence of this in diel migrations. Diel migrations are 24-h cycles in which krill descend at dawn to depths in the hundreds of meters, and then ascend to the water surface at dusk, or sometimes vice versa (Tarling et al., 2001). Tarling et al. (2001) reported that northern krill (*M. Norvegica*) and pteropods (*Cavolina inflexa*) at the leading edge of a swarm during an ascending phase tend to travel more slowly relative to those at median depths. The authors suggested this may be a behavioral response that enables cohesive swarms.

Wiebe et al. (1992) also reported this effect for euphausiid swarms that consisted of a six euphausiid species. Heywood (1996) reported this effect for zooplankton, indicating a kind of compression effect among both the upward and downward direction swarms in which leading edge animals move more slowly relative to followers, thus maintaining higher group cohesion.

We suggest that this behavior is in fact what we would expect in the presence of an energy saving mechanism. For example, even for dead krill descending collectively through water at  $2.5 \text{ cm s}^{-1}$  (Kils, 1982) we would expect a sedimentation effect in which a “drafting, kissing, tumbling” process occurs repeatedly, as is demonstrated among inert spheres in fluid (Wang and Guo, 2014). However, the effect is exaggerated with increased speeds and, with an energy saving mechanism, we would expect a compression effect to occur in both directions, particularly when leaders are working nearer to maximum while followers exert relatively lower effort to sustain the speeds of leaders; i.e. leaders are effectively pushed backwards relative to followers, generating increased compression.

## 18. Summary

There are various mechanisms in biological systems by which the interactions of coupled organisms facilitate energy saving for at least one member of the coupled system. We have identified a few such mechanisms. Moreover, the occurrence of drafting in non-biological systems indicates the process is a basic physical one that represents a basin of attraction in the energetic landscape, consistent with thermodynamic principles and a tendency for systems to maximize entropy. All of these mechanisms provide the beneficiaries with varying magnitudes of energy saving, in terms of percentages, and the literature indicates these quantities range from ~7% to ~70%, with some exceptions. Broadly the size or mass variation ranges follow in remarkable accordance with values as predicted by the variation range hypothesis. See Table 6 for a summary.

We have identified certain fundamental dynamical processes that flow from the presence of energy saving mechanisms. One of these processes involves convective effects, characterized by high frequency and magnitude passing among organisms at sufficiently low collective outputs (Trenchard, 2015). Convective behavior self-organizes over short timescales in a variety of biological systems, including bicycle pelotons, bird flocks, fish schools, penguin huddles, krill, and bacteria. Over long time scales, convective behavior occurs in phyllotactic formations. The convective processes are a dynamical phase, and a property that may represent a class of systems.

When speeds increase above a critical threshold, but below a decoupling threshold, coupled organisms lock their positions and sustain the speeds of those ahead by exploiting the energy saving mechanism while being unable to pass others or share the most costly front positions. This is observed in pelotons, for example, when cyclists are proceeding at near maximal outputs. We propose that sperm agglomerations are examples of this process in nature, since sperm competitively advance at near maximal speeds, thereby locking in relative positions through the equalizing effect of an energy saving mechanism.

We propose that this position locking, which results from the high output phase in the presence of the energy saving mechanism, precedes sperm agglomerative behavior in its evolutionary lineage. This high output phase resides in the stressed region of the thermodynamic branch, as shown in Fig. 1. This phase is also indicative of a rigid state, as described by Csermely (2015), in which resources are strained due to maximal energy or resource consumption. By contrast, the convective phase exhibits higher degree plasticity (Csermely, 2015) due to its greater abundance of accessible energetic resources and fluidity.

In addition, we have adduced evidence for the variation range hypothesis, perhaps first proposed in by Makoto in 1970 in the specific case of fishes. Trenchard (2015) demonstrated by computer simulation that the variation range of cyclists in a peloton (group of cyclists) tends to converge on the equivalent percent energy saving when cyclists are driven to their near maximal speeds because decoupling between cyclists occurs and sub-groups form.

We propose this is a universal sorting principle that applies when collectives are driven to near maximal speeds. The principle is independent of the causes of these near maximal speeds, whether such speeds are, for example, a result of being chased by predators, a foraging effect, or a scaling effect in which collective strength diminishes from fatigue over long range migrations. We suggest that this group sorting process is an evolutionary principle that can lead to speciation; and, when repeated continuously over geologic time, the entire diversity of species emerges in which each species

**Table 6**  
Summary of approximate energy saving quantities and approximate variation ranges in coupled systems.

System	Energy saving mechanism	Indicated energy saving (% difference except where given as multiple)	Length range; Mass where noted (% difference except where given as multiple)	Pacesetter equivalence	Reference
Non-biological					
Particles in optical vortice	hydrodynamic drafting	15		leading particle	Grujic and Helleso (2007)
Particles in chain	hydrodynamic drafting	50		leading particle	Šiler et al. (2012)
Biological					
Bacteria <i>Bacillus subtilis</i>	transverse vortices	five-fold	up to ten-fold	front position	Cisneros et al. (2007); Trueba and Woldringh (1980)
Cyclists	aerodynamic drafting	39	36	front position	McCole et al. (1990)
Caribou	trail breaking	40			Mattfeld (1973)
Dolphins	Bernoulli suction; hydrodynamic drafting	up to 90 (neonates) ; 20-28 (older infants)		mother	Noren et al. (2008); Weihs (2004)
Ducklings on water	hydrodynamic drafting	7.8–62.8	16.5 (wing length, juveniles and adults) 9.3 (body-length, juveniles and adults)	decoy (mother)	Fish (1994); Owen and Montgomery (1978)
Eels (European)	undulatory synchronization	30	34; 29–44	parallel motion	Burgerhout et al. (2013); Vøllestad (1992)
Fishes (general)			~30	front position	Pitcher and Parrish (1993)
Fishes (horse mackerel)	hydrodynamic drafting; Karman gait	15–29		front position	Zuyev and Belyayev (1970)
Fishes (Grey mullet)	hydrodynamic drafting; Karman gait	28.5 8.8–19.4	29.7	front position	Marras et al. (2015) Koutrakis et al. (1994) [see Table 1 for further quantities]
Fishes (Roach)	hydrodynamic drafting; Karman gait	7.3 11.9 11.6	7–14 17–41(mass)	front position	Svendsen et al. (2003)
Fishes (Sea bass)	hydrodynamic drafting; Karman gait	9–14 9–23		front position	Herskin and Steffensen (1998)
Fishes (Euro. Minnow)	hydrodynamic drafting; Karman gait		39.5	front position	Ward and Krause (2001)
Krill ( <i>E. Superba</i> )	hydrodynamic uplift	up to seven-fold	34	front position	Ritz (2000); Watkins et al. (1992) [see Table 5 for further quantities]
Locusts	wing-beat coupling	16		front position	Camhi et al. (1995)
Northern bald ibis	vortice upwash			front position	Voelkl et al. (2015)
Geese (Canada)	vortice upwash	36		front position	Hainsworth (1987)
Geese (Canada) simulation	vortice upwash	16		front position	Maeng et al. (2013)
Geese (Pink-footed)	vortice upwash	14		front position	Cutts and Speakman (1994)
Pelicans (Brown)	vortice upwash (ground effect)	49		front position	Hainsworth (1988)
Pelicans (white)	vortice upwash	11.4–14		front position	Weimerskirch et al. (2001)
Penguins (Emperor)	huddling	51		birds peripherally exposed to wind	Gilbert et al. (2008) [see Gilbert et al. (2010) for review of huddling systems]
Spermatozoa (Bull)	flagellar synchronization	32		front position	Woolley et al. (2009)
Spermatozoa (Zebra finch)			27	front position	Birkhead and Fletcher (1995) [see Table 4 for further species]
Spiny lobsters	queue formation	65	45	front position	Bill and Herrnkind (1976); Kanciruk and Herrnkind (1978)
			54		
			57		
			54		
			52		
Turtle hatchlings	granular fluid drafting	71	53	front position	Rusli and Booth (2016); Kolbe and Janzen (2002)
			55		
			64 (mass)		



exhibits its own unique maximal strength variation range, usually in the form of size or mass, that corresponds proportionately to the available energy saving quantity.

We have provided some evidence of a correlation between the size ranges of a variety of species and the energy saved by coupling. This assumes that size, in terms of body-length or mass, correlates with strength, as the evidence bears out. We have modelled the circumstance in which the size of the group modulates the variation range, because weaker individuals may decelerate relative to others and remain within the system boundaries and within proximity of energy saving zones. Thus if the mean group speed falls, weaker individuals have opportunities to remain within the group. It is not clear how much the size of the system (flock, school, etc.) affects the variation range.

One implication of the variation range hypothesis is that when nascent offspring are too weak to fall within the variation range, mothers and/or conspecifics must invest increased marginal energy sufficient to ensure offspring survive *until* the offspring's physiological capacity reaches the lower boundary of the variation range. Similarly, in other circumstances, weak young must grow in relatively sedentary conditions for some extended period so as to grow to the minimum boundary of the variation range in order to undertake high cost migrations. Once offspring grow to achieve this minimum physiological capacity, they capably sustain the pace set by stronger members of the collective without further conspecific investment. This has implications for increased understanding of the timing of migratory patterns.

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