

2008

Medusan Morphospace: Phylogenetic Constraints, Biomechanical Solutions, and Ecological Consequences

John H. Costello
Providence College

Sean Colin
Roger Williams University, scolin@rwu.edu

John O. Dabiri
California Institute of Technology

Follow this and additional works at: http://docs.rwu.edu/fcas_fp



Part of the [Biology Commons](#)

Recommended Citation

Costello, J.H., Colin, S. P., Dabiri, J.H. 2008. Medusan Morphospace: Phylogenetic Constraints, Biomechanical Solutions, and Ecological Consequences. *Invert. Biol.* 127: 265-290.

This Article is brought to you for free and open access by the Feinstein College of Arts and Sciences at DOCS@RWU. It has been accepted for inclusion in Feinstein College of Arts & Sciences Faculty Papers by an authorized administrator of DOCS@RWU. For more information, please contact mwu@rwu.edu.

Medusan morphospace: phylogenetic constraints, biomechanical solutions, and ecological consequences

John H. Costello,^{a,1} Sean P. Colin,² and John O. Dabiri³

¹ Biology Department, Providence College, Providence, Rhode Island 02819, USA

² Environmental Sciences, Roger Williams University, Bristol, Rhode Island 02809, USA

³ Graduate Aeronautical Laboratories and Bioengineering, California Institute of Technology, Pasadena, California 91125, USA

Abstract. Medusae were the earliest animals to evolve muscle-powered swimming in the seas. Although medusae have achieved diverse and prominent ecological roles throughout the world's oceans, we argue that the primitive organization of cnidarian muscle tissue limits force production and, hence, the mechanical alternatives for swimming bell function. We use a recently developed model comparing the potential force production with the hydrodynamic requirements of jet propulsion, and conclude that jet production is possible only at relatively small bell diameters. In contrast, production of a more complex wake via what we term rowing propulsion permits much larger sizes but requires a different suite of morphological features. Analysis of morphometric data from all medusan taxa independently confirms size-dependent patterns of bell forms that correspond with model predictions. Further, morphospace analysis indicates that various lineages within the Medusozoa have proceeded along either of two evolutionary trajectories. The first alternative involved restriction of jet-propelled medusan bell diameters to small dimensions. These medusae may be either solitary individuals (characteristic of Anthomedusae and Trachymedusae) or aggregates of small individual medusan units into larger colonial forms (characteristic of the nectophores of many members of the Siphonophorae). The second trajectory involved use of rowing propulsion (characteristic of Scyphozoa and some hydromedusan lineages such as the Leptomedusae and Narcomedusae) that allows much larger bell sizes. Convergence on either of the differing propulsive alternatives within the Medusozoa has emerged via parallel evolution among different medusan lineages. The distinctions between propulsive modes have important ecological ramifications because swimming and foraging are interdependent activities for medusae. Rowing swimmers are characteristically cruising predators that select different prey types from those selected by jet-propelled medusae, which are predominantly ambush predators. These relationships indicate that the different biomechanical solutions to constraints on bell function have entailed ecological consequences that are evident in the prey selection patterns and trophic impacts of contemporary medusan lineages.

Additional key words: morphology, hydrodynamics, emergent properties, plankton

Medusae are a diverse array of planktonic cnidarians occupying all of the world's oceans and some freshwater habitats. The Cnidaria is an ancient clade with origins in an early radiation within the basal lineage that gave rise to the rest of the animal kingdom (Valentine 2004). Although the exact relation-

ship between the ancient Cnidaria and the rest of the Metazoa remains unresolved, it is clear that the cellular inheritance of medusae rivals even the sponges in the restricted number of cell types available for body construction (Bonner 1965; Valentine et al. 1994). Yet, unlike sponges, medusae are characterized by the evolutionary innovation of muscle-powered motility. Diversification of this muscular body plan allowed medusae to radiate into a variety of ecological niches within planktonic and some benthic

^a Author for correspondence.

E-mail: costello@providence.edu

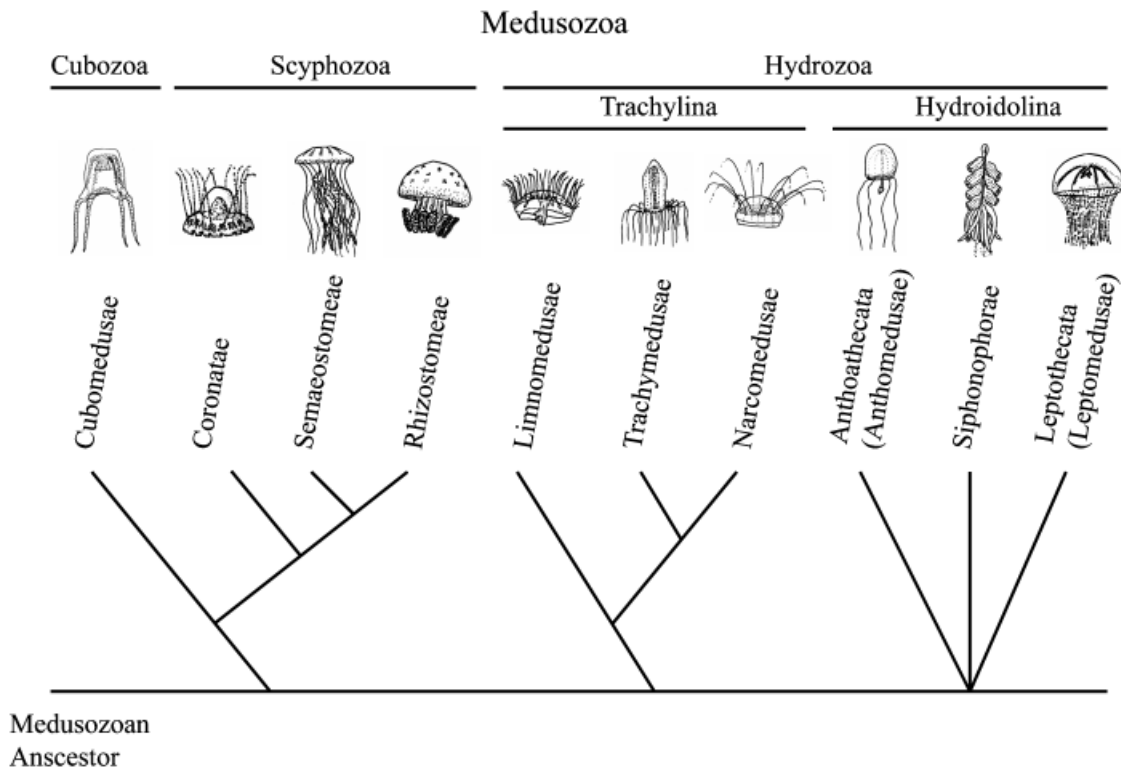


Fig. 1. Medusan diversity illustrating phylogenetic hypotheses based on Collins et al. (2006). Only extant lineages containing medusae are shown. Parenthetical lineage names reflect historical nomenclature when referring to the medusan portions of life cycles rather than current systematic nomenclature. Medusozoan drawings after Ford et al. (1997), Colin & Costello (2002), and Colin et al. (2006).

marine environments. However, the limited cellular repertoire of the medusae also provides the opportunity to examine the means by which a major animal lineage resolved constraints dictated by its ancestry. By examining both constraints and evolutionary solutions, we seek to define basic principles that organize the structure and function of medusae.

Medusan diversity

Medusae are members of the subphylum Medusozoa, which is characterized by possession of a medusan stage during the life cycle of many members of the constituent classes. The extant medusa-producing taxa within the Medusozoa include the classes Hydrozoa, Scyphozoa, and Cubozoa. A fourth class, the Staurozoa, is an early medusozoan taxon (Collins et al. 2006; Van Iten et al. 2006) but produces no medusae.

Although possession of a medusa stage characterizes many members of the Medusozoa, the form and organization of medusae vary substantially between and even within the major medusozoan lineages. Among the extant medusozoans, the Cubozoa and

Scyphozoa bear a number of shared characters (Marques & Collins 2004; Collins et al. 2006) and appear to form an early medusozoan clade (Collins et al. 2006). The Cubozoa may represent the oldest class (Fig. 1) and it contains medusae noted for their box-like shape (often known as “box jellies”). The Cubozoa is not as species rich as the other medusozoan classes (Mianzan & Cornelius 1999) and are generally thought to move via jet propulsion (Gladfelter 1973; Shorten et al. 2005) and capture prey on extended tentacles (Larson 1976). The largest medusae are found in the Scyphozoa, which includes three orders: Coronatae, Semaestomeae, and Rhizostomeae. Among these, the latter two orders are the most diverse. Members of these orders possess developed oral arms that often extend well below the margin of the swimming bell. Among the Rhizostomeae, these oral arms are fused into complex oral arm cylinders containing hundreds to thousands of small mouthlets used to consume prey.

The most diverse medusozoan class, the Hydrozoa, is comprised of two major clades, the Trachylina and the Hydroidolina, that have each radiated into several medusa-producing lineages (Collins et al.

2006; Fig. 1). The lineages within Trachylina appear to be well differentiated as the Limnomedusae, Trachymedusae, and the Narcomedusae. The second hydrozoan clade, the Hydroidolina, has produced the most species-rich lineages, and the phylogenetic relationships between some of these groups remain incompletely resolved at present (Collins et al. 2006). We have chosen to use nomenclature that refers to the medusan component of the life history and is therefore congruent with the medusan literature, rather than more recent and systematically appropriate nomenclature that is less readily connected to the functional ecology literature. Hence, our use of the terms Anthomedusae and Leptomedusae refer to the taxa Anthoathecata and Leptothecata (Marques & Collins 2004; Collins et al. 2006), respectively (as in Fig. 1). The Hydroidolina additionally contains a taxon that possesses clonal aggregations of medusae as components of larger colonies—the Siphonophorae (Fig. 1).

Life-history organization within the Medusozoa varies substantially, with some species maintaining holoplanktonic life histories while a large number alternate between benthic, asexually reproducing forms, and sexually reproducing medusae (e.g., see Boero et al. 1992). Although medusae are frequently independent, sexually mature, feeding individuals, their function may be limited to brief periods of free swimming before reproduction. In some forms, termed medusoids, the medusa form may remain attached to the colony and is functionally reduced solely to reproduction.

Paralleling the diverse shapes and life-history variations, medusae extend through a spectrum of sizes spanning three orders of magnitude for mature individuals. Sexually mature hydromedusae include species as small as 2.0 mm in diameter while some adult scyphomedusae may exceed 2.0 m in diameter (Omori & Kitamura 2004). Siphonophoran colonies consisting of hundreds of individual members may extend tens of meters in length (Tregouboff & Rose 1957).

The taxonomic diversity of the Medusozoa, combined with the array of sizes, shapes, and clonal organizations of its members, has produced a diverse collection of extant medusae. Our goal is identification of unifying patterns that underlie this variation.

Patterns of swimming bell design within the Medusozoa

One of the chief defining characters of a medusa is the possession of a swimming bell. Planktonic motility alone does not distinguish the medusozoans

because many non-medusan cnidarians possess planular larval stages, which swim via cilia. However, possession of a muscular swimming bell capable of propulsion is unique to the Medusozoa. For many medusae, it is also the largest portion of the body and houses most, if not all, of the digestive, reproductive, and neural systems. Its dominance as an essential medusan structure makes the swimming bell an appropriate first character for describing medusan morphological patterns.

Is there an appropriate single variable that can be used to describe patterns of swimming bell morphology among medusae? Conveniently, the radial symmetry of a medusan bell allows us to simplify the shape from three to two dimensions by describing the bell as a hemiellipsoid with a measurable aspect ratio. This approach was first used for hydrodynamic analyses of bell shape by Daniel (1983, 1985) and, subsequently, by others (Colin & Costello 1996, 2002) for comparison of swimming performance among medusae possessing widely divergent bell shapes. In these cases, bell shape was quantified as the fineness ratio (F), where bell height (h) is compared with bell diameter (d) as $F = h/d$. High bell fineness values (>1.0) represent streamlined, or prolate, shapes, whereas low values (<0.5) represent flattened, or oblate, shapes.

We used the concepts of theoretical morphospace analysis (Raup & Michelson 1965) to organize patterns of medusan bell-shape variations. A morphospace refers to the range of morphological variability within a multidimensional space produced by varying parameter values that describe the geometric forms of a taxon (McGhee 1999). We generated a medusozoan morphospace by compiling average bell diameter and height values published or illustrated in monographs describing hydromedusae (Kramp 1961), scyphomedusae (Mayer 1910), or siphonophores (Pugh 1999). Combinations of variables that share a parameter, such as bell diameter in this analysis, should be considered with caution because of the potential to generate spurious relationships without biological significance. However, with the use of appropriate bounding considerations, the use of such ratios can be of substantial biological value (Prothero 1986; Prairie & Bird 1989). The empirically determined natural distribution of bell fineness among medusae is limited to a minimum of 0.1 and a maximum of 3.5 (Kramp 1961). When these values are set as the limits of bell height relative to bell diameter, and distributed evenly across the range of common bell diameter, an otherwise random combination of bell heights and diameters results in a relatively homogeneous distribution of bell fineness values that

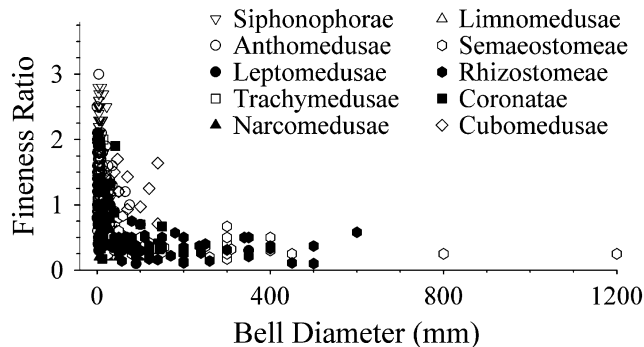


Fig. 2. An empirically determined medusan swimming bell morphospace. Data on swimming bell dimensions of extant species were taken from Kramp (1961), Mayer (1910), and Pugh (1999).

might be expected to accompany the range of bell diameters for medusae in nature.

However, the actual pattern of bell fineness as a function of bell diameter is not randomly or homogeneously distributed among medusae (Fig. 2). Instead, the observed pattern found in nature, or the empirical morphospace based on the parameters of bell size and shape, exhibits two outstanding non-random traits. First, most medusae are small relative to the full range of the medusan morphospace and, second, bell shape exhibits an apparent dependence on bell size. At small bell diameters (<50 mm), bell shape is highly variable between oblate and prolate forms. However, at larger bell diameters (>200 mm), only oblate bell forms exist in nature. As a result, there is a large region of potential bell size and shape combinations unoccupied by any medusa. We do not rule out the possibility that some other probability distributions may exist (e.g., gamma distribution) that could produce similar distributions by randomly combining the variables of bell height and diameter. However, we suggest that the combinations of medusan bell heights and diameters are not random in nature and that the large unoccupied morphospace region is unlikely to have remained empty over the long evolutionary history of the Medusozoa unless constraints have prevented its exploitation. Such constraints on medusan bell form appear to be size scale dependent and are relaxed at small bell diameters but inflexible at large bell diameters.

What factor(s) might constrain this medusozoan morphospace? Our approach to this question is influenced by two fundamental functional considerations. First, the chief function of the medusan bell is to provide thrust during swimming. Therefore, changes in bell shape affect swimming and activities that depend on swimming. Second, comparison with

other animal swimmers having similar means of propulsion indicates that the prohibited region of the medusozoan morphospace is unique to the medusae. For example, both medusae and squid are frequently characterized as jet-propelled swimmers (Mackie 1990; Vogel 1994). Large, prolate morphologies are found among squid, such as members of the genus *Architeuthis* that reach lengths of >18 m (Roper & Boss 1982). However, such large, prolate jetting morphologies do not occur in the medusan morphospace. Thus, our approach to understanding patterns of size and shape among the Medusozoa has focused on the mechanisms of medusan swimming and the unique characteristics of this taxon that might influence morphological patterns. But what factors might constrain swimming and how can they be evaluated quantitatively?

Foundations of morphological pattern: swimming mechanics

Swimming by any organism involves the interaction between the propulsive forces originating from the internal actions of the organism and the forces resisting motion from the surrounding fluid environment. Our approach was to compare the magnitude of the internal, physiologically dominated forces with that of the external, hydrodynamically dominated forces (Daniel 1995). Medusan swimming mechanics have most commonly been analyzed based on jet propulsion by either hydromedusae (Daniel 1983, 1985; DeMont & Gosline 1988a,b,c; Colin & Costello 1996, 2002; Dabiri et al. 2006) or siphonophores (Bone & Trueman 1982). These studies have established a framework for understanding the process of medusan swimming and provided a basis for a quantitative description of swimming by a hydrozoan medusa. An idealized hydromedusan bell resembles a hollow sphere (Fig. 3). The interior of the sphere, or subumbrellar cavity, is continuous with the exterior fluid environment via a narrow aperture. A thin flap of elastic tissue, termed the velum, surrounds the aperture. The aperture diameter can constrict or expand via muscles within the velum (Gladfelter 1972a). Swimming via jet propulsion (Fig. 4) involves contraction of circular muscle fibers lining the subumbrellar surface (and therefore termed subumbrellar muscles). Shortening of the subumbrellar muscles contracts the bell and reduces the subumbrellar volume. This action forces fluid out of the bell as a jet through the velar aperture. Simultaneously, the force of the exiting jet produces thrust and propels the medusa forward (Daniel 1983; Dabiri et al. 2006).

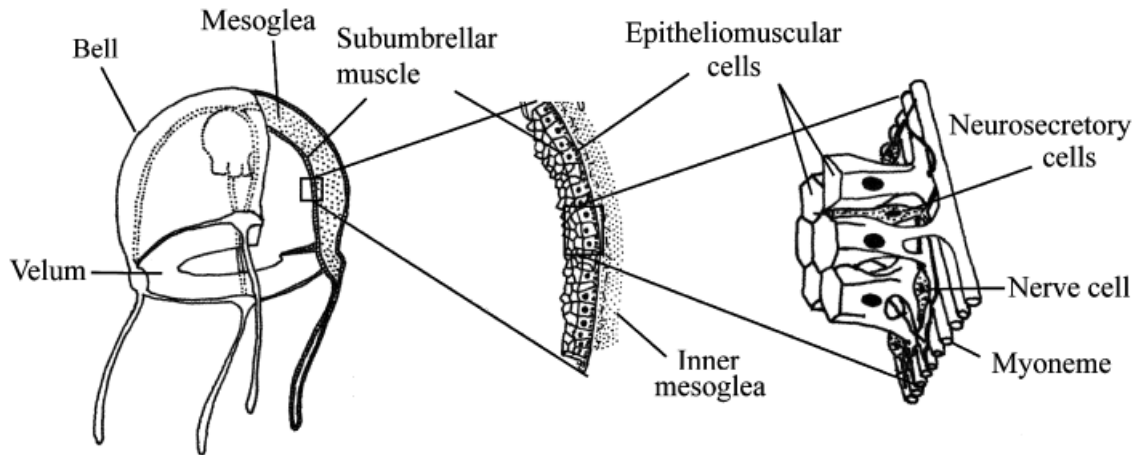


Fig. 3. Hydromedusan swimming bell and muscle fiber structures (after Seipel & Schmid 2005; Brusca & Brusca 2003).

The force that the subumbrellar muscles can produce is directly related to the pressure (force/subumbrellar area) that expels the fluid through the velar aperture and to the thrust resulting from the jet production (DeMont & Gosline 1988a). Subsequently, the subumbrellar muscles relax, and the bell returns to its original relaxed form due to antagonistic interactions of elastic fibers within the mesoglea of the medusan bell (Megill et al. 2005). Bell relaxation is accompanied by refilling of the subumbrellar cavity with fluid. Bell contraction is more rapid than bell relaxation and the asymmetry in the timing of the two phases results in greater fluid velocities, and hence momentum, during bell contraction than during bell relaxation. As a result, swimming by hydromedusae involves pulsed, unsteady motion (Daniel 1983).

Medusan subumbrellar muscles

The structure and function of medusan muscular contraction provides a potential mechanism that may limit the range of bell shapes possible at larger bell diameters. Medusan subumbrellar muscular tissues share many traits with striated muscles that are involved in motion of most other metazoans. From a molecular perspective, sequence analysis of muscle-specific myosin heavy-chain genes, from striated muscle fibers of the hydromedusa *Podocoryne carnea* Sars 1846, strongly resemble those of bilaterian striated muscle tissues (Seipel & Schmid 2005). Structurally, medusan subumbrellar myofibrils show a banding structure similar to vertebrate skeletal muscles (Bolsterli 1977; Schuchert et al. 1993), and sarcomere lengths of medusan subumbrellar myofibrils (2–3 μm ; Chapman 1974) are similar to those of

vertebrate skeletal muscles (2.0–2.8 μm ; Biewener 2003). Sarcomere length is generally related to force production (Vogel 1994; Biewener 2003), and maximum isometric stress estimates of medusan subumbrellar muscles (0.13–0.20 N mm^{-2} ; Bone & Truman 1982; DeMont & Gosline, 1988b) are of a magnitude similar to those of frog and rat leg muscles (0.15–0.36 N mm^{-2} ; Alexander 2003). The molecular, structural, and functional similarities between medusan striated muscle fibers and those of higher metazoans suggest that force production patterns of medusan swimming muscle tissue might parallel those of higher metazoan striated muscles.

However, despite these similarities, medusan subumbrellar muscle tissues are organized in a fundamentally different pattern from the striated muscles used for movement in other animal phyla. The most important distinction involves the epithelial nature of cnidarian muscular tissues. Myocytes of most animal muscle tissues are elongated, multinucleate entities that are highly specialized for muscular contraction and, along with enervating motor neurons, are bundled into motor units of variable thickness and length. Although dynamics of contractions differ between muscle types (Alexander 2003; Biewener 2003), the conservative nature of actin and myosin in striated muscles of a variety of animal phyla results in force generation that is relatively similar per unit of muscle cross-sectional area. Consequently, thicker layers of muscle fibers typically generate greater total force (reviewed in Biewener 2003).

In contrast to the striated myocytes of most metazoans, medusan subumbrellar myofibrils are restricted to epithelial cells termed epitheliomuscular cells (Fig. 3). These cells are typically cylindrical or squamous in shape, and myofibrils are located in the basal

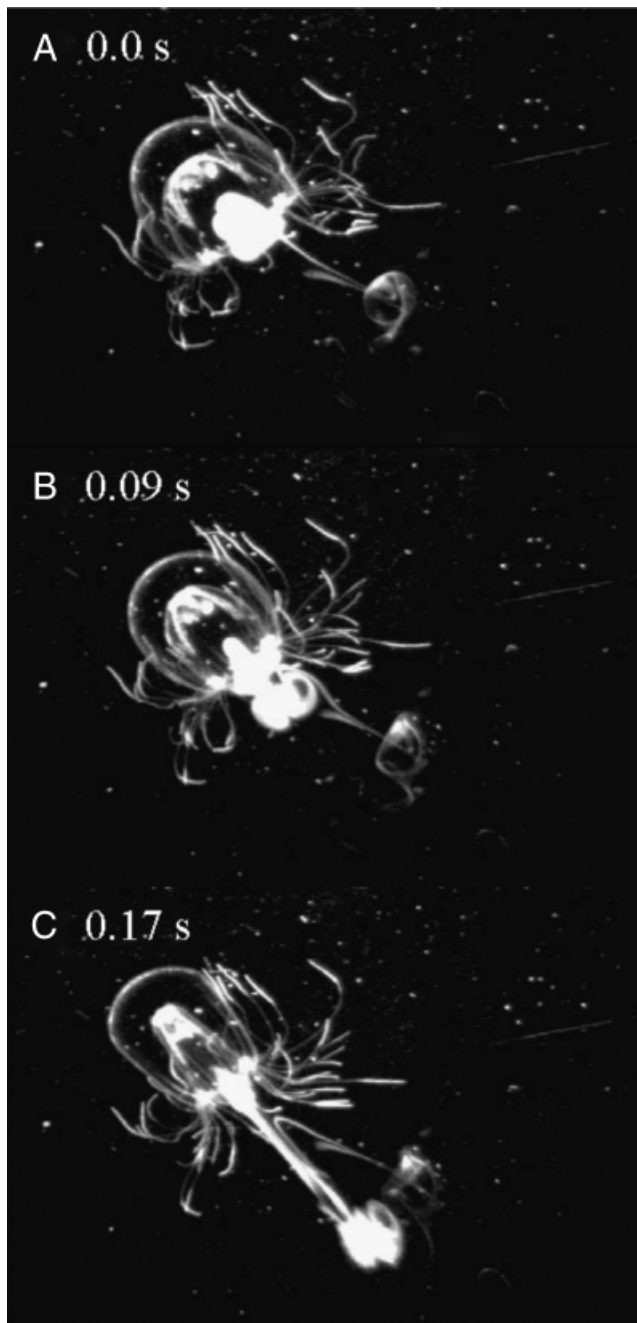


Fig. 4. Time course of jet propulsion by the anthomedusa *Nemopsis bachei*. The pulsation cycle begins with a fully relaxed, expanded bell (7.9 mm relaxed bell diameter) (A). Initially, the subumbrellar cavity encircles a large fluid volume that is partially marked by dye. Jet production entails contraction of the subumbrellar muscles and rapid reduction of the subumbrellar volume, accompanied by expulsion of a fluid bolus through the velar aperture (B). Note the central jet ejected through the velar aperture (C) and the jet's dominant starting but negligible stopping vortex (described by Dabiri et al. 2006).

portion of the cell only (Fig. 3). Most importantly, the epitheliomuscular cells lining the medusan subumbrellar surface are only one cell thick. Consequently, the myofibrils available to generate force for bell contraction are limited in depth, and hence cross-sectional area, to this single cell layer. Bundles of myofibrils formed at the basal ends of epitheliomuscular cells encircle the subumbrellar cavity, and it is the contraction of these circularly oriented muscle fibers that reduces bell volume and produces jet thrust (Gladfelter 1973). Myofibril thickness of even large, muscular scyphomedusae, such as *Cyanea capillata* LINNAEUS 1758, is thin (3.5 μm ; Gladfelter 1972b).

In scyphomedusae, this myofibrillar sheet may be folded and interdigitates with the mesogleal region (Gladfelter 1972b; Anderson & Schwab 1981), thereby contributing a secondary means of increasing muscle cross-sectional area. Such folding can result in an approximately fivefold increase in the effective cross-sectional area of myoepithelial tissues (Gladfelter 1972b). Although evident within some scyphomedusae, epitheliomuscular cell folding does not appear to be widespread among medusan lineages and has been documented within only a few hydromedusae and no cubomedusae (Gladfelter 1973; Satterlie et al. 2005). The restriction of striated myofibrils to epithelial cells is a cnidarian trait (Chapman 1974) and the limited cross-sectional area of subumbrellar epitheliomuscular tissues represents a phylogenetic constraint upon force production by swimming medusae.

Force production and bell dimensions

The constrained architecture of medusan subumbrellar muscles critically influences size-dependent patterns of medusan bell morphology. The muscular contractile forces required to achieve jet propulsion do not scale favorably with increasing medusa size for several reasons. The major reason is that for an idealized hemispherical hydromedusa, muscular capacity to be used for force generation increases as a *linear* function of bell diameter (D) because muscle fiber depth is phylogenetically constrained to one cell layer, and muscular cross-sectional area is then only proportional to the *circumference* of the subumbrellar cavity. In contrast, the hydrodynamic force requirements for accelerating the mass of fluid in a jet used for propulsion increase as a *cubic* function of bell diameter (D^3) because they depend on the *volume* of the subumbrellar cavity. Hence, the force required for jet propulsion increases with animal size more rapidly than the available physiological force.

A similar force-scaling pattern dictates the upper limit on the size of squid, another animal known to use jet propulsion (Pauly 1997; O'Dor & Hoar 2000). An alternative reason why contractile forces do not scale favorably with size is that the pressure in the subumbrellar cavity that is used to expel the fluid jet is caused by tension in the bell due to muscle contraction. However, in accordance with Laplace's law, the amount of pressure created per unit bell tension decreases with increasing bell diameter (for a sphere: pressure = tension/radius). Further, the amount of force available for jet production is further diminished because only a portion of the force generated by contraction of the subumbrellar muscle sheet is available to generate hydrostatic pressure on the subumbrellar fluid and generate a fluid jet. A substantial fraction does not directly impact fluid jet production (DeMont & Gosline 1988b; Megill et al. 2005) but is instead stored as elastic recoil energy within the mesoglea.

Hydrodynamic patterns of medusan swimming

The prevailing models of medusan swimming assume that fluid interactions rely on simple jet propulsion and that thrust forces for swimming are generated solely during the swimming power stroke. Following bell contraction, a single vortex ring is formed in the wake (termed the "starting" vortex) and the momentum imparted to the fluid during this power stroke provides the force available for forward motion (Fig. 4; see Dabiri et al. 2006). The force available for thrust is directly related to, but less than, the force of the contracting muscles.

Observations of swimming by oblate medusae have indicated more complex wake structures than those of jetting medusae. The contraction phase of swimming by oblate medusae generates a starting vortex similar to that of traditional jetting medusae. However, during the relaxation phase, the paddling motion of the bell causes the formation of a second vortex ring with opposite rotational orientation relative to the starting vortex termed the "stopping" vortex. Stopping vortices are either absent or negligible in the simple form of jet propulsion described previously (Fig. 5; Dabiri et al. 2005).

Stopping vortex ring production fundamentally affects the force requirements of medusan swimming. Because the force required to create this recovery phase vortex is directed opposite to the force applied during the power phase of swimming, the stopping vortex retards the starting vortex forward velocity. Simultaneously, the net time-averaged force required for locomotion is reduced. Importantly, the force to

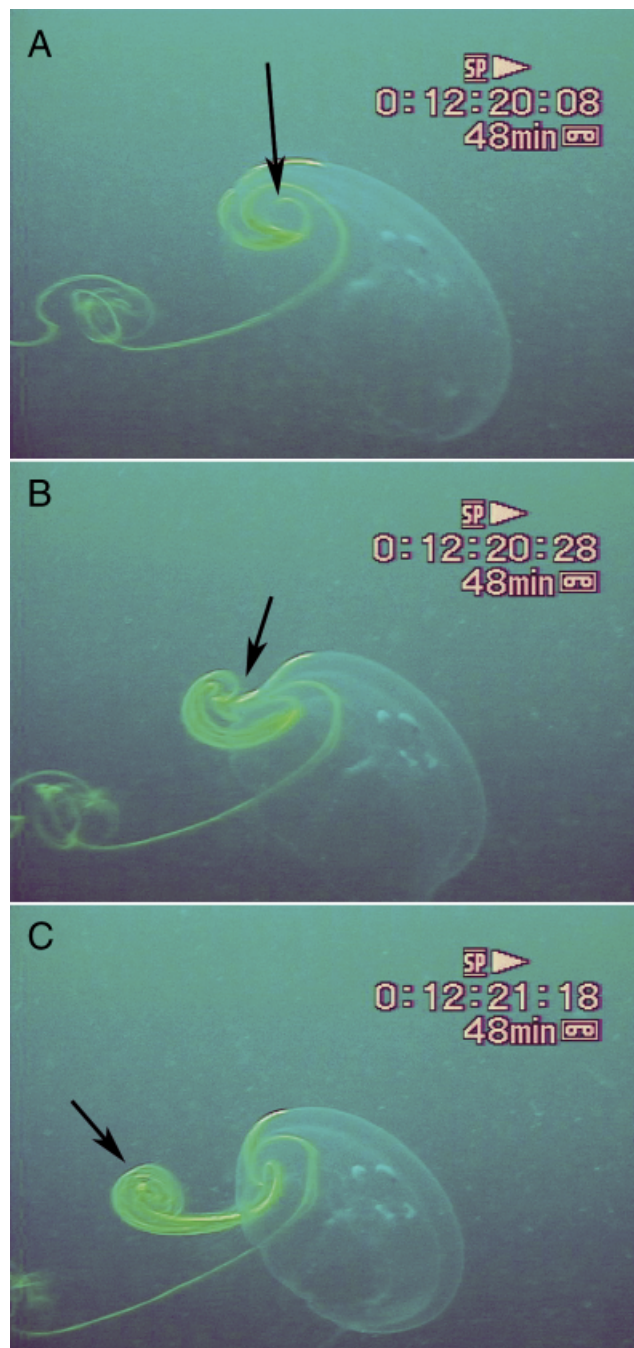


Fig. 5. Vortices produced during swimming by *Aurelia aurita*, a rowing-propelled scyphomedusae. **A.** Relaxation phase during which the formation of the stopping vortex is visible inside the bell. **B.** Start of the contraction phase during which the starting vortex is forming from fluid originating both inside and outside the bell. **C.** End of contraction phase with the starting vortex superstructure trailing in the wake (the vortex from the previous pulse is visible just behind it). Arrows indicate the described vortices.

generate this stopping vortex during the recovery phase arises from elastic strain storage in the bell (DeMont & Gosline 1988a,b,c; Megill et al. 2005). Because this propulsive mode generates both stopping and starting vortices during swimming, we term it rowing propulsion to distinguish it from jet propulsion.

The interactions of the starting and stopping vortices in the wakes of oblate medusae influence the energetic efficiency of medusan swimming. Wake dynamics determine the energy requirements of propulsion and therefore the force requirements of swimming. The magnitude of the energy lost to the wake during swimming, also known as induced drag, is directly proportional to the amount of rotational motion in the medusan wake. As described previously, the stopping vortex interacts with the contraction-phase starting vortex of the next swimming cycle, reducing the total rotational motion in the water behind the animal (Dabiri et al. 2005). This motion-canceling interaction between the starting and stopping vortices in the rowing swimming mode acts to reduce the energy lost in the wake, thereby increasing the swimming efficiency.

Interestingly, a similar energy-recovery mechanism has been identified in the swimming of bony fishes (Ahlborn et al. 1991, 1997). The existence of such energy-saving behaviors has not been appreciated previously in lineages as primitive as medusae, but can strongly influence the energetics of swimming and therefore merits evaluation when estimating the muscular force requirements of medusan swimming. An important consequence of these wake dynamics is that there is a smaller difference between forward-swimming velocities and wake velocities of oblate medusae compared with prolate medusae (Colin & Costello 2002). Consequently, the Froude propulsion efficiencies of rowing medusae are high compared with jetting medusae (Ford et al. 1997).

Modeling medusan propulsion

Here, we used a model developed by Dabiri et al. (2007) that compared the forces produced by medusae with the forces required for propulsion. Specifically, the model compared the forces generated by the muscles (F_M) during bell contraction with the hydrodynamic forces required for jet-propelled locomotion (F_J). In order to swim, F_M must be $\geq F_J$. The parameter F_M is the product of muscle cross-section area and the isometric stress of the muscle tissue; therefore, its magnitude is a function of bell size and shape. F_J is based on the model of Daniel (1983) for jet propulsion and is the force associated with the

fluid jet generated during bell contraction. Therefore, it is equal to the force required to expel fluid from a subumbrellar cavity of a particular volume through an oral cavity of a particular area. The magnitude of F_J is not only related to the volume of the subumbrellar cavity and oral cavity exit area but also the rate and amount that they change throughout the contraction (Daniel 1983; Dabiri et al. 2006, 2007).

The size-limiting curve $F_M = F_J$ for medusa shape (quantified by the fineness ratio $f = \text{bell height } H / \text{bell diameter } D$) versus bell diameter D for various swimming frequencies is plotted in Fig. 6A (dotted-dashed line). These limiting upper-bound curves illustrate that for most bell shapes (i.e., fineness ratios), medusae > 10 cm cannot produce a sufficient muscle force to swim via jet propulsion.

When the effect of the stopping vortex is included in the model, the net time-averaged locomotive force F_L required for medusan swimming can be approximated by the equation

$$F_L = \frac{T_J}{T} F_J - \frac{T_R}{T} F_R \quad (1)$$

where T_J and T_R are the durations of the jetting and relaxation phases, respectively, T is the duration of the entire swimming cycle (i.e., $T = T_J + T_R$), and F_J and F_R are the locomotive forces occurring during the jetting and relaxation phases, respectively. F_R is estimated from the strength of the stopping vortex (Dabiri et al. 2007). The locomotive forces during jetting and bell relaxation are weighted in equation (1) according to the fraction of the swimming cycle that is spent in each phase. The negative sign before the second term accounts for the direction of the relaxation phase force opposite to the contraction phase force.

With additional derivation (see Dabiri et al. 2007), equation (1) can be used in conjunction with the physiological constraint, $F_L \leq F_M$, to predict the morphological distribution of medusa fineness ratio f versus bell diameter D :

$$f \leq \sqrt{\frac{9}{4\pi\rho} \left(\frac{\pi\rho}{32} + \frac{\sigma_M t_M}{2g(\omega)D^3} \right)} \quad (2)$$

In equation (2), ρ is the density of the water, σ_M is the maximum isometric stress produced by the subumbrellar muscle layer, t_M is the thickness of the muscle layer, and $g(\omega)$ is a trigonometric function of the swimming frequency (Dabiri et al. 2007). Using an average of reported physiological and kinematic values (Gladfelter 1972a,b; Bone & Trueman 1982) for σ_M (160 kPa), t_M of 3.5 μm (Gladfelter 1972a,b; Anderson & Schwab 1981), and $g(\omega)$, Fig. 6A (solid

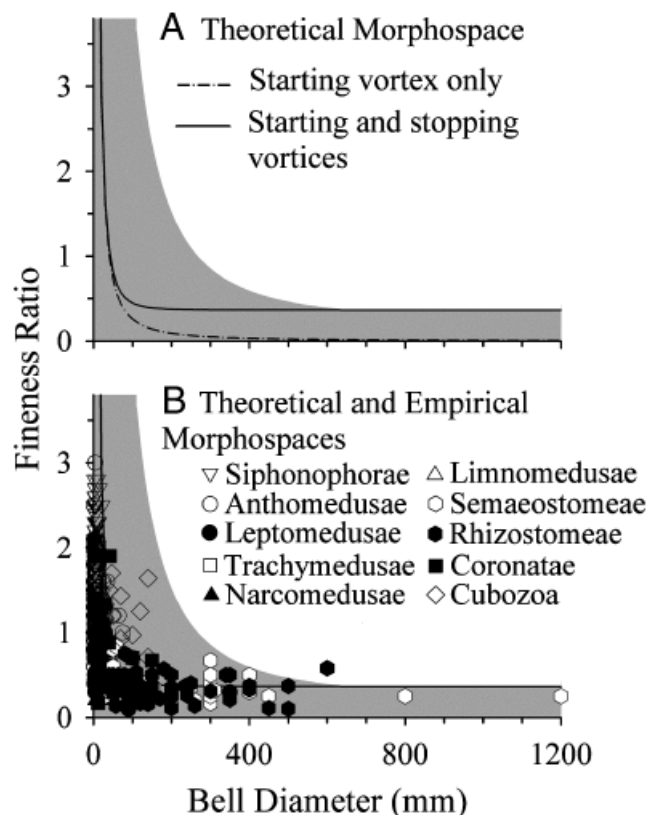


Fig. 6. Model (A) compared with empirical (B) medusan morphospaces. The model morphospace is bounded (shaded region) by bell diameter and fineness conditions for which the time-averaged locomotive force (F_L) \leq potential muscular force (F_M). The solid line in both panels indicates the case of a medusa pulsing at a rate of 2 Hz, when locomotive forces associated with the starting vortex created during the jetting contraction phase (F_J) and generated during the stopping vortex of the bell relaxation phase (F_R) are both included in the calculation of F_L . When the locomotive force associated with the stopping vortex of the relaxation phase is ignored (dashed line in [A]), medusae larger than ~ 200 mm in diameter cannot produce sufficient muscular force to swim. The shaded region represents model limits when the bell pulsation rate is varied between 0.5 and 3.0 Hz and isometric stress of the muscular tissue is varied by an order of magnitude of the mean estimate (i.e., $\pm 0.1F_M$ or $10F_M$). Symbols represent the average diameter and fineness values of species within various medusan lineages (as in Fig. 2B).

line) plots the predicted morphological distribution of fineness ratio versus bell diameter for medusae that create both stopping and starting vortices during pulsation.

The new model predicts that bell diameters of prolate, jet-propelled medusae are limited by physiological constraints on force production by swimming muscles, but that oblate rowing-propelled medusae

are physiologically capable of propulsion over a wide range of bell diameters. This is because medusae with lower fineness ratios create sufficient stopping vortices during bell relaxation to effectively reduce the forces required for locomotion. Consequently, oblate medusae of large bell diameters are able to generate sufficient muscle forces to swim. Because medusae are known to possess a variety of mesogleal conformations that might affect the transmission of contractile muscle fiber force (e.g., Megill et al. 2005), and neural organizations that influence contraction timing (e.g., Satterlie 2002), variability in the muscular force that is available for bell contraction is estimated in Fig. 6A. This region is estimated by varying the isometric stress values used in the model by two orders of magnitude (i.e., $0.1F_M$ or $10F_M$) and the pulsation rate over contraction frequencies from 0.5 to 3 Hz.

Model function

The predicted morphological distribution of fineness ratio versus bell diameter for various swimming frequencies is plotted in Fig. 6, which compares these predictions with the morphological data. The model predictions correspond well with the observed bounds on the morphological distribution of medusae. If the formation of the stopping vortex is neglected in the model, as in the traditional jet propulsion perspective, Fig. 6A also shows that the largest medusae would appear to violate the constraints imposed by the available muscular capacity.

The model developed is especially useful because of the small number of input parameters required to make predictions. Nonetheless, it relies on a quasi-steady approximation of transient swimming dynamics and muscle mechanics. There may potentially exist variations in muscle performance across medusan lineages due to differences in muscle myosin isoforms, twitch durations, shortening velocities, sarcomere geometries, etc. (Biewener 2003). Likewise, as noted previously, differences in both mesogleal responses to muscle fiber contraction (e.g., Megill et al. 2005) and neural organization (Satterlie 2002) may influence swimming performance of individual medusan species. Models explicitly incorporating effects such as these have been shown to require a large number of input parameters (Daniel 1995), which detracts from the goals of the present model. However, Fig. 6B (shaded region) shows that even if the combined effect of these variations were to change the nominal physiologically available force computed above by two orders of magnitude, the predicted morphological distribution would be relatively

unaffected. Mathematically, this robustness of the model follows from the relatively weak (i.e., square-root) dependence of the limiting curves on the physiological force (Equation 2).

We suggest that this model and the supporting morphological data indicate that animal–fluid interactions provide organizing principles underlying the morphological and propulsive design of medusae. We view these principles as setting broad limits on the potential range of medusan bell forms. Within these limits, a variety of other factors, such as the type of neural organization controlling pulsation and the interactions of muscles with the elastic strain storage traits of the mesoglea, contribute to variations in medusan form and function. An important outcome of these broad patterns is that, amidst considerable apparent diversity in medusan form, two essential evolutionary trajectories have emerged during medusan evolution: medusan bells may either be small and jet propelled, or oblate and rowing propelled.

Lineage-dependent solutions to propulsive constraints

Morphospace patterns of medusan taxa indicate that propulsive constraints on bell morphology have been negotiated differently between medusan lineages. For example, within the Hydrozoa, both anthomedusan and trachymedusan species are commonly considered to be jet propelled (Gladfelter 1973), and bell dimensions of both lineages correspond well with force model predictions for small, jet-propelled medusae (Fig. 7A). The evolutionary trajectories of these lineages have entailed a simple solution to force production constraints—bell size has been maintained within limits, allowing adequate jet thrust production for swimming. Consequently, these lineages consist of small, solitary individuals. The Siphonophorae, a lineage closely allied to the Anthomedusae within the Hydroidolina (Bouillon & Boero 2000; Marques & Collins 2004; Collins et al. 2006), extended this design solution to the level of colonial rather than solitary organization. Siphonophoran swimming bells (termed nectophores) maintain size limits compatible with the constraints of jet thrust production (Fig. 7B). However, large aggregate colonies can be propelled by chaining multiple small nectophore units together into a coordinated propulsive whole. Hence, the colonial organization of siphonophores typically maintains a small size for individual nectophores, but allows a large aggregate size of the colony. Consequently, colonial siphonophores can measure many meters in length (Tregouboff & Rose

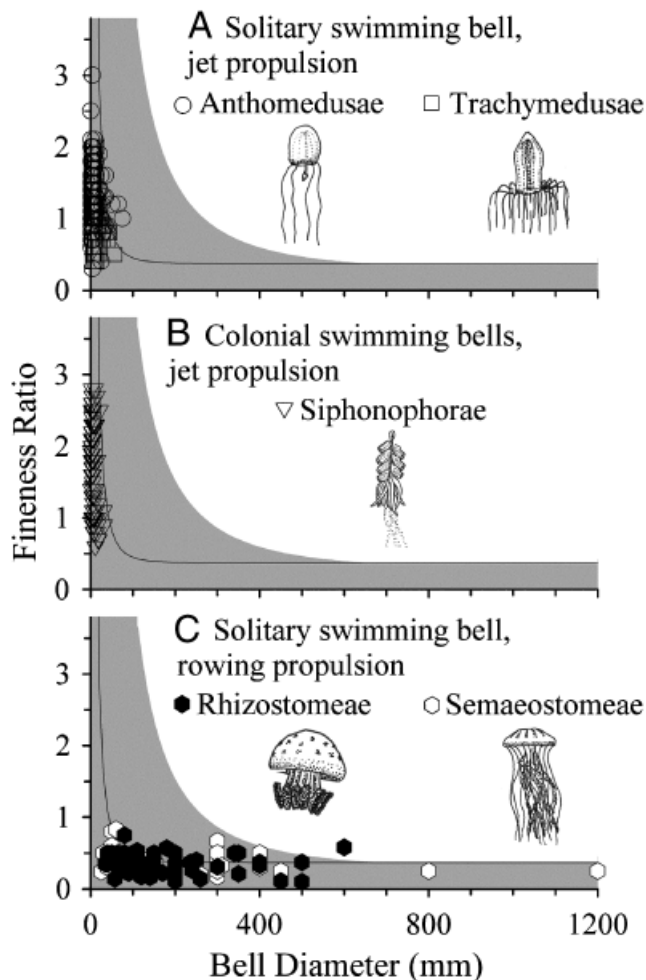


Fig. 7. Alternative solutions to physiological constraints on medusan bell performance. Data points represent empirical morphospaces for respective lineages; the shaded region and the solid line are the same as in Fig. 6B.

1957) but may be propelled by a collection of small nectophores.

Use of stopping vortices during propulsion relaxes size constraints on medusan bell diameters and has allowed rowing-propelled medusan lineages within the Scyphozoa and Hydrozoa to evolve large, oblate medusan bells. Departures from expectations based on simple jet production and solely starting vortex thrust production are most evident within the semaestome and rhizostome scyphomedusae (Fig. 7C). These lineages possess members that exceed by more than an order of magnitude the expected size limits for medusan jet propulsion.

Correlates of propulsive modes

The empirically determined morphospace reflects swimming bell shape limitations associated with

medusan propulsive modes. For jet propulsion, we expect bell size limitation but relatively few limitations on bell shape, because force production for jet propulsion places few constraints on bell shape. Accordingly, bell fineness is highly variable for these medusae (Fig. 7A,B). Daniel (1983, 1985) noted that streamlining reduces form drag and added mass forces during swimming by jetting medusae, and is therefore favorable for high swimming performance. However, it has been noted that other selective forces may also affect bell fineness, with the result that a wide range of bell fineness values characterize jet-propelled medusae (Daniel 1983). In contrast, size limits are more relaxed for rowing medusae, but shape is constrained by the requirement of low fineness so that the swimming bell acts as a flexible, circular paddle that produces a substantial stopping vortex. Hence, swimming bells of most rowers are flattened along the oral–aboral axis and characterized by fineness values generally <0.5 (Fig. 7C). Although rowing propulsion is compatible with a small size, such as scyphozoan ephyrae (2–7 mm diameter) or the leptomedusa *Obelia* sp. (1–5 mm diameter), many rowers are relatively large (Fig. 7C). The clade-wide relationships between medusan size and shape primarily reflect the aggregated constraints imposed by the two propulsive modes on the medusan morphospace.

The relationship between swimming bell morphology and propulsive mode is expressed in the distinctive morphologies of each medusan lineage. From a broad perspective, lineages that have been described as jet propelled (Cubomedusae: Gladfelter 1973; Trachymedusae and Anthomedusae: Colin & Costello 2002; Siphonophorae: Bone & Trueman 1982) are characterized by significantly higher average bell fineness ratios (Kruskal–Wallis ANOVA, $p < 0.001$) and lower bell diameters (Kruskal–Wallis ANOVA, $p < 0.001$) than lineages that have been described as rowing propelled (Semaestomeae and Rhizostomeae: Costello & Colin 1994, 1995; Narcomedusae: Raskoff 2002; Leptomedusae: Colin & Costello 2002) (Fig. 8). Importantly, the distribution of these traits within related lineages demonstrates convergence on either propulsive solution via parallel evolution between medusan lineages. This is most evident within two hydrozoan clades: the Hydroidolina (giving rise to the Anthomedusae, Siphonophorae, and the Leptomedusae) and the Trachylina (giving rise to the Narcomedusae and the Trachymedusae). Both are recognized as distinct, monophyletic clades based on morphometric and developmental (Bouillon & Boero 2000; Marques & Collins 2004) or molecular criteria (Collins 2002; Collins et al. 2006). Within each clade,

lineages possess rowing or jetting propulsion and morphometric traits—bell size and shapes—associated with either propulsive mode.

Within the Hydroidolina, the average bell diameter is smaller (Kruskal–Wallis ANOVA, $p < 0.001$) and bell fineness is higher (Kruskal–Wallis ANOVA, $p < 0.001$) for the jet-propelled members of the Anthomedusae compared with the rowing-propelled members of the Leptomedusae. Likewise, within the Trachylina, the average bell diameter is smaller (Kruskal–Wallis ANOVA, $p < 0.001$) and bell fineness is higher (Kruskal–Wallis ANOVA, $p < 0.001$) for the jet-propelled members of the Trachymedusae compared with the rowing-propelled members of the Narcomedusae (Fig. 9). Parallel evolution of propulsive modes and morphological similarities within and between closely related lineages indicates that despite the variation in medusan morphologies, propulsive mode and bell morphology appear to be co-evolved traits with a limited range of possible combinations.

Interestingly, the adaptations for rowing propulsion in the two hydrozoan lineages involve recruitment of different body parts as paddle structures and use of different components of the resulting fluid flows for feeding. The narcomedusan species most studied for swimming, *Solmissus albicans* GEGEBAUR 1856, does not use its velum to constrict centralized jet flow during bell contraction. Instead, the structure and function of the velum are modified to act as part of the paddle structure that creates broad vortices at the bell margin (Colin et al. 2006). Similar to many Narcomedusae (Fig. 10), members of *Solmissus* spp. swim with tentacles oriented aborally (Larson et al. 1989) and use flow that is “upstream” of the bell margin to capture gelatinous prey such as siphonophores or salps (Raskoff 2002) that are capable of rapid escape swimming.

Such use of upstream flow allows for the approach of the cruising predator toward their prey with minimal hydrodynamic disturbance to startle prey. In contrast, rowing propulsion within the Leptomedusae is more similar to that of most scyphomedusae, and prey are captured in the flow “downstream,” or after fluid has passed the bell margin. In species such as *Aequorea victoria* MURBACH and SHEARER 1902 and *Mitrocoma cellularia* A. AGASSIZ 1865, the velar aperture is wide and provides little constriction of subumbrellar flow during bell contraction (Colin & Costello 2002). For these species, the velum plays largely a vestigial role in propulsion and has been completely abandoned by the cosmopolitan genus *Obelia*.

Consequently, although both the leptomedusan and the narcomedusan lineages within the Hydrozoa

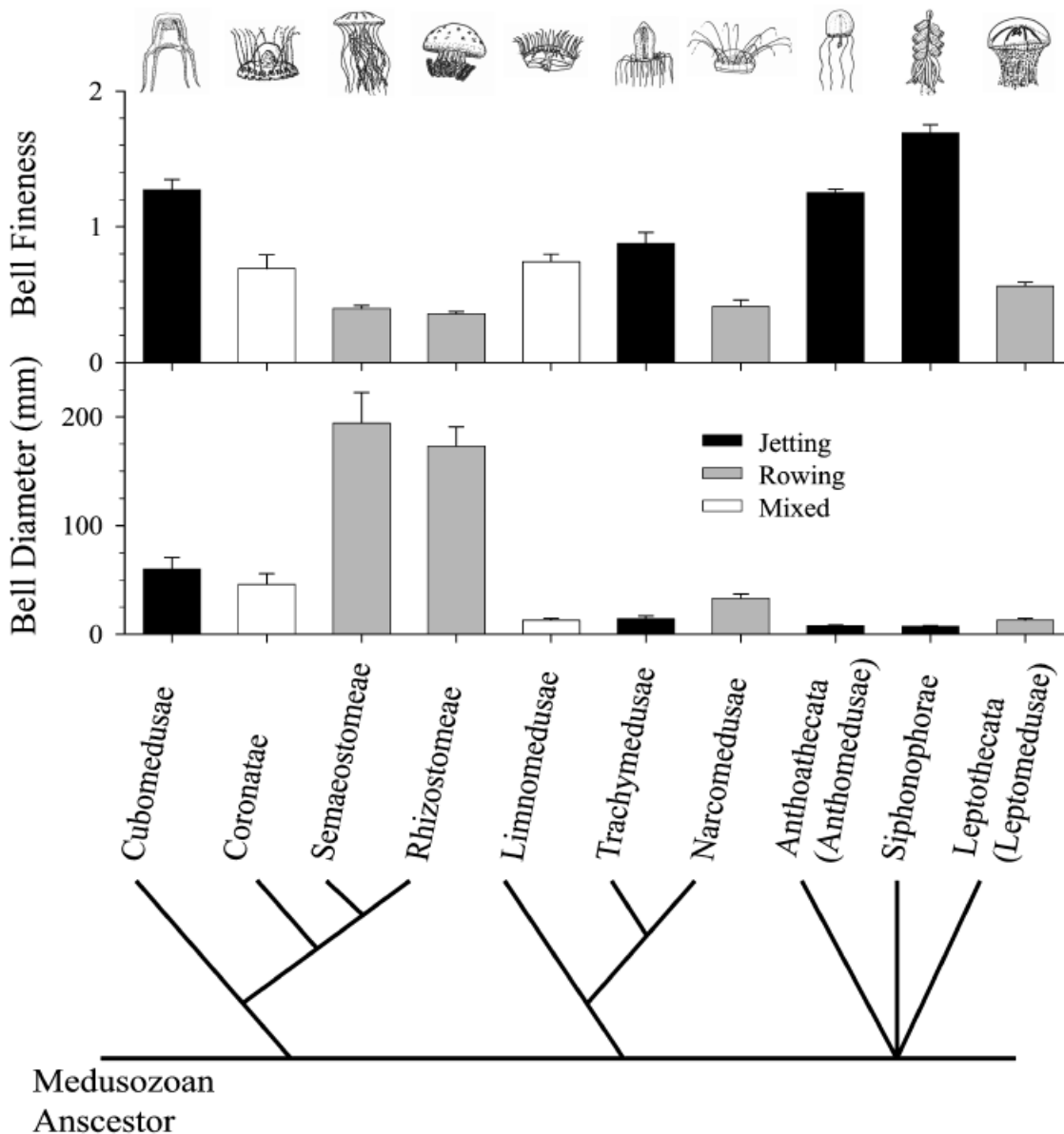


Fig. 8. Comparison of medusan swimming bell diameter and fineness among major medusan clades. Histograms represent the average diameter and fineness values of species within various medusan lineages based on Mayer (1910), Kramp (1961), and Pugh (1999). Error bars represent one standard error from the mean. Phylogenetic relationships are based on our interpretation of the hypotheses described by Marques & Collins (2004) and Collins et al. (2006).

use rowing propulsion, the independent evolution of rowing propulsion within the two lineages involved parallel but different structures for thrust generation and different positions of tentacles within the flows surrounding the medusae.

Plasticity of propulsive modes

Medusan lineages vary in the fidelity with which their members can be identified as possessing either of the propulsive modes and their associated mor-

phological characters. Although some lineages appear to be characteristically one mode or the other (Fig. 8), the parallel existence of sister lineages characterized by different modes (Fig. 9) suggests considerable plasticity in evolution of a propulsive mode. Several lines of evidence suggest that transitions between modes may require relatively few morphological alterations and that recruitment of different morphological structures can result in convergence upon either propulsive mode. Within a species, development of an individual in leptomedusan genera

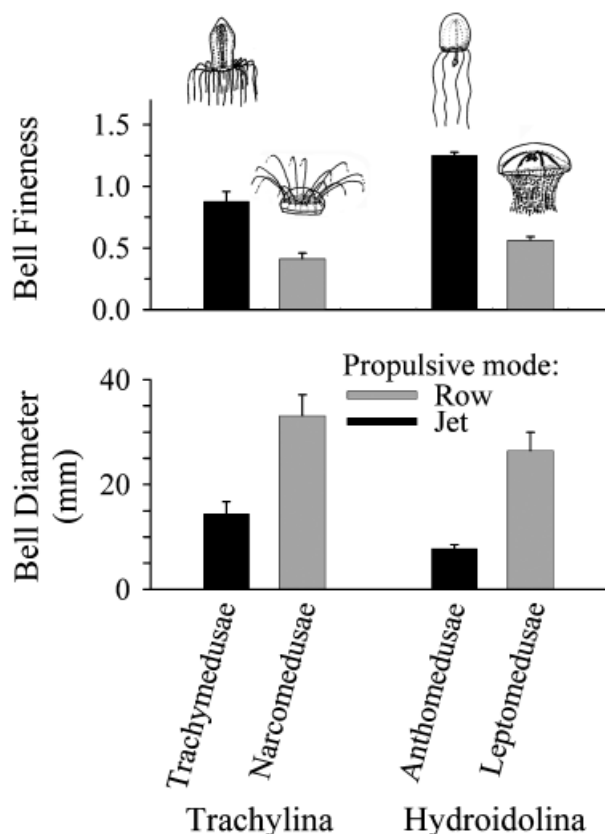


Fig. 9. Comparison of swimming bell morphologies of jet- and rowing-propelled lineages within the hydrozoan clades of the Trachylina and the Hydroidolina. Error bars indicate standard error of the mean. Note the parallel convergence upon high fineness and small-bell-diameter bells for jetting lineages, in contrast to low fineness and larger bell diameters of rowing-propelled lineages within both of the hydromedusan clades.

such as *Clytia*, *Aequorea*, and *Mitrocoma* involves a prolate, jetting juvenile medusae that alters swimming bell shape during the growth into oblate, rowing-propelled adults (Fig. 11). In these cases, the underlying swimming bell morphology remains fundamentally intact, but the proportions of bell and velum dimensions alter during development.

Within some lineages, not all members can be categorized as strictly one or the other propulsive types because even adult members may be of different propulsive and morphological types. Analogous evolution of propulsive structures, such as the hydromedusan velum and the cubomedusan velarium (Hyman 1940), or use of the narcomedusan velum to pulse in a manner functionally similar to the leptomedusan or scyphomedusan bell, suggests that a variety of body parts have been recruited to form the mechanical structures required for each propulsive

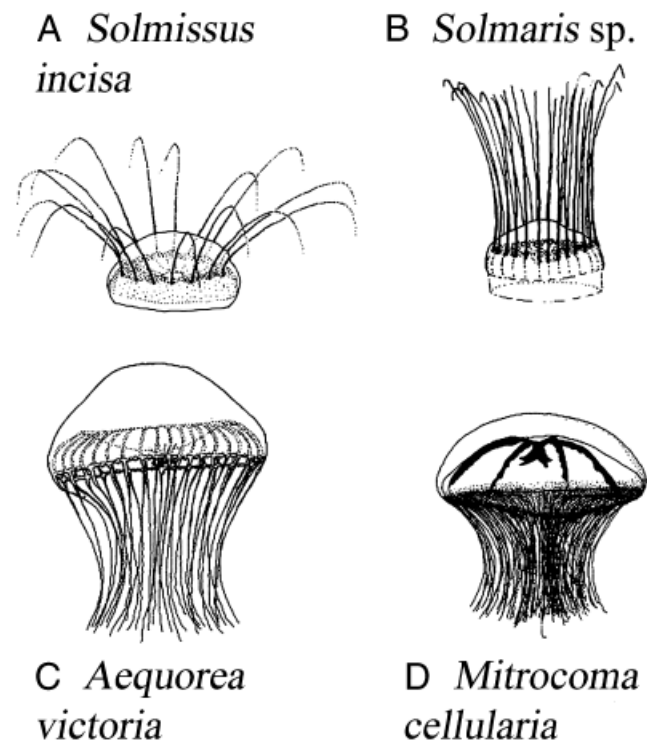


Fig. 10. Tentacle position during swimming. Upstream feeding by narcomedusae (A, B) and downstream feeding by leptomedusae (C, D). (A) After Colin et al. (2006); (B) after Larson et al. (1989); and (C, D) after Colin & Costello (2002).

mode. The flexibility with which structures have been recruited to build either propulsive mode suggests that the simplicity of the medusan morphospace is based on repeated directional selection within and between lineages toward either jet or rowing propulsion.

The variety of routes by which either propulsive mode has been reached implies that intermediate propulsive modes may exist. Are intermediates between rowing and jet propulsion operational and exemplified by any group? At present, few studies provide sufficient quantitative information about hydrodynamic regimes and swimming modes to answer this question definitively. However, if bell fineness serves as a reliable indicator, the distribution of bell shapes indicates two principal adaptive peaks and these peaks appear to be associated with either rowing or jet propulsion (Fig. 12).

Although the empirical morphospace of adult medusae argues for a highly polarized distribution of morphologies and associated propulsive modes, there is evidence for the existence of intermediate modes. Both the leptomedusan and limnomedusan transitions from prolate juveniles to oblate adult medusae

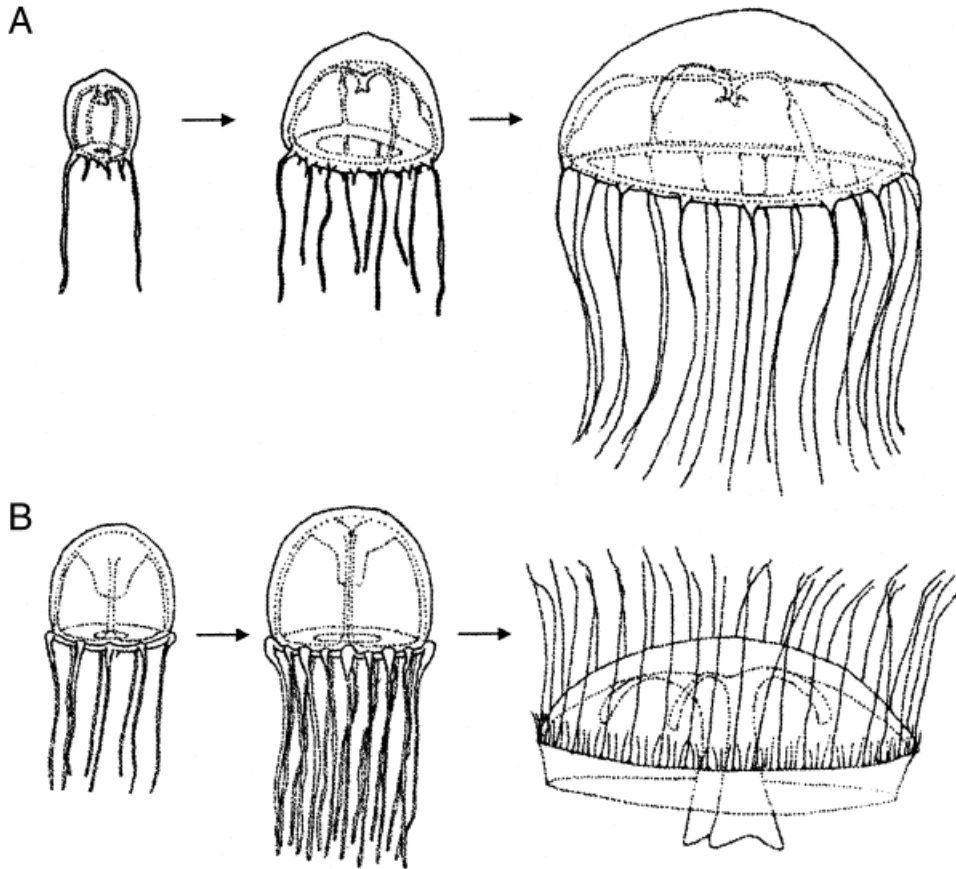


Fig. 11. Morphological changes during development of hydromedusae. Typical morphological variations of (A) the leptomedusa *Mitrocoma cellularia* (0.9, 2.6, and 5.6 mm diameter from left to right, respectively, after Widmer 2004) and (B) the limnomedusa *Craspedacusta sowerbyi* (0.4, 0.65, and 4.5 mm diameter from left to right, respectively, during development, after Boulenger & Flower 1928). Note that the early stages in development of both species are prolate with narrow velar apertures, characteristic of jetting medusae, but that adults of both species are oblate with very wide velar apertures. Prey capture and fluid motions during swimming of adults are characteristic of downstream (*M. cellularia*: Colin & Costello 2002) and upstream (*C. sowerbyi*: Colin et al. 2006) rowing medusae.

indicate the existence of intermediate propulsive states that swim and feed successfully during life cycle development (Fig. 11). The multiple origins of rowing propulsion among hydrozoan lineages and the shared possession of prolate juvenile stages among all medusa-producing hydrozoan lineages suggest a jet-propelled ancestor within the Hydrozoa. The poor fossil record of medusan forms provides little evidence about the transitions between lineages, but each stage in the transition, like those occurring during leptomedusan and limnomedusan development, may have maintained viable propulsion and feeding mechanisms.

Despite the interest of intermediate propulsion types, adult forms possessing intermediate propulsive modes probably represent a minor portion of the extant species comprising the medusan empirical morphospace. Among the species of which we have

sufficient morphological data, all lie within the theoretical morphospace bounded by the constraints of either jetting or rowing propulsion. The low frequency of intermediate propulsive forms suggests strong selection against their persistence, possibly due to unfavorable energetic characteristics. One interpretation of this pattern is that the two propulsive modes and their associated morphological traits represent adaptive peaks in the medusan morphospace and that the valleys between these peaks are only sparsely populated by intermediate species (Fig. 12). The range of developmental pathways, variations in recruitment of morphological structures for analogous propulsive components, and parallel evolution of similar propulsive solutions between medusan lineages indicate the strong selection toward these two propulsive solutions among the Medusozoa. All of these variations may be viewed as different

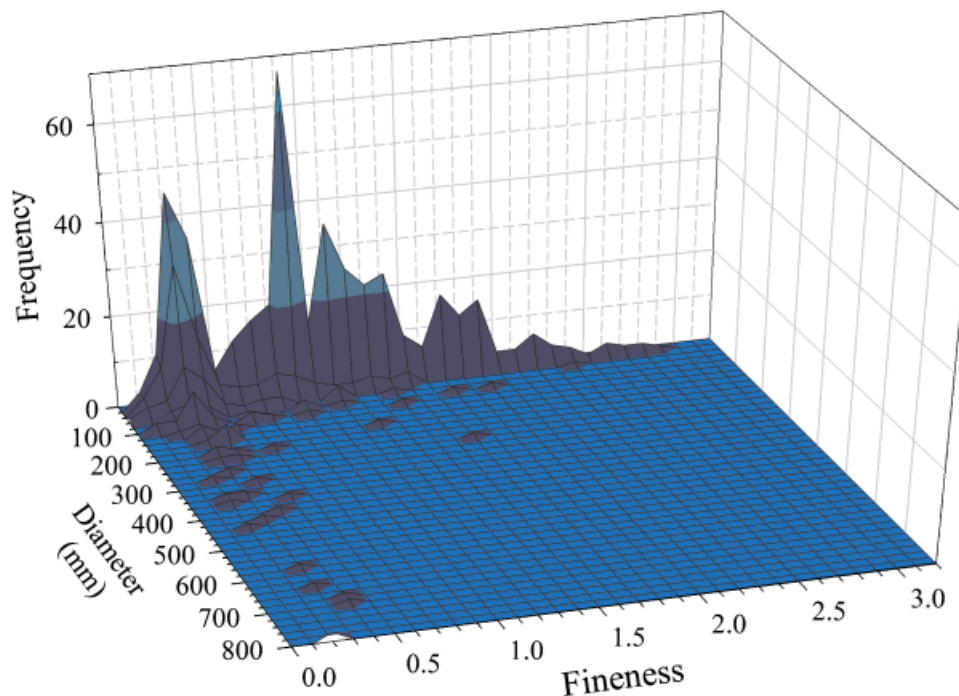


Fig. 12. Adaptive landscape of medusan bell forms based on the empirical medusan morphospace. Frequency refers to the number of species within a particular diameter (20 mm interval bins) and bell fineness (0.1 bins) category. The extreme representatives of both large bell diameter and high fineness have been left out (99% of quantified species represented in the figure).

pathways leading to either of the two propulsive destinations.

Propulsive mode and species diversity

Is either propulsion mode so advantageous as to become a dominant trait among medusae? In other words, does possession of either mode contribute to elevated species diversity within clades? We considered this question by comparing medusan species di-

versity within medusozoan lineages that could be characterized as possessing either rowing or jetting propulsion. Diversity of medusan species within the lineages served as the variable of comparison. We regard the values we used for species diversity within lineages (Table 1) as provisional due to periodic additions of new species and revisions of existing taxa. However, even when this qualification is considered, the disparities in diversity within medusan lineages are substantial. For our purpose, medusan species

Table 1. Provisional list of propulsive modes, polyp organization, and medusan species diversity within major medusan lineages.

Order	Propulsive mode	Polyp type	No. species	References
Rhizostomeae	Rowing	Noncolonial	56	Mayer (1910)
Semaeostomeae	Rowing	Noncolonial	52	Mayer (1910)
Coronatae	Mixed	Colonial	19	Mayer (1910)
Cubomedusae	Jetting	Noncolonial	16	Mayer (1910)
Trachymedusae	Jetting	Noncolonial	51	Bouillon & Boero (2000)
Narcomedusae	Rowing	Noncolonial	38	Bouillon & Boero (2000)
Anthomedusae	Jetting	Colonial	404	Bouillon & Boero (2000)
Siphonophora	Jetting	Colonial	134	Totton (1965)
Leptomedusae	Rowing	Colonial	204	Bouillon & Boero (2000)
Limnomedusae	Mixed	Noncolonial	38	Bouillon & Boero (2000)

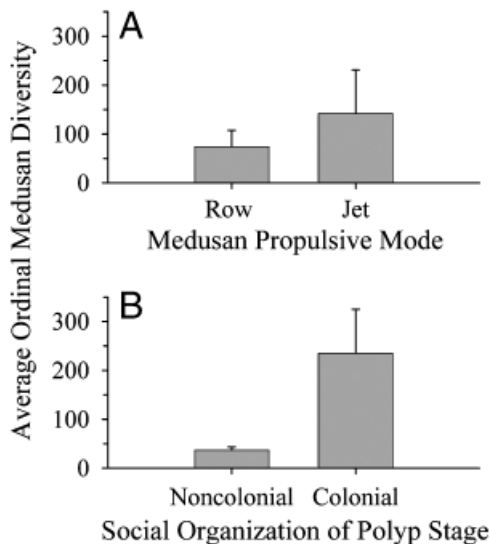


Fig. 13. Correspondence between medusan species diversity and (A) propulsive mode, and (B) the social organization of the polyp stage of the life cycle. Error bars represent standard error of the mean.

within the Limnomedusae and Coronatae were excluded from the propulsive comparison because of the potential for mixed propulsive modes within those lineages.

Propulsive mode did not contribute significantly (Mann–Whitney U , $p = 1.0$) to explaining the diversity of medusan species within a medusozoan lineage at the ordinal level (Fig. 13A). The most diverse lineages are the sister lineages of the Leptomedusae and the Anthomedusae (Table 1). The former is characterized by rowing and the latter by jetting medusae as adults. The species diversity of either of these sister lineages exceeds those of any other order possessing medusae. Therefore, some other variable or variables may contribute more importantly than propulsive mode to medusan diversity within any particular lineage. In fact, lineage-dependent patterns of medusan species diversity may be better explained by factors other than medusan propulsive mode.

One feature that is common to both the leptomedusan and the anthomedusan lineages is the possession of colonial, often polymorphic, benthic polyps. This trait is absent in most other lineages, except for the Siphonophorae. For example, medusozoan lineages with colonial polyps are significantly (Mann–Whitney U , $p = 0.025$) more species rich than are lineages without colonial polyps (Fig. 13B). In other words, whether jet or rowing propelled, the number of medusan species within a medusozoan lineage is significantly correlated with the evolution of a colonial life mode by the polyp generation of the life

cycle. Therefore, although propulsive mode explains the chief features of adaptive peaks in medusan form and function, variations in propulsive mode do little to explain the success in terms of species number enjoyed by some medusan lineages relative to others.

Evolution of the colonial habit and the potential for polymorphic specialization accompanying coloniality may more favorably explain species diversification within medusozoan lineages than does propulsive mode. However, diversification within clades may involve complex interactions (Mayr 2001) and polyp coloniality alone may not be a decisive factor explaining medusan diversity (e.g., compare coronate and semeanostome medusan diversities). Instead, polyp coloniality may be only one of a variety of factors that has influenced the comparative success of the polyp generation within medusozoan lineages. Most importantly, for our consideration of the medusan life state, species diversity within medusan lineages is not significantly correlated with propulsive mode. Instead, we suggest that the species diversity of medusan lineages may be better understood through further examination of the polyp counterparts that are a component of the life cycles of most medusozoan lineages.

Ecological correlates of swimming bell form and function

Links between propulsive and foraging modes

The physiological constraints on force production by medusan muscle tissues are reflected in two divergent patterns of propulsion by medusae. But are these constraining patterns of bell structure and function reflected in the ecological roles played by medusae? Foraging behavior provides an insight into this question because the process of foraging relates an animal's motion to its ecological role. Foraging success among planktonic animals may be optimized by either of two strategies, termed ambush and cruising foraging modes (Gerritsen & Strickler 1977). Encounter rates of ambush predators with their prey are generally dependent on prey motility patterns. In contrast, cruising predators are more mobile than their prey and encounter rates reflect the relative velocities of both predators and prey. Mobility is therefore essential for feeding by planktonic cruising predators, whereas passive drifting characterizes planktonic ambush predators.

Jet propulsion is generally accompanied by ambush foraging among medusae. Ambush foragers drift motionlessly, waiting for actively motile prey to swim into the predator's outstretched tentacles

(Mills 1981; Arkett 1984; Madin 1988; Colin et al. 2003, 2005). For these predators, prey capture is uncoupled from medusan swimming, and therefore propulsion. Consequently, swimming serves the sole function of transportation—both to new locations and away from potential predators. The high swimming performance, i.e., rapid acceleration and high velocities, of jet-propelled ambush foragers is particularly effective for predator avoidance (Colin & Costello 2002).

This pattern is exemplified perhaps most clearly by colonial siphonophores in which nectophores serve only the function of swimming and other functions, such as feeding, are performed by other individuals within the colony that are specialized for those purposes. Morphological traits that favor high swimming performance include small bell size, high bell fineness (reduces drag and acceleration reaction; Daniel 1983, 1985; Colin & Costello 1996, 2002), and low velar aperture ratio. Low velar aperture ratios favor flow constriction and production of a high-speed jet during bell contraction (Gladfelter 1973; Colin & Costello 2002). Furthermore, bell contraction is typically rapid for these species (Colin & Costello 2002), imparting higher velocity and thus momentum for thrust production to the medusa's wake.

The strong jet produced by these medusae is evident within their wakes as a high-velocity core region originating from the velar aperture (Fig. 4). These species typically retract their tentacles during swimming (Colin et al. 2003), thus reducing drag associated with trailing tentacles and maximizing forward acceleration during swimming. The energetic tradeoff paid for this strategy is the low energetic efficiency of jet propulsion (Vogel 1994). Jet-propelled species have extremely low propulsive efficiencies relative to their rowing counterparts within the medusae (Ford & Costello 2000) and estimates of their cost of transport are relatively high, near those of flying animals (Daniel 1985). However, the unfavorable energetic efficiency of jet propulsion is partially offset by the low proportions of time spent swimming by jetting species (Colin et al. 2003).

Rowing propulsion is generally accompanied by cruising foraging among medusae. Although cruising species may at times sit motionless with tentacles extended, and thus act as ambush predators, they typically spend the majority of their time actively swimming with tentacles extended (Costello et al. 1998; Colin et al. 2003). In contrast to jet propulsion, rowing propulsion involves primarily contraction at the bell margins (Ford & Costello 2000), creating a wake in which most flow is entrained from the area

outside the bell margin (Colin & Costello 2002) to form a series of interconnected vortices (Dabiri et al. 2005) that transport fluid through a variety of capture surfaces. Flows past the bodies of adult scyphomedusae are typically characterized by $Re > 10^2$ (Larson 1987b; Costello & Colin 1994, 1995; D'Ambra et al. 2001; Colin & Costello 2002). Consequently, inertial forces dominate the hydrodynamic regimes around these medusae, and flows around these medusae transport entrained planktonic prey to nematocyst-studded capture surfaces, such as tentacles and oral arms (Costello & Colin 1994, 1995; Colin & Costello 2002; Dabiri et al. 2005; Colin et al. 2006). Once encountered prey contact prey capture surfaces, nematocyst properties play an important role in prey retention (Purcell & Mills 1988) and, hence, overall patterns of prey selection (Fig. 14).

Prey capture by cruising medusae may use either the upstream or the downstream regions of flow surrounding the swimming medusae. Upstream tentacle deployment is the less documented of the foraging strategies, but has been described for a number of Narcomedusae (Larson et al. 1989) and the relationships between tentacle position and prey capture have been well documented for *Solmissus* sp. (Raskoff 2002; Colin et al. 2006). The low shear region upstream of an advancing medusa is a favorable location to deploy the tentacles for medusan predators depending on hydrodynamic stealth to approach prey possessing rapid escape abilities. Many of the target prey of mid-water cruising medusae appear capable of rapid escape swimming and upstream tentacle deployment has evolved within the Narcomedusae (Larson et al. 1989; Raskoff 2002) as well as a number of mid- and deep-water coronate scyphomedusae (Larson 1979; Youngbluth & Bamstedt 2001; Sotje et al. 2007).

Downstream tentacle deployment appears to be more common among surface and coastal-dwelling cruising medusae and, consequently, has been described in greater detail for both hydrozoan and scyphozoan cruising medusae. Maps of prey capture locations for cruising medusae using downstream flow have demonstrated that the majority of captured prey contacted capture surfaces such as tentacles and oral arms near the bell margins (Ford et al. 1997). This is also the region of maximum wake velocities for these typically oblate medusae.

While prey capture strategies for upstream and downstream oblate medusae differ, the role of swimming is the same. Both use swimming to efficiently maximize the volume of fluid delivered through capture surfaces (Fig. 15). The oblate bell forms and rowing propulsion of these species entail

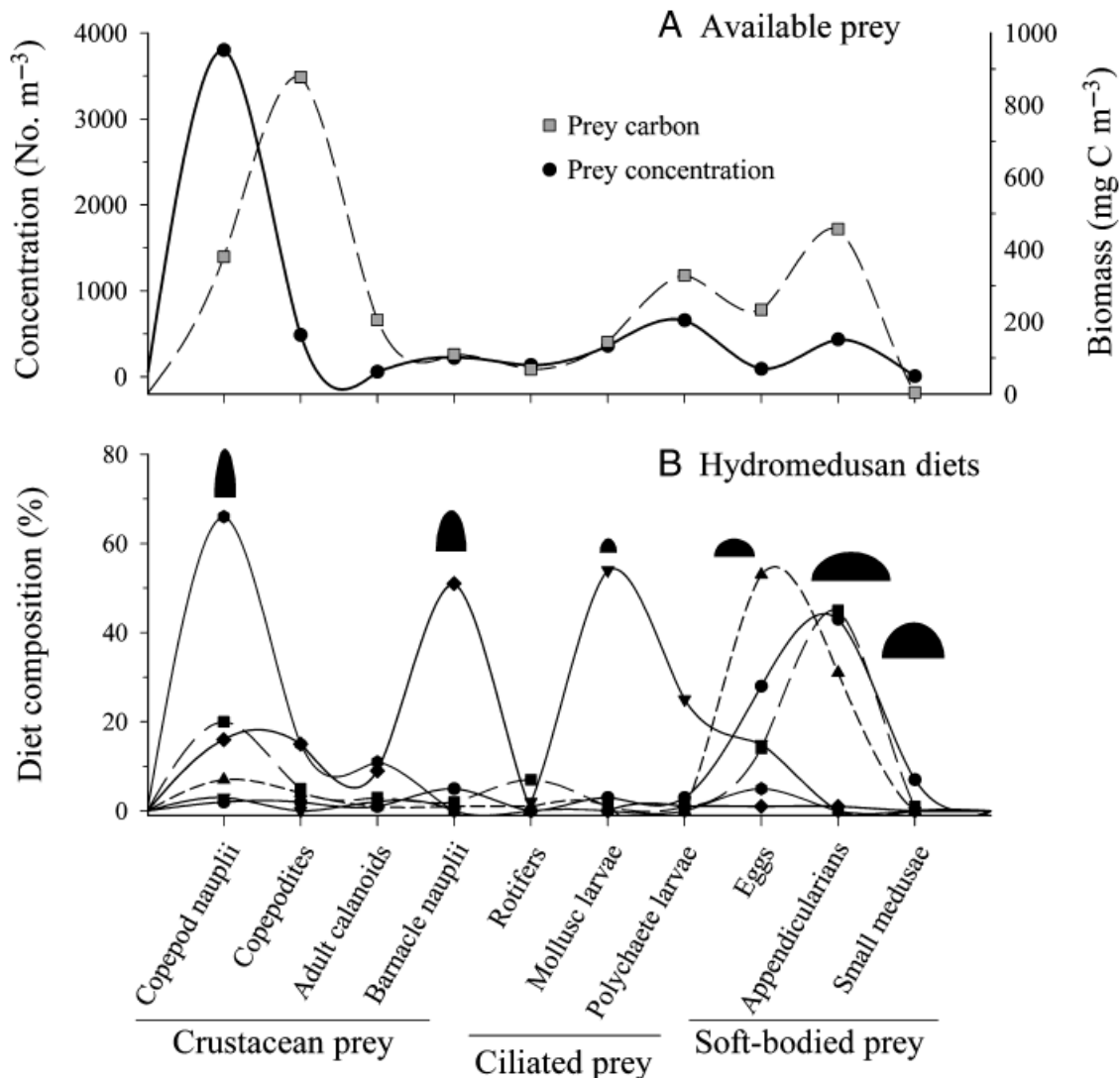


Fig. 14. Selective feeding by co-existing hydromedusae in waters surrounding Friday Harbor Laboratories, San Juan Island, WA, USA. The available prey assemblage (A) is utilized selectively (B) by the prolate species *Aglantha digitale*, *Sarsia tubulosa*, and *Proboscicactyla flavicirrata*, as illustrated by their peak diet compositions (the three leftmost peaks, respectively). In contrast, the three oblate cruising medusae, *Phialidium gregarium*, *Mitrocoma cellularia*, and *Aequorea victoria* (three overlapping peaks on right of bottom panel), share relatively similar diets. After Costello & Colin (2002).

hydrodynamic costs, such as high drag and added-mass forces, that oppose rapid acceleration. However, the high drag and added-mass properties of their swimming also contribute to the mass flux of fluid, and entrained prey, to their capture surfaces. Therefore, the same factors that preclude rapid acceleration ensure transport of large volumes of prey-containing fluid past medusan capture surfaces. Wake velocities of oblate species are often similar in magnitude to medusan forward velocities, allowing high Froude propulsion efficiencies (Ford & Costello 2000). Cost of transport estimates for a relatively large scyphomedusa (*Stomolophus meleagris* L. AGAS-

siz 1862) are comparable with, or lower, than fish (Larson 1987b). The low energetic costs of swimming and high potential for fluid entrainment past capture surfaces appear to favor a cruising foraging mode for rowing-propelled medusae.

Foraging modes and trophic niches

The two optima in planktonic foraging modes should result in encounter and ingestion of different prey types by cruising and ambush foragers (Gerritsen & Strickler 1977). Owing to their low motility during foraging, ambush predators rely on prey

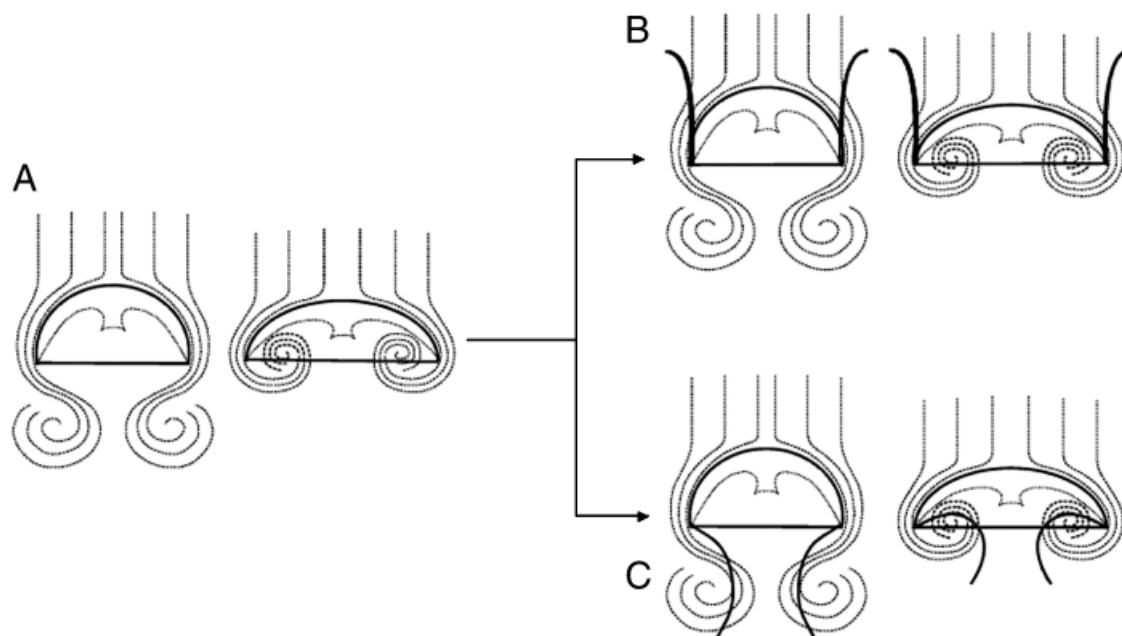


Fig. 15. Flow (dotted lines) around cruising predatory medusae with oblate-shaped bells during (A) contraction (left) and relaxation (right) phases of the swimming cycle, and of tentacle placement in flow around (B) upstream and (C) downstream cruising foragers. The starting vortex ring is visible during the contraction phase and the stopping vortex ring is visible during the relaxation phase. Note that flows around both upstream and downstream cruising foragers are similar. After Colin et al. (2006).

motions to initiate predatory encounters. Hence, an ambush foraging mode would primarily impact highly motile, actively swimming prey (Purcell 1981; Greene 1986; Colin et al. 2005; Hansson & Kiorboe 2006). In contrast, cruising foragers typically swim more rapidly than their prey and encounter depends primarily on motions generated by the predator relative to the prey (Costello & Colin 1994, 1995). For these medusae, feeding and swimming are concurrent activities, and prey selection (Fig. 14) appears to depend on, first, vulnerability of prey to entrainment within medusan water motions and, second, a prey-size threshold when encountering medusan capture surfaces (Costello & Colin 1994, 1995; Sullivan et al. 1994; Hansson et al. 2005). Cruising medusae examined thus far appear capable of retaining a variety of hard- or soft-bodied prey (e.g., Sullivan et al. 1994; Hansson et al. 2005). Hence, a cruising foraging mode results in trophic impacts primarily upon prey that are either stationary or are slow swimmers relative to the predator's motions (Fig. 14).

Are these predictions based on encounter theory realized in the dietary niches of medusae using ambush or cruising foraging modes? A number of studies have examined ingestion patterns of hydromedusae (Larson 1987a; Purcell & Mills 1988; Mills 1995; Purcell 1997), siphonophores (reviewed in

Mackie et al. 1987), and scyphomedusae (reviewed in Arai 1997). Among other results, these studies have demonstrated that prey ingestion patterns are strongly influenced by the relative availability of different prey. Therefore, testing the applicability of encounter theory expectations to actual dietary niches of medusae requires quantification of the dietary patterns of a variety of medusan species using different foraging modes during exposure to the same prey conditions.

In situ studies of prey selection that meet these criteria demonstrate that the dietary niches of co-occurring hydromedusae are strongly influenced by the predator's foraging mode. A comparison of the dietary niches of co-occurring hydromedusae from Friday Harbor, WA, USA, found that ambush-foraging, jet-propelled species fed primarily upon motile plankton such as crustaceans, rotifers, and mollusk larvae (Costello & Colin 2002). The dietary niches of these medusae centered on different fractions of available prey and, consequently, the ambush-foraging medusae effectively partitioned the available prey spectrum with minimal dietary overlap.

In contrast, rowing-propelled, cruising foraging, species consumed primarily slowly moving, soft-bodied prey such as eggs and appendicularians. Because the three cruising foragers (*Aequorea victoria*,

Mitrocoma cellularia, *Phialidium (Clytia) gregarium* L. AGASSIZ 1862) consumed similar prey, their diets overlapped extensively. Owing to the similarities in prey selection and feeding mechanisms, the cruising foraging medusae can appropriately be considered to be a medusan feeding guild, whereas the ambush-foraging medusae cannot. The predatory pressure exerted by the cruising predatory guild of medusae may be ecologically important because the soft-bodied plankton fraction is often a substantially more limited food resource, both in terms of prey concentration and total carbon availability, than the crustacean component of the zooplankton (Fig. 14). Consequently, strong predatory selection by a guild of cruising hydromedusae can substantially affect field populations of soft-bodied prey (Purcell 1990; Purcell & Grover 1990; Purcell 2003).

Competition among a guild of predators for a limited resource also fosters intraguild predation (Polis et al. 1989). Whereas intraguild predation occurs frequently among oblate, rowing-propelled, cruising foragers—both hydromedusae (Purcell & Mills 1988; Purcell 1991a,b; Mills 1995; Costello & Colin 2002; Raskoff 2002) and scyphomedusae (Purcell 1991a; Hansson 1997)—it is rare among ambush-foraging medusae and siphonophores (Purcell 1991a), except for a few highly specialized medusae (e.g., *Stomatoca atra* L. AGASSIZ 1862). Consequently, foraging mode affects both prey selection and patterns of interspecific interactions among medusae (Costello & Colin 2002).

Trophic niches and ecosystem impacts

In contrast to digestion limitation due to gut fullness in some ambush-foraging medusae (Hansson & Kiorboe 2006), guts of cruising medusae appear frequently to be adapted for high consumption, and are either large and elaborated or very extensible. Consequently, neither gut fullness nor digestion-rate limitation is likely to limit prey ingestion of cruising medusae. In fact, prey ingestion is often a linear function of prey concentration (Clifford & Cargo 1978; Uye & Shimauchi 2005; Titelman & Hansson 2006) for cruising medusae and rarely found to saturate at high prey concentrations.

The combination of cruising foraging mode, relatively large size, and virtually unlimited consumption rates contributes to influential predatory impacts of cruising medusae (Fig. 16). In contrast, ambush-foraging hydromedusae (e.g., Purcell & Nemazie 1992) and siphonophores (e.g., Purcell 1997) may, under some circumstances, substantially affect prey populations, but more generally, do not appear to limit

prey standing stocks severely (e.g., Daan 1986). In fact, all reports of substantial standing stock reductions of plankton by medusae involve either cruising scyphomedusae or cruising hydromedusae (Table 2). However, because few studies exist that have examined the predatory impact of small ambush hydromedusae, more work is needed to understand their trophic role fully.

In addition to direct reduction of prey populations, cruising scyphomedusae may exert indirect predatory impacts. For example, the scyphomedusa *Chrysaora quinquecirrha* DESOR 1848 influences copepod standing stocks in Chesapeake Bay via predation upon a highly efficient copepod predator, the ctenophore *Mnemiopsis leidyi* A. AGASSIZ 1862 (Fig. 16; Purcell & Decker 2005). In this case, reduction of the ctenophore standing stocks by *C. quinquecirrha* reduces predation pressure upon the copepod *Acartia tonsa* DANA 1849 by the ctenophore and results in alterations of the planktonic community structure. Likewise, indirect trophic effects of selective predation by the scyphomedusa *Aurelia aurita* LINNAEUS 1758 on small copepods release flagellate populations of Baltic Sea communities from copepod predatory pressure, with a resulting shift in microplanktonic community structure (Schneider & Behrends 1998). Taken together, the evidence from studies documenting both direct and indirect trophic effects indicates that oblate, cruising medusae, particularly scyphomedusae, are most frequently related to important trophic impacts within marine planktonic communities.

A synthetic perspective

The cnidarian cellular heritage has influenced multiple levels of medusan organization. The limitations on force generation imposed by cnidarian epitheliomuscular cells are expressed as the dichotomous pattern of propulsive organization within the medusae. The rather simple medusan morphospace, characterized by pronounced peaks related to rowing and jetting propulsion, reflects the strong directional selection that has resulted in the varied morphologies using either a jetting or a rowing propulsive mode. We suggest that the diversity of functional solutions—whether for solitary or colonial organization of jet-propelled forms, or upstream versus downstream feeding by rowing medusae—are variations of these two major propulsive themes underlying medusan swimming.

The developmental and structural means of arriving at either propulsive mode have varied between lineages, and parallel evolution has converged on the

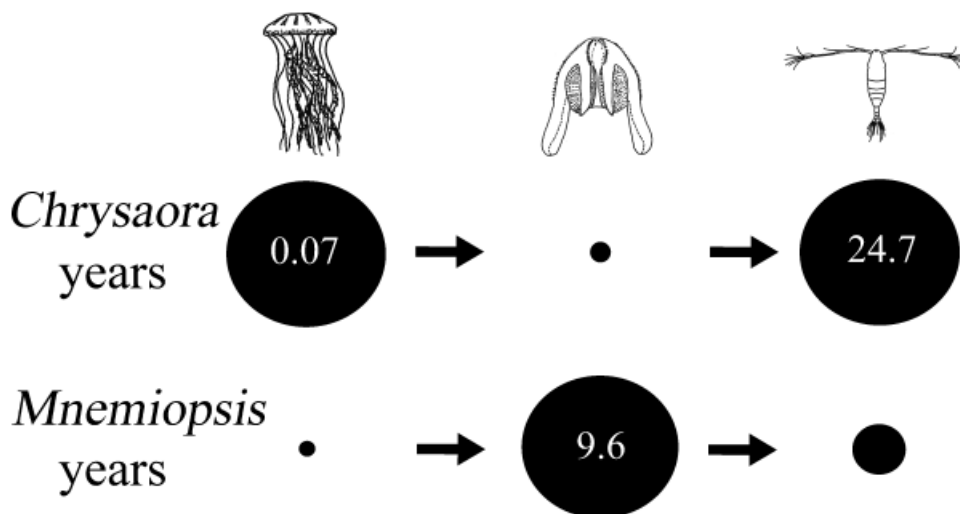


Fig. 16. Impact of selective feeding by an oblate scyphomedusa, *Chrysaora quinquecirrha*, on a planktonic community in mesohaline regions of Chesapeake Bay, USA, that contain the ctenophore *Mnemiopsis leidy* and copepods. Data based on Purcell & Decker (2005; annual variations detailed therein). The circumference of the spheres under each organism represents the relative average proportions of those species in the plankton during years of high abundance in individuals of *C. quinquecirrha* (*Chrysaora* years: 1987–1990 and 1995) or *M. leidy* (*Mnemiopsis* years: 1996–2000). The maximum concentrations of each organismal group are normalized to the same circumferences. Within each organismal group, the relative circumferences of the two time periods are proportionately dimensioned and the average abundances of each group (no. m⁻³ for *C. quinquecirrha* and *M. leidy*, no. L⁻¹ for copepods) are listed within the circles. Values for smaller circles (*C. quinquecirrha*: 0.007 m⁻³, *M. leidy*: 1.1 m⁻³, copepods: 7.7 L⁻¹) were not listed in the figure. Arrows represent a simplification of trophic interactions because members of *C. quinquecirrha* prey upon both individuals of *M. leidy* and copepods, but selectively prey upon ctenophores relative to copepods. Predation by individuals of *C. quinquecirrha* upon the ctenophore *M. leidy* reduces the latter with a cascading effect on the ctenophore’s principle prey items, the copepods. Consequently, the relative abundance of copepods in the plankton is dominated by trophic interactions that depend on the prey selection characteristics of the oblate scyphomedusa *C. quinquecirrha*.

relatively limited array of functional solutions comprising the medusan morphospace. But these convergent solutions have also entailed ecological parallels

because of the close relationship between propulsive and foraging modes. Similarities and distinctions in the ecological roles played by medusae result from

Table 2. Studies indicating standing stock limitation by medusan predation. 1, crustacean zooplankton; 2, barnacle nauplii; 3, fish eggs and larvae; 4, ctenophores.

Predator	Prey	Foraging mode	Location	Reference
<i>Aurelia aurita</i>	1	Cruising predator	Kiel Bight	Moller (1979)
<i>Aurelia aurita</i>	1	Cruising predator	Gullmar Fjord	Lindahl & Hernroth (1983)
<i>Aurelia aurita</i>	1	Cruising predator	Bedford Basin, NS	Matsakis & Conover (1991)
<i>Aurelia aurita</i>	1	Cruising predator	Kertinge, Denmark	Olesen (1995)
<i>Aurelia aurita</i>	1	Cruising predator	Kiel Bight	Behrends & Schneider (1995)
<i>Aurelia aurita</i>	2,3	Cruising predator	Limfjorden	Hansson et al. (2005)
<i>Chrysaora quinquecirrha</i>	1	Cruising predator	Chesapeake Bay	Feigenbaum & Kelly (1984)
<i>Chrysaora quinquecirrha</i>	4	Cruising predator	Chesapeake Bay	Purcell & Decker (2005)
<i>Aequorea victoria</i>	3	Cruising predator	Vancouver Island, BC	Purcell (1989)
<i>Aequorea victoria</i>	3	Cruising predator	Vancouver Island, BC	Purcell & Grover (1990)
<i>Aurelia aurita</i>	3	Cruising predator	Kiel Bight	Moller (1984)
<i>Cyanea capillata</i>	3	Cruising predator	P. Phillip Bay, Australia	Fancett (1988)
<i>Pseudorhiza haeckeli</i>	3	Cruising predator	P. Phillip Bay, Australia	Fancett (1988)
<i>Craspedacusta sowerbii</i>	1	Cruising predator	Lake Alsdorf, Germany	Jankowski et al. (2005)

the variations in capture surfaces (i.e., tentacle type and placement, oral arm structure) and nematocyst complements that have been married to the two basic propulsive alternatives.

The fundamental importance of propulsion for medusan body architectures and ecological roles might be interpreted to confer selective advantage and, hence, greater species diversity associated with either of the modes. However, medusan species rich-

ness within medusozoan lineages does not appear to be closely related to propulsive mode. Hence, selection for either propulsive mode is unlikely to drive speciation but is a strong influence after a planktonic medusa has evolved within a life cycle. Variations in propulsive modes within and between lineages indicate that possession of either propulsive mode is not fixed during the evolution of a lineage. Yet, despite the flexibility with which different propulsive modes

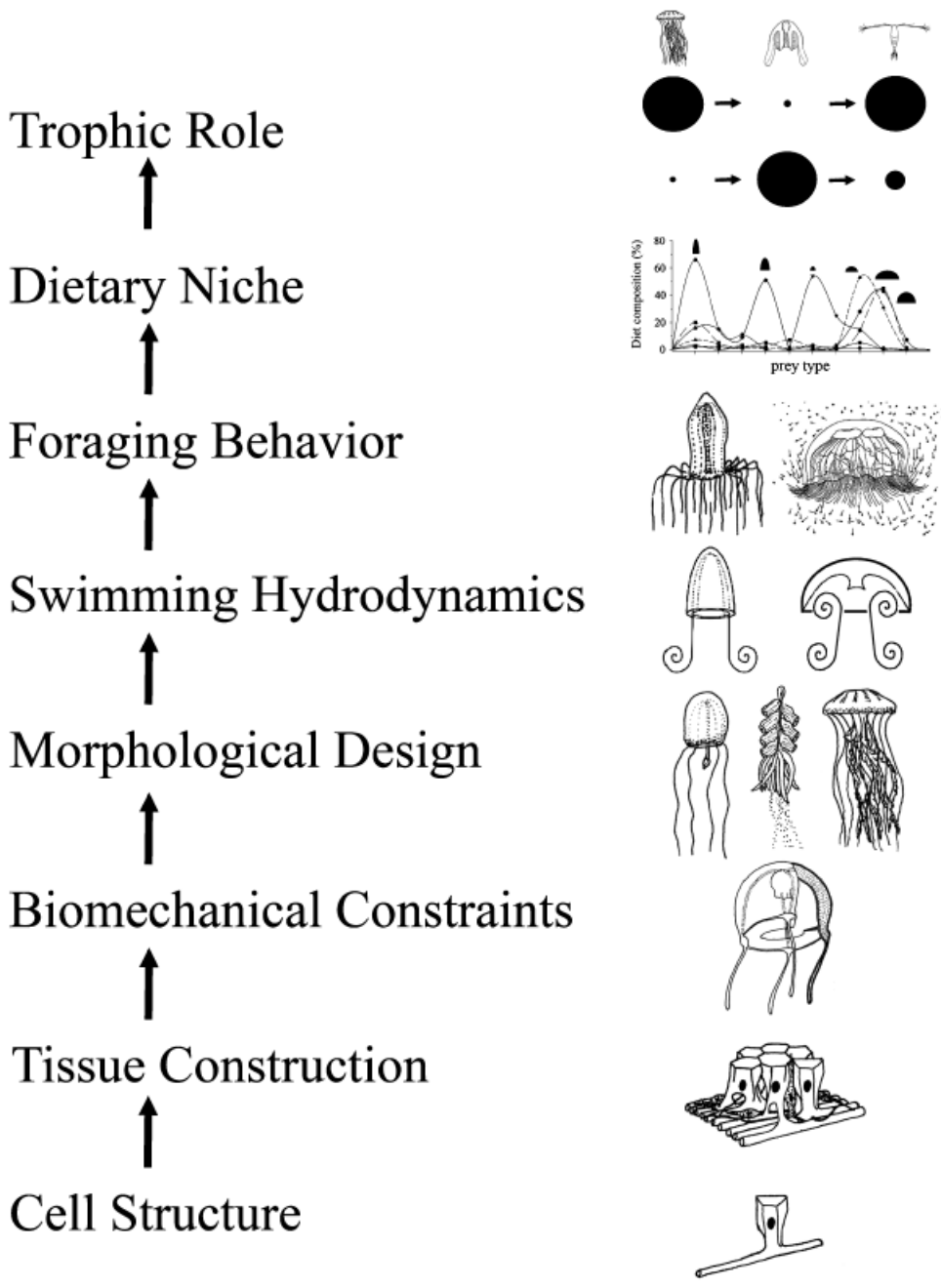


Fig. 17. Levels of integration influencing medusan form and function.

can be derived, most medusan lineages appear to have maintained characteristic propulsive and ecological patterns.

Owing to their relatively simple organization, the Medusozoa represent an unusual opportunity to piece together causal relationships that connect cellular, tissue, morphological, biomechanical, behavioral, and trophic processes of an animal group. We depict these in a linear pattern summarizing the links that occur at each level (Fig. 17). This schematic depiction is a simplification because many of the links between levels are bi-directional or interact in a more complex manner than the schematic synopsis. For example, prey availability certainly affects the success of particular dietary niches and foraging modes. In turn, the latter may affect natural selection on bell morphologies and propulsive modes. Yet despite its clear limitations, the synopsis provides a framework for understanding the integration of hierarchical levels of organization from cells to communities for one of the earliest planktonic animal groups.

We envision medusan evolution to be inextricably bound to this series of relationships, with each successive level of biological organization, from cellular to ecosystem, emerging from constraining traits of preceding levels. In this way, the “primitive” level of medusan organization provides a uniquely simple opportunity to assemble the interlocking parts of an evolutionary story. Our view begins at the cellular level, but progress on the molecular and developmental levels may reveal even more fundamental patterns underlying medusan organization.

Acknowledgments. We are grateful for financial support from the US National Science Foundation (OCE-0350834 and OCE-0623508 to J.H.C.; OCE-0351398 and OCE-0623534 to S.P.C.; OCE-0623475 to J.O.D.). We are grateful to J.E. Purcell and M.B. Decker for sharing their data (Fig. 17) with us. We thank A. Marques and H. Mianzan for valuable comments and discussion that improved earlier versions of the manuscript. We also thank P. Reynolds for help with graphic design.

References

- Ahlborn B, Harper DG, Blake RW, Ahlborn D, & Cam M 1991. Fish without footprints. *J. Theor. Biol.* 148: 521–533.
- Ahlborn B, Chapman S, Stafford R, & Harper R 1997. Experimental simulation of the thrust phases of fast-start swimming of fish. *J. Exp. Biol.* 200: 2301–2312.
- Alexander RMcN 2003. *Principles of Animal Locomotion*. Princeton University Press, Princeton, NJ. 371 pp.
- Anderson PAV & Schwab WE 1981. The organization and structure of nerve and muscle in the jellyfish *Cyanea capillata* (Coelenterata; Scyphozoa). *J. Morph.* 170: 383–399.
- Arai MN 1997. *A Functional Biology of Scyphozoa*. Chapman & Hall, London, UK. 316 pp.
- Arnett SA 1984. Diel vertical migration and feeding behavior of a demersal hydromedusan (*Polyorchis penicillatus*). *Can. J. Fish. Aquat. Sci.* 41: 1837–1843.
- Behrends G & Schneider G 1995. Impact of *Aurelia aurita* medusae (Cnidaria, Scyphozoa) on the standing stock and community composition of mesozooplankton in the Kiel Bight (western Baltic Sea). *Mar. Ecol. Prog. Ser.* 127: 39–45.
- Biewener AA 2003. *Animal Locomotion*. Oxford University Press, Oxford, UK. 281 pp.
- Bolsterli U 1977. An electron microscopic study of early developmental stages, myogenesis, oogenesis and cni-dogenesis in the Anthomedusa, *Podocoryne carnea* M. Sars. *J. Morph.* 154: 259–289.
- Boero F, Bouillon J, & Piraino S 1992. On the origins and evolution of hydromedusan life cycles (Cnidaria, Hydrozoa). In: *Sex Origin and Evolution. Selected Symposia and Monographs UZI*, 6. Dallai R, ed., pp. 59–68. Mucchi, Modena, Italy.
- Bone Q & Trueman ER 1982. Jet propulsion of the calycophoran siphonophores *Chelophyes* and *Abylopsis*. *J. Mar. Biol. Assoc. UK* 62: 263–276.
- Bonner JT 1965. *Size and Cycle: An Essay on the Structure of Biology*. Princeton University Press, Princeton, NJ.
- Bouillon J & Boero F 2000. The hydrozoa: a new classification in the light of old knowledge. *Thalassia Salentina* 24: 1–296.
- Boulenger MA & Flower WU 1928. The Regent’s Park medusa, *Craspedacusta sowerbyi*, and its identity with *C. (Microhydra) ryderi*. *Proc. Zool. Soc. Lond.* 66: 1005–1015.
- Brusca RC & Brusca GJ 2003. *Invertebrates*, 2nd Ed. Sinauer Associates, Sunderland, MA. 936 pp.
- Chapman DM 1974. Cnidarian histology. In: *Coelenterate Biology*. Muscatine L & Lenhoff HM, eds., pp. 1–92. Academic Press, New York, NY.
- Clifford HC & Cargo DG 1978. Feeding rates of the sea nettle, *Chrysaora quinquecirrha*, under laboratory conditions. *Estuaries* 1: 58–61.
- Colin SP & Costello JH 1996. Relationship between morphology and hydrodynamics during swimming by the hydromedusae *Aequorea victoria* and *Aglantha digitale*. *Sci. Mar.* 60: 35–42.
- 2002. Morphology, swimming performance and propulsive mode of six co-occurring hydromedusae. *J. Exp. Biol.* 205: 427–437.
- Colin SP, Costello JH, & Klos E 2003. In situ swimming and feeding behavior of eight co-occurring hydromedusae. *Mar. Ecol. Prog. Ser.* 253: 305–309.
- Colin SP, Costello JH, Graham WH, & Higgins J 2005. Omnivory by the small cosmopolitan hydromedusa *Aglaurea hemistoma*. *Limnol. Oceanogr.* 50: 1264–1268.

- Colin SP, Costello JH, & Kordula H 2006. Upstream foraging by medusae. *Mar. Ecol. Prog. Ser.* 327: 143–155.
- Collins AG 2002. Phylogeny of Medusozoa and the evolution of cnidarian life cycles. *J. Evol. Biol.* 15: 418–432.
- Collins AG, Schuchert P, Marques AC, Jankowski T, Medina M, & Schierwater B 2006. Medusozoan phylogeny and character evolution clarified by new large and small subunit rDNA data and an assessment of the utility of phylogenetic mixture models. *Syst. Biol.* 55: 97–115.
- Costello JH & Colin SP 1994. Morphology, fluid motion and predation by the scyphomedusa *Aurelia aurita*. *Mar. Biol.* 121: 327–334.
- 1995. Flow and feeding by swimming scyphomedusae. *Mar. Biol.* 124: 399–406.
- 2002. Prey resource utilization by coexistent hydromedusae from Friday Harbor, Washington. *Limnol. Oceanogr.* 47: 934–942.
- Costello JH, Klos E, & Ford MD 1998. In situ time budgets of the scyphomedusae *Aurelia aurita*, *Cyanea* sp, and *Chrysaora quinquecirrha*. *J. Plankton Res.* 20: 383–391.
- Daan R 1986. Food intake and growth of *Sarsia tubulosa* (Sars, 1835), with quantitative estimates of predation on copepod populations. *Neth. J. Sea Res.* 20: 67–74.
- Dabiri JO, Colin SP, Costello JH, & Gharib M 2005. Flow patterns generated by oblate medusan jellyfish: field measurements and laboratory analyses. *J. Exp. Biol.* 208: 1257–1265.
- Dabiri JO, Colin SP, & Costello JH 2006. Fast-swimming jellyfish exploit velar kinematics to form an optimal vortex wake. *J. Exp. Biol.* 209: 2025–2033.
- 2007. Morphological diversity of medusan lineages is constrained by animal–fluid interactions. *J. Exp. Biol.* 210: 1868–1873.
- D’Ambra I, Costello JH, & Bentivegna F 2001. Flow and prey capture by the scyphomedusa *Phyllorhiza punctata* von Lendenfeld 1884. *Hydrobiologia* 451: 223–227.
- Daniel TL 1983. Mechanics and energetics of medusan jet propulsion. *Can. J. Zool.* 61: 1406–1420.
- 1985. Cost of locomotion: unsteady medusan swimming. *J. Exp. Biol.* 119: 149–164.
- 1995. Invertebrate swimming: integrating internal and external mechanics. In: *Biological Fluid Dynamics*. Ellington CP & Pedley TJ, eds., pp. 61–89. The Company of Biologists Ltd., Cambridge, UK.
- DeMont ME & Gosline JM 1988a. Mechanics of jet propulsion in the hydromedusan jellyfish, *Polyorchis penicillatus*. I. Mechanical properties of the locomotor structure. *J. Exp. Biol.* 134: 313–332.
- 1988b. Mechanics of jet propulsion in the hydromedusan jellyfish, *Polyorchis penicillatus*. II. Energetics of the jet cycle. *J. Exp. Biol.* 134: 333–345.
- 1988c. Mechanics of jet propulsion in the hydromedusan jellyfish, *Polyorchis penicillatus*. III. A natural resonating bell and the importance of a resonant phenomenon in the locomotor structure. *J. Exp. Biol.* 134: 347–361.
- Fancett MS 1988. Diet and selectivity of scyphomedusae from Port Phillip Bay, Australia. *Mar. Biol.* 98: 503–509.
- Feigenbaum D & Kelly M 1984. Changes in the lower Chesapeake Bay food chain in the presence of the sea nettle *Chrysaora quinquecirrha* (Scyphomedusa). *Mar. Ecol. Prog. Ser.* 19: 39–47.
- Ford MD & Costello JH 2000. Kinematic comparison of bell contraction by four species of hydromedusae. *Sci. Mar.* 64 (Suppl. 1): 47–53.
- Ford MD, Costello JH, Heidelberg KB, & Purcell JE 1997. Swimming and feeding by the scyphomedusa *Chrysaora quinquecirrha*. *Mar. Biol.* 129: 355–362.
- Gerritsen J & Strickler JR 1977. Encounter probabilities and community structure in zooplankton: a mathematical model. *J. Fish. Res. Board Can.* 34: 73–82.
- Gladfelter WG 1972a. Structure and function of the locomotory system of *Polyorchis montereyensis* (Cnidaria, Hydrozoa). *Helgol. Wiss. Meeresunters.* 23: 38–79.
- 1972b. Structure and function of the locomotory system of the Scyphomedusa *Cyanea capillata*. *Mar. Biol.* 14: 150–160.
- 1973. A comparative analysis of the locomotory systems of medusoid Cnidaria. *Helgol. Wiss. Meeresunters.* 25: 228–272.
- Greene CH 1986. Patterns of prey selection: implications of predator foraging tactics. *Am. Nat.* 128: 824–839.
- Hansson LJ 1997. Capture and digestion of the scyphozoan jellyfish *Aurelia aurita* by *Cyanea capillata* and prey response to predator contact. *J. Plankton Res.* 19: 195–208.
- Hansson LJ & Kiorboe T 2006. Prey-specific encounter rates and handling efficiencies as causes of prey selectivity in ambush feeding hydromedusae. *Limnol. Oceanogr.* 51: 1849–1858.
- Hansson LJ, Moeslund O, Kiorboe T, & Riisgard HU 2005. Clearance rates of jellyfish and their potential predation impact on zooplankton and fish larvae in a neritic ecosystem (Limfjorden, Denmark). *Mar. Ecol. Prog. Ser.* 304: 117–131.
- Hyman LH 1940. *The Invertebrates: Protozoa Through Ctenophora*, Vol. 1. McGraw-Hill, New York, NY. 726 pp.
- Jankowski T, Strauss T, & Ratte HT 2005. Trophic interactions of the freshwater jellyfish *Craspedacusta sowerbii*. *J. Plankton Res.* 27: 811–823.
- Kramp PL 1961. Synopsis of the medusae of the world. *J. Mar. Biol. Assoc. UK* 40: 1–469.
- Larson RJ 1970. Feeding in coronate medusae (Class Scyphozoa, Order Coronatae). *Mar. Behav. Physiol.* 6: 123–129.
- 1976. Cubomedusae: feeding—functional morphology, behavior and phylogenetic position. In: *Coelenterate Ecology and Behavior*. Mackie GO, ed., pp. 236–245. Plenum Press, New York, NY.
- 1979. Feeding in coronate medusae (class Scyphozoa, Order Coronatae). *Mar. Behav. Phys.* 6: 123–129.
- 1987a. Trophic ecology of planktonic gelatinous predators in Saanich Inlet, British Columbia: diets and prey selection. *J. Plankton Res.* 9: 811–820.

- 1987b. Costs of transport for the scyphomedusa *Stomolophus meleagris* L. Agassiz. *Can. J. Zool.* 65: 2690–2695.
- Larson RJ, Mills CE, & Harbison GR 1989. In situ foraging and feeding behaviour of narcomedusae (Cnidaria: Hydrozoa). *J. Mar. Biol. Assoc. UK* 69: 785–794.
- Lindahll O & Hernroth L 1983. Phyto-zooplankton community in coastal waters of western Sweden—an ecosystem off balance? *Mar. Ecol. Prog. Ser.* 10: 119–126.
- Mackie GO 1990. Giant axons and control of jetting in the squid *Loligo* and the jellyfish *Aglantha*. *Can. J. Zool.* 68: 799–805.
- Mackie JE, Pugh RR, & Purcell JE 1987. Siphonophore biology. *Adv. Mar. Biol.* 24: 97–262.
- Madin LP 1988. Feeding behavior of tentaculate predators: in situ observations and a conceptual model. *Bull. Mar. Sci.* 43: 413–429.
- Marques AC & Collins AG 2004. Cladistic analysis of Medusozoa and cnidarian evolution. *Invert. Biol.* 123: 23–42.
- Matsakis S & Conover RJ 1991. Abundance and feeding of medusae and their potential impact as predators on other zooplankton in Bedford Basin (Nova Scotia, Canada) during spring. *Can. J. Fish. Aquat. Sci.* 48: 1419–1430.
- Mayer AG 1910. *Medusae of the World*. Carnegie Institute of Washington, Washington, DC. 735 pp.
- Mayr E 2001. *What Evolution Is*. Perseus Books, New York, NY. 318 pp.
- McGhee GR 1999. *Theoretical Morphology: The Concept and Its Applications*. Columbia University Press, New York, NY. 316 pp.
- Megill WM, Gosline JM, & Blake RW 2005. The modulus of elasticity of fibrillin-containing elastic fibres in the mesoglea of the hydromedusa *Polyorchis penicillatus*. *J. Exp. Biol.* 208: 3819–3834.
- Mianzan HW & Cornelius PFS 1999. Cubomedusae and Scyphomedusae. In: *South Atlantic Zooplankton*. Boltovskoy D, ed., pp. 513–559. Backhuys Publishers, Leiden, the Netherlands.
- Mills CE 1981. Diversity of swimming behaviors in hydromedusae as related to feeding and utilization of space. *Mar. Biol.* 64: 185–189.
- 1995. Medusae, siphonophores, and ctenophores as planktivorous predators in changing global ecosystems. *ICES J. Mar. Sci.* 52: 575–581.
- Moller H 1979. Significance of coelenterates in relation to other plankton organisms. *Meeresforsch Rep. Mar. Res.* 27: 1–18.
- 1984. Reduction of a larval herring population by jellyfish predator. *Science* 224: 621–622.
- O’Dor RK & Hoar JA 2000. Does geometry limit squid growth? *ICES J. Mar. Sci.* 57: 8–14.
- Olesen NJ 1995. Clearance potential of jellyfish *Aurelia aurita*, and predation impact on zooplankton in a shallow cove. *Mar. Ecol. Prog. Ser.* 124: 63–72.
- Omori M & Kitamura M 2004. Taxonomic review of three Japanese species of edible jellyfish (Scyphozoa: Rhizostomeae). *Plankton Biol. Ecol.* 51: 36–51.
- Pauly D 1997. Geometrical constraints on body size. *Trends Ecol. Evol.* 12: 442.
- Polis GA, Myers CA, & Holt RD 1989. The ecology and evolution of intraguild predation: potential competitors that eat each other. *Ann. Rev. Ecol. Syst.* 20: 297–330.
- Prairie YT & Bird DF 1989. Some misconceptions about the spurious correlation problem in the ecological literature. *Oecologia* 81: 285–288.
- Prothero J 1986. Methodological aspects of scaling in biology. *J. Theor. Biol.* 118: 259–286.
- Pugh PR 1999. Siphonophorae. In: *South Atlantic Zooplankton*. Boltovskoy D, ed., pp. 467–511. Backhuys Publishers, Leiden, the Netherlands.
- Purcell JE 1981. Selective predation and caloric consumption by the siphonophore *Rosacea cymbiformis* in nature. *Mar. Biol.* 63: 283–294.
- 1989. Predation on fish larvae and eggs by the hydromedusa (*Aequorea victoria*) at a herring spawning ground in British Columbia. *Can. J. Fish. Aquat. Sci.* 46: 1415–1427.
- 1990. Soft-bodied zooplankton predators and competitors of larval herring (*Clupea harengus pallasii*) at herring spawning grounds in British Columbia. *Can. J. Fish. Aquat. Sci.* 47: 505–515.
- 1991a. A review of cnidarians and ctenophores feeding on competitors in the plankton. *Hydrobiologia* 216/217: 335–342.
- 1991b. Predation by *Aequorea victoria* on other species of potentially competing pelagic hydrozoans. *Mar. Ecol. Prog. Ser.* 72: 255–260.
- 1997. Pelagic cnidarians and ctenophores as predators: selective predation, feeding rates, and effects on prey populations. *Ann. Inst. Oceanogr. Paris* 73: 125–137.
- 2003. Predation on zooplankton by large jellyfish (*Aurelia labiata*, *Cyanea capillata*, *Aequorea aequorea*) in Prince William Sound, Alaska. *Mar. Ecol. Prog. Ser.* 246: 137–152.
- Purcell JE & Mills CE 1988. The correlation between nematocyst types and diets in pelagic Hydrozoa. In: *The Biology of Nematocysts*. Hessinger DA & Lenhoff HM, eds., pp. 463–485. Academic Press, San Diego, CA.
- Purcell JE & Grover JJ 1990. Predation and food limitation as causes of mortality in larval herring at a spawning ground in British Columbia. *Mar. Ecol. Prog. Ser.* 59: 55–61.
- Purcell JE & Nemazie DA 1992. Quantitative feeding ecology of the hydromedusan *Nemopsis bachei* in Chesapeake Bay. *Mar. Biol.* 113: 305–311.
- Purcell JE & Decker MB 2005. Effects of climate on relative predation by scyphomedusae and ctenophores on copepods in Chesapeake Bay during 1987–2000. *Limnol. Oceanogr.* 50: 376–387.
- Raskoff KA 2002. Foraging, prey capture, and gut contents of the mesopelagic narcomedusa *Solmissus* spp. (Cnidaria: Hydrozoa). *Mar. Biol.* 141: 1099–1107.

- Raup DM & Michelson A 1965. Theoretical morphology of the coiled shell. *Science* 166: 994–995.
- Roper CFE & Boss KJ 1982. The giant squid. *Sci. Am.* 246: 96–105.
- Satterlie RA 2002. Neuronal control of swimming jellyfish: a comparative story. *Can. J. Zool.* 80: 1654–1669.
- Satterlie RA, Thomas KS, & Gray GC 2005. Muscle organization of the cubomedusa *Tripedalia cystophora*. *Biol. Bull.* 209: 154–169.
- Shorten M, Davenport J, Seymour JE, Cross MC, Carrette TJ, Woodward G, & Cross TF 2005. Kinematic analysis of swimming in Australian box jellyfish, *Chiropsalmus* sp. and *Chironex fleckeri* (Cubozoa, Cnidaria: Chiropodidae). *J. Zool. London* 267: 71–380.
- Schneider G & Behrends G 1998. Top-down control in a neritic plankton system by *Aurelia aurita* medusae—a summary. *Ophelia* 48: 71–82.
- Schuchert P, Reber-Muller S, & Schmid V 1993. Life stage specific expression of a myosin heavy chain in the hydrozoan *Podocoryne carnea*. *Difference* 54: 11–18.
- Seipel K & Schmid V 2005. Evolution of striated muscle: jellyfish and the origin of triploblasty. *Dev. Biol.* 282: 14–26.
- Sotje I, Tiemann H, & Bamstedt U 2007. Trophic ecology and the related functional morphology of the deepwater medusa *Periphylla periphylla* (Scyphozoa, Coronata). *Mar. Biol.* 150: 329–343.
- Sullivan BK, Garcia JR, & Klein-MacPhee G 1994. Prey selection by the scyphomedusan predator *Aurelia aurita*. *Mar. Biol.* 121: 335–341.
- Titelman J & Hansson LJ 2006. Feeding rates of the jellyfish *Aurelia aurita* on fish larvae. *Mar. Biol.* 149: 297–306.
- Totton AK 1965. A Synopsis of the Siphonophora. British Museum of Natural History, London, UK. 230 pp.
- Tregouboff G & Rose M 1957. Manuel de planktonologie mediterraneene, Vol. 2. Centre National de la Recherche Scientifique, Paris, France. 589 pp.
- Uye S & Shimauchi H 2005. Population biomass, feeding, respiration and growth rates, and carbon budget of the scyphomedusa *Aurelia aurita* in the Inland Sea of Japan. *J. Plankton Res.* 27: 237–248.
- Valentine JW 2004. On the Origin of Phyla. University of Chicago Press, Chicago, IL. 614 pp.
- Valentine JW, Collins AG, & Meyer CP 1994. Morphological complexity increase in metazoans. *Paleobiology* 20: 131–142.
- Van Iten H, de Moraes Lerne J, Guimaraes Simoes M, Marques AC, & Collins AG 2006. Reassessment of the phylogenetic position of conulariids (?Eldiacaran–Triassic) within the subphylum Medusozoa (phylum Cnidaria). *J. Syst. Palaeontol.* 4: 109–118.
- Vogel S 1994. Life in Moving Fluids: The Physical Biology of Flow, 2nd ed. Princeton University Press, Princeton, NJ. 467 pp.
- Widmer CL 2004. The hydroid and early medusa stages of *Mitrocoma cellularia* (Hydrozoa, Mitrocomidae). *Mar. Biol.* 145: 315–321.
- Youngbluth MJ & Bamstedt U 2001. Distribution, abundance, behavior and metabolism of *Periphylla periphylla*, a mesopelagic coronate medusa in a Norwegian fjord. *Hydrobiologia* 451: 321–333.