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动物行为中的流体力学及其对人造系统的启示

张逸凡,李 博*

(武汉大学 高等研究院,湖北 武汉 430072)

摘要: 流体是动物适应和进化重要的生态位,因此在多尺度上深刻影响生物个体行为与群体组织形式。从个体层面的飞行与游动,到群体层面的协同行为与集群运动,生态系统中的多种现象均受到流体动力学机制的调控。尽管这些过程涉及不同物种与尺度,其基本行为同样可在连续介质框架下,由质量、动量与能量守恒统一描述,并受惯性与黏性相互作用的约束,从而表现出一定的动力学共性。从统一的流体力学视角出发,围绕动物个体与群体两个层级,对流体与生物行为相互作用的进展进行系统综述,重点关注运动产生的流场结构、流体介导的信息与能量传递,以及由此引发的群体协同与自组织现象。这些流体动力学进展揭示了生态系统中行为调控与结构形成的物理基础,并为工程编队设计与多尺度流动建模提供了理论基础。

关键词: 流体动力学;动物行为;跨尺度普适性;无量纲参数;仿生设计

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Fluid mechanics in animal behaviour and its implications for artificial systems

ZHANG Yifan, LI Bo*

(The Institute for Advanced Studies, Wuhan University, Wuhan 430072, Hubei, China)

Abstract: Fluids constitute a critical ecological niche for animal adaptation and evolution, thereby profoundly influencing individual behavior and collective organization across multiple scales. From flight and swimming at the individual level to coordinated behaviors and collective motion at the group level, a wide range of phenomena in ecosystems are regulated by fluid dynamical mechanisms. Although these processes involve different species and scales, their fundamental behaviors can be uniformly described within a continuum framework by the conservation laws of mass, momentum, and energy, and are constrained by the interplay between inertia and viscosity, thus exhibiting certain dynamical commonalities. From a unified fluid dynamics perspective, this paper provides a systematic review of recent advances in the interactions between fluids and biological behaviors at both the individual and collective levels, with a focus on flow structures generated by locomotion, fluid-mediated information and energy transfer, and the resulting collective coordination and self-organization phenomena. These fluid dynamical insights reveal the physical basis underlying behavioral regulation and structural formation in ecosystems, and offer theoretical foundations for engineering formation design and multiscale flow modeling.

Key words: fluid dynamics; animal behavior; cross-scale universality; dimensionless parameters; biomimicry design

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作者简介: 张逸凡(2001-),女,硕士生,研究方向为流体力学,E-mail: lilablsmp@163.com

* 通信作者: 李博(1990-),男,博士,教授,主要从事生命系统和材料物理交叉学科研究工作,E-mail: libo@whu.edu.cn

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0 引言

生态学研究生物与环境相互作用,生态位反映生物对资源利用与行为方式。对飞行与游动物而言,空气与水可视为连续介质下的流体环境,其流场影响运动与能量消耗。动物通过附肢运动与流体相互作用并加以调节,因此,动物行为可在一定程度上理解为对流场结构的适应与反馈。

1 飞行与游动的动力学相似规律

飞行与游动中不同尺度动力学行为具有相似性,如鱼类与鸟类在涡脱落节律与动量输运上可比,其推进源于附肢运动驱动的动量与压差^[1],并伴随前缘涡(leading-edge vortex, LEV)与涡-结构耦合等效应^[2]。生态系统流体现象可通过无量纲参数统一描述。雷诺数可分解为表征流动强度与动力学特征的流速 u ,以及雷诺数扣除流速后得到的组合项 $\rho d/\mu$,其整合了流动尺度与介质性质,并将生物运动映射至统一参数空间,如图1所示,多类生物及人造推进器多处于惯性主导区间,表现出相似涡脱落与动量输运特征。这种相似性可由纳维-斯托克斯方程无量纲化框架解释,使不同系统在一定参数范围内呈现可比流动特征^[3]。其中,雷诺数可以反映惯性与黏性的相对作用^[4];同时,鱼类与鸟类在巡航状态下的斯特劳哈尔数多集中于0.2~0.4,有相近

脱落节律^[5]。此外,涡形成时间可用于描述附着涡由增长趋于饱和并接近脱落的过程,其对尺度与流动条件的依赖相对较弱^[6]。由此,这些现象在一定程度上可理解为相近动力学参数条件下的表现。

在上述视角下,本文从飞行与游动两类运动出发,分别在个体与群体尺度上进行综述:个体尺度涉及不同运动方式及其流动结构特征,群体尺度则关注编队与尾流相互作用。在此基础上,讨论动物行为对人造系统的可能启示,经典工程流体问题不在本文范围内。

2 动物个体的流体动力学

在生态流体系统中,个体运动为基本动力单元,关键在于其与流体耦合及对局部涡结构的调控。涡结构参与动量与能量输运,并关联推进、升力与姿态控制,因此鸟类飞行与鱼类游动可视为不同介质中相似机制的体现。

2.1 鸟类个体飞行

鸟类个体飞行研究可以大致分为流场分析、生物体形态以及运动模式3个部分,如图2(a)所示。相关研究主要从流场结构演化、形态结构与运动调控3方面展开,探究鸟类飞行的流体动力学特征及动物如何通过飞行器官结构进化和运动模式调整有效利用流场,提升飞行效率。

在飞行过程中流场研究方面,涡结构是一类重

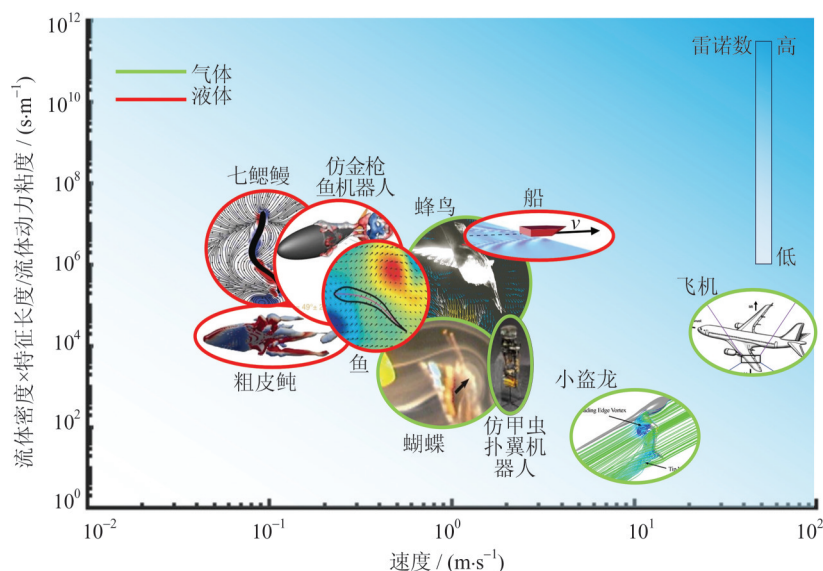


图1 不同生态学环境所匹配的雷诺数条件

Figure 1 Reynolds number conditions matched by different ecological environments

注:横轴为 u (m/s),纵轴为 $\rho d/\mu$ (s/m)。颜色条代表雷诺数的大小。不同生态学环境分别为七鳃鳗^[7]、鱼类^[8]、蝴蝶^[9]、蜂鸟^[10]、小盗龙^[11]、仿金枪鱼机器人^[12]、粗皮鲀^[13]、仿甲虫扑翼机器人^[14]、飞机^[15]、船舶^[16]。

Note: x-axis, u (m/s); y-axis, $\rho d/\mu$ (s/m). The color bar represents the magnitude of the Reynolds number. Different ecological cases: lamprey^[7], fish^[8], butterfly^[9], hummingbird^[10], *Microraptor*^[11], tuna-like robot^[12], *Rudarius ercodes*^[13], beetle flapping-like robot^[14], airplane^[15], ship^[16].

要的议题。在扑翼飞行中,涡会在有限时间内发展并周期性脱落^[6],不同飞行阶段对应不同涡结构分布特征^[17]。尽管不同物种在翼形态与运动模式上存在差异,但其LEV与翼尖涡的耦合仍构成涡结构的常见形式。例如,LEV沿翼展方向的延展与连接是维持气动升力连续的关键,如图2(a)的气流相互作用部分所示,蝴蝶的LEV可从翼根延伸至翼尖并与翼尖涡相连^[9];而在某些情况下,LEV会呈现锥形分布,这种形态有助于增强涡的稳定性,雨燕便是典型代表^[18];此外,LEV的贡献还表现出明显的阶段性,下拍阶段往往是涡升力的主要产生期,蜂鸟即依靠强下拍涡结构来支撑其悬停飞行^[10]。综合来看,不同飞行动物的LEV虽形态各异,但在空间延展、稳定性调节和相位贡献上仍存在可归纳的共性特征。相关研究还涉及效率调节^[19]、气味输运^[20]及环境流动利用^[21]。除涡结构外,涉及翼尖涡诱导下洗主导的垂向动量输运以及分离泡等局部流动现象^[18];鸟类滑翔过程中边界层可能发生层流-转捩变化,下洗流通过改变有效迎角与压力分布影响诱导阻力^[21]。另一类研究将重点放在生物体结构上,探究这些因素作为边界条件影响流动过程,优化飞行效率。如图2(a)的躯体构型部分所示,小翼羽与LEV稳定相关^[22],果蝇翅膀后缘与气味输运能力相关^[20]。整体结构中,羽毛开闭影响气动过程^[23],刚毛翅降低惯性与能耗^[24],展弦比与翼载荷对应不同飞行模式与速度范围^[25],翼形差异与效率及环境条件相关^[26]。第三类研究重点聚焦运动方式影响流动状态,多翼系统中前后翼相互作用影响局部流动^[11],不同姿态对应不同升阻分布,如图2(a)的飞行动作部分所示,小盗龙在不同姿态下表现出差异^[27]。进一步而言,参数调节对应不同功能取向,例如,熊蜂飞行中翅膀的振幅变化^[28]与果蝇感知行为差异^[20]。同时,能量利用方式也随涡结构的生成与脱落而被重构^[29]。此外,飞行过程中升力与阻力可随运动方向与姿态变化发生转换^[30],多部位协同运动与升力维持相关^[31],同时,非对称拍动对应净升力产生^[32],并与环境流动条件共同影响飞行策略^[21]。

2.2 鱼类个体游动

鱼类游动研究可大致分为流场分析、生物体形态、运动模式以及水面生物运动4个部分,如图2(b)所示。相关研究主要从外部流动结构演化、边界层与分离流动特征,以及周期性运动所引发的非定常输运机制展开,探究鱼类如何通过对流场环境的感知与调控,在不同尺度上优化阻力与推进效率。

流场分析方面的研究显示,鱼类游动涉及各类

复流场结构(层流、涡流、湍流等)间的平衡和转化。鱼体尾部会形成尾迹涡并诱导轴向高速射流,其强度决定推力,也可被感知用于定位与追踪^[33]。同时,还存在分离与再附着等局部现象,如鳃后、鳍根或胸鳍大攻角运动下形成的层流分离泡,可在较低阻力代价下维持附着流动并增强升力^[34]。在流动利用策略上,如图2(b)的流场相互作用部分所示,鱼可选择相邻涡间低耗能区并通过微小姿态调整实现推进^[8],推进亦可在摆动生成与滑行利用之间切换^[35]。生物体形态方面,鱼体通过粘液与盾鳞维持较稳定边界层,延缓转捩,降低阻力,并抑制噪声,有利于侧线感知;流线型体型亦有助于抑制边界层分离^[36]。局部结构上,胸鳍刚柔差异改变涡生成与脱落,如图2(b)的躯体构型部分所示,通过刚度与姿态调节兼顾升力与阻力,提升操控稳定性^[37];尾鳍闭合与张开分别对应低阻加速与尾流增强两种模式^[13]。多鳍通过耦合变形形成连续流场调节以维持稳定^[38],悬停则依赖持续鳍调节^[39]。运动模式方面,周期性身体变形驱动整体流场演化,如图2(b)的游动动作部分所示,前后反相弯曲在多尺度上组织流动结构以实现高效推进^[40];连续变形可在体表建立低压区形成吸力推进^[7],不同参数对应不同效率与流动分布。水面生物运动方面,以水黽为例,其运动依赖表面张力与界面动量交换,如图2(b)的气-液界面部分所示,双极涡承担主要动量传递,使动量向后释放并推动身体前进^[41],体现界面效应与流动结构的共同作用^[42]。低雷诺数下的浮游生物运动方面,不同鞭毛构型会直接改变游动效率,形成专属摄食流场,辅助猎物沿顶丝完成转运^[43]。

2.3 仿生单体运动

在人造流动系统内,空气中主要分为传统设计,结构设计与材料设计3部分,如图2(c)所示;水中主要分为航船,潜艇,水下仿生体与水面仿生体4部分,如图2(d)所示。相关研究从流动结构演化、边界层与分离特性及界面耦合输运展开,探究通过结构设计与主动控制实现流场调制以提高升力、减阻与推进效率。

首先,在空气动力学系统中,鸟类与飞行器在不同尺度上呈现出高度一致的流体结构控制逻辑。在经典飞机设计中,如图2(c)的传统设计部分所示,大迎角条件下机翼前缘分离形成稳定LEV,并通过涡诱导低压增强升力^[44]。同时,通过结构设计实现剪切层与分离点的被动稳定化,如图2(c)的结构仿生部分所示,受鸟类覆羽启发的多排被动襟翼可实现分离点后移并扩大稳定附着流范围^[45]。在小尺度飞

行器中,通过诱导前缘局部分离并快速再附着,可降低升力波动并增强抗扰动能力^[46]。随着控制尺度进一步向边界层与瞬态流动细节推进,仿生设计不仅用于结构与动态优化拓展^[14],材料仿生也开始介入流动调控过程,在跨音速条件下,如图2(c)的材料仿生部分所示,多孔后缘结构通过引入动量交换改变尾流与边界层状态,从而间接稳定激波位置^[15]。

此外在水环境系统中,水面与水下人造器械的运动由流体结构与界面效应共同控制。在水面船舶中,剪切流与有限水深显著影响波阻及临界速度^[16]。图2(d)的船部分可见船首波与反射波之间的抵消机制^[47]。潜航器则以三维涡结构为主,如图2(d)的潜艇部分所示,斜航产生的非对称尾涡增强^[48];此外,自由面约束进一步导致尾流吸附与变形^[49]。工程上发展为几何优化与主动控制双路径,并逐步走向仿生与智能闭环调控^[50]。在仿生推进中,水下机器鱼可通过尾部集中摆动^[51]与刚度进行调控^[52]。进一步延伸到自由界面系统,如图2(d)的水面仿生部分所示,水电机器人依赖超疏水结构与表面张力实现低阻支撑^[53]。当界面作用作为动态运动调控机制

时,水面运动还表现出多样化特征,可以通过弹跳-滑翔等多模式实现界面驱动运动^[54]。在低雷诺数下的浮游生物仿生系统中,通过借鉴幼虫纤毛结构,开发出超声驱动的仿生纤毛带微机器人系统,可实现流体驱动、微粒捕获与微尺度推进^[55]。

3 动物群体的流体动力学

进入群体尺度后,多体共享流场中的相互作用与协同组织逐渐主导系统演化。尾流持续影响后续个体,使群体处于动态重构的共同流场中,个体间通过流体结构形成耦合,从而使群体流体动力学呈现尾流主导的相互作用特征,并表现为耦合反馈驱动的集体现象。

3.1 鸟类群体飞行

鸟类群体飞行研究可大致分为群体编队结构、局部流动感知及大尺度迁徙三个部分,如图3(a)所示。相关研究从群体构型与流动耦合、局部流场响应及环境流动引导展开,探究鸟类通过空间组织调节实现能量优化与迁徙效率提升。

鸟类群体中经典的V形与斜列编队揭示了群体

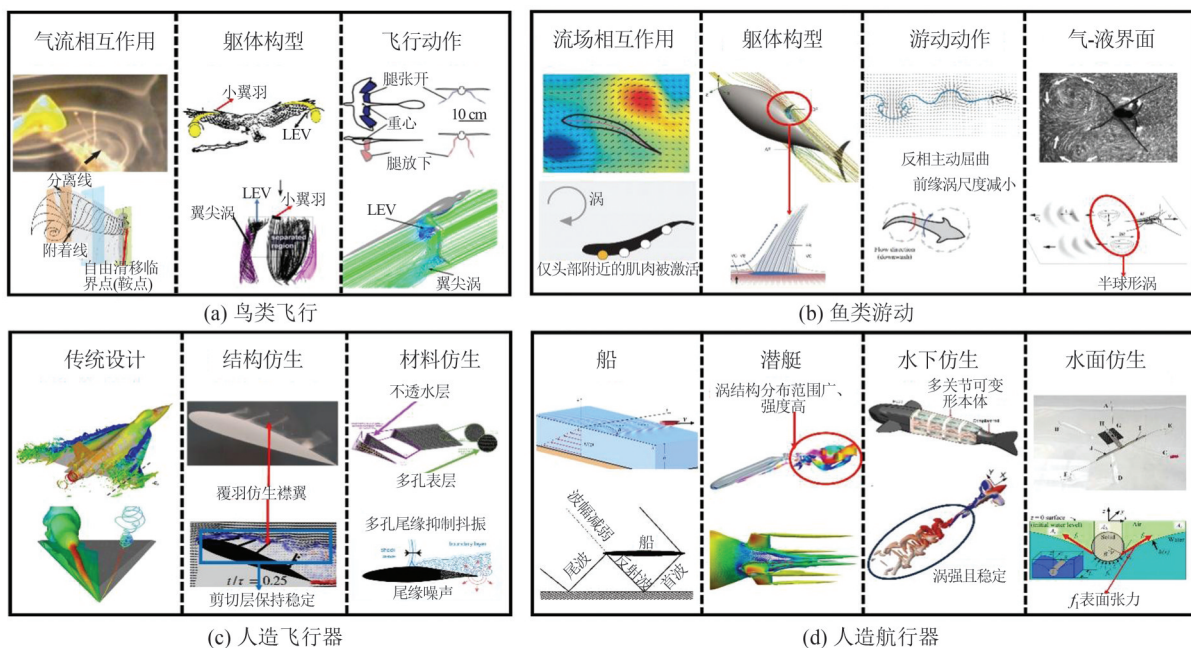


图2 动物个体的流体动力学

Figure 2 Fluid dynamics of individual animals

注:(a)鸟类飞行(旋涡调控个体升力^[9],机翼调节流场^[22],飞行姿态调控远航性能^[11,27]);(b)鱼类游动(节约漩涡能耗^[8],躯体构型调控稳定性^[37],运动模式调控能耗^[40],界面涡推进^[41]);(c)人造飞行器(LEV影响性能^[44],剪切层稳定机制^[45],材料构型调控抖振^[15]);(d)人造航海器(波动叠加效应^[16,47],非对称流动推进性能^[48-49],多关节结构调控推力^[51],表面张力稳定漂浮^[53])。

Note: (a) Avian flight (vortex modulation of individual lift^[9], wing modulation of flow^[22], flight posture modulation of cruising performance^[11,27]); (b) fish swimming (vortex energy saving^[8], body configuration modulation of stability^[37], motion modulation of power consumption^[40], interface-vortex propulsion^[41]); (c) artificial aircraft (LEV affecting performance^[44], shear-layer stabilization^[45], material configuration modulation of buffeting^[15]); (d) artificial vehicle (wave superposition effects^[16,47], asymmetric-flow propulsion^[48-49], multi-joint structure modulation of thrust^[51], surface tension-stabilized floating^[53]).

构型与翼尖涡结构之间的耦合关系,如图3(a)的集群队形部分所示,前鸟翼尖产生的反向旋涡对形成上升/下降交替区域,后鸟占据上升区获得额外升力^[56]。而不同群体构型能量收益存在差异,如鸽群等密集无规则编队中,个体需提高拍翅频率以维持飞行并避免碰撞^[57]。大规模群体中可能因相位耦合出现流动波动放大现象,影响编队稳定性^[58]。因此,鸟类群体构型与流体相互作用之间存在一定耦合关系。此外,流体结构影响个体位置的选择,如图3(a)的流场结构部分所示,在侧后方省力位,后鸟与前鸟同相拍翅以利用上升流增压;正后方则通过反相拍翅避开下降流以减阻^[59]。在大尺度环境流动中,如白鹤利用热气流时,领飞个体锁定上升流核心区,跟飞个体停留于高上升区附近^[60]。在更大的迁徙尺度上,如图3(a)的迁徙运动部分所示,候鸟路径与季风风场一致,因海洋通道风场更稳定,沿海成为最优迁徙路线^[61]。

3.2 鱼类群体游动

鱼类群体游动研究可大致分为群体编队结构、局部流场重构以及扰动条件下的群体组织与状态转变3个部分,如图3(b)所示。相关研究从群体构型与流动耦合、局部流场响应及扰动驱动重组展开,探究鱼类通过阵型与行为调控实现能量优化与稳定适应。

规则阵型可通过尾流结构获得水动力收益,如图3(b)的集群队形部分所示,菱形或交错编队中后续个体位于前方尾流有利区,实现减阻增效^[62],同时涡锁定与尾流相干结构约束下,自由系统可自发形成半纵列等稳定阵型^[63]。此外,鱼群结构呈状态依赖特征,如低速菱形与高速方阵切换^[64],并受流速、规模及行为参数调制^[65]。

局部流场结构重构可影响系统整体稳定性与行为,如图3(b)的流场结构部分所示,涡诱导流重定向局部受力,使得并列阵可以稳定^[66];也可延伸至行为层面,如帆鱼通过涡破裂与声学单极子实现猎物围困^[67]。从结构生成机制来看,鱼群组织主要受相位调控主导^[68],并受时间调制与环境耦合影响^[69]。此外,由尾流相位匹配主导^[70],近场减耗,远场累积节能^[71],同时,多体相互作用^[72]与压力分布共同约束能量收益上限^[73]。出现外部扰动后,鱼类可以通过感知圈-安全圈实现群体组织与状态切换,形成如图3(b)的外部扰动部分所示的喷泉式分裂、磨坊球等结构^[74],并受流速与规模影响^[75];此外,也可以通过涡结构重构限制群体运动^[67],共同构成非平衡动力

过程。

3.3 仿生群体运动

仿生群体的研究可大致分为飞行器、无人水面航行器(unmanned surface vehicle, USV)、自主水下航行器(autonomous underwater vehicle, AUV)以及流体执行器4个部分,如图3(c)所示。相关研究从尾流升力与稳定性、多体协同控制及尾流引导与能量优化展开,探究编队系统的高效推进与协同调控机制。

飞行器系统的研发关键在于获取升力增益的同时抑制尾流诱导的不稳定性,如图3(c)的飞行器部分所示,僚机在长机尾流中的受益位置为侧向偏移至特定阈值后进入的上洗区域^[76],马蹄涡使最优气动位置兼具高性能与稳定性。同时,通过引入局部速度对齐与制动机制可实现稳定编队^[77]。在无人水面航行器系统中,如图3(c)的水面航行器部分所示,编队通过可视、速度匹配与避碰聚集约束形成感知协同,实现无人船在复杂水流中的稳定跟随^[78]。同时,此系统可以进一步扩展为多平台协同,通过自主导航在复杂流场中执行任务并维持整体协同状态^[79]。在自主水下航行器系统中,如图3(c)的水下航行器部分所示,前体产生的低压涡尾流会对后体形成明显的吸引与偏转作用^[80],同时通过对接方向与涡旋相位匹配,使个体持续处于有利流场位置,实现节能^[81]。在流体执行器系统中,群体纤毛通过可编程协同运动产生流场叠加与干涉的复合效应,可在低雷诺数环境下构建多样化流场拓扑,实现微流体的精准操控^[82]。

4 总结与展望

在生态系统中,流体力学通过个体与群体两个层面体现普适性。个体尺度上,鱼类和鸟类运动与流体相互作用紧密,推进过程伴随流场的扰动与调控,其效率取决于局部流场利用方式;群体尺度上,个体尾流形成共享流场,使空间分布与运动协调呈现流体耦合下的集体动力学特征。工程与应用中,上述机制进一步被抽象为可设计的控制策略,涵盖飞行器编队、水面无人系统以及水下航行器网络等方向,通过局部流场调控和大尺度通讯的平衡,实现稳定性与能效之间的优化。

动物行为的复杂性和流体的混沌特征是阻碍生态学中流体研究从物理现象观测和应用数学描述到可预测、可应用的设计规律的主要原因。未来应将经典流体动力学研究和人工智能及动物生理深入结

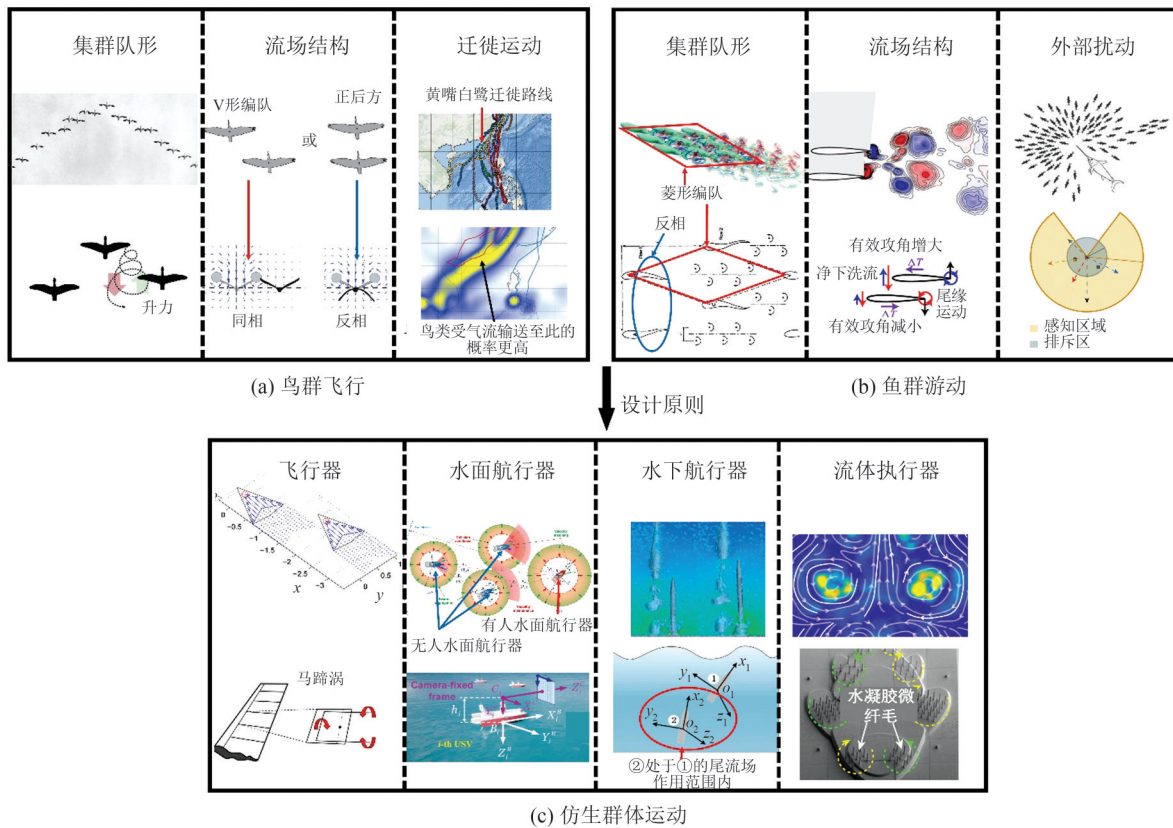


图3 动物群体的流体动力

Figure 3 Fluid dynamics of animal groups

注:(a)鸟群飞行(队形影响能耗^[56],结构影响阻力^[59],风场影响路径^[61]);(b)鱼群游动(队形节能^[62,83],流场结构调控生物位置^[66],应急行为转变^[74,84]);(c)仿生群体运动(前体调控后体性能^[76],USV对有人水面航行器的跟随及USV可视聚集行为^[78],AUV的尾流扰动轨迹^[80],集体运动影响流场^[82]).

Note: (a) Avian collective flight (formation affects energy use^[56], flow affects drag^[59], wind field shapes paths^[61]); (b) fish schooling swimming (formation energy saving^[62,83], flow structure modulation of biological position^[66], emergency behavior shift^[74,84]); (c) biomimetic group motion (forebody influence of afterbody performance^[76], USV following manned surface vehicle and visible collective behavior of USVs^[78], wake-disturbed trajectories of AUV^[80], collective motion influences the flow field^[82]).

合。前者可以依托流体理论挖掘航行器、飞行器设计规律,并结合深度学习解析流场涡演化特征,确定最优流动控制策略^[85];后者可以从基础科学层面更深刻地理解动物适应流体环境的生物学机制,例如,依托昆虫本体感知原理研发生物驱动控制方法,结合翼面传感数据与流体仿真解析自适应飞行机理,以此连接流场建模与仿生设计^[86]。

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