

REVIEW

Cool your jets: biological jet propulsion in marine invertebrates

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ABSTRACT

Pulsatile jet propulsion is a common swimming mode used by a diverse array of aquatic taxa from chordates to cnidarians. This mode of locomotion has interested both biologists and engineers for over a century. A central issue to understanding the important features of jet-propelling animals is to determine how the animal interacts with the surrounding fluid. Much of our knowledge of aquatic jet propulsion has come from simple theoretical approximations of both propulsive and resistive forces. Although these models and basic kinematic measurements have contributed greatly, they alone cannot provide the detailed information needed for a comprehensive, mechanistic overview of how jet propulsion functions across multiple taxa, size scales and through development. However, more recently, novel experimental tools such as high-speed 2D and 3D particle image velocimetry have permitted detailed quantification of the fluid dynamics of aquatic jet propulsion. Here, we provide a comparative analysis of a variety of parameters such as efficiency, kinematics and jet parameters, and review how they can aid our understanding of the principles of aquatic jet propulsion. Research on disparate taxa allows comparison of the similarities and differences between them and contributes to a more robust understanding of aquatic jet propulsion.

KEY WORDS: Squid, Jellyfish, Salps, Swimming efficiency, Pulsed jets, Particle image velocimetry

Introduction

Animal locomotion and the impact of the fluid environment on the evolution of body forms in swimming animals has long been a focus of evolutionary and functional biologists (e.g. Thompson, 1961; Vogel, 2013) and, more recently, to those within the field of engineering who work on ‘bio-inspired’ designs and focus on marine invertebrate animals (e.g. Villanueva et al., 2011; Gu and Guo, 2017; Tang et al., 2020). Pulsatile jet propulsion, the focus of this Review, is a common swimming mode employed by a number of distantly related marine taxa (Fig. 1).

Many of these animals have relatively simple shapes and swim using few propulsive structures (i.e. control surfaces; see Glossary) for locomotion. This has allowed for basic theoretical models of both propulsive and resistive forces to be developed. In contrast, animals that swim with predominantly oscillating appendages, such as fins, exhibit more complex motions and generate more complex

fluid patterns, which make the analyses of resistive forces, such as drag, more difficult (Daniel, 1983). An additional consideration that makes jet-propelled animals an attractive target for investigation is the fact that a pulsed jet can result in greater average thrust than a steady jet of the same mass flow rate (see Glossary) (Siekmann, 1963; Weihs, 1977; Mohseni et al., 2002; Krueger and Gharib, 2003, 2005). However, to gain a robust understanding of aquatic jet propulsion, it is imperative to consider the wide array of morphological and taxonomic diversity present among jetting swimmers (Fig. 1). This is a significant challenge because there have been few attempts at approaching locomotion questions from a comparative framework. Thus, the primary objective of this Review is to summarize the current state of the literature for the major taxonomic groups of jet-propelled swimmers and identify similarities and differences between these groups. By providing this information along with a historical context of experimental and modeling approaches, we aim to better facilitate comparative analyses to aid our understanding of the principles of aquatic jet propulsion.

Measuring and modeling biological jet propulsion

Two challenges common to almost all biological propulsion in fluids are that the surrounding medium is transparent and the ‘footprints’ of the organism are transient. The former can be addressed by introducing tracers, e.g. fluorescent dye (Shorten et al., 2005), giving clear visualizations of the impact of the animal on the surrounding fluid (Fig. 2). The advent of high-speed videography and quantitative visualization tools, such as 2D (Bartol et al., 2009a) and 3D (Gemmell et al., 2015b) particle image velocimetry (PIV; see Glossary), has addressed the latter challenge, enabling wake dynamics to be captured in high spatiotemporal resolution (Fig. 2; Box 1).

As more jet-propelled taxa have been studied, it has become clear that the generic term ‘jet propulsion’ belies a variety of propulsion modes much greater than that traditionally associated with engineered systems, where the thrust from conventional jet propulsion is idealized as a steady stream of excess rearward momentum. Indeed, some jetters (i.e. certain pelagic tunicates) create a nearly persistent, rearward efflux of fluid reminiscent of the exhaust from a rocket or jet engine (Bone, 1998). This can be modeled based on direct measurements of the jet speed relative to the background flow and the jet cross-sectional area. Daniel (1983) derived a kinematic model that eliminated the need to directly measure the flow and that has proved effective in describing the swimming of jet-propelled swimmers whose wakes resemble the steady rearward stream implicit in the thrust model (Dabiri and Gharib, 2003).

However, a more common occurrence is the periodic ejection of pulses of fluid, each of which forms a toroidal ring of fluid, such as a vortex ring (see Glossary) or tails of vorticity, in the animal’s wake. Organisms that produce the jet in a series of pulsed vortex rings have been observed to generate thrust exceeding that predicted by a steady flow model. The thrust enhancement has been attributed to the vortex formation process and two associated phenomena. The first is a transient increase in pressure behind the animal as the jet is initiated.

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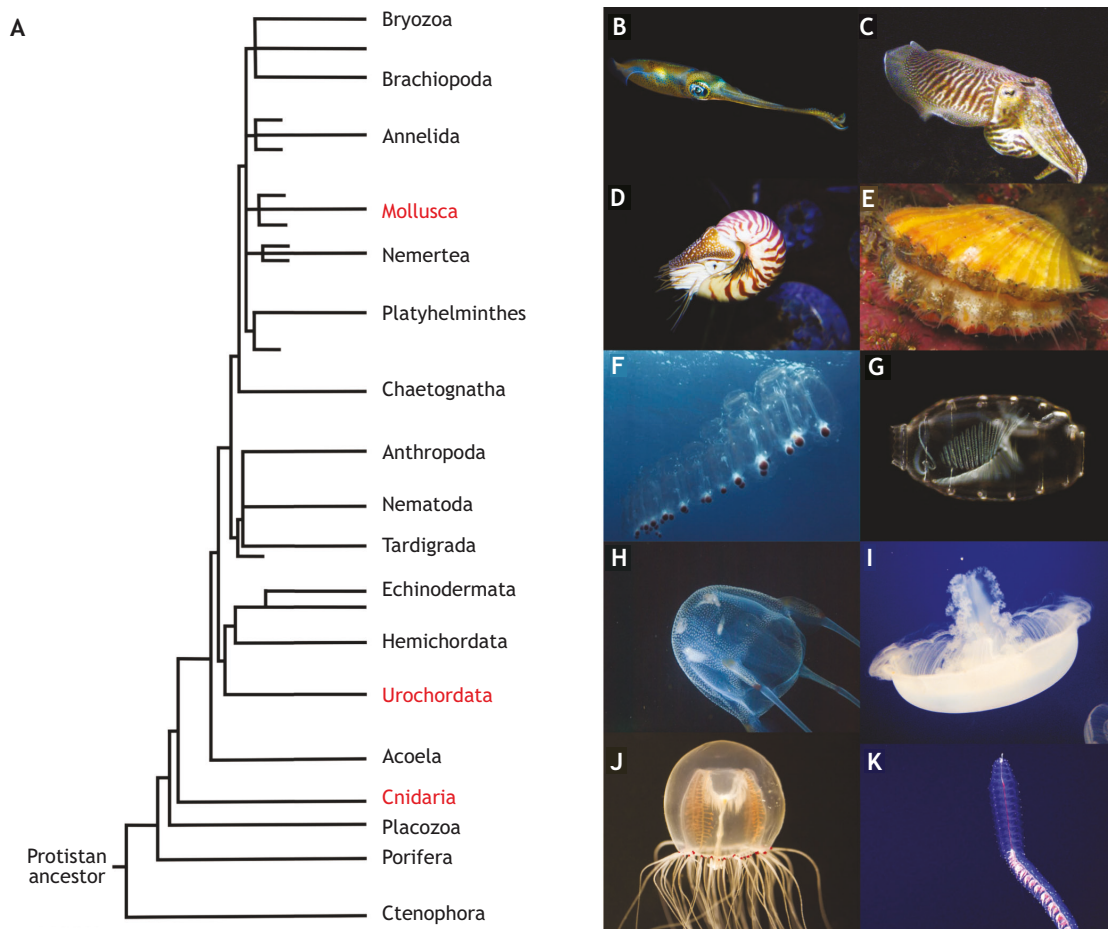


Fig. 1. Distribution of jet propulsion within the animal kingdom. (A) Three major phyla (highlighted in red) possess jet propelled swimmers. The topology has been broadly adapted from Laumer et al. (2019), with unlabeled limbs representing minor taxa. (B–E) Jet-propelled molluscs include (B) squid, (C) cuttlefish, (D) nautilus and (E) scallop bivalves. (F–K) Urochordate jetters include (F) salps and (G) doliolids. Jet propulsion is widely employed by cnidarians, including (H) cubomedusae, (I) scyphomedusae, (J) solitary hydromedusae and (K) colonial siphonophores. Images in B–K were obtained through Creative Commons Licensing (CC-BY) and image credits in the order presented are as follows: Francois Libert, Brent Moore, Desirae, Dan Hershman, Kelly Sutherland, Richard Kirby, Seascapeza, Jim G, Nathan Rupert and NOAA Photo Library.

In mechanical models, this ‘overpressure’ has been found to increase thrust by almost 30% relative to a steady jet (Krueger and Gharib, 2003). Second, the vortex rings formed in the wake can interact (Dabiri et al., 2005), modifying the local pressure field encountered by the animal and the resulting thrust (Gemmell et al., 2021).

Models that explicitly incorporate vortex ring formation are necessarily more complex and are often incompatible with simple equations relating the animal’s kinematics to the resulting locomotive forces [for a more in-depth description and example, see Dabiri et al. (2006), equation 11]. However, the inclusion of vortex dynamics does enable pulsatile jet-propelled swimmers to be modeled as accurately as their simpler steady-jet counterparts.

In the past decade, advances in both experimental and computational tools have facilitated studies of biological jet propulsion that are not limited to a focus on wake dynamics (Box 1). PIV has been especially valuable in these efforts, as the pressure field can be inferred from the measured velocity field using readily available software tools (Dabiri et al., 2014). This ability to resolve fluid as it interacts directly with animals’ bodies can help to alleviate many previously identified problems (Schultz and Webb, 2002), where estimates of efficiency and separation of thrust and drag are problematic for many types of swimmers (see also Box 2). Ongoing efforts to expand the utility of these techniques from 2D to

3D flows would enable the study of jet propulsion in animals with more complex morphologies, such as siphonophores and other colonial jetters (see Box 1).

Concurrent with these experimental breakthroughs has been a dramatic increase in computational power, which enables the simulation of 3D self-propelled analogs to the real swimmers (Box 1). These numerical simulations are a powerful complement to empirical investigations, as they provide controlled tests of swimmer designs found in nature and of those that are not extant (Mohseni, 2006; Sahin et al., 2009). Finally, these techniques have now evolved to a stage in which muscle contraction can be directly represented in the computational models (Hoover et al., 2019). This presents new opportunities to understand the evolutionary constraints encountered by primitive but extant jet-propelled swimmers and to inform the design of actuators for bioinspired robots that use jet propulsion.

Pulsatile jet-propelled swimmers

Chordates: one-way flow in single or multi-jet form

Pelagic tunicates (phylum: Chordata; subphylum: Tunicata; class: Thaliacea) comprise 72 described species and include salps, doliolids and pyrosomes (Govindarajan et al., 2011). Salps are barrel shaped with incurrent (oral) and excurrent (atrial) siphons

Glossary

Control surface

Structure that allows animals (or devices) to adjust orientation.

Cost of transport (COT)

A measure of the energetic efficiency of movement normalized to the size of different organisms that use different modes of transport (energy/mass $\times$ velocity). Useful for comparisons across taxa. Also see Box 2.

Froude equation

Calculates Froude efficiency, a classic analysis of hydrodynamic efficiency that has been applied to propellers and more recently to jet-propelled animals.

Jump distances

Distance traveled during a jump, a locomotory burst of high acceleration during unsteady swimming.

Mass flow rate

Movement rate of fluid per unit time.

Mesoglea

Jelly-like matrix in jellyfish swimming bell that stores elastic energy during bell contraction. The stored elastic strain allows the bell to return to a relaxed state.

Particle image velocimetry (PIV)

A technique to quantify fluid motion around aquatic organisms. A two-dimensional laser sheet illuminates reflective particles added to the water. Movements of the particles are imaged and analyzed.

Propulsive efficiency

A mechanical measure of efficiency that considers wake dynamics in relation to forward speed of the jetting animal, but not the metabolic/energetic costs of swimming. Various hydrodynamic measures including Froude efficiency and whole-cycle efficiency have been used previously.

Reynolds number (Re)

A dimensionless number used to estimate the relative ratio of viscous to inertial forces. When $Re \ll 1$, viscosity dominates and when $Re \gg 1$, inertia dominates.

Rowing propulsion

An alternative to jet-propulsion. Some oblate (plate-shaped) medusae use a paddling motion to entrain water from outside the bell margin during contraction.

Siphon

An anatomical structure that conveys fluid in or out.

Slip

Wasted energy calculated based on how much the jet speed exceeds swimming speed. It can be calculated as $slip = \text{jet speed} / 1 - \text{swimming speed}$ (Anderson and Grosenbaugh, 2005). Low slip is indicative of high swimming efficiency.

Vortex ring

A toroidal volume of rotating fluid produced during pulsatile swimming.

Whole-cycle propulsive efficiency

Incorporates effects of passive refill by jet-propelled swimmers. Developed by Anderson and Demont (2000).

Zoid

A single-animal, functional unit that is part of a multi-unit colony.

(see Glossary) at opposing ends of their bodies. Muscle bands that encompass the cylindrical body, along with elastic properties of the tunic, generate a pulsed jet by taking water up through the incurrent siphon and then a muscular contraction expels the water through the excurrent siphon. These pulsed jets act to propel the animals forward but the water moved through the body is also used for feeding and respiration.

During forward swimming, the oral siphon closes just prior to muscle contraction, which forces water out through the atrial siphon. When the muscles relax, the body expands owing to the elastic properties of the tunic and water enters through the oral siphon to fill the body chamber (Bone and Trueman, 1983). Visualizing the flows of the resulting jet using *in situ* fluorescein dye (Fig. 2A) and laboratory PIV demonstrated that salps propel themselves using

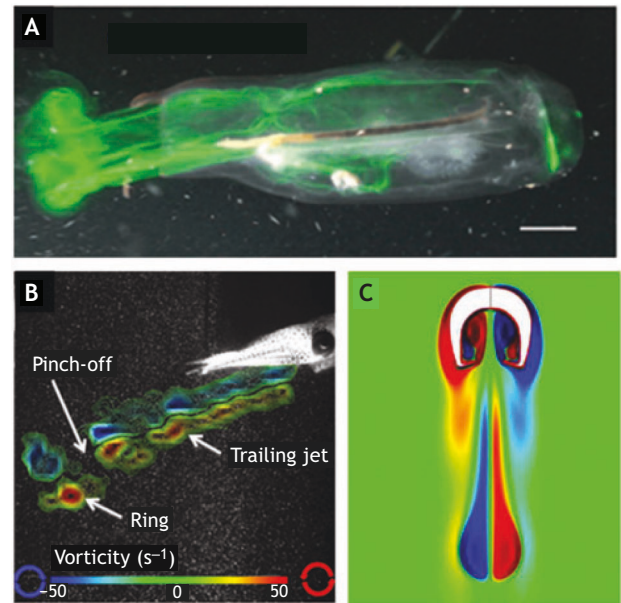


Fig. 2. Visualizing the fluid involved in jet-propelled animal swimming.

(A) *In situ* wake structure made with fluorescein dye (green) in the solitary salp *Cyclosalpa affinis*. From Sutherland and Madin (2010a). Scale bar: 1 cm.

(B) Vorticity of wake structures in free-swimming Atlantic brief squid (*Lolliguncula brevis*) showing the jet mode of swimming using particle image velocimetry (PIV). Adapted from Bartol et al. (2009a,b). (C) Vorticity (red=positive or counterclockwise fluid rotation; blue=negative or clockwise fluid rotation) of wake structure of the hydromedusae *Sarisa tubulosa* used to compare propulsive performance via computational fluid dynamics (CFD).

Warm colours represent positive vorticity and cool colours represent negative vorticity. From Sahin et al. (2009).

vortex rings and that, similarly to squids, siphon diameter is variable during jet production (Sutherland and Madin, 2010a), aiding entrainment of additional fluid and enhancing forward thrust (Dabiri and Gharib, 2005). This manipulation of the fluid to achieve hydrodynamic efficiency may help to explain the low energetic cost of transport (COT; see Glossary) in some salps (as low as $1 \text{ J kg}^{-1} \text{ m}^{-1}$) (Bone and Trueman, 1983; Trueman et al., 1984). The jet speeds measured in three different salp species (40–60 mm zoid size; see Glossary) were found to be remarkably similar at approximately 3.3 cm s^{-1} with a Reynolds number (Re ; see Glossary) between 200 and 400 (Sutherland and Madin, 2010a). This is roughly an order of magnitude less than jet speeds of squids of similar size and is reflected in the comparatively low mean swimming speeds of salps, which range from 1.2 to 1.7 cm s^{-1} (~ 0.3 body lengths s^{-1}). Jet pulse frequency for salps ranges between 0.8 and 2 Hz .

The arrangement of salp chains differs strikingly among groups, comprising wheel-shaped, transverse and linear forms (Madin, 1990). In the most streamlined linear forms, the blastozoids lie end to end with the central axes parallel to the chain axis. During pulsed jetting, swimming efficiency can be reduced (i.e. drag is increased) when the body accelerates and decelerates. This creates an alternating build-up and shedding of the fluid boundary layer around the body as well as the acceleration reaction. Mathematical models and experiments showed that when the swimming jets are produced at different times (Bone and Trueman, 1983) – instead of simultaneously – the colony swims at a constant velocity, thereby negating the drag penalty associated with pulsed jetting and improving swimming efficiency (Sutherland and Weihs, 2017). Interference between the swimming wakes is also minimized during asynchronous swimming and aids in maximizing thrust

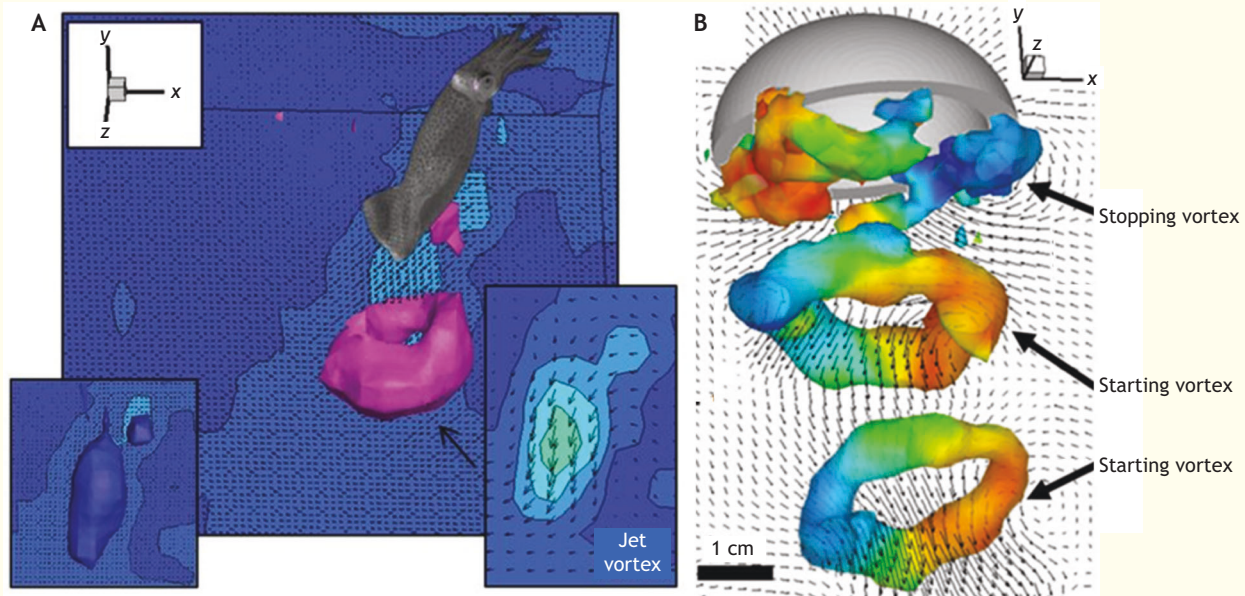
Box 1. Measurement methods for jet propulsion

Kinematics measurements

Early efforts to characterize the swimming of jet-propelled organisms captured videos of organisms coupled with pressure measurements inside the body cavity to infer locomotive forces (O'Dor, 1988). These indirect measurements of force relied on an assumed balance between the negative buoyancy of the organism and a partitioning of swimming forces between the jet and auxiliary appendages (i.e. the lateral fins of the squid). Additional kinematic studies have focused on subsystems of jet-propelled animals, such as modulation of the jet nozzle during propulsion (Bartol et al., 2001).

Flow measurements

Qualitative visualization of the efflux from jet-propelled organisms has been accomplished using tracers, such as brine shrimp eggs (Bartol et al., 2001). The advent of non-invasive flow velocimetry, specifically particle image velocimetry (Willert and Gharib, 1991; Müller et al., 1997; Drucker and Lauder, 1999), enabled more quantitative studies of jet propulsion in freely swimming organisms using a combination of laser illumination and high-speed imaging of small tracer particles in the water. Recent work has achieved three-dimensional, three-component measurements of the wakes of jet-propelled squid (A; adapted from Bartol et al., 2016) and jellyfish (B; adapted from Gemmell et al., 2015a,b) showing 3D vorticity iso-surfaces of shed vortex rings, which has revealed the importance of vortex ring formation in various modes of jet-propelled locomotion (Gemmell et al., 2015a,b; Bartol et al., 2016).



Numerical simulations

Computational fluid dynamics has enabled studies of jet-propelled swimming that are infeasible experimentally. A particularly successful technique has been the immersed boundary method, because of its ability to simulate complex, deforming bodies (Mittal and Iaccarino, 2005; Hamlet et al., 2011). Sahin et al. (2009) used an arbitrary Lagrangian–Eulerian (ALE) method to conduct a comparative analysis of prolate and oblate hydromedusae. Because parameters of the numerically simulated organisms, such as their pulse rate, swimming direction, swimming duration and background flow, could be controlled, the study was able to isolate specific effects, such as those of body geometry, on the propulsive performance of the organisms.

(Athanassiadis and Hart, 2016). The hydrodynamic efficiency of linear chain forms helps facilitate their diel vertical migrations of hundreds of meters (Wiebe et al., 1979; Madin et al., 1996).

Swimming speed, pulse rate and the degree of musculature vary among species. Fast swimming forms are characterized by higher pulse rates and streamlined morphologies (Sutherland and Madin, 2010b). The depth of contraction and, therefore, percentage of the overall fluid that is expelled, also varies with species and ranges from 18 to 30% (Sutherland and Madin, 2010b). It is thought that species with weaker hydrodynamic performance may compensate by having relatively low energetic demands (Biggs, 1977; Cetta et al., 1986).

Doliolids are barrel-shaped ascidians. A unique feature is that they use ciliary motion as the primary means of feeding, which produces a slow, steady water current that propels the animal through the water at low speeds (Bone and Trueman, 1984). Muscular jetting is used to escape or to reposition in the water column (Bone and Trueman, 1984). These rapid muscular contractions produce single jets that propel the animal at velocities of up to 21 cm s^{-1} (over 50 body lengths s^{-1}).

Cephalopods: high proficiency jet propulsion from a high-speed jet

Some of the earliest scientific interest in animal jet propulsion was devoted to squids (Phylum: Mollusca; Class: Cephalopoda) (e.g. Stevenson, 1934; Williamson, 1965; Trueman and Packard, 1968; Bradbury and Aldrich, 1969). Cephalopods are an abundant and diverse group within the world's oceans, composed of approximately 800 species (Sanchez et al., 2018). Unlike other jet-propelling taxa, squid can propel by a combination of fin and jet propulsion. During low-speed swimming, both fin and jet propulsion are used, with 'finning' gaits used most frequently, especially when ascending from vertical migrations (Flaspohler et al., 2019). As swimming speed increases, jet propulsion increasingly contributes to total thrust production among shallow-water squid species. At the greatest swimming speeds, squid will often keep the fins wrapped tightly against the mantle, using jetting only (Williamson, 1965). Squid are thought to be the most proficient invertebrate swimmers, with maximum speed estimates ranging from 5 to 10 m s^{-1} (Vogel, 1987). Such high proficiency in speed is a result of the production of a powerful jet. Indeed, squid in the family Ommastrephidae are the only jetting taxa known to be able to propel themselves fully out of

Box 2. A note on swimming efficiency

As highlighted by Schultz and Webb (2002), the concept of swimming efficiency is ill-posed for many modes of locomotion. In contrast to most engineered propulsion systems, it is often impossible to unambiguously disentangle thrust and drag forces exerted by a self-propelled animal swimmer. Indeed, the same propulsive surfaces can contribute to either thrust or drag depending on the phase of the swimming stroke.

In jet-propelled swimmers, this challenge is often circumvented by attributing thrust to the jet efflux, and by ascribing drag to the hydrodynamic forces on the outer surface of the animal. Anderson and Grosenbaugh (2005), Bartol et al. (2008) and others have leveraged this partitioning of thrust and drag in order to define measures of efficiency that enable comparative studies. However, it is important to recall that this partitioning is an assumption, and the numerical efficiency values are not directly connected to the underlying mechanisms that create thrust and drag at the organism's propulsive surfaces. Rather, these measures primarily provide a quantitative means to compare swimmers with similar morphology and swimming kinematics.

Other measures of efficiency that consider metabolic costs, such as the cost of transport (COT) (e.g. $\text{J m}^{-1} \text{kg}^{-1}$), can be more directly related to the underlying biomechanics and physiology of animals, since they reflect energy consumption required for locomotion. However, because this measure has dimensional units and may not scale isometrically, it is of more limited utility in comparing across ontogeny or in animals with significantly different sizes or physiology. Indeed, the observation that one animal group has a lower COT than another might be attributable to differences in their hydrodynamics, their physiology, their relative size or all three.

the water (Muramatsu et al., 2013). Squid draw water into their cylindrical mantle cavity via openings on either side of the head and then expel it under high pressure through a funnel. This involves contraction of the mantle as a muscular hydrostatic system. A thick layer of circular muscle is divided into regular bands by thin layers of radial muscle and sandwiched between an inner and outer tunic made up of fibrous connective tissue (Kier, 1988). Refilling of the mantle cavity is driven by the elastic properties of the mantle tissue (Gosline and Shadwick, 1983), contraction of antagonistic radial muscles (Gosline et al., 1983) and internal positive pressures within the mantle induced by fluid flow (Vogel, 1987).

To increase speeds during continuous swimming, small squid will increase the pulse duration and the resulting degree of elongation of the vortex structure, leading to higher impulse while maintaining relatively constant jet velocity (Bartol et al., 2009b). Larger squid can employ a variety of approaches to increase speed, such as increasing jet velocity through alterations in mantle contraction frequency, volume and/or duration (O'Dor, 1988; Bartol et al., 2001; Anderson and Grosenbaugh, 2005). Over short distances, small individuals performing an escape response can swim at high relative speeds of up to 25 body lengths s^{-1} . During such escape swimming behaviors, the mantle can undergo hyperinflation, where the outside diameter of the mantle increases by 10% relative to the relaxed state and the volume of the internal cavity increases by ~22% (Gosline and DeMont, 1985). The entire escape swim cycle takes approximately one second and can be repeated up to 10 times to put distance between the squid and the perceived threat. The excurrent funnel that forms the jet is highly dexterous and can direct fluid forwards or backwards, allowing squid to change direction rapidly. Squid exhibiting arms-first swimming can achieve speeds of ~70% that of squids exhibiting mantle-first swimming (Bartol et al., 2016).

Using digital PIV, it was determined that the average jet velocities for steadily swimming *Doryteuthis pealeii* ($10.1\text{--}59.3 \text{ cm s}^{-1}$)

ranged from 19.9 to 85.8 cm s^{-1} and always exceeded animal swimming speed, whereas maximum fluid velocities within jets varied from 25.6 to 136.4 cm s^{-1} (Anderson and Grosenbaugh, 2005). In terms of forces resisting forward motion of squids, it has been suggested that skin friction and working fluid intake are the two most important sources of drag (Anderson et al., 2001). A number of jet patterns involving interconnected vortex rings, long jets with ring elements and turbulent jets have been found in squid wakes (Bartol et al., 2016), but two distinct jet modes have been consistently observed during squid swimming. In jet mode I, fluid ejected from the funnel rolls up into an isolated vortex ring in the wake. In jet mode II, the expelled fluid becomes a leading vortex ring that 'pinches off' from the long trailing jet (Bartol et al., 2009a) (Fig. 2). The ratio of jet length to jet diameter (L_w/D_w) defines the jet mode and is <3.0 for jet mode I and >3.0 for jet mode II. The use of jet mode II appears to result in greater time-averaged thrust and it is the jet mode most commonly observed (Bartol et al., 2009a). Jet mode I exhibits a greater propulsive efficiency (see Glossary), lower slip (see Glossary) and shorter jet periods than jet mode II and is more likely to be associated with the simultaneous use of the mantle fins (Bartol et al., 2009a).

As adults, squid are the largest known jet propellers in nature; however, as paralarvae they are also some of the smallest. This transition from small larvae, which are faced with the problem of jet propulsion being ineffective at $Re < 10$ (Herschlag and Miller, 2011), to large adults in fully inertial fluid regimes, has provided an opportunity to learn about jet propulsion across multiple scales. Several investigations have identified the importance of continuous swimming over pulsatile or burst-and-coast swimming at low and intermediate Re (Hunter, 1972; Weihs, 1974; Batty, 1984; Muller et al., 2000). Therefore, it is interesting to consider the squid as an example in which even the smallest developmental stage employs pulsatile jet propulsion.

Unlike adults, which frequently travel great distances, squid larvae spend the majority of their time station holding in the water column, where they produce a frequent, high-volume, vertically directed jet (Bartol et al., 2009a). Larval squid also have comparatively large funnel complexes (Packard, 1969; Thompson and Kier, 2002) and higher mantle contraction rates (Thompson and Kier, 2006) relative to larger juveniles and adults. These short stroke ratios (length of ejected plug of fluid to the diameter of the jet aperture) have been suggested to aid in improving both thrust and propulsive efficiency (Bartol et al., 2009a). Bartol et al. (2009b) found that, during the contraction phase of swimming, mean and peak propulsive efficiencies of paralarvae were 75% and 88%, respectively, which are only about 10% lower than the juvenile/adult stages, where mean and peak efficiencies of 86% (swimming speeds exceeding 0.65 mantle lengths s^{-1}) and 95–97%, respectively, were reported (Anderson and Grosenbaugh, 2005). The high contraction phase efficiency at the paralarval stage is due to a combination of jets being more directly aligned with the direction of motion than in juvenile and adult squids (Bartol et al., 2001; Anderson and Grosenbaugh, 2005; Bartol et al., 2009b), low slip values related to the morphology of small paralarvae, which have larger funnel apertures (Packard, 1969; Thompson and Kier, 2002; Bartol et al., 2009b), and the proportionally larger volumes of water that paralarval squids hold in their mantle cavities (Gilly et al., 1991; Preuss et al., 1997; Thompson and Kier, 2001). These factors allow smaller squid to eject larger water volumes at low speeds to produce sufficient thrust.

Work by Staaf et al. (2014), which focused on the efficiency of the entire swim cycle, found that reducing the aperture during

mantle contraction promotes greater propulsive efficiency at all body sizes. However, this same study found the smallest (1 mm) squid paralarvae suffered from low efficiency (20%) because of a limited speed of contraction. The whole-cycle swimming efficiency increases to a peak of 40% for a 1 cm squid and then slowly declines beyond that (Fig. 3). Squid larger than 6 cm must increase aperture size and/or reduce contraction speeds to maintain tensional muscle stress within maximal tolerance. Ecological pressures, such as the need to capture prey or avoid predators, where high swimming velocities are important, may lead squid to increase aperture size, which will temporarily reduce efficiency.

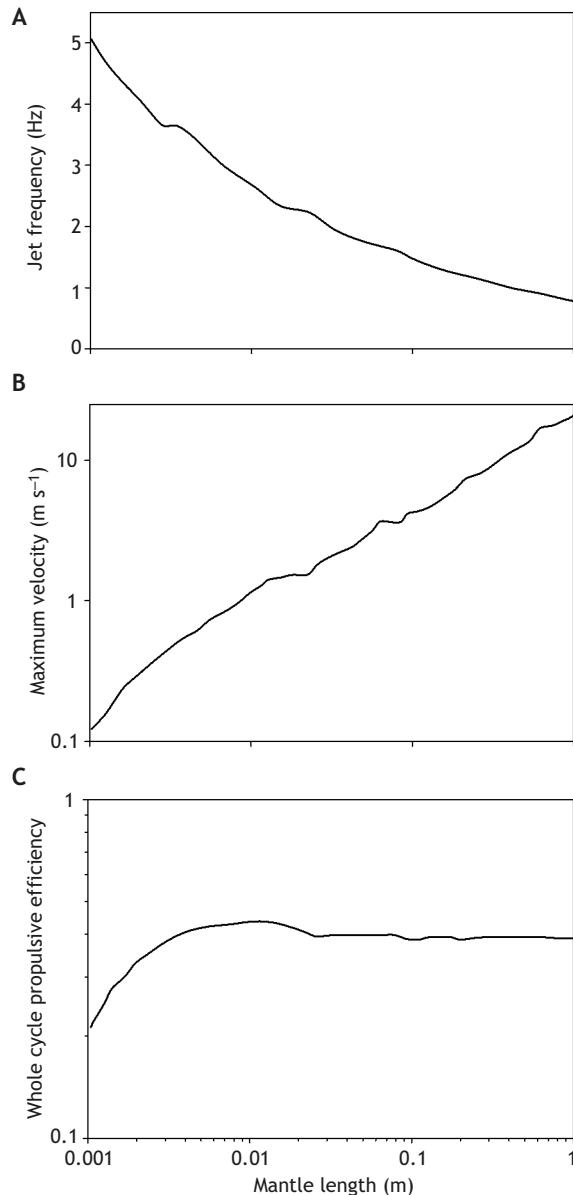


Fig. 3. Relationship between various swimming performance metrics and squid size. (A) Jet frequency declines rapidly with body size when squid are small, but more slowly as they grow. (B) Theoretical results of using jet frequency (from A) for maximal squid velocity. Velocity also shows the greatest change at small body sizes (C) Hydrodynamic efficiency also increases most rapidly at small body sizes, peaks at an intermediate body size and then actually declines slightly at moderate to large body sizes. Replotted from Staaf et al. (2014).

Although squid are by far the most well studied group of jetting cephalopods, other members of the Cephalopoda employ jetting as well. *Nautilus* swim at lower relative speeds (0.5–1.5 body lengths s^{-1}) than squid (up to 25 body lengths s^{-1}) using either jet mode I or jet mode II (Neil and Askew, 2018). Interestingly, the whole-cycle propulsive efficiency (see Glossary) is higher than that of squid, despite the lower swim speeds, and ranges from 48 to 76% during anterior-first swimming (Neil and Askew, 2018). This high efficiency is thought to be an adaptation for reducing the metabolic cost of swimming as these animals frequently encounter hypoxic conditions in the water column, which demand low oxygen consumption. Cuttlefish appear unable to swim using jet propulsion at moderate to high swim speeds for sustained periods and instead rely more heavily on their fins (Aitken and O'Dor, 2004). However, the cuttlefish *Sepia bandensis* uses jet propulsion in combination with fins to achieve high maneuverability and one of the smallest turning radii of any taxa (Jastrebsky et al., 2016). Octopus use jet propulsion frequently as larvae, especially to catch prey (Villanueva et al., 1997), but are primarily benthic as adults, employing jet propulsion intermittently for escape and predation. In addition to conventional jetting, some octopods exhibit 'medusoid' locomotion analogous to that of some jellyfish, whereby they spread their arms and webs to gather water and then bring these appendages together to eject large volume jets at relatively low speeds (Hanlon et al., 2018).

Bivalves: periodic jetters with clapping shells and high cost of transport

Although the vast majority of bivalves (Phylum: Mollusca; Class: bivalvia) are fully sessile as adults (Gould, 1971), scallops and file shells are capable of jet-propulsive swimming. Typically in response to a would-be predator, these bivalves rapidly 'clap' the two halves (valves) of their shells using the well-developed adductor muscle, that rebounds through stiff, elastic ligaments (Gould, 1971). Clapping draws water in from the ventral side of the animal and produces jets of water that emerge on either side of the hinge connecting the valves at the dorsal end (Gould, 1971; Cheng and DeMont, 1996a,b). The result is an unsteady, pulsed thrusting force that propels the animal along the ventral edge first (Cheng and DeMont, 1996a). Scallops only cover short distances of >30 m over less than 1 min per swimming bout, whereas file shells are known to swim much greater distances for upwards of 15 min at a time (Gould, 1971; Baldwin and Lee, 1979; Dadswell and Weihs, 1990).

The maximum velocity during each adduction cycle, for most species, ranges from 19 to 43 $cm s^{-1}$ (Ansell et al., 1998; Bailey and Johnston, 2005) with a mean velocity during level swimming of up to 24 $cm s^{-1}$ (Ansell et al., 1998). One large species, *Amusium balloti*, has been estimated to swim up to 160 $cm s^{-1}$ (16.8 body lengths s^{-1}) and covers 23 m in a single swim event (Joll, 1989). A full swim or adduction cycle consists of an opening, closing and glide phase averaging 1.5 adductions s^{-1} . Swimming in scallops begins with 2–5 adduction cycles ('take-off phase') followed by 1–14 adductions during level swimming (Ansell et al., 1998). The energetic COT for swimming bivalves ranges from 21 (scallops) to 66 (file shells) $J kg^{-1} m^{-1}$, of which up to 65% is aerobically produced (O'Dor and Webber, 1991; Donovan and Baldwin, 1999). Scallops from cold waters have reduced shell and muscle mass but increased resilience in abductin (elastic protein found in the hinge ligament) to help maintain performance (Denny and Miller, 2006). To date, there are no detailed measurements quantifying the jet produced by swimming bivalves. Thus, fluid dynamic comparisons to other jetting taxa cannot be made in this regard.

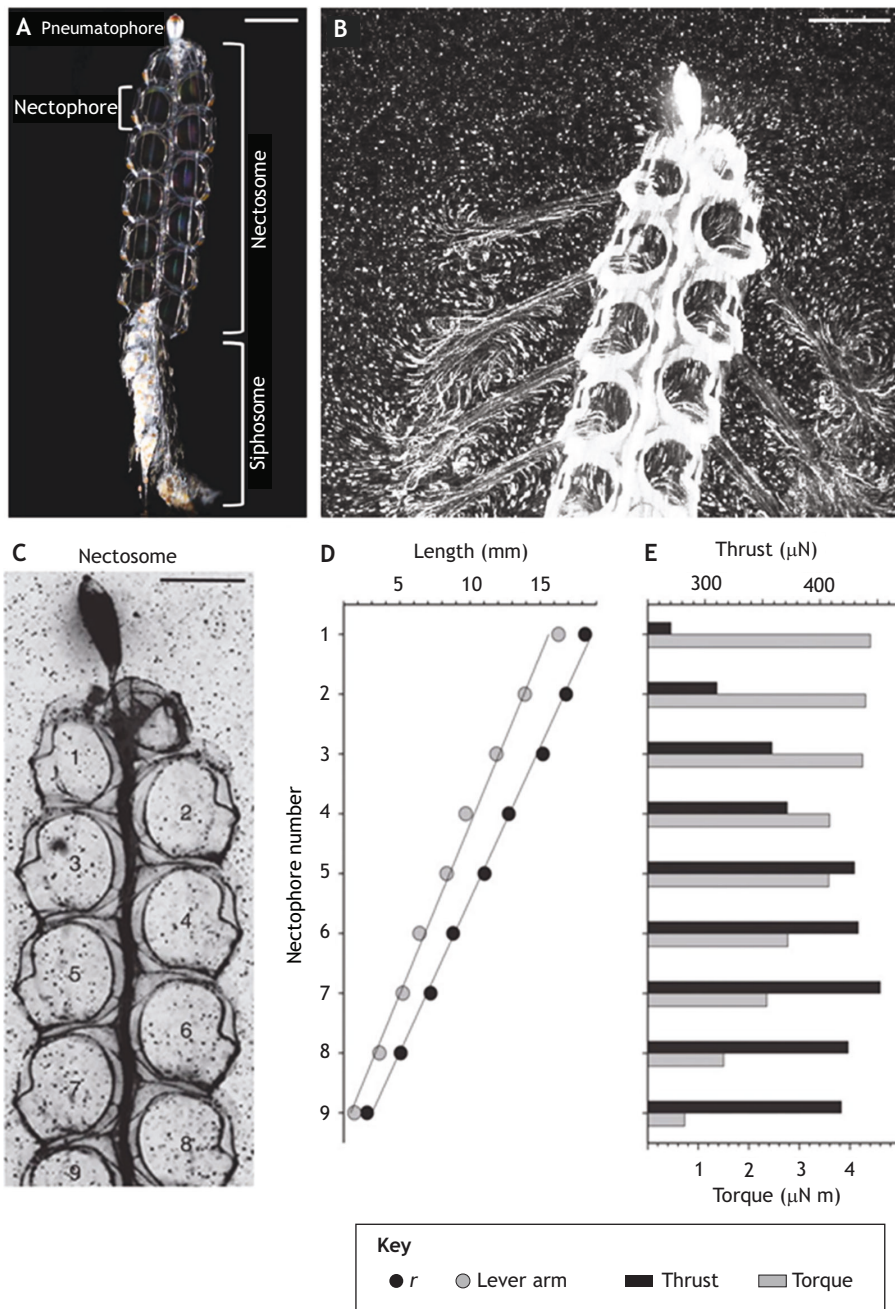


Fig. 4. Jet wakes and maneuvering by the multi-jet siphonophore *Nanomia bijuga*. (A) Anatomical structures. (B) Narrow, high-speed jets produced by the nectophores shown as particle tracer paths. From Sutherland et al. (2019a,b). (C–E) The relationship between nectophore position and size relative to the contribution to thrust and torque, showing that the smaller nectophores, while creating the lowest thrust values, actually contribute the most to torque for turning owing to their position furthest from the center of mass (maximum lever arm effect). r =distance from nectosome–siphosome border. From Costello et al. (2015). Scale bars: 3 mm.

Siphonophores: high performance multi-jet jellies

Siphonophores (Phylum: Cnidaria; Class: Hydrozoa; Subclass: Hydroidolina) are colonial cnidarians that have a cosmopolitan distribution from icy polar waters to the tropics and from surface waters to the abyssal depths (Totton and Bargmann, 1965). They range in size from millimeters to meters. Many species contain multiple jet-propelled swimming units, called nectophores, and use jet propulsion for long-distance migrations (Robison et al., 1998), rapid bursts and quick turning maneuvers (Costello et al., 2015) (Fig. 4).

Nectophores propel the animal by producing pulsed, high-speed jets, and are capable of directing the jets in a way that facilitates forward or reverse swimming (Mackie, 1964; Costello et al., 2015). These jets are very narrow (1–2 mm) and reach speeds of up to 1 m s^{-1} (Sutherland et al., 2019a,b) (Fig. 4). These maximum jet

speeds are on par with the highest speeds recorded in squids; however, the squid body is many times the size of an individual nectophore. Scaled to the 3 mm nectophore length, jet speeds reach $>300 \text{ lengths s}^{-1}$. The coordination of multiple jets makes physonect siphonophores highly effective swimmers capable of extensive diel vertical migrations. These individuals may travel hundreds of meters daily (Robison et al., 1998).

Fluid is directed out of the nectophore by a highly maneuverable velum, which changes diameter and shape rapidly to control fluid during jetting and refill (Sutherland et al., 2019b). During nectophore refilling, the velum is opened fully in a very short period of time ($\sim 0.03 \text{ s}$) and the greatly expanded diameter slows the fluid as it enters the nectophore cavity. This allows a 0.95:1 ratio of time spent jetting to time spent refilling in *Nanomia bijuga* despite a short overall jet cycle time of 0.26 s (Sutherland et al.,

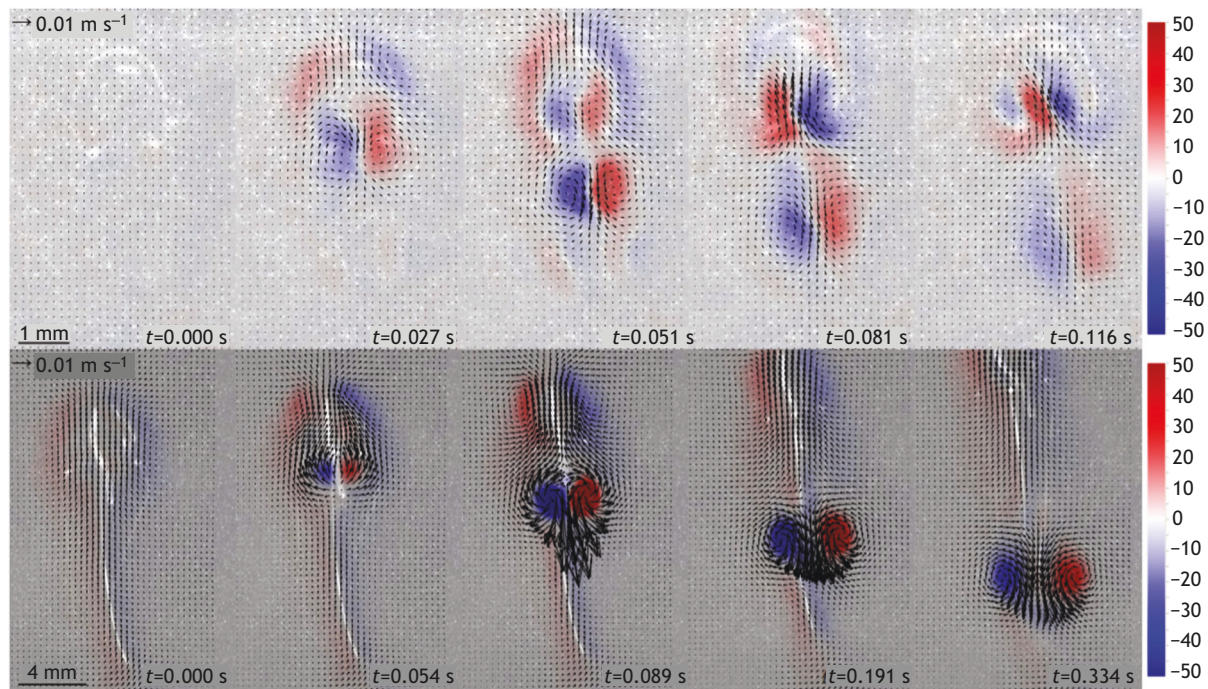


Fig. 5. Velocity and vorticity fields of the hydromedusa *Sarsia tubulosa* over a contraction cycle, showing the development of the jet wake for two different size classes. Velocity is represented by black vectors, vorticity by red and blue filled contours. Bell diameters are 1 mm (A) and 4 mm (B). From Katija et al. (2015).

2019b). The siphonophore *Chelophyes appendiculata* has a jetting to refill ratio of 0.8:1 (Bone and Trueman, 1982). These ratios are higher than that in other jetting species (Sutherland et al., 2019b), which allows more time for the animals to create forward thrust.

To change direction, siphonophores rely on the smaller, younger nectophores located at the apex, whose jets are less powerful; however, with a longer lever arm and more lateral jet angles they are able to provide greater torque (Fig. 5). In terms of turning rates, *N. bijuga* turns with a mean length-specific turning radius of 0.15 ± 0.10 and achieves an angular velocity of $104 \pm 41 \text{ deg s}^{-1}$ with maximum velocities of 215 deg s^{-1} (Sutherland et al., 2019a). This is in line with many other swimming animals, but exceeds a number of vertebrates with more complex body forms and neurocircuitry (Sutherland et al., 2019a). For comparison, some cephalopods, such as the brief squid (*Lolliguncula brevis*) and dwarf cuttlefish (*S. bandensis*) can use both jet propulsion and fins to achieve very high turning rates of 725.8 and 485.0 deg s^{-1} (Jastrebsky et al., 2016). In terms of maneuverability, siphonophores really excel in their ability to swim rapidly in both forward and reverse directions. *N. bijuga* is capable of a 1:1 ratio of forward to reverse swimming speed, which has not been recorded in other swimming organisms. This is due in part to the highly dexterous velum, which can change the jet angle by nearly 180° . This combination of colony architecture and highly controlled pulsatile jets allows *N. bijuga* to exhibit a diverse array of movements. Combined with the advantages of scalability and redundancy that exist in colonies, siphonophores could serve as a novel platform to inform designs for underwater propulsion through complex environments.

Medusae: efficient single jet jellies

Medusan morphology and propulsive mode

Cnidarian medusae (Phylum: Cnidaria; Class: Hydrozoa, Scyphozoa, Cubozoa) were the first animals to evolve muscle-powered swimming and most likely used jet propulsion (Gold, 2018). Extant medusan

species exhibit highly variable shapes and sizes, but most species are small ($<1 \text{ cm}$) and prolate or bullet shaped (Costello et al., 2008). Not all medusae use jet propulsion; however, because most medusae are small, and small medusae overwhelmingly use jet propulsion (Colin and Costello, 2002), jet propulsion is the most common swimming type among medusae. Among the taxa of medusae, the hydrozoan and cubozoan classes primarily swim via jet propulsion (Costello et al., 2008; Colin et al., 2013). Scyphozoan medusae, primarily use rowing propulsion (see Glossary) with minimal jet formation (Costello et al., 2008). Whether a medusa swims via jet or rowing propulsion depends primarily upon the aspect ratio (defined as the fineness ratio, where $f = \text{height/diameter}$) of their bell (Colin and Costello, 2002; Dabiri et al., 2010). Medusae with relatively high aspect ratios (e.g. $f \geq 1$), termed prolate medusae, use jet propulsion for thrust during bell contraction. Medusae with low fineness ratios, termed oblate medusae, primarily use rowing propulsion because the low aspect ratio of their bells results in fluid from outside their bells being entrained during bell contraction and this serves as the source of their swimming thrust (Colin et al., 2012; Gemmell et al., 2014, 2015a).

Limits on medusan jet propulsion

Medusan jet propulsion is initiated when the medusa contracts its bell using muscle cells that line the inner surface of the bell cavity. Bell contraction is rapid and quickly decreases the subumbrellar volume as a fluid jet is expelled out the bell cavity and through the velar aperture. After contraction, the subumbrellar muscles relax and the elastic properties of the mesoglea (see Glossary) cause the bell to expand and draw fluid back into the bell cavity. This process is constrained by physiological limits inherent to the phylogenetically basal position of these ancient metazoans. The muscle fibers used to contract their bells are only a single layer of epithelial cells, limiting the forces that medusae can generate (Costello et al., 2008).

For small medusae (<5 cm), muscular force does not constrain jet propulsion. Because the volume of fluid expelled increases by their bell diameter cubed, medusae with bell diameters larger than 5 cm are not able to generate jets with sufficient thrust to overcome the drag resisting forward motion (Dabiri et al., 2007). To overcome this limitation, larger medusae are oblate-shaped, where paddling-type locomotion can supplement jetting. Material resonance can also play a role in swimming performance. Hoover and Miller (2015) found that jellyfish swimming speed is maximal when the animal contracts at the bell's material resonant frequency, but the COT is optimized when jellyfish contract the bell at lower frequencies and passively coast between pulsation cycles, where they receive a boost from a stopping vortex ring. Here, the thrust generated by passive energy recapture (PER), defined as positive pressure generated in the bell cavity by the inward movement of fluid that accumulates inside the bell (Sahin et al., 2009; Gemmell et al., 2013), depends most strongly on the elastic properties of the jellyfish bell.

The smallest medusae also experience limitations on their jet propulsion. However, these limitations are imposed by fluid viscosity. Cantwell (1986) calculated that jet vortices do not form in flows with $Re < 6$. Medusae with bell diameters around 1 mm swim with peak $Re \leq 10$ (Blough et al., 2011; Katija et al., 2015) (Fig. 6). Below $Re = 10$, the work required to generate jets greatly increases, and the distance traveled with each pulse sharply decreases with size (Herschlag and Miller, 2011). At this small scale, the wakes produced by jets no longer resemble the wakes of larger jellyfish at higher Re , where inertia is important (Dabiri et al., 2010; Herschlag and Miller, 2011; Katija and Jiang, 2013). Compared with other impulsive swimmers of similar size, such as copepods, the swimming performance of these smallest medusae is much lower at slower velocities and shorter jump distances (see Glossary) (Katija and Jiang, 2013). As medusae grow, their swimming performance increases linearly, and the corresponding hydrodynamic costs of transport improve. However, this size-related pattern does not affect relative travel distance or overall hydrodynamic efficiency (Katija et al., 2015).

Hydrodynamics of medusan jet propulsion

Similarly to many jetting animals, the cyclic motion of medusan jet propulsion interacts with the surrounding fluid to generate starting and stopping vortices during bell contraction and relaxation, respectively. Until recently, most studies examining the hydrodynamics of medusan jet propulsion have focused on the flow during the contraction phase, i.e. the starting vortex (Dabiri et al., 2006; Lipinski and Mohseni, 2009; Katija and Jiang, 2013; Park et al., 2015).

Recent hydrodynamic studies have also begun to reveal the important role of vortex interactions that occur at the interface of vortices inside and outside the bell cavity (Costello et al., 2019; Krieg and Mohseni, 2020). As already mentioned, bell kinematics generate several vortices throughout the swimming cycle. Fluids are accelerated at locations where these vortices interact with each other, which enhances momentum transfer to the fluid and, therefore, thrust (Costello et al., 2019). Recent numerical studies have shown that bell contraction and expansion kinematics are able to control the timing and location of these vortex interactions to enhance swimming acceleration at the very beginning of bell contraction and decrease energy costs during bell expansion (Krieg and Mohseni, 2020).

Assessing the pulsatile jet-propelled swimmers

Thrust production by pulsatile jet propulsion and the associated hydrodynamics are relatively simple (compared with other modes of

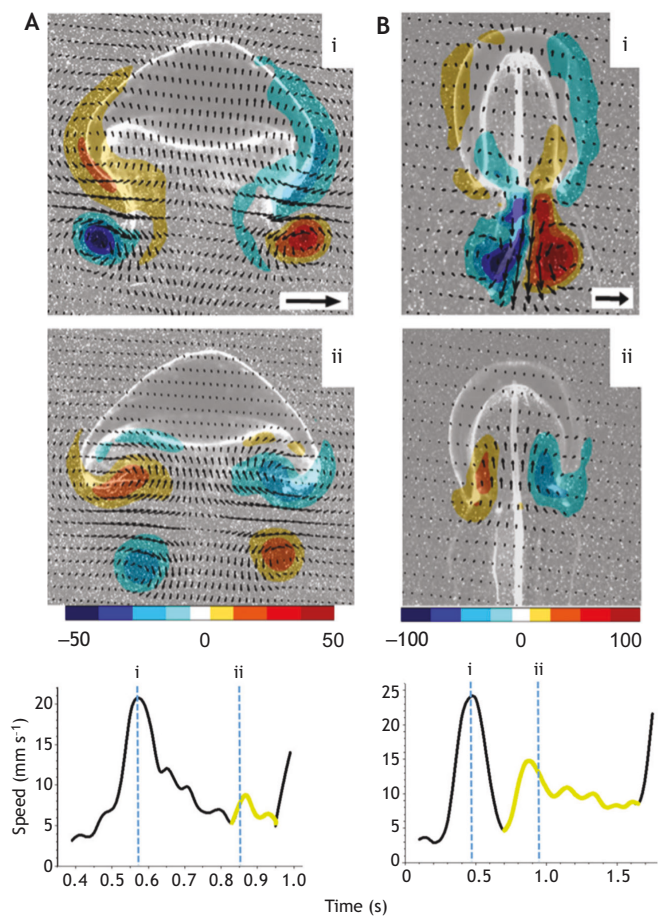


Fig. 6. Wake structure vorticity, velocity vectors and passive energy recapture by rowing and jetting medusae. Vorticity (red and blue), velocity vectors and passive energy recapture by (A) rowing (*Aequorea victoria*) and (B) jetting (*Sarsia tubulosa*) medusae. The top panels (i) show the contraction phase and the middle panels (ii) show the relaxation phase of the swim cycle. Bottom panels show portion of the cycle where passive energy recapture (PER) is utilized (highlighted in yellow). Note the large proportion of PER achieved in the jetting species (B). The vorticity scale (black arrow) represents 10 and 15 cm s^{-1} for A and B, respectively. Adapted from Gemmell et al. (2018).

propulsion), in the sense that thrust is always generated by muscle contractions that eject fluid through an orifice. However, despite the relatively few degrees of freedom associated with jet propulsion, it is used by a diverse range of taxonomic groups that have very different functions of jet propulsion and very different physical and biological constraints.

Many jet-propelled animals use jet propulsion for rapid swimming to escape predation, capture prey or to reposition. Squid have evolved to generate high thrust using jet propulsion to swim at very high speeds (Fig. 7). Squid achieve high thrust by using strong muscle contractions that expel fluid rapidly. The trade-off is that squid have some of the highest net costs of transport among jetting animals at $5\text{--}7 \text{ J kg}^{-1} \text{ m}^{-1}$, with other cephalopods such as the Nautilus (*N. pompilius*) and the cuttlefish (*Sepia officinalis*) doing only moderately better at $3 \text{ J kg}^{-1} \text{ m}^{-1}$ (O'Dor and Webber, 1991) (also see COTs; Fig. 7). However, squid can modulate their jets (type I versus II) to increase hydrodynamic efficiency and presumably their COT. Only scallops, which are primarily benthic and only swim occasionally (primarily for avoiding potential predators), have a higher net COT than squid at

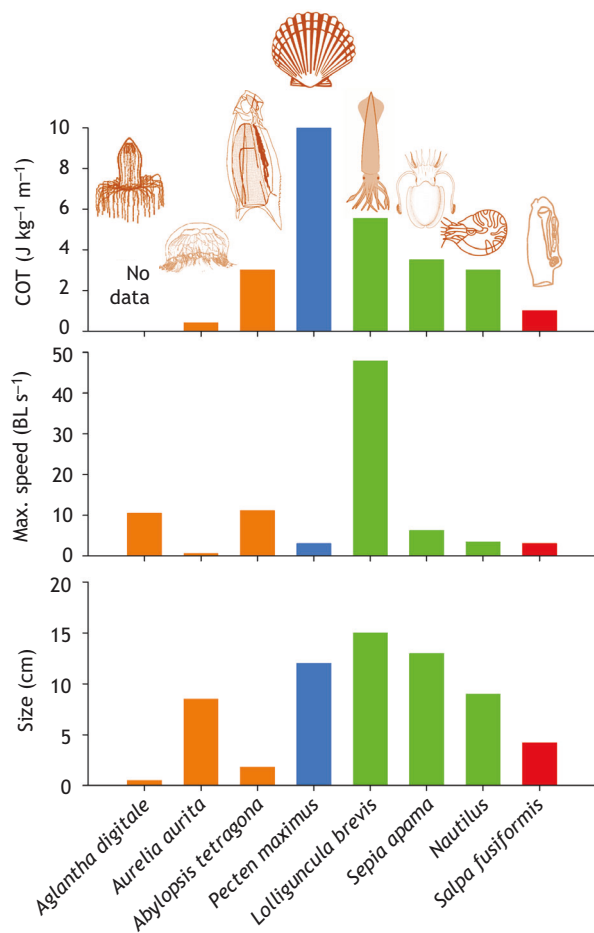


Fig. 7. Comparison of swimming performance of representative jetting taxa. Orange bars are cnidarians (Bone and Trueman, 1982; Colin and Costello, 2002; McHenry and Jed, 2003). Blue bar is a bivalve (O'Dor and Webber, 1991; Neil, 2016). Green bars are cephalopods (O'Dor et al., 1990; O'Dor and Webber, 1991; York and Bartol, 2016). Red bar is a salp (Bone and Trueman, 1984). BL, body length; COT, cost of transport.

$21 \text{ J kg}^{-1} \text{ m}^{-1}$ (O'Dor and Webber, 1991). However, scallops still have a lower COT for swimming than crustaceans, such as copepods, krill and shrimp ($>30 \text{ J kg}^{-1} \text{ m}^{-1}$) (Morris et al., 1985).

In contrast, animals that use jet propulsion for generating a feeding current, such as salps (as low as $1.07 \text{ J kg}^{-1} \text{ m}^{-1}$) and oblate medusa (as low as $0.4 \text{ J kg}^{-1} \text{ m}^{-1}$), have the lowest COTs among jetting animals (Trueman et al., 1984; Gemmell et al., 2013) (Fig. 7). Propulsion by salps and oblate medusae has been altered in different ways from typical jet propulsion. Salps, and doliolids, are unique among jet propellers in that they draw water in from the front and expel it from the rear. This one-way movement of fluid appears to have significant advantages in terms of efficiency, because fluid does not need to be redirected to create thrust (Trueman et al., 1984). In contrast, oblate medusae have lower energetic costs associated with their propulsion by using a hybrid mode of propulsion, jet-paddling (or rowing propulsion). When oblate medusae contract their bells during swimming, they do receive some thrust from fluid being jetted out of their body cavity, but most of their thrust results from negative pressure fields aligned along the outside of their bells that pull forward (Gemmell et al., 2015a). As a result, they use slow and much weaker muscle contractions to generate sufficient thrust to swim and feed and have the lowest recorded COT among swimming animals (Fig. 7).

Not all jetting species that use typical jet propulsion, whereby water is drawn and ejected from a rearward facing orifice, suffer from the COT issues that squid and scallops do. In medusae, the refilling phase (drawing in water) can actually play an important role in overall swimming efficiency (COT) (Gemmell et al., 2013, 2018) (Fig. 6). Additional thrust is observed as a small boost in swimming speed just after the bells stops expanding (Blough et al., 2011; Gemmell et al., 2013; Katija et al., 2015; Gemmell et al., 2018). The additional boost comes from PER, which significantly reduces the COT of swimming oblate medusae and likely lowers the COT of prolate jetting medusa given the high degree to which they can use PER (Fig. 6). However, net COTs for jetting medusae have not been estimated.

Like medusae, siphonophores appear to have mechanisms that minimize the negative impacts of the refilling phase that likely contribute to a relatively low net COT of 2.86 (Bone and Trueman, 1982). High-pressure regions inside the nectophores have been observed during refilling and appear to be analogous to the medusae PER mechanism (Sutherland et al., 2019b). Given that squid bodies are not transparent as adults, it is currently unknown how much, if any, PER contributes to swimming performance in this taxonomic group. Given the relatively high COT for squid and the fact that PER requires a considerable pause duration between jet pulses, these animals do not appear to be able to benefit substantially from this process. It is possible that PER may play a larger role in deep-dwelling squid which exhibit slower jetting cycles, but deep sea squid appear to rely almost exclusively on fin locomotion over most of the speed range (Vecchione et al., 2002; Kubodera et al., 2007).

Laboratory studies have shown that there is a physical limit on the maximum size of a starting vortex that can be generated by a pulsatile jet, termed formation number. This number is the ratio of jet length to jet diameter (L/D). After this limit is reached, any additional fluid ejected does not end up in the starting vortex and forms a region of unorganized vorticity termed the trailing jet. The emergence of a trailing jet results in energy loss and, therefore, less efficient jet propulsion (Gharib et al., 1998). The maximum formation number observed for efficient jets produced by mechanical laboratory apparatuses is ~ 4 . Beyond this value, the vortex ring at the front of the fluid discharge stops growing and separates from the jet stream behind it. However, medusae have been shown to be able to extend the formation number to ~ 8 by altering their velar aperture area during bell contraction (Dabiri et al., 2006). This means that medusae may be able to produce strong jets more efficiently than jets produced by mechanical jet generators (Dabiri et al., 2005). Jetting medusae regularly produce jets with trailing jets (Dabiri et al., 2010), suggesting that they have evolved to maximize thrust at the expense of efficiency. Some squid produce even longer trailing jets, and with their powerful, muscular mantles achieve L/D ratios in excess of 30 (Bartol et al., 2001; Anderson and Grosenbaugh, 2005), although propulsive efficiency is highest at lower L/D ratios, where jet fluid rolls up into an isolated vortex ring (Bartol et al., 2009a). In *Nautilus*, which display high whole-cycle propulsive efficiency, L/D ratio varies by speed and jet mode from 0.79 to 2.16 in jet mode I and from 3.16 to 6.29 in jet mode II (Neil and Askew, 2018).

One interesting aspect of jet-propelled swimmers is that, unlike other swimmers such as fish, there is no significant relationship between body size and maximum swim speed (Fig. 8A). Only mean swimming speed is significantly correlated with size (Fig. 8B). The lack of a relationship between body size and peak swim speeds suggests that many jetting species do not possess an ability to significantly increase the strength of their jet, resulting in low burst

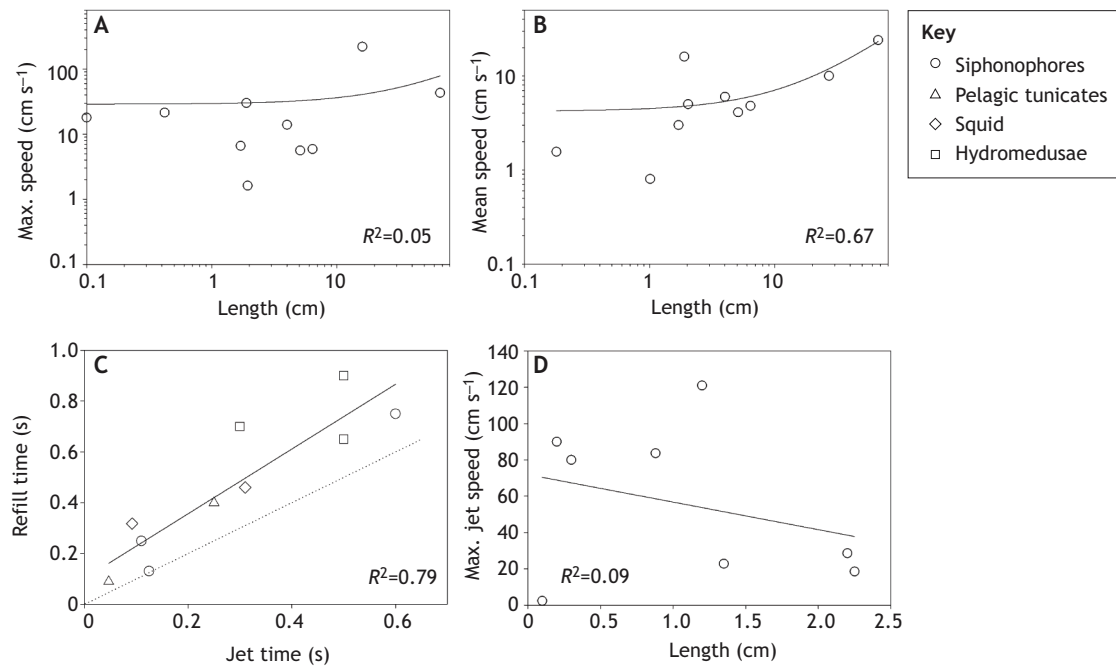


Fig. 8. Comparative propulsion features across jet-propelled taxa. (A) Maximum speed versus body length. (B) Speed versus body length. Note that the relationship between maximum speed and body size is very weak but a significant positive relationship exists for mean swimming speed and body size. (C) Jetting time versus refill time (s) shows that all species spend more time refilling than jetting but a siphonophore can achieve very close to 1:1 jet to refill ratio (dotted line indicates a 1:1 jet:refill ratio) (modified from Sutherland et al., 2019a). (D) Maximum jet speed vs body length comparisons. Data for panels A, B and D from: Sutherland and Madin, 2010a,b; Bone and Trueman, 1982, 1983, 1984, Bartol et al., 2009a,b; Anderson and Grosenbaugh, 2005; Packard, 1972; Sutherland et al., 2019a,b; Costello et al., 2015; Colin and Costello, 2002; Costello et al., 2019; Katija et al., 2015; Ansell et al., 1998.

speeds. This is likely the case for groups such as medusae, which are limited in muscle mass. In contrast, squid have thick, muscular mantles and have been recorded swimming at speeds approaching 8 m s^{-1} (Packard, 1966). However, unlike for some of the larger species of fish (e.g. Mako shark and sailfish), we do not have reliable estimates on swimming speeds for the larger species of squid (e.g. *Mesonychoteuthis hamiltoni*), so the upper bound of speed is currently unknown for jet-propelled species. However, given the fact that these animals can attain lengths in excess of 10 m, it is possible they could exceed the fastest fish in terms of absolute maximum speed. Squid do have the highest propulsive efficiency during the jetting phase (equivalent to rocket motor efficiency) of all currently measured jetting taxa with values that can exceed 90% (Anderson and Grosenbaugh, 2005; Bartol et al., 2009a), whereas the propulsive efficiency of salps is lower, with mean values ranging from 65 to 78% (Sutherland and Madin, 2010a). The Froude equation (see Glossary) has often been used as a measure of mechanical swimming efficiency; however, it is known to underestimate propulsive efficiencies of squid jet periods while simultaneously overestimating whole-cycle propulsive efficiency (Anderson and DeMont, 2000).

The Re of jet-propelled locomotion can vary by many orders of magnitude: early developmental stages of medusae (1 mm diameter *Sarsia tubulosa*) and squid [1.0 and 1.8 mm mantle length (ML) for Ommastrephid hatchlings and *D. pealeii*, respectively] jet effectively at an Re of 15 and 25, respectively (Bartol et al., 2009b; Katija and Jiang, 2013; Staaf et al., 2014), whereas adult squid can have Re of 160,000 (30 cm ML *D. pealeii*) (Anderson and Grosenbaugh, 2005) to roughly 800,000 (40 cm ML *Loligo vulgaris*) (Packard, 1972). The speed of the resulting jet has been measured for several species and shows no significant relationship with body size (Fig. 8), suggesting again that some jetting taxa are limited in their ability to generate

strong jets. Jet speeds range from $<3 \text{ cm s}^{-1}$ for paralarvae squid (*D. pealeii*) and a salp (*Cyclosalpa affinis*) to over 1 m s^{-1} for larger squid (*D. pealeii*) and siphonophores (*Namonia bijuga*). The frequency at which these jets occur is less variable than the magnitude and ranges from $<1 \text{ Hz}$ in some salps (*Salpa fusiformis* and *C. affinis*) (Trueman et al., 1984; Sutherland and Madin, 2010a) to $>4 \text{ Hz}$ for some siphonophores (e.g. *N. bijuga*) (Costello et al., 2015) and up to 5.4 Hz for paralarval squid (Staaf et al., 2014). This range in frequency of thrust-producing jets is lower than the range for swimmers that use other propulsive structures, such as fish, which can beat their tails in excess of 20 Hz (Bainbridge, 1958), and krill, which beat their pleopods in excess of 9 Hz (Thomasson et al., 2003).

The limited range in jet frequency may relate to the time it takes for fluid in a large cavity to be ejected through a small opening such that propulsion is efficient. This results in a jet period (ejection phase only) between 0.2 and 0.7 s for most jet-propelled species (Colin and Costello, 2002; Anderson and Grosenbaugh, 2005; Bartol et al., 2009a; Sutherland and Madin, 2010a; Costello et al., 2019). Only the siphonophores and paralarval squid exhibit a more rapid jet period of approximately 0.1 s (Bartol et al., 2009b; Staaf et al., 2014; Sutherland et al., 2019b), which also explains their ability to jet with the highest observed frequencies. Another factor that limits jetting frequency is that refilling cannot be done too rapidly or the animal risks losing significant forward momentum. This results in the majority of jet-propelled swimmers exhibiting a ratio of jetting time to refill time of less than 1 (Fig. 8). In single-jet animals, a longer relative jetting duration is required in order for the contraction phase to create a greater amount of forward thrust than the opposite flow during the refilling phase of swimming. However, in animals with multiple jets, such as siphonophores (e.g. *N. bijuga*), the refill time is almost the same as the jetting time (Sutherland et al., 2019b), because the high refill velocities are

reduced by a highly dynamic velum that rapidly increases in diameter to slow water intake speed greatly during refill.

Summary

Biological jetters have been shown to leverage several features – including flexible propulsive structures, variable jet orifice diameter, vortex interactions and energy capture during refill – that significantly enhance their propulsion capabilities over mechanical systems. However, to further elucidate the underlying mechanisms of aquatic jet propulsion, we need robust data in a comparative framework and the development of model species that can provide access to quantifying body–fluid interactions both inside and outside of the body cavity. To allow for better comparative data, a combination of rapidly evolving new methods, such as computational fluid dynamics (Krieg and Mohseni, 2013; Hou et al., 2020; Luo et al., 2020), robotics (Marut et al., 2012; Giorgio-Serchi et al., 2016), *in situ* diver-operated PIV (Sutherland et al., 2014) and even genetic techniques that can eliminate pigmentation in opaque jetting species (Crawford et al., 2020), will be crucial for success.

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Competing interests

The authors declare no competing or financial interests.

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