

## Locomotion by *Abdopus aculeatus* (Cephalopoda: Octopodidae): walking the line between primary and secondary defenses

Christine L. Huffard

Department of Integrative Biology, University of California, Berkeley, CA 94720-3415, USA

e-mail: chuffard@berkeley.edu

Accepted 10 July 2006

### Summary

Speeds and variation in body form during crawling, bipedal walking, swimming and jetting by the shallow-water octopus *Abdopus aculeatus* were compared to explore possible interactions between defense behaviors and biomechanics of these multi-limbed organisms. General body postures and patterns were more complex and varied during the slow mode of crawling than during fast escape maneuvers such as swimming and jetting. These results may reflect a trade-off between predator deception and speed, or simply a need to reduce drag during jet-propelled locomotion. Octopuses swam faster when dorsoventrally compressed, a form that may generate lift, than when swimming in the head-raised posture. Bipedal locomotion proceeded as fast as swimming and can be considered a form of fast escape

(secondary defense) that also incorporates elements of crypsis and polyphenism (primary defenses). Body postures during walking suggested the use of both static and dynamic stability. Absolute speed was not correlated with body mass in any mode. Based on these findings the implications for defense behaviors such as escape from predation, aggression, and ‘flatfish mimicry’ performed by *A. aculeatus* and other octopuses are discussed.

Supplementary material available online at  
<http://jeb.biologists.org/cgi/content/full/209/19/3697/DC1>

Key words: hydrostatic, multi-legged, bipedal, camouflage, velocity, mimicry.

### Introduction

Unlike other examples of multi-limbed hydrostats such as caterpillars (Mezoff et al., 2004), onychophorans (Manton, 1950) and molting crabs (Taylor and Kier, 2003), octopuses move using eight flexible and independent, sucker-lined arms. Because of the diversity of possible movements and potential applications to the fields of biomimetics and soft robotics (Walker et al., 2005), the structure, use and control of individual octopus arms have been well studied. The arrangement of muscles offers movement in infinite degrees of freedom (Kier and Smith, 1985). Yet for at least one type of octopus (*Octopus vulgaris*), reaching movements are stereotyped (Gutfreund et al., 1996), and arms form vertebrate-like joints where two opposing waves of muscle activation meet during fetching (Sumbre et al., 2005; Sumbre et al., 2006). Although the nervous control of locomotion is poorly understood, these single-arm movements do not necessarily require complex control. Nervous control of reaching is decentralized and can proceed without involvement of the brain’s motor control region [the peduncle lobe (Messenger, 1967; Williamson and Chrachri, 2004)], allowing for simple feed-forward movements capable of incorporating feedback (Gutfreund et al., 1996; Gutfreund et al., 1998; Matzner et al.,

2000; Sumbre et al., 2001; Yekutieli et al., 2005a; Yekutieli et al., 2005b).

By contrast, few biomechanic aspects of octopus locomotion have been documented. Gaits have been illustrated for crawling by the deep-sea finned octopods (Octopoda: Cirrata) *Grimpoteuthis* sp. and *Cirrotheuthis* sp. (Villanueva et al., 1997), and bipedal walking by the shallow-water octopus (Octopoda: Incirrata) *Abdopus aculeatus* (Huffard et al., 2005). A few reports have noted speeds of crawling, jet-propulsion or bipedal locomotion (Wells et al., 1987; Wells, 1990; Huffard et al., 2005), but to my knowledge speeds across all modes, or for animals of different masses, have not been published previously for any single species.

Qualitative descriptions of body postures and modes of locomotion have been provided for some octopuses (Packard and Sanders, 1971; Roper and Hochberg, 1988; Hanlon and Wolterding, 1989; Mather, 1998; Hanlon et al., 1999; Norman et al., 2001). Fig. 1 illustrates the diversity of locomotion by seven species, providing a small window into the richness of their movements. In general, octopuses crawl by pushing and pulling themselves along the bottom using what appear to be irregular (Mather, 1988) and intermittent movements of multiple arms (Wells et al., 1987; Forsythe and Hanlon, 1997).

Where known, crawling is the most common form of locomotion in the wild, used at relatively slow paces during activities away from the den [as in *Octopus cyanea* (Forsythe and Hanlon, 1997) and *Abdopus aculeatus* (Huffard, 2005)]. Fast transport typically involves jet propulsion, in which octopuses bring water into the mantle cavity and then expel it quickly through the funnel (Wells, 1990). Although it is the main form of fast escape (*via* swimming and jetting), jet propulsion is physiologically inefficient, quickly leading to oxygen debt and requiring internal mantle pressures high enough to stop the hearts (Wells et al., 1987; Wells, 1990). Bipedal locomotion provides some octopuses with another means to move faster than crawling during threatening situations, while freeing six arms for use in cryptic postures (Huffard et al., 2005).

Crypsis is the primary defense of shallow-water octopuses (Hanlon and Messenger, 1996). However, immobility is a major requirement for background matching in most animals (Edmunds, 1974), presenting a possible behavioral dilemma. Each move, whether to forage for food or to retreat from the vicinity of a predator, may compromise camouflage and trigger the predator's search image, putting the animal at risk. Whereas locomotion and traditional camouflage are often conflicting needs for many animals, some octopuses employ behaviors that may help circumvent this problem. By performing frequent shape change ['polyphenism' as in *Octopus cyanea* (Hanlon et al., 1999)], moving like unpalatable animals ['dynamic mimicry' as in *Thaumoctopus mimicus* (Norman et al., 2001)], or by moving while assuming the shape of inedible objects ['moving rock' of *O. cyanea* (Hanlon et al., 1999); during bipedal locomotion in *Amphioctopus marginatus* and *Abdopus aculeatus* (Huffard et al., 2005)], octopuses may employ predator deception during locomotion. Such behaviors may inhibit a predator's ability to form a search image for these octopuses as prey, allowing them to move about while visually noticeable but undetected as a meal (Hanlon et al., 1999).

Jetting and fast swimming are secondary defenses enacted once polyphenism and/or other forms of predator deception have initially failed (Hanlon and Messenger, 1996). These modes of locomotion may reflect measures to maximize speed or biomechanical efficiency during escape, rather than to prevent detection by predators. Where jetting octopuses have been described or illustrated, they tend to be similarly elongate, smooth and show limited color patterns, a streamlined form that appears remarkably consistent across many species (Fig. 1A) (Hartwick et al., 1978; Roper and Hochberg, 1988; Hanlon and Messenger, 1996; Hanlon et al., 1999). Swimming (forward jet-propulsion) often takes place with the head raised (HR), the body in a somewhat fusiform shape, and arms trailing close to or under the body (Fig. 1C) (Forsythe and Hanlon, 1988; Hanlon et al., 1999). Additionally (or instead), some octopuses swim while dorsoventrally compressed (DVC) with the arms held out to the side (Fig. 1D). When performed by the dark and light-striped *Thaumoctopus mimicus* DVC swimming has been attributed to mimicry of a similarly colored toxic flatfish (Norman et al., 2001). However, this form of swimming is

widespread among other long-armed octopuses without such striking body patterns [e.g. *A. aculeatus*, personal observations; *Octopus* sp. 2 (Hoover, 1998); *Octopus* sp. 18 (Norman, 2000)] and may serve as a faster and possibly more efficient way to swim than other means. *Abdopus aculeatus* performs both types of swimming and I hypothesize that individuals will swim faster while dorsoventrally compressed than with the head raised.

These reports suggest a role of locomotion in both primary and secondary defenses of octopuses, with possible trade-offs between predator deception and fast-escape. Body posture and skin patterns are predicted to be more complex and varied during slow modes such as crawling (when an octopus is more likely to encounter a predator) than during fast escape maneuvers such as swimming and jetting (for which the main objective is to flee). Bipedal locomotion is predicted to represent an intermediary between fast escape and camouflage (Huffard et al., 2005) both in terms of speed, and in terms of the number of body patterns exhibited. *Abdopus aculeatus* has among the most complex skin patterning and camouflage capabilities of any octopus (Norman and Finn, 2001; Huffard, 2005). It performs the four main modes of octopus locomotion, and tends to behave relatively naturally in large aquaria (Huffard, 2005), making it an ideal subject in which to address these hypotheses. Additionally, the speeds attained by differently sized animals relate to their abilities to escape aggression and predation (Rezende et al., 2006). Here speeds of differently sized *A. aculeatus* are compared to explore the role of locomotion in defensive situations related to these behavioral processes.

### Materials and methods

Eleven foraging octopuses *Abdopus aculeatus* (d'Orbigny 1834) were captured with a hand net from intertidal reef flats and returned to the Lizard Island Research Station, Great Barrier Reef, Australia (14°40'S, 145°28'E) for observation (August 2005). They were maintained individually in 18 liter tubs with flow-through seawater, and fed once daily a variety of crustaceans from the groups Xanthidae, Portunidae, Grapsidae, Paguridae, Stomatopoda, Panaeidae, and *Calappa*. Each individual was sexed, sized, weighed and identified by arm injury. Calipers were used to measure the distance from between the eyes to the posterior end of the mantle while the mantle was in a contracted state, estimating a minimum mantle length (*ML*) for each animal. To obtain wet masses, animals were held in a net above the water until they stopped dripping and then allowed to crawl from the net into a small beaker of water on an electric balance. *A. aculeatus* is an arm-dropping animal and individuals in the wild are often missing several arms. Individuals missing two full arms or more were not included in analyses because their locomotor abilities might be significantly impacted by their injuries.

Observations were performed in a 2.5 m diameter circular tank with flowthrough seawater. Water depth was approximately 0.3 m, which simulates tidal level during peak active periods of this species (Huffard, 2005). Substrate was

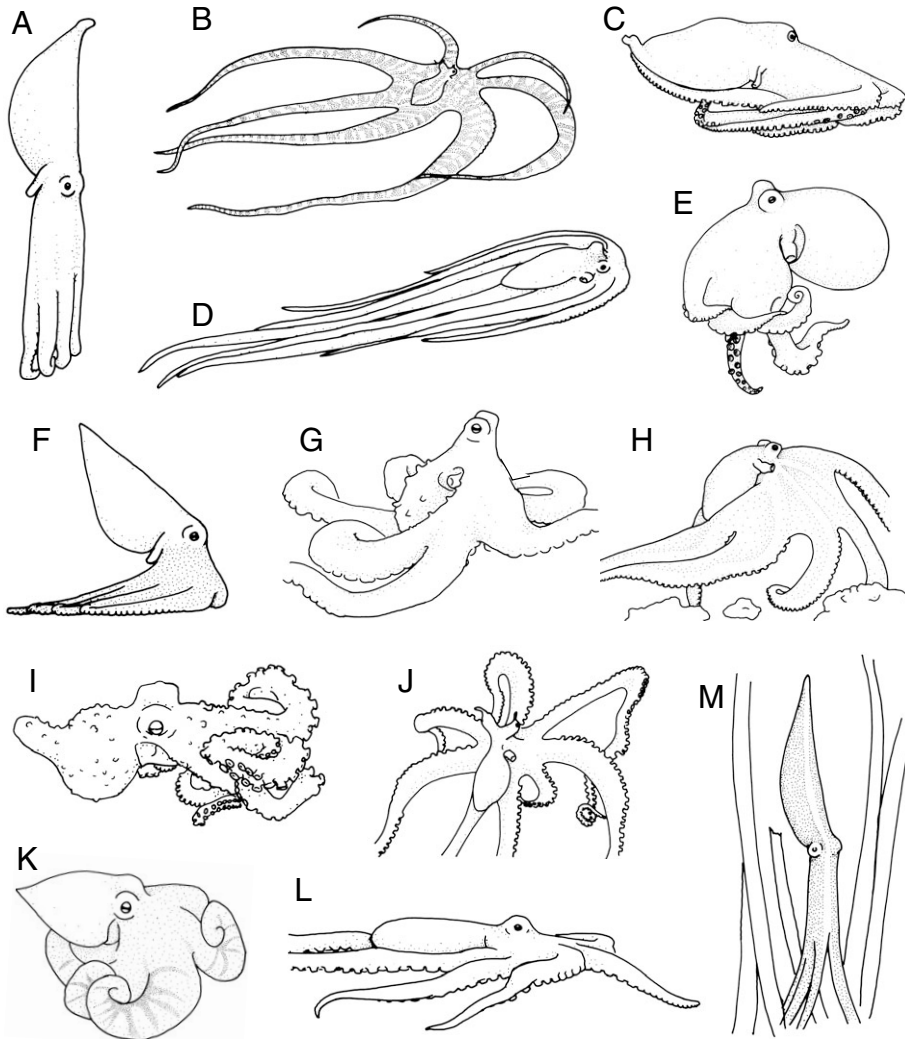


Fig. 1. Examples of body positions during: (A) jetting, (B–D) swimming, (E) walking and (F–M) crawling by a variety of octopuses, in which all except A show movement from the left to right side of the page. (A) *Hapalochlaena lunulata* jetting vertically up and down in the water column, drawn from the video *Shape of Life: Survival Game* Sea Studios, Inc., cameraman Bob Cranston. (B) *Thaumoctopus mimicus* swimming slightly above the substrate, drawn from a frame of a video taken by Annie Crawley (damaged arm I idealized, but missing arm not created). (C) *H. lunulata* swimming in the water column, drawn from photograph by R. L. Caldwell. (D) *Octopus* sp. 18 (Norman, 2000) swimming close to the substrate, drawn from photograph by Roger Steene (Norman, 2000). (E) *Amphioctopus marginatus* drawn from the video *Shape of Life: Survival Game* Sea Studios, Inc., cameraman Bob Cranston. (F) *H. lunulata* drawn from a photograph by R. L. Caldwell. (G) *Octopus* cf. sp. 18 (Norman, 2000) drawn from photograph by Jeffrey Rosenfeld. (H) *Octopus* sp. 2 (Hoover, 1998) drawn from photograph. (I) *Callistoctopus luteus*, drawn from photograph by Roberto Sozzani. (J) *Octopus* sp. 20 (Norman, 2000) drawn from a photograph by Denise Tackett. (K–M) *A. aculeatus* (North Sulawesi) drawn from frames of a video and field drawings.

semi-natural and consisted of a thin layer of sand (0–1 cm depth) scattered sparsely with rubble (5–15 cm diameter). Each octopus was observed for 30–60 min at a time. Because octopuses demonstrate highly variable responses to stimuli (Hanlon and Messenger, 1996), and to prevent habituation, a variety of stimuli (waving a net near the animal, touching the animal gently with a net, moving the rubble on which it sat, placing it on open sand and waiting for it to move to cover, lifting the animal to the surface and letting it fall to the bottom) were used to induce locomotion. I attempted to film each octopus performing each mode of locomotion (crawling, walking, swimming, and jetting; Fig. 2) three times. Efforts to randomize the order of stimuli and locomotion performed were abandoned because octopuses did not respond consistently enough to stimuli. I did not aim to show maximum speeds because motivation necessary to yield them may have lead to exhaustion or the use of jetting only. If the animal resisted movement, appeared fatigued, or would not perform a certain type of locomotion, then observations on that animal were stopped and resumed at least 4 h later, for up to four more trials. All bouts were video-taped using a Sony DCR-VX-2000 mini-

DV camera mounted on a tripod (1.25 m high), and pointed nearly straight down over the side of the tank. I analyzed video clips in which bouts of locomotion proceeded over bare sand in a straight line from left to right (or *vice versa*) directly in front of the camera. Representative video sequences of each form of locomotion were filmed with this camera in an Amphibico underwater housing (see supplementary material).

Definitions used here attempt to clarify terms already in use for octopuses and other cephalopods (Trueman and Packard, 1968; Wells et al., 1987; Hanlon and Messenger, 1996; Mather, 1998; Huffard et al., 2005). In the past, the terms ‘walking’ and ‘swimming’ appear to have been used to encompass crawling and jetting, respectively (Trueman and Packard, 1968; Wells et al., 1987; Forsythe and Hanlon, 1988), and jetting and swimming have been called backward and forward swimming, respectively (Forsythe and Hanlon, 1988; Hanlon and Messenger, 1996). The term ‘jetting’ is used here because it is analogous to the form of locomotion used by squids, for which the same term is used widely in the literature. Anatomical description follows that used in conventional cephalopod taxonomy, with the arms being anterior, the end of the mantle

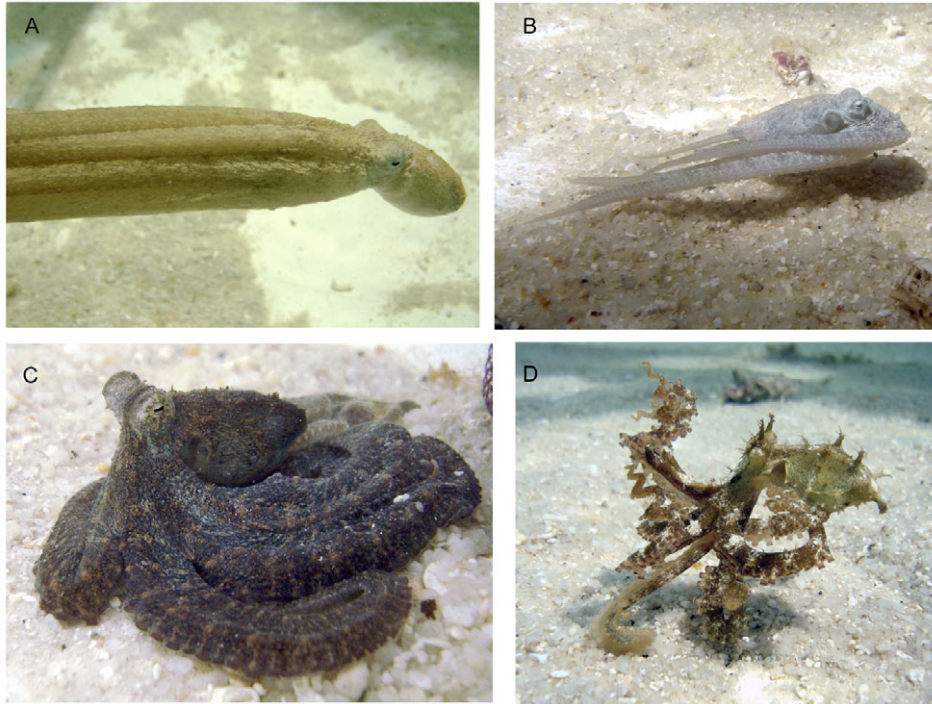


Fig. 2. Locomotion by *Abdopus aculeatus* (Lizard Island, Australia). (A) Jetting (see also Movie 1 in supplementary material for ‘medusoid’ jetting, which incorporates the arms); (B) swimming; (C) crawling; (D) walking (see Movies 2 and 3 in supplementary material).

posterior, arm pair I being dorsal, and arm pair IV being ventral (Roper and Voss, 1983). Fig. 2 shows photographs of *A. aculeatus* performing the types of locomotion measured in this study.

#### Jet

The octopus expels water from the mantle through the funnel, which is pointed away from the posterior mantle to propel the animal backward (led by the posterior end of the mantle). The body and arms trail behind the mantle and do not bear weight (although arms of some long-armed species do occasionally brush the bottom during jetting). Arms are held tightly together (Fig. 2A), in a V-formation, or spread laterally.

#### Swim

The octopus expels water from the mantle through the funnel, which is pointed backward toward the posterior mantle to propel the animal forward (led by the head, eyes, and arm crown). Swimming may or may not incorporate undulations of the body and arms. No portion of the body rests on the bottom (Fig. 1B–D, Fig. 2B).

#### Crawl

The octopus uses the sucker edge of more than two of eight arms to push and pull along the bottom in any direction. Each arm typically contacts the bottom at multiple points (Fig. 1F–M, Fig. 2C).

#### Bipedal walk/run

The octopus pushes and/or rolls along the bottom using

alternating movements of a single pair of arms [currently known only to be arm pair IV [(Huffard et al., 2005), Fig. 1E, Fig. 2D]].

Using Dvgate Plus 1.2.01.09250 software, video was downloaded onto a computer and edited into clips of video in which an octopus maintained a relatively uniform body shape and moved in a straight line. Frames ( $30 \text{ frames s}^{-1}$ ) were extracted using IrfanView 3.95 software. The locations of naturally occurring, discrete features [pupil of the eye, posterior mantle papilla, dorsal mantle white spots and frontal white spot (*sensu* Packard and Sanders, 1971)], the midpoint between the eyes, the posterior end of the mantle, the two most distant points of the animal, stationary control points on the sand, and the edges of an object of known size, were digitized using ScionImage Beta 4.0.2. These data were used to calculate relative speed in body lengths per second, and absolute speed in centimeters per second. Speeds achieved by each type of locomotion were averaged for each individual before inclusion into group analyses.

Data analyses were performed using StatXact 4.0.1, Systat 11.00.00, and SigmaStat 3.1. Pearson’s Correlation Coefficients (PCC) were calculated to identify correlations between size (mass) and average speeds per mode of locomotion. The Friedman test was used to determine whether or not the average speeds of locomotory modes differed. Because ten tests were performed to compare absolute and relative speeds per mode, respectively, pairwise Wilcoxon sign rank tests were adjusted for multiple comparisons (significance determined at  $\alpha_e=0.005$ ) (Bland and Altman, 1995). A paired Student’s *t*-test was used to compare speeds of different modes of swimming.

## Results

### Size relationships

Eleven *A. aculeatus* were filmed during this study. One individual, octopus no. 11 (O-11) was captured having already lost four arms, including both arms IV (ventral-most arm pair) and one arm III (third arm pair back from dorsal). The speeds of locomotion by this animal were calculated but were not included in statistical analyses, and are addressed in the discussion. All individuals were considered adult or sub-adult because they copulated either during the experimental period or within the following week. They ranged in size from 24–43 mm *ML* (11.3–62.3 g). At this period in their ontogeny the relationship between mantle length and mass was linear (Fig. 3), for which the equation:  $\text{mass}=2.42\text{ML}-46.61$  explains 94.6% of the variation between mass and mantle length. As with other octopuses (Semmens et al., 2004), *A. aculeatus* hatchlings and juveniles may show a very different relationship between mass and *ML* from that observed for adults. Because I aimed to describe this relationship for adults only, and not the early stages of growth, the *y*-intercept was not forced to zero.

### Variation in locomotion

Individuals in this study demonstrated considerable variation in the body form assumed (Fig. 4), and the speeds attained (Fig. 5) during locomotion. Body patterns and postures are described briefly per mode of locomotion and summarized in Table 1. Detailed descriptions of skin components consistent with these body patterns are presented elsewhere (Huffard, 2005). The most common varieties (aside from those in Fig. 2) are shown in Fig. 5, and given names if the body position (1) was different from the common positions in Fig. 2, (2) involved consistent chromatophore and papillae patterns, and (3) was demonstrated consistently by the octopuses.

### Jetting

A total of 62 examples of jetting were analyzed for ten animals. Neither absolute nor relative jetting speed correlated with mass [mass vs relative speed ( $BL\ s^{-1}$ ), where *BL*=body

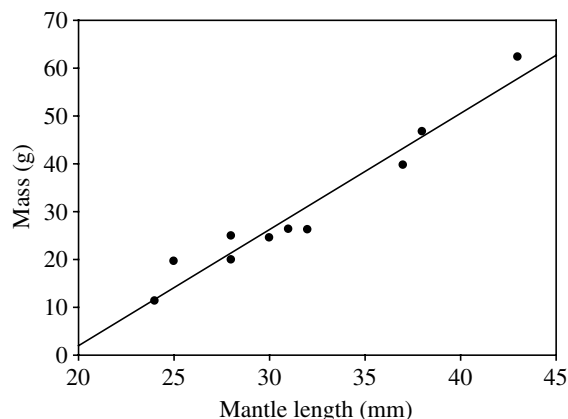


Fig. 3. Relationship between mantle length (mm) and mass (g) of adult *Abdopus aculeatus*, with the trendline  $\text{mass}=2.42\text{ML}-46.61$ ;  $R^2=0.95$ .

length: PCC  $-0.48$ ,  $N=10$ ,  $P=0.16$ ; mass vs absolute speed ( $\text{cm}\ s^{-1}$ ): PCC  $-0.058$ ,  $N=8$ ,  $P=0.89$ ). Jetting speeds averaged  $1.73\pm 0.80\ BL\ s^{-1}$  and  $45.3\pm 19.4\ \text{cm}\ s^{-1}$ . Maximum jetting speeds calculated were  $3.29\ BL\ s^{-1}$  and  $70.1\ \text{cm}\ s^{-1}$ .

In nearly every case of jetting the body was completely elongated with the straight arms held tightly together, and the skin smooth (Fig. 2A). Two octopuses also exhibited a total of four cases of curled arm jetting [curled arm swimming (*sensu* Packard and Sanders, 1971) (Fig. 4E)]. In the two side-by-side comparisons possible, curled arm jetting was slower than elongate jetting. This form was rare and not included in analyses. During elongate jetting, octopuses were consistently pale except for four cases (two animals) when they were dark brown with pale medial stripe, and two cases (two animals) when they exhibited black and white stripes consistent with aggressive interactions (as also exhibited by the mating male in Fig. 4H). Medusoid jetting occurs when octopuses open and close the arms and arm crown like an umbrella to supplement jet propulsion (Forsythe and Hanlon, 1988). *Abdopus aculeatus* occasionally use this form in the wild during sustained jetting to chase conspecifics (see Movie 1 in supplementary material) or prey items such as swimming crabs (C.L.H., personal observation). It was not observed during this study, perhaps because the water was not deep enough, the stimuli were not appropriate, or the tank was too small for sustained jetting.

### Swimming

Forty-five examples of swimming from nine animals were analyzed. Larger, heavier octopuses took longer than small octopuses to swim their body length past a given point [mass vs relative speed ( $BL\ s^{-1}$ ): PCC  $-0.76$ ,  $N=9$ ,  $P=0.018$ ]. Absolute speed in  $\text{cm}\ s^{-1}$  did not correlate with octopus mass (PCC  $-0.065$ ,  $N=9$ ,  $P=0.90$ ). Swimming speeds averaged  $1.27\pm 0.32\ BL\ s^{-1}$  and  $10.8\pm 6.4\ \text{cm}\ s^{-1}$ . Maximum swimming speeds calculated were  $3.06\ BL\ s^{-1}$  and  $20.2\ \text{cm}\ s^{-1}$ .

Body form during swimming ranged gradually from the head raised (HR) posture with arms held close to and under the body (cf. Fig. 1C), to dorsoventrally compressed (DVC) with the head and mantle lowered to the same plane as the arms, which were held both forward and to the side (cf. Fig. 1D). Coloration ranged from dark brown to pale during HR swimming. Octopuses were consistently pale during DVC swimming. No erect papillae were visible during either form. Most individuals swam using an intermediate posture (Fig. 2B). In the four cases in which animals swam using clear examples of each form, DVC swimming was faster than HR swimming (paired *t*-test:  $P=0.004$ ,  $N=4$ ) by 23–59% (Fig. 5A).

### Crawling

Ten octopuses crawled a total of 86 times. Octopus crawling speed in  $BL\ s^{-1}$  and  $\text{cm}\ s^{-1}$  did not correlate with mass [mass vs  $BL\ s^{-1}$ : PCC  $-0.36$ ,  $N=10$ ,  $P=0.30$ ; mass vs absolute speed ( $\text{cm}\ s^{-1}$ ): PCC  $-0.23$ ,  $N=10$ ,  $P=0.53$ ]. Relative speed in  $ML\ s^{-1}$  (calculated for each animal from speeds in  $\text{cm}\ s^{-1}$  because of variability in body shape) declined with increasing octopus mass (PCC  $-0.58$ ,  $N=9$ ,  $P=0.10$ ). Crawling speeds averaged



Fig. 4. Variety of body positions of *A. aculeatus* during locomotion. (A) Walking backward, arms coiled close to the body; (B) walking obliquely backward; (C) walking forward, arms raised; (D) conical crawling (any direction), mantle conical, arms tucked under or pulled close to the body; (E) curled arm jetting; (F) walking, arms tucked under the body; (G) crawling forward upright; (H) female (right) crawling dragging mating male (left); (I) crawling (any direction), mantle upright, arms tightly coiled; (J) hopping, arm tips coiled tightly; (K) Individual O-11 hopping on the hectocotylus. Note small regenerating arms, including arm pair IV.

$0.62 \pm 0.01 \text{ BL s}^{-1}$ ,  $1.54 \pm 0.03 \text{ ML s}^{-1}$  and  $7.3 \pm 2.1 \text{ cm s}^{-1}$ . Maximum crawling speeds calculated were  $1.94 \text{ BL s}^{-1}$ ,  $4.31 \text{ ML s}^{-1}$  and  $21.3 \text{ cm s}^{-1}$ .

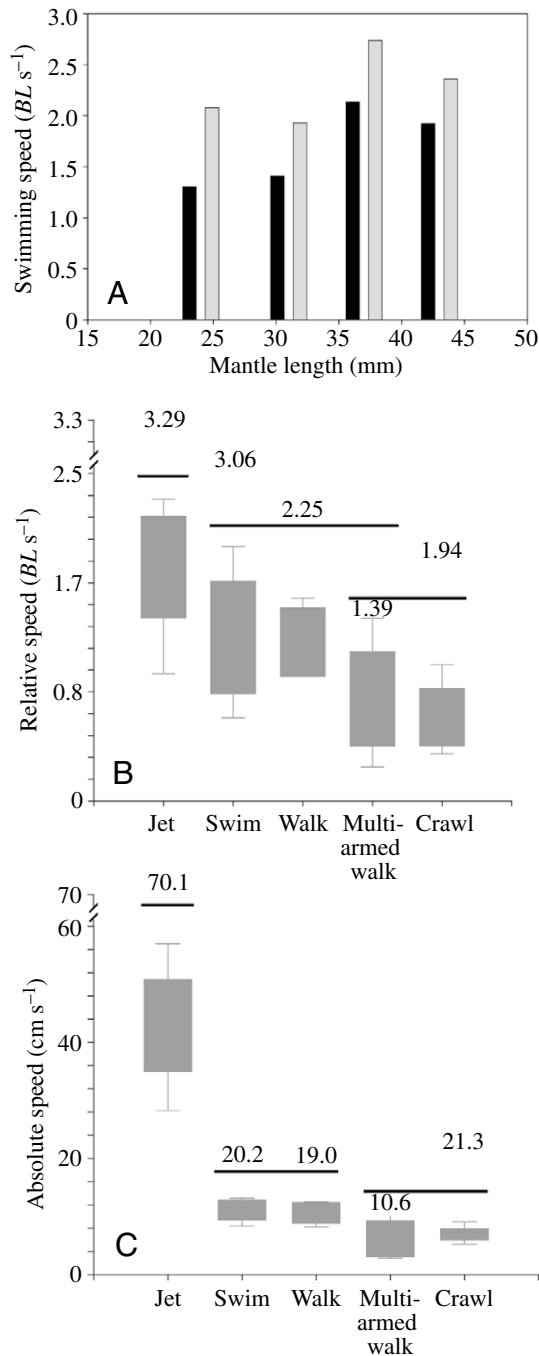
Octopuses demonstrated more variation in body posture while crawling than during any other form of locomotion. Most of this variation occurred between individuals rather than within the repertoire of any given octopus. Consistent variations involved: (1) Arms sprawled about the body, color and papillae patterns variable (Fig. 2C). (2) Upright crawling, in which the mantle was pointed and upright (Fig. 4G) with the arms typically dragged straight under or trailed behind the body, but coiled tightly on a few occasions (Fig. 4I). The color was dark with a pale medial stripe and the posterior mantle papilla lobate. (3) Conical crawling, which involved rolling along the sucker edge of arm pairs III and IV, or using several arms in unison to push and pull the octopus forward in jerky movements. The arms were curved backward, held close to body or to the side. The mantle was conical, gray or pale and the arms dark brown mottled. Secondary papillae gave a shaggy appearance (Fig. 4D). (4) Ball crawling, which involved rolling along the sucker edge of arm pairs III and IV, or moving on

stiffened, curved arms, with the mantle and arms forming a ball. Ball-crawling may be similar to 'moving rock' described previously (Forsythe and Hanlon, 1997; Hanlon et al., 1999).

#### Walking

Five of ten *A. aculeatus* walked bipedally a total of 23 times by rolling backward or obliquely backward (Fig. 4B) along the sucker edge of arm pair IV. During many instances of walking, a third and sometimes fourth arm was involved briefly (Fig. 4A). This form of locomotion was categorized as multi-armed walk (MAW) and the data were analyzed separately from bipedal walking. I found no relationship between octopus mass and walking speed, but none of the three largest octopuses walked [mass vs relative speed ( $\text{BL s}^{-1}$ ): PCC  $-0.71$ ,  $N=5$ ,  $P=0.18$ ; mass vs absolute speed ( $\text{cm s}^{-1}$ ): PCC  $-0.71$ ,  $N=5$ ,  $P=0.19$ ]. Octopuses walked at average speeds of  $1.34 \pm 0.19 \text{ BL s}^{-1}$  and  $13.1 \pm 11.5 \text{ cm s}^{-1}$ , reaching maximum speeds of  $2.25 \text{ BL s}^{-1}$  and  $19.0 \text{ cm s}^{-1}$ . Speeds for MAW averaged  $0.80 \pm 0.16 \text{ BL s}^{-1}$  and  $0.68 \pm 0.15 \text{ cm s}^{-1}$ , and reached  $1.39 \text{ BL s}^{-1}$  and  $10.6 \text{ cm s}^{-1}$ .

In addition to walking backward, octopuses also walked



forward on stiffened, bent alternate arms IV while occasionally dragging or possibly supporting weight briefly with a third arm (Fig. 4C; see Movie 2 in supplementary material). They also hopped backward on arm pair IV while sometimes incorporating jetting (Fig. 4J). These two examples were rare and were not included in analyses. O-11, which was missing arm pair IV, hopped on the hectocotylus, its only arm III (Fig. 4K). During both backward and forward walking, octopuses took on one of two different body positions: (1) arms coiled helically, raised high above the substrate, [cf. flamboyant display *sensu* Packard and Sanders (Packard and Sanders, 1969)], body ochre mottled, primary and supraocular

Fig. 5. (A) Swimming speed of *A. aculeatus* using the head raised (HR, black) vs flat, dorsoventrally compressed (DVC, gray) body forms. DVC swimming was consistently faster per individual than HR swimming (paired *t*-test  $P=0.004$ ). (B) Relative speed of modes. Mean speeds of *A. aculeatus* during modes of locomotion measured in  $BL s^{-1}$  (Friedman test statistic 16.00;  $P=0.003$ ). Horizontal lines are drawn over groups that are not significantly different from each other, as determined by pairwise Wilcoxon signed rank tests adjusted for multiple comparisons ( $\alpha_e=0.005$ ). Maximum speeds are given above these lines. Bars indicate standard error (s.e.m.),  $N=10$  (jet), 9 (swim), 5 (walk), 5 (multi-armed walk), 10 (crawl). (C) Absolute speed of modes. Mean speeds of *A. aculeatus* during modes of locomotion measured in  $cm s^{-1}$  (Friedman test statistic 11.80;  $P=0.019$ ). Horizontal lines are drawn over groups that are not significantly different from each other, as determined by pairwise Wilcoxon signed rank tests adjusted for multiple comparisons ( $\alpha_e=0.005$ ). Maximum speeds are given above these lines. Bars indicate s.e.m.,  $N=8$  (jet), 9 (swim), 5 (walk), 5 (multi-armed walk), 10 (crawl).

papillae erect and branched; (Fig. 2D, Fig. 4C), or (2) arms held close to or under the body, body typically dark mottled or sometimes dark with pale medial stripe, primary and secondary papillae erect and branched, although less so than in the flamboyant posture (Fig. 4F).

#### Comparison of speeds across modes

Average relative and absolute speeds were compared for jetting, swimming, crawling, walking and multi-armed walking (Fig. 5B,C). Average speeds differed between modes (Friedman  $P<0.05$  for both sets), but I found few pair-wise differences. Jetting was the fastest form of locomotion, followed by swimming and walking. Crawling and multi-armed walking proceeded at equivalent speeds on average, although maximum crawling speeds were faster and exceeded maximum absolute swimming speed.

#### Discussion

Locomotion can play a role in crypsis and polyphenism (primary defenses) of *A. aculeatus*, but biomechanical limitations may be just as important. Body patterns and postures were more varied during slower modes of locomotion than during faster, jet-propelled modes of locomotion. Crawling was the most diverse mode of locomotion observed here, incorporating so many postures and patterns that few could be defined. It is also the mode during which these octopuses are most likely to encounter a predator. By contrast, *A. aculeatus* showed little variation in body form and color pattern while jetting and swimming (two discernable shapes each, with limited color patterns and minimal involvement of the papillae), indicating that predator deception may not be an objective after the initiation of fast escape. However, the intricate body postures and skin textures often involved in primary defenses simply may not be possible during jet propulsion because of biomechanical limitations. Friction drag is a major force hindering squid jetting (Anderson et al., 2001) and would pose a significant obstacle for small octopuses as

Table 1. *Combinations of body patterns, postural components, and papillae employed by locomoting *Abdopus aculeatus**

Body patterns and prominent skin components	Example figures	Prominent postural components	Papillae patterns	Mode of locomotion
1. Ochre mottled (dorsal mantle white spots)	2D, 4C	Mantle held horizontal to substrate away from body; arms sprawled around the body, coiled helically while walking	Primary and supraocular papillae branched, flaplike	Crawling, walking, multi-armed walking
2. Dark mottled	4E,F	Arms drawn near or under body, or curled at tips as while jetting	Primary unbranched or slightly branched, supraocular unbranched, secondary small, posterior lobate	Crawling, walking, multi-armed walking, curled-armed jetting*
3. Dark with pale medial stripe	4A,B,G,I–K	Mantle typically held upright elongate, sometimes falls behind head; arms typically dragged straight below body, or sometimes tightly coiled	Posterior lobate	Crawling, walking, swimming*, jetting*
4. Mantle gray, arms dark mottled	4D	Arms curved backward, mantle conical	Secondary	Crawling with by using curved arms to push the body forward or to the side in jerky movements
5. Uniformly dark	2C	None consistent	Secondary, none	
6. Uniformly pale	2A,B	Elongate while jetting; head raised and dorsoventrally compressed while swimming	None	Crawling, swimming, jetting

\*Rare combinations.

well. To reduce drag by flattening the skin, octopuses must relax the papillae muscles. These muscles are controlled by the same brain lobe (the posterior chromatophore lobe) that controls chromatophore expansion (Miyan and Messenger, 1995; Williamson and Chrachri, 2004), which can couple the expression of skin texture and color (Miyan and Messenger, 1995). As a result, fast-jetting *A. aculeatus* may turn pale as a byproduct of flattening the skin to minimize drag, rather than some behavioral preference not to employ primary defenses.

Walking took place with only two body patterns, but they involved complex body positions, color and papillae patterns expressed consistently during camouflage of this species (Huffard, 2005). This form of locomotion appears to offer a means of escape that is intermediate in terms of defenses – approximately as fast as swimming, yet nearly as camouflaged and variable as crawling.

Bipedal walking by *A. aculeatus* proceeded as fast as swimming and can be considered a form of fast escape that does not rely on jet propulsion. The rolling movement of their walking arms (Huffard et al., 2005) appears similar to a low-drag arm-extension movement performed by *Octopus vulgaris* (Yekutieli et al., 2005a). However, given the body shape and papillae expression of walking octopuses, octopuses are clearly not more streamlined while walking than while swimming. Drag is further increased when each walking arm moves faster than the body during the initiation of a new step. In order to

overcome such drag and attain these speeds, certain elements of the bipedal gait might be remarkably efficient, and the forces involved require study.

A large footprint and/or dynamic stability might enable bipedal locomotion by octopuses. Underwater, gravitational forces are reduced by upward buoyancy, which renders gaits involving inverted pendula (such as walking on land) inefficient, and more stable postures are required to move along the bottom (Martinez et al., 1998). *Abdopus aculeatus* walks using a rolling gait with a large footprint [illustrated previously (Huffard et al., 2005)], even over rugged terrain. In general, static stability requires a moving organism's center of mass to remain within the polygon of support offered by the limbs involved in that particular gait (reviewed in Jindrich and Full, 2002). Octopuses that walked using a very large footprint might have been statically stable. However, several individuals used what appeared to be a smaller footprint and leaned back considerably while walking (Fig. 2D; Movie 3 in supplementary material). Although center of mass and gaits were not measured, they appeared to violate this condition of static stability. In those cases, *Abdopus aculeatus* may rely on dynamic stability to walk bipedally. In general, animals that are dynamically stable use momentum to overcome periods of static instability (reviewed by Jindrich and Full, 2002). Underwater, momentum is decreased by drag and the viscosity of water (Vogel, 1994). Any momentum these octopuses might



generate would decrease as an animal slows down, and might explain the observations of multi-armed walking. If some *Abdopus aculeatus* rely on dynamic stability to walk bipedally, then they might occasionally support their gait with another arm at lower speeds.

*Abdopus aculeatus* and *Amphioctopus marginatus* are the only two animals currently known to move bipedally without the support of a rigid skeleton (Huffard et al., 2005). They do so at equivalent speeds while adopting different body forms in different environments. Each of these octopuses lives in areas with strong and variable tidal currents, however, it is not yet known how body shape, speed, and the ability to walk may vary with hydrodynamic environment. In Sulawesi, Indonesia and some regions of Queensland, Australia, *Abdopus aculeatus* lives in macro-algae and/or seagrass-dominated intertidal reef flats, and exhibits the color patterns, textures, and motion of nearby plants for crypsis (Huffard, 2005). Any of the forms and colors demonstrated by walking octopuses in this study (Fig. 1D, Fig. 4A,B,F) may be perceived either as algae that commonly breaks loose from the substrate and drifts in the surge, or dead leaf-litter that washes in from the beach. In addition to allowing for a large footprint, the long arms of *A. aculeatus* contribute postural elements to these forms of crypsis. By contrast, *Amphioctopus marginatus* often lives on visually homogenous sand plains. Small round objects such as coconut shells, rocks, and sponges are among the sparse visually prominent elements of this environment. By holding the arms at the side and/or tucked under the body, adult *A. marginatus* may look similar to these objects, particularly coconut shells (without husks) that may roll slightly in the strong currents. In this posture, the dark arm stripes characteristic of many octopuses in this genus (Huffard and Hochberg, 2005) form a dark 'shaded' region under the animal that may contribute to its rounded appearance. Regardless of the objects they may resemble (and unlike jetting octopuses), these walking octopuses use crypsis and polyphenism during fast escape, which may inhibit recognition by a predator.

Although little is known about the speeds of other octopuses, values measured for *Abdopus aculeatus* are somewhat similar. They jetted and crawled slower than the larger *O. vulgaris* (jetting maximum:  $70 \text{ cm s}^{-1}$  vs  $100 \text{ cm s}^{-1}$ ; crawling average:  $7.3 \text{ cm s}^{-1}$  vs  $9 \text{ cm s}^{-1}$  for *A. aculeatus* and *O. vulgaris*, respectively) (Wells et al., 1987; Wells, 1990). Walking speeds of *A. aculeatus* were about the same as documented for the slightly larger *A. marginatus* [ $3 \text{ ML s}^{-1}$  vs  $2.6 \text{ ML s}^{-1}$ ;  $13 \text{ cm s}^{-1}$  vs  $14 \text{ cm s}^{-1}$ , respectively (Huffard et al., 2005)]. Jetting was the fastest form of locomotion by *Abdopus aculeatus*, and would provide the most obvious means of escape when being actively pursued by a predator. However, the bodies of jetting octopuses were so elongate that they took nearly as long as walking and swimming octopuses to pass their entire body over a given distance. If this distance is past a lie-in-wait predator, then that predator might be just as capable of grabbing any portion of a jetting *A. aculeatus* as a walking one, even though a jetting octopus would move four times as fast (in  $\text{cm s}^{-1}$ ).

As predicted, body form was related to swimming speed: *A. aculeatus* swam faster while dorsoventrally compressed than with the head raised. This shape, which provides flatfish with lift during swimming (Webb, 2002), appears to do the same for these octopuses. By contrast one individual was missing four adjacent arms, an injury that compromised its ability to assume this shape. Although it jetted as fast as other octopuses of the same mantle length, it swam more than half as slowly, possibly unable to generate lift. Shallow-water octopuses tend to be negatively buoyant, and upward forces of lift may also be important during jet-propulsion, particularly of large individuals. *Octopus vulgaris*, *O. californicus* and *Enteroctopus dofleini* jet with the arms spread laterally [(Wells, 1990); (Norman, 2000), figs on pp. 213 and 290], a position that may also enable lift in these fairly large species.

In addition to being perhaps more biomechanically efficient than HR swimming, DVC swimming may have been exapted for the defensive behavior of flatfish mimicry. Several long-armed octopuses such as *T. mimicus*, *A. aculeatus*, *Octopus* sp. 2 (Hoover, 1998) and *Octopus* sp. 18 (Norman, 2000) co-occur with a rich diversity of bottom-dwelling gape predators (Allen, 1997) similar to the scorpionfish that prey on temperate octopuses (Taylor and Chen, 1969). They also co-occur with several similarly colored, typically non-toxic flatfish (Allen, 1997), and utilize DVC swimming. So far, only *T. mimicus* has been reported to mimic flatfish because its coloration is similar to that of a toxic sole (Norman et al., 2001). However, whereas the flexible body of an octopus can be slurped up easily, a bony flatfish would be an impossible mouthful for many gape predators. Thus, regardless of model toxicity, mimicry of a flatfish should be investigated as a defense for long-armed octopuses.

Unlike in many animals (Bejan and Marden, 2006), absolute speed ( $\text{cm s}^{-1}$ ) was not correlated with body size of *A. aculeatus* during any form of locomotion. A small octopus covered a given distance just as fast as a larger octopus did, and *vice versa*, a result that may have particular importance for jetting octopuses. Unlike the situation experienced by many birds (Veasey et al., 1998), smaller octopuses may not experience increased predation rates because of slower velocities during escape (typically jetting). Jetting is also the main form of locomotion used during intraspecific aggressive interactions between male *A. aculeatus* (Huffard, 2005) (Movie 2 in supplementary material) and *Octopus bimaculoides* (Cigliano, 1993), which can lead to intense physical contact. Large males 'win' interactions with smaller males, which then flee *via* jetting. Whereas fighting ability of *A. aculeatus* depends on size (Huffard, 2005), jetting speed does not. Large males are thus not likely to catch up with small males that jet away from aggressive interactions.

### Conclusions

Locomotion by *A. aculeatus* appears to reflect both behavioral needs and biomechanic limitations. Individuals used numerous elements of crypsis and polyphenism during crawling, when they may be most likely to encounter a

predator. This mode may also have fewer physical limitations than jet-propelled swimming and jetting, which were much faster, but far less variable in form. Bipedal locomotion demonstrated elements of predator deception during fast escape, despite the potential for large drag forces. When interpreted in a behavioral context, variation (or lack thereof) of speeds revealed the potential for biomechanical influences on predation, aggression, and mimicry, which may ultimately impact survivorship and reproduction of these animals.

#### List of abbreviations

Arms I	dorsal, front-most arm pair
Arms II	second arm pair back from dorsal
Arms III	third arm pair back from dorsal
Arms IV	ventral-most arm pair
BL	body length
DVC	dorsoventrally compressed (body shape while swimming)
HR	head raised (during swimming)
MAW	multi-armed walk
ML	mantle length
PCC	Person's correlation coefficient

Roy L. Caldwell provided the video equipment necessary for this project, as well as advice on fieldwork. Becky Williams and Michelle Weber helped to locate, feed, and motivate the octopuses. I am grateful to Lyle Vail, Anne Hoggett, Bob Lamb and Tania Lamb at the Lizard Island Research Station (LIRS) for logistical support at many levels. Bench fees for work at LIRS were paid by an anonymous benefactor. Permits were granted by the Great Barrier Reef Marine Park Authority and the Australian Government Department of the Environment and Heritage. Drafts of this manuscript were greatly improved by comments from Sheila Patek, Roy Caldwell, Becky Williams, Stephanie Bush, Callie Martinez, Emily Griffen and two anonymous reviewers.

#### References

- Allen, G. R. (1997). *Marine Fishes of Tropical Australia and South-East Asia*. Perth: Western Australian Museum.
- Anderson, E. J., Quinn, W. and DeMont, M. E. (2001). Hydrodynamics of locomotion in the squid *Loligo pealei*. *J. Fluid Mech.* **436**, 249-266.
- Bejan, A. and Marden, J. H. (2006). Unifying structural theory for scale effects in running, swimming and flying. *J. Exp. Biol.* **209**, 238-248.
- Bland, J. M. and Altman, D. G. (1995). Multiple significance tests: the Bonferroni method. *Br. Med. J.* **310**, 170.
- Cigliano, J. A. (1993). Dominance and den use in *Octopus bimaculoides*. *Anim. Behav.* **46**, 677-684.
- Edmunds, M. (1974). *Defense in Animals. A Survey of Anti-predator Defenses*. New York: Longman.
- Forsythe, J. W. and Hanlon, R. T. (1988). Behavior body patterning and reproductive biology of *Octopus bimaculoides* from California USA. *Malacologia* **29**, 41-56.
- Forsythe, J. W. and Hanlon, R. T. (1997). Foraging and associated behavior by *Octopus cyanea* Gray, 1849 on a coral atoll, French Polynesia. *J. Exp. Mar. Biol. Ecol.* **209**, 15-31.
- Gutfreund, Y., Flash, T., Yarom, Y., Fiorito, G., Segev, I. and Hochner, B. (1996). Organization of octopus arm movements: a model system for studying the control of flexible arms. *J. Neurosci.* **16**, 7297-7307.
- Gutfreund, Y., Flash, T., Fiorito, G. and Hochner, B. (1998). Patterns of arm muscle activation involved in octopus reaching movements. *J. Neurosci.* **18**, 5976-5987.
- Hanlon, R. T. and Messenger, J. B. (1996). *Cephalopod Behaviour*. Cambridge: Cambridge University Press.
- Hanlon, R. T. and Wolterding, M. R. (1989). Behavior body patterning growth and life history of *Octopus briareus* cultured in the laboratory. *Am. Malacol. Bull.* **7**, 21-46.
- Hanlon, R. T., Forsythe, J. W. and Joneschild, D. E. (1999). Crypsis, conspicuousness, mimicry and polyphenism as antipredator defences of foraging octopuses on Indo-Pacific coral reefs, with a method of quantifying crypsis from video tapes. *Biol. J. Linn. Soc. Lond.* **66**, 1-22.
- Hartwick, B., Thorarinsson, G. and Tulloch, L. (1978). Anti predator behavior in *Octopus dofleini*. *Veliger* **21**, 263-264.
- Hoover, J. P. (1998). *Hawaii's Sea Creatures: A Guide to Hawaii's Marine Invertebrates*. Honolulu, HI: Mutual Publishing.
- Huffard, C. L. (2005). *The Behavioral Ecology and Locomotion of *Abdopus aculeatus* (d'Orbigny, 1834)*. Berkeley, CA: University of California.
- Huffard, C. L. and Hochberg, F. G. (2005). Description of a new species of the genus *Amphioctopus* (Mollusca: Octopodidae) from the Hawaiian islands. *Molluscan Res.* **23**, 113-128.
- Huffard, C. L., Boneka, F. and Full, R. J. (2005). Underwater bipedal locomotion by octopuses in disguise. *Science* **307**, 1927.
- Jindrich, D. L. and Full, R. J. (2002). Dynamic stabilization of rapid hexapod locomotion. *J. Exp. Biol.* **205**, 2803-2823.
- Kier, W. M. and Smith, K. K. (1985). Tongues, tentacles and trunks: the biomechanics of movement in muscular-hydrostats. *Zool. J. Linn. Soc.* **83**, 307-324.
- Manton, S. M. (1950). The evolution of arthropod locomotory mechanisms. Part 1. The locomotion of *Periapatus*. *Zool. J. Linn. Soc.* **45**, 251-484.
- Martinez, M. M., Full, R. J. and Koehl, M. A. R. (1998). Underwater punting by an intertidal crab: a novel gait revealed by the kinematics of pedestrian locomotion in air versus water. *J. Exp. Biol.* **201**, 2609-2623.
- Mather, J. A. (1998). How do octopuses use their arms? *J. Comp. Psychol.* **112**, 306-316.
- Matzner, H., Gutfreund, Y. and Hochner, B. (2000). Neuromuscular system of the flexible arm of the octopus: physiological characterization. *J. Neurophysiol.* **83**, 1315-1328.
- Messenger, J. B. (1967). The Peduncle Lobe: a visuo-motor centre in octopus. *Proc. R. Soc. Lond. B Biol. Sci.* **167**, 225-251.
- Mezoff, S., Papastathis, N., Takesian, A. and Trimmer, B. A. (2004). The biomechanical and neural control of hydrostatic limb movements in *Manduca sexta*. *J. Exp. Biol.* **207**, 3043-3053.
- Miyani, J. A. and Messenger, J. B. (1995). Intracellular recordings from the chromatophore lobe of octopus. In *Cephalopod Neurobiology: Neuroscience Studies in Squid, Octopus and Cuttlefish* (ed. J. A. Abbott, R. Williamson and L. Maddock), pp. 415-429. Oxford: Oxford University Press.
- Norman, M. D. (2000). *Cephalopods: A World Guide*. Hackenheim: ConchBooks.
- Norman, M. D. and Finn, J. (2001). Revision of the *Octopus horridus* species-group, including erection of a new subgenus and description of two member species from the Great Barrier Reef, Australia. *Invertebr. Taxon.* **15**, 13-35.
- Norman, M. D., Finn, J. and Tregenza, T. (2001). Dynamic mimicry in an Indo-Malayan octopus. *Proc. R. Soc. Lond. B Biol. Sci.* **268**, 1755-1758.
- Packard, A. and Sanders, G. (1969). What the octopus shows to the world. *Endeavour* **28**, 92-99.
- Packard, A. and Sanders, G. D. (1971). Body patterns of *Octopus vulgaris* and maturation of the response to disturbance. *Anim. Behav.* **19**, 780-790.
- Rezende, E. L., Kelly, S. A., Chappell, M. A. and Garland, T. J. (2006). Effects of size, sex, and voluntary running speeds on costs of locomotion in lines of laboratory mice selectively bred for high wheel-running activity. *Physiol. Biochem. Zool.* **79**, 83-99.
- Roper, C. F. E. and Hochberg, F. G. (1988). Behavior and systematics of cephalopods from Lizard Island Australia based on color and body patterns. *Malacologia* **29**, 153-194.
- Roper, C. F. E. and Voss, G. L. (1983). Guidelines for taxonomic descriptions of cephalopod species. *Mem. Natl. Mus. Vic.* **44**, 49-63.
- Semmens, J. M., Pecl, G. T., Villanueva, R., Jouffre, D., Sobrino, I., Wood, J. B. and Rigby, P. R. (2004). Understanding octopus growth: patterns, variability and physiology. *Mar. Freshw. Res.* **55**, 367-377.
- Sumbre, G., Gutfreund, Y., Fiorito, G., Flash, T. and Hochner, B. (2001). Control of octopus arm extension by a peripheral motor program. *Science* **293**, 1845-1848.

- Sumbre, G., Fiorito, G., Flash, T. and Hochner, B.** (2005). Motor control of flexible octopus arms: The octopus borrows a jointed-vertebrate strategy to transfer an item between points. *Nature* **433**, 595-596.
- Sumbre, G., Fiorito, G., Flash, T. and Hochner, B.** (2006). Octopuses use a human-like strategy to control precise point-to-point arm movements. *Curr. Biol.* **16**, 767-772.
- Taylor, J. R. A. and Kier, W. M.** (2003). Switching skeletons: hydrostatic support in molting crabs. *Science* **301**, 209-210.
- Taylor, P. B. and Chen, L. C.** (1969). The predator prey relationship between the octopus *Octopus bimaculatus* and the California scorpionfish *Scorpaena guttata*. *Pac. Sci.* **23**, 311-316.
- Trueman, E. R. and Packard, A.** (1968). Motor performances of some cephalopods. *J. Exp. Biol.* **49**, 495-507.
- Veasey, J. S., Metcalfe, N. B. and Houston, D. C.** (1998). A reassessment of the effect of body mass upon flight speed and predation risk in birds. *Anim. Behav.* **56**, 883-889.
- Villanueva, R., Segonzac, M. and Guerra, A.** (1997). Locomotion modes of deep-sea cirrate octopods (Cephalopoda) based on observations from video recordings on the Mid-Atlantic Ridge. *Mar. Biol.* **129**, 113-122.
- Vogel, S.** (1994). *Life in Moving Fluids: The Philosophical Biology of Flow*. Princeton: Princeton University Press.
- Walker, I. D., Dawson, D. M., Flash, T., Grasso, F. W., Hanlon, R. T., Hochner, B., Kier, W. M., Pagano, C. C., Rahn, C. D. and Zhang, Q. M.** (2005). Continuum robot arms inspired by cephalopods. In *Unmanned Ground Vehicle Technology VII*. Vol. 5804 (ed. G. R. Gerhart, C. M. Shoemaker and D. W. Gage), pp. 303-314. SPIE Digital Library.
- Webb, P. W.** (2002). Kinematics of plaice, *Pleuronectes platessa*, and cod, *Gadus morhua*, swimming near the bottom. *J. Exp. Biol.* **205**, 2125-2134.
- Wells, M. J.** (1990). Oxygen extraction and jet propulsion in Cephalopods. *Can. J. Zool.* **68**, 815-824.
- Wells, M. J., Duthie, G. G., Houlihan, D. F. and Smith, P. J. S.** (1987). Blood flow and pressure changes in exercising octopuses *Octopus vulgaris*. *J. Exp. Biol.* **131**, 175-187.
- Williamson, R. and Chrachri, A.** (2004). Cephalopod neural networks. *Neurosignals* **13**, 87-98.
- Yekutieli, Y., Sagiv, R., Aharonov, R., Engel, Y., Hochner, B. and Flash, T.** (2005a). Dynamic model of the octopus arm. I. Biomechanics of the octopus reaching movement. *J. Neurophysiol.* **94**, 1443-1458.
- Yekutieli, Y., Sagiv, R., Hochner, B. and Flash, T.** (2005b). Dynamic model of the octopus arm. II. Control of reaching movements. *J. Neurophysiol.* **94**, 1459-1468.