

Biomechanics and Behavioral Adaptations associated with Cuttlefish Locomotion

by

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INTRODUCTION

Cuttlefish are a unique order of invertebrates within the class Cephalopoda. The 700 living species of recognized cephalopods are divided into two major groups: the shelled nautiloids and the reduced-shelled coleoids (Clarke 1988, Hanlon and Messenger 1996). Cuttlefish, squids, and octopods are represented in the latter category (Hanlon and Messenger 1996). The cuttlefish order Sepioidea is well represented within the coleoids; the genus *Sepia* alone contains over 100 species (Hanlon and Messenger 1996). These complex marine animals all bear the defining characteristics of the Sepioidea: a flattened internal shell (the cuttlebone) divided by numerous gas and fluid filled chambers, a muscular mantle covering the body, paired lateral fins, and 8 flexible arms and 2 long tentacles bearing adhesive suckers (Okutani 1987, Pearse et al. 1987).

Cuttlefish are mobile animals, generally inhabiting the shallow waters of continental shelves in temperate and tropical regions (Amaratunga 1987). Most commonly found living in the shallow neretic zone, they spend much of their time hovering above sandy bottoms and coral reefs (Amaratunga 1987, Hanlon and Messenger 1988, 1996). This hovering ability is directly related to the buoyancy of the calcified internal shell and is an important evolutionary trend in the adaptive radiation of cephalopods (Hanlon and Messenger 1996).

In order to understand cuttlefish locomotion, the evolutionary modifications of the external shell must be considered. Much of the fossil record of early cephalopods comes from the ectocochliates, the externally shelled cephalopods, of which over 10,000 species have been discovered (Lehmann 1981). Though this part of the fossil record is rich in species, only one genus of living shelled cephalopods, the *Nautilus*, exists today (Ward and Bandel 1987).

Packard (1972) proposed that significant radiation of coleoids appeared during the Mesozoic era, 65-195 M.y. B.P., proliferating important buoyancy adaptations that gave rise to present day cephalopods. Early work by Denton and Gilpin-Brown (1973) suggested patterns of morphological development that introduced gas spaces within the calcified external shell, followed by a reduction and internalization of the shell. Clarke (1988) suggested that the shell modification, along with the concurrent development of strengthened mantle muscles, aided in expelling water from the mantle cavity, effectively launching the prominent mechanism of current cuttlefish locomotion, jet propulsion. The increased buoyancy and stability created by these adaptations was important in maintaining position in the mid-water environment. These modifications gave cuttlefish the mobility to successfully compete with epipelagic fishes (Packard 1972, Clarke 1988).

The purpose of this paper is to discuss the biomechanics of cuttlefish locomotion and the behavioral adaptations facilitated by these mechanisms. Examining the morphological features that cuttlefish use to move, their energetics, and their integration into all aspects of cuttlefish behavior will foster a more comprehensive understanding of these unique animals.

MORPHOLOGY RELATED TO LOCOMOTION

There are many design features integral to cuttlefish locomotion. One important structure is the internal cuttlebone. Rounded and shaped similar to a small, thickened shield, the cuttlebone is divided into many thin chitinous partitions, separating gas filled anterior chambers and fluid filled posterior chambers (Boletzky 1987, Pearse et al. 1987). Functionally similar to fish swim bladders (Webber et al. 2000), the forward most gas- filled chambers are used to control buoyancy, aiding in easy hovering over the substrate (Clarke 1988). The smaller posterior chambers contain fluid that cuttlefish can manipulate, using strong mantle muscles to increase or decrease the internal volume (Trueman 1983, Webber et al. 2000). This specialized region of the shell enables the animals to angularly orient their bodies in the water column (Pearse et al. 1987, Webber 2000).

Along with the specialized cuttlebone, the muscular mantle cavity is also an important feature that increases the diversity of locomotion. Rogers et al. (1997) describe structure and function. Used in jet propulsion as well as in respiration, the mantle cavity is arranged with tightly packed, obliquely striated radial and circular muscle fibers. Contraction of the circular muscles within a mantle cavity of constant volume causes opposing extension of the radial muscles, effectively expelling water used for jetting. The mantle cavity refills with water when the muscle movements are reversed (Fig. 1, Trueman 1975). Along with these muscles, Kier (1988) describes a meshwork of connective-tissue fibers that penetrate the mantle muscles, storing elastic energy and working to antagonize the circular muscles. This opposing force assists in the expulsion of water from the mantle by hydrostatic forces (Curtin et al. 2000). Kier (1988) suggests that the elasticity of the connective tissue fibers plays an important role in the hydrostatic system. There seems to be a correlation between the thickness of mantle muscles and jetting ability (Kier 1988, Hanlon and Messenger 1996).

The mantle cavity contains another structure significant for cuttlefish locomotion: a membranous funnel. Wells (1988) describes the development of the mobile funnel as an enhancement of the hydrostatic skeleton, allowing for rapid jetting and steering by increasing the inflatable volume of the mantle. Wells (1988) explains that two infoldings of the mantle form joined lateral flaps leading to a ventral tubular siphon with the opening facing anteriorly. Contraction of the circular mantle muscles to expel water from the funnel enables the cuttlefish to swiftly propel itself backward. Trueman (1983) reasons that jet swimming is effectively accomplished by the contraction of mantle muscles and respiratory exchange through funnel membranes. Depending on the strength of muscle contraction, the resulting internal pressure change can create slow gliding or fast escape swimming (Trueman 1983). The ejection of water from the funnel may also allow a cuttlefish to hollow a depression in the substrate in order to bury itself for camouflage (Wells 1988).

Physiology studies performed by Wells (1988) describe the specialized system of giant neural fibers with large axons housed within the cuttlefish mantle cavity. This giant fiber system, which is used to facilitate jet propulsion, consists of three separate groups of giant nerve cells connecting to nerve fibers and extending the length of the mantle cavity. The system radiates from the stellate ganglion and connects to the mantle musculature. The giant fibers have varying grades of thickness and send nerve impulses that trigger maximal response from all other interacting nerve fibers. The giant-fiber system allows cuttlefish to contract mantle muscles quickly and powerfully. Wells (1988) states that these “all or nothing” nerve impulses can elicit very rapid water expulsion that increases the velocity of jet swimming.

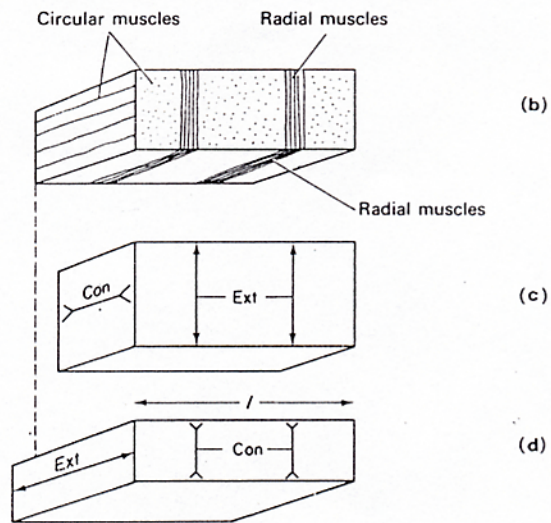
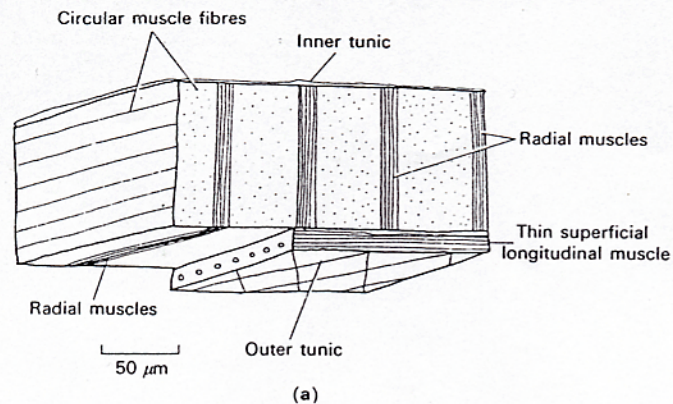


Figure 1. Structure of mantle musculature of *Sepia*. (a) shows a section of mantle with a layer of longitudinal muscle, circular muscle fibers, and transverse radial muscle bands; (b) resting stage of muscle; (c) thickening resulting from contraction (con $\rangle\langle$) of circular muscles and extension (ext $\langle\rightarrow$) of radial muscles. Circular muscle contraction produces a jet pulse. (d) radial muscles contracted and circular muscles extended during hyperinflation of the mantle. b-d shown at constant length and volume. (Adapted from Trueman 1975).

Specialized fin design also gives cuttlefish an edge in locomotory diversification. The paired undulatory fins on either side of the mantle allow for increased maneuverability and rapid directional change (Clarke 1988, Wootton 1999). Small amplitude waves can be generated along the mantle fins to move the animal in either the forward or backward direction (Trueman 1983). Hovering by slight rippling of these laterally fringing fins along with respiratory water exchange gives cuttlefish a “dynamic lift” that can alter their position from passive suspension to active propulsion (Boletzky 1987).

Kier (1988) describes another key feature of locomotory design: the arm and tentacle structure, which is specialized for bending and grasping. Cuttlefish have ten muscular appendages, including two longer tentacles that can be rapidly extended from the mantle. Attachment suckers are located on the terminal portion of the two tentacles, allowing for easier prey capture. Suckers are also located on the oral arm surfaces, giving cuttlefish an advantage in turning and bending prey in order to position the food toward the mouth.

Kier (1982) details the tentacle musculature. Tightly packed peripherally located longitudinal muscles surround dense transverse muscle fibers, forming a “tentacular stalk.” This stalk design functions to elongate and shorten the tentacles while providing the ability to exert torsional force on an object. While the tentacular stalk maintains a static internal volume, the process of muscle contraction will exert hydrostatic pressure, and the arms will elongate or shorten, depending on the muscle being controlled.

Kier (1982) proposes that cuttlefish are able to use their tentacles to exert torsional force on an object. He suggests that these directional movements are produced by the antagonism of two helical muscle layers within the tentacles. While working in conjunction with other modes of locomotion, the tentacular-stalk design has given cuttlefish many options to manipulate objects in their environment.

ENERGETICS OF LOCOMOTION

While cuttlefish exhibit a diverse array of functional morphology related to locomotion, their adaptations for movement come at an energetic cost. Jet swimming by propulsive water bursts is an energetically expensive and inefficient means of locomotion and is difficult to sustain for extended periods (Siebel et al. 1997). Successful jet propulsion requires the maintenance of high internal fluid pressure in order to expel a maximal amount of water for the most efficient power jetting (Kramer and McLaughlin 2001).

To offset the cost of this metabolically expensive activity, cuttlefish use intermittent locomotion. They pause and change the speed of their movements while adjusting to their surroundings (Kramer and McLaughlin 2001). Full or partial recovery of expended energy during these pauses is an important benefit. Quickly accelerating from a motionless state adds energetic costs to intermittent locomotion, but these costs might be offset by the energetic benefit derived from the residual gliding between jet bursts (Kramer and McLaughlin 2001).

Trueman (1980) used experimental measurements of swimming performance in several cephalopod species to assess jet-propulsion energetics. The results showed a reasonably good relationship of thrust performance for the cuttlefish *Sepia officinalis* compared to *Octopus vulgaris* and *Loligo vulgaris* (Table 1). Although cuttlefish demonstrate effective thrusting ability, drag forces add significant costs to jet propulsion (Webber et al. 2000). Fluid drag forces can be offset by the neutral buoyancy capabilities and hovering strategies of shallow-water cuttlefish, suggesting reduced metabolic rates in relationship to energy expenditure (Webber et al. 2000).

The difficulty in extracting oxygen from the water may also increase the energetic costs of jet propulsion (Webber et al. 2000). Slow water movement over the gills obtains maximal oxygen removal (Siebel et al. 1997), but jet thrusting for peak locomotory performance opposes this concept (Webber et al. 2000). Slow undulating fin motions and buoyant hovering are positive adaptations that may balance this inefficiency (Clarke 1988, Siebel et al. 2000).

Table 1: Comparison of swimming performance by jet propulsion. Velocity measurements refer to maximum instantaneous velocity (Adapted from Trueman 1980).

Animal	% of body vol expelled	Mantle muscle as % of body wt	Mantle pressure resp.-max. jet (kPa)	Frequency of jetting (Hz)	Velocity (m/sec)
<i>Loligo vulgaris</i> (350 g)	50	35	0.5-30	2	2
<i>Sepia officinalis</i> (250 g)	25	30	0.2-20	3	0.8
<i>Octopus vulgaris</i> (220 g)	15	<10	0.02-20	NA	NA

CUTTLEFISH BEHAVIORS RELATED TO LOCOMOTION

Relating the locomotory methods used by cuttlefish to adaptive behaviors enhances our understanding of cuttlefish biology. Through unique locomotory mechanisms, three essential life processes are maintained: feeding, defense, and reproduction.

Feeding

The carnivorous cuttlefish have developed specialized strategies for hunting and capturing prey. Utilizing the cuttlebone's fluid-filled posterior chambers, they contract their mantle muscles to reduce the volume of water while increasing the volume of air (Trueman 1988). This allows them to orient themselves in a head down posture to hunt for partially buried prey on the substrate (Hanlon and Messenger 1996). By then using the jet force of the mantle funnel, they can expel a jet of water over the bottom, making buried prey more visible (Hanlon and Messenger 1996).

Another strategy practiced by cuttlefish is the rapid extension of their tentacles to capture swimming prey (Halm et al. 2000). This method is important in the ambush hunting described by Hanlon and Messenger (1996). The cuttlefish partially bury themselves in the substrate. When the prey comes near, the cuttlefish utilizes the dynamic lift provided by jetting to quickly rise from the substrate, extend its tentacles, seize the prey, and bring it back to the mouth.

Observations by Messenger (1968: cited in Hanlon and Messenger 1996) explain a different type of ambush hunting that depends on the specialized hovering ability of cuttlefish. While cuttlefish move their fins in slight waves, they often use luring techniques to draw prey closer. Cuttlefish hover above the substrate and present interesting arm displays to potential prey. They commonly use cryptic colorations while waving their arms in multiple directions. This seems to attract the curiosity of prey, usually shrimp, which often stop and watch. This becomes deadly to the prey when cuttlefish rapidly eject their long tentacles and strike.

Messenger (1968) also observed cuttlefish attacking prey using a ballistic method of pursuit and capture. In ballistic attacks, cuttlefish detect the prey and begin a swimming pursuit. They fix the prey's position in the water and then forcefully propel themselves at the target by a powerful jet of water, effectively launching a missile-like attack. Studies by Boucher-Rodoni et al. (1987) and Halm et al. (2000) have also described observations of this type of attack behavior.

Considering the diversity of feeding strategies exhibited by cuttlefish, I wonder if there might be patterns to the particular capture method employed. Laboratory experiments by Halm et al. (2000) have shown a degree of prey-specific capture methods using crabs and shrimp, but field research lacks sufficient data to support a comprehensive evaluation (Hanlon and Messenger 1996). Cuttlefish locomotory abilities suggest that they have many options for foraging and capture (Boucher-Rodoni 1987). I think it would be worth exploring how they select their prey in order to understand the success rates achieved using these different capturing methods. Open water studies in a natural environment should be beneficial in obtaining a more accurate assessment of prey preferences. I might design a field experiment utilizing coral reef communities. I would assess viable reefs for cuttlefish populations and prey species diversity. I would then use SCUBA and underwater video cameras to record direct observations of cuttlefish foraging behavior and capture methods.

This type of field research would work well with a large aggregation such as the annual spawning group of Australian cuttlefish studied by Hall and Hanlon (2002). Non-invasive observations of extensive group activity in this natural environment would allow for more comparative analysis of possible behavior patterns related to prey-specific capture efficiency.

Defense

Cuttlefish have exploited their diverse locomotory methods by developing several interesting modes of defense. The most obvious defensive maneuver used by cuttlefish is escape jetting. The rapid muscle contractions that expel water through the funnel are an effective method of evasion (Boyle 1986). Observations by Hanlon and Messenger (1996) also describe a particularly successful defensive adaptation cuttlefish use in combination with escape jetting: ink ejection. A release of a dense ink cloud from an internal sac maximizes the evasion response by distracting predators from the actual escape path (Boletzky 1987, Hall and Hanlon 2002). The inking may appear in two forms: acting as a visual smoke screen to confuse predators or by actually resembling the shape of the cuttlefish and eliciting attack of the ink cloud (Hanlon and Messenger 1996). The control of ink discharge is maintained by a combination of the giant nerve fibers sending electrical signals to the mantle muscles and coordinating contraction of propulsive jetting (Boletzky 1987).

Another type of defensive posture uses protracted fin undulations and extensive arm displays. While slowly swimming horizontally, the cuttlefish contorts its arms laterally, stretching upward and downward (Boletzky 1987). It changes its internal shell volume and floats with its head positioned downward, disguising itself as floating algae or plant material (Boletzky 1987, Hanlon and Messenger 1996).

Hanlon and Messenger (1988) describe a defensive maneuver they refer to as "Clandestine escape" in which they observed juvenile cuttlefish utilizing a combination of jet pulses, fin and tentacle posturing, and cryptic coloration in order to escape predatory fish. In the shallow waters

these young cuttlefish inhabit, wave surges create movement of sand and floating algae on the substrate. When a predator comes near, the cuttlefish releases its suction grip on the bottom, gently jet pulses upward with the wave flow, displays a cryptic “Disruptive pattern” breaking up the body outline, and presents its fins and tentacles in a position that mimics the floating algae. The cuttlefish would perform this maneuver irregularly while slowly moving away from the predator.

I think important aspects of defensive maneuvers might be explored more broadly in population studies of cuttlefish in different environments. Might particular predator species such as the bony fish *Serranus cabrilla* or the barracuda affect the defensive response cuttlefish use in order to escape? Could cuttlefish display substrate specificity that would enhance either escape jetting or cryptic hovering? Experiments of defensive maneuvering should be performed in open-ocean environments to observe natural responses to predation pressures. Regional distinctions in response mechanisms could be examined using cuttlefish populations with different primary predators. Response patterns to predation by *Serranus cabrilla*, indigenous to Mediterranean waters, could be compared to reactions toward tropical species such as barracuda.

Boletzky (1987) suggests that benthic cephalopods should exhibit a greater degree of complex behaviors because their environment is more complex than that of pelagic cuttlefish. He offers that manipulating substrates as well as open-water investigations may play a part in learned defensive responses of juvenile cuttlefish. Hanlon and Messenger (1996) and Boyle (1986) suggest that expanded research into cuttlefish learning ability, specifically responses to predation pressures, could significantly enhance the limited information available today. Responding to predators by escape or mimicry has obvious value if successful, so it would follow that early learning of these behaviors during juvenile development would increase survival. To what extent these particular behaviors are learned or inherent are interesting questions that might be addressed with comparative studies of laboratory-reared and open-water populations.

I think it would be instructive to examine this idea of learned defensive behaviors in a variety of environments. This type of experiment could be performed with laboratory-reared cuttlefish in a controlled environment. I would use juvenile cuttlefish at various developmental stages and manipulate the substrate to observe any differences in defensive response. I would develop sandy-bottom and reef habitats for comparison. I would also design artificial predator mimics that would facilitate defensive maneuvers. This type of experiment might provide valuable insight into preferred locomotory techniques for escape.

Reproduction

Cuttlefish use their diversity of locomotion to employ several characteristic reproductive behaviors. They actively participate in elaborate courtship displays, agonistic behaviors, mating rituals, and guarding tactics in order to reproduce.

Although no categorically documented courtship displays have been observed in males, females often preferentially choose or reject mates according to criteria that are yet unknown (Hanlon et al. 1999, Adamo et al. 2000). In laboratory (Adamo et al. 2000) and open-ocean studies (Hall and Hanlon 2002), females have been observed to initiate copulation by orienting themselves to face a male, hovering, and then spreading their arms wide or extending them

forward and waving excitedly to elicit contact. This type of display usually results in successful mating (Hall and Hanlon 2002).

Along with choosing a mate, females have also been observed to reject mating attempts by rapidly jetting in the opposite direction, blowing streams of water at the male, and occasionally inking while escaping (Mangold 1987, Hall and Hanlon 2000). Escape jetting may contribute to reproductive success by promoting female choice that rejects potentially unsuitable mates (Adamo et al. 2000).

While males generally do not display courtship behaviors, they do participate in a variety of agonistic displays with other males. These marked behaviors are important competitive strategies for successful mating. Hanlon et al. (1999) and Hanlon and Messenger (1996) describe observations of male reproductive behavior. The typical pattern of male behavior when females approach is to swiftly jet forward from a hovering position, advance toward the female, and slowly fin swim along side her. The males next compete with each other for copulation rights by rapidly jetting toward one another and exhibiting intense coloration patterns. The most common pattern is characterized as “Intense Zebra Display” (Hanlon and Messenger 1996). They display this bold striped pattern while expanding their arms in wide aggressive postures, hovering side-by-side as aggressions escalate. If neither male retreats, the intensity of behavior increases and physical contact takes place. Using internal mantle pressure to pulse jet, the males forcefully ram into each other, often flipping over and biting each other’s mantle tissue (Hanlon and Messenger 1996, Hanlon et al. 1999, Adamo et al. 2000). During this process, they continually jet and often ink in large quantities. These contests generally result in the female copulating with the dominant male (Hanlon and Messenger 1996, Hall and Hanlon 2002).

During field studies, Hall and Hanlon (2002) observed mating acts in which the male utilized his hovering ability by extending his arms and grasping the female by the head. The pair locked arms and the male blew a jet of water from his funnel into the female’s buccal cavity, possibly as an attempt to flush out spermatophores from other males who might have mated previously. While hovering in mid-water, the pair continued the mating process with the male transferring his spermatophores to the female’s buccal area with his modified hectocotylus arm (Mangold 1987, Hall and Hanlon 2002). The ability to easily hover for an extended period allows males to transfer many spermatophores to the female, increasing the chance of reproductive success (Hanlon et al. 1999).

Mate-guarding behavior is another factor that may ensure a particular male’s genetic material is propagated. Often, after mating, the dominant male will hover very close to the female, blocking all potential competitors from contact (Hanlon and Messenger 1996, Hanlon et al. 1999). If provoked, the protective male will use rapid fin undulations to maneuver himself between the female and the challenger (Hall and Hanlon 2002). I believe this could be an important technique utilized for individual reproductive success. Guarding the female from other competitors gives the dominant male some insurance that his genes are passed on to the next generation.

Mate-guarding as a form of sperm competition has been observed in many species. Studies of spawning squid (Smale et al. 2001) and insects such as the dung fly *Scatophaga* (Parker 1970) and the dragonfly *Anisoptera* (Waage 1984) have presented evidence that mate-guarding behavior plays a prominent role in post-copulatory reproduction. Closely shadowing the female and driving away competition decreases the chance of fertilization by others and increases the probability of

individual gene propagation (Waage 1984). A study of post-copulatory mate-guarding behavior could be performed in a controlled laboratory environment while observing separate cuttlefish populations. Genetic sampling of future progeny could then be analyzed for a possible correlation between mate-guarding behavior and paternity. The genetic data might be able to measure fitness (Hanlon and Messenger 1996) and compare populations utilizing different locomotory methods to achieve reproductive success.

The energetics of reproductive behaviors might be another avenue for further research. There seems to be a great deal of investment in the elaborate activities cuttlefish perform in order to reproduce, but little data is available observing these activities in the field (Hanlon et al. 1999). There have been many laboratory studies examining cuttlefish locomotory energetics (Trueman 1983, Siebel et al. 1997, Webber et al. 2000). Perhaps more field observations of reproductive behaviors would provide important information in evaluating the energetic expenditures the locomotory mechanics of these behaviors require. Considering the energetic cost of reproduction: production of spermatophores, copulation and transfer of gametes, and agonistic contests, mate guarding seems to be a positive behavior that ensures a benefit from the metabolic investment. Evaluating the metabolic cost of reproductive success might offer insight into the evolution of cuttlefish diversity of locomotion.

CONCLUSION

The locomotory mechanisms of jet propulsion, buoyancy hovering, and undulatory fining have clearly enabled cuttlefish to develop behaviors significant for survival. The specialized design of the cuttlebone, mantle, and fins has increased the capacity for diverse movements. The ability to move slowly or quickly, easily changing body position and patterning, has provided cuttlefish with opportunities for a wide variety of hunting techniques and defensive maneuvers. The diversity of locomotion has also permitted cuttlefish to evolve behaviors that may increase reproductive success. Considering the degree of diversity that cuttlefish exhibit, there seems to be many opportunities for further research into locomotory abilities and behavioral adaptations.

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