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Squid dances: an ethogram of postures and actions of *Sepioteuthis sepioidea* squid with a muscular hydrostatic system

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KEYWORDS

Squid, *Sepioteuthis sepioidea*, postures, movements, ethogram

ABSTRACT

A taxonomy of the movement possibilities for any species, within the constraints of its neural and skeletal systems, should be one of the foundations of the study of its behaviour. Caribbean reef squid, Sepioteuthis sepioidea, appear to have many degrees of freedom in their movement as they live in a three-dimensional habitat and have no fixed skeleton but rather a muscular hydrostatic one. Within this apparent lack of constraints, there are regularities and patterns of common occurrences that allow this article to describe an ethogram of the movements, postures and positions of squid. Squid have a combination of bent, spread and twisted maintained postures of the eight arms and two tentacles that enhance camouflage. Their body–arm posture combinations are actively maintained in the water but also influenced by gravity. Positions related to conspecifics are stereotyped and important for communication. For locomotion, squid use a well-coordinated dual fin–jet locomotion system. This motor system uses tonic postures for camouflage and maintains body position in courtship, though squid seldom touch. The interdependence of movement control by different units is seen in fins and jet propulsion, and bilateral symmetry is maintained even for the eight arms. It is argued that the repertoire is well adapted for a soft-bodied animal in its three-dimensional, open but near-shore demersal habitat.

Introduction

One of the foundations of the study of animal behaviour must be an ethogram, seldom produced in vertebrates and almost never in cephalopods (though see Mather 1998; Huffard 2007). Barlow (1977) commented on the necessity of knowing the Modal Action Patterns, the units of behaviour, and Fentress (1978, 1991) followed with a comment on the necessity to first define a behavioural phenomenon if one wished to seek mechanisms for it. Pellis (1989) noted that “When exploring an uncharted behavioural landscape it would seem prudent to begin the analysis with a description of its constituent movements” (p. 363). More recently, Jing et al. (2004) described how they could dissect complex motor acts into combinations of a small number of modules, using *Aplysia* feeding as a model. Flash and Hochner (2005) discussed the idea of Motor Primitives, elementary building blocks of motor actions and behaviour, with

octopus arm movement as one example. All these authors agree that to investigate the behaviour of a species, we must first know what movement units are actually used, and this article contains such a description for the Caribbean reef squid, *Sepioteuthis sepioidea*.

Such a basic description (Gallistel 1980; Golani 1992; Alexander 2002) is made difficult for the cephalopod molluscs because they have no fixed skeletal system but instead have a muscular hydrostat in which several sets of muscles contract in opposition to each other to act both as force generator and skeleton (Kier and Smith 1985; Kier 1989). Such flexibility gives a great number of degrees of freedom of movement, and octopuses (Mather 1998; Huffard 2006; Grasso 2008) and squid (Moynihan and Rodaniche 1982) produce actions and postures that express this variety. However, recent work on octopus arm movement (Gutfreund et al. 1996; Yekutieli et al. 2005a, 2005b) has demonstrated that arm extension has stereotypies that reduce the variation considerably and simplify the action. Such simplification might be even more prominent for the squid as it has eight cephalopod arms and a pair of extensible tentacles used mainly for prey capture (Messenger 1977) and controlled by a different brain region (Nixon and Young 2003), as well as a dual jet-propulsion and fin locomotion system (O'Dor and Webber 1986; Hoar et al. 1994). These movement systems are more specialized than those of the larger manipulative octopus arms.

One of the constraints on movement of squid is the medium in which they move, since water has a high density that reduces the demand of the gravitational pull but increases the drag on movement (Wootton 1999) and constrains actions. Water affects locomotion of Grapsus crabs, which use a 'punting' walk in it (Martinez et al. 1998) in contrast to their gait on land, and octopuses, needing only to attain dynamic stability during walking, have only a loosely coordinated gait (Huffard 2006). Some cephalopods avoid the problem of gravity's pull by adopting anti-sinking strategies (Clarke 1988; Webber et al. 2001) including buoyancy mechanisms such as air-filled shells or ammonia-filled tissues (Clarke et al. 1979; Voight et al. 1994). However, the loliginid squid such as *Sepioteuthis* have no buoyancy mechanism and must constantly use a combination of jet propulsion (O'Dor and Webber 1986; Anderson et al. 2001) and movement of the fins (Hoar et al. 1994) to stay in place. Gravity should constrain squid movement to some extent and make sudden actions or position changes less common. In addition to constraining movement, water's physical characteristics may select the sensory modality of incoming information, as squid can use the excellent vision of the cephalopods (Muntz 1999) as well as mechanoreception from the sensitive Lateral Line Analogue (Budelmann 1995) to guide their actions.

More than just the medium, the specific habitat within the ocean in which a squid species is found should affect its anatomy, physiology and repertoire of movement. Pörtner (2002) points out that the highest energy turnover in movement is found in open-ocean squid such as *Illex illecebrosus*, whereas the near-shore *Lolliguncula brevis* have a lesser jetting performance (Finke et al. 1996) and more dependence on agility. Similarly, fin shape and usage vary amongst species, from the small posterior ones of *Illex* to the lateral-mantle ribbon of *Sepia*. Given the physical limitations of its near-shore demersal habitat (Moynihan and Rodaniche 1982) we expect that *S. sepioidea* will use jet propulsion but also make extensive use of its lateral fins to aid in maintenance of position in the water column and increase its mobility. Such actions might include spreading the fins to 'soar' on currents like birds on thermal currents of air (Sauer et al. 1997) or reducing energy expenditure by choosing microhabitats with lower current velocity (O'Dor et al. 2002).

Besides the constraints of habitat, squid face the predation pressure that stems from their lack of a protective exoskeleton and answer it with excellent skin pattern generation for camouflage (Messenger 2001). The near-shore environment of the Caribbean where *S. sepioidea* is found (Roper et al. 1984) has an abundance of fish predators (Randall 1967). Cephalopods have a variety of responses to their threat (Hanlon and Messenger 1996; Mather submitted), but one of the most obvious is avoidance by

concealment (Ruxton et al. 2004). Countershading is one ability (Ferguson et al. 1994; Preuss and Budelmann 1995) but another is maintaining a variety of body and arm postures accompanied by concealing patterns. This is particularly found in young squid near features of the microhabitat such as sea grass and floating objects (Moynihan and Rodaniche 1982), and is also used by octopuses out on the sea bottom (Huffard 2006). Combinations of these displays and specific postures serve to make the cephalopod look nothing like an animal. Moynihan (1985) described some of these postures for *S. sepioidea* and made vivid drawings, but never attempted a systematic catalogue of them, only listing them with skin displays as 'ritualized patterns'. Yet these postures are also actions and should be constrained by the anatomy of the squid into particular combinations.

The objective of this article is to catalogue the postures, relative positions and actions of *S. sepioidea* from field observation, to describe the actions of the body units including jet propulsion, fin movement and arm postures, as well as build these into combinations to produce a taxonomy of squid behaviour.

Methods

This description is the result of a 5-year observational study of the squid *S. sepioidea* on the island of Bonaire in the Caribbean. *Sepioteuthis sepioidea* is a near-shore species found across the Caribbean (Roper et al. 1984), with a life span of approximately 1 year (Laroe 1971). Eggs are laid on the substrate in up to 100 strings by females, who offer no parental care. Young emerge and move to near the water surface, where they grow from 9mm mantle length at birth to approximately 20 cm at adulthood. While Moynihan and Rodaniche (1982) found squid in different habitats, *Thalassia* sea grass beds for juveniles and coral reefs and rubble for adults, squid of all ages were found in the same habitat in Bonaire. They were 2–40m from shore, inshore of the steep drop-off and in water depths of 1–8m over sand and coral rubble (Boom et al. 2001). Squid are obligate daytime schoolers (Moynihan and Rodaniche 1982), preferring to school with individuals of similar sizes. Observation was carried out mainly in the daytime by snorkellers, who recorded notes on an underwater slate and entered them into a computer shortly thereafter. Squid habituated readily if divers remained fairly motionless. Observation totaling approximately 1200 h was carried out in summer from 1998 to 2002, mainly in the early morning (07:00 to 10:00) and late afternoon (15:00 to 18:00) because the squid's activity cycle was crepuscular. Limited observation was carried out at night as squid behaviour was disrupted by divers' lights.

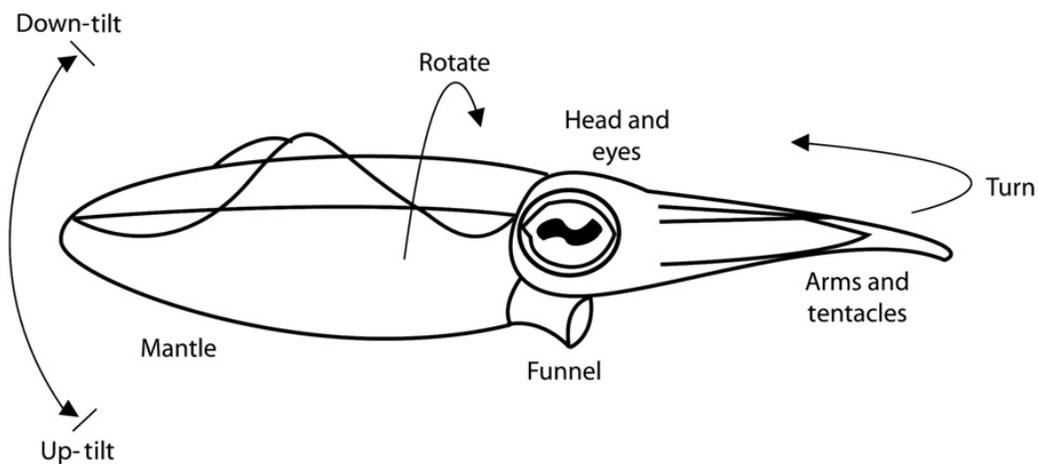
Observation was complemented by video film footage. This was taken in 1999 and 2000 and to a much greater extent in 2001 by a professional camera team making a film of the squid research. Some exemplary video clips can be viewed at www.byrne.at/squiddances.¹ Fourteen hours of footage was made available to us. The authors watched and classified behaviours, discussed and returned to the film footage to confirm them and extract duration of some postures. Some details, such as the use of the funnel in passing eggs to the arms and the miniature fin undulations on the outer quarter, would not have been recognized without film analysis.

In 2008, the senior author conducted some observations to check on resting postures and body–arm position combinations. For observations of body angle with relation to other squid and tilt, three groups of subadults ($n=10, 8, 20$) were observed. Every 2 min for five observations, the heading and then the body and arm postures were recorded. To check on arm curl, a second set of observations was made on two groups ($n=6, 8$) recording the body tilt and the presence of arm curl up and down, again every 2 min for five observations.

Results

Squid are generally located in the water just above the ocean floor, and thus all positions and actions can be expressed in three dimensions. They have no skeleton and so the movement of the body parts is limited only by attachment, although the mantle is stiffened by a cartilaginous sheet and can only contract or expand. The two fins are attached along the lateral-mantle margins and, although they are also a muscular hydrostat (Kier 1985), can only move with relation to it. The head is attached to the anterior end of the body and moves only minimally in relation to it. The eight arms and the two elastic tentacles (hence a decapod) are attached to the anterior of the head (thus a cephalopod) and have a wide range of movement (Figure 1). This description will start with position and movement of smaller components, as in Mather (1998) for octopuses, and continue to combinations of these. The first mention of any motor unit will be italicized and subsequent ones will be capitalized.

Figure 1. Diagram of a squid with the areas and dimensions of movement labelled.

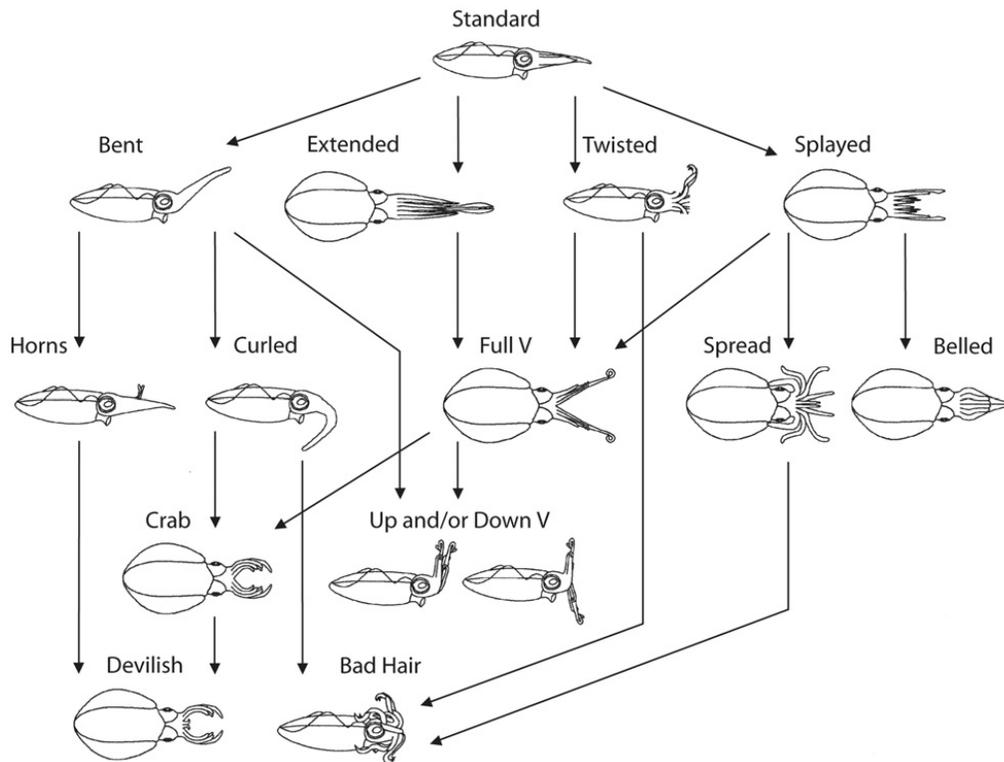


Arm and tentacle positions

A squid's arms and tentacles can be described as in their basic position when they are *Linear*, extended from the body along a line approximately through its centre and *Appressed* to one another (in *Standard*). There are four basic units of departure from *Linear* (Figure 2). The first is movement along this axis, in *Extended* and *Contracted*. Second, arms can remain *Linear* yet separate from the mid-line in *Splayed*. Third, they can deviate from this axis at a single point in *Bent* or along much of their length in *Curled* (Moynihan 1985, Figure 5). Downward *Bent* was held for 5.35 s (SD=4.5, $n=25$) and Upward *Bent* 2.9 s (SD=1.5, $n=37$). Upward *Curled* was held a mean of 5.1 s (SD=3.9, $n=16$) and downward *Curled* 10.5 s (SD=20.2, $n=15$). Fourth, one or several arms/tentacles can also be *Twisted*, rotated around their own axis. Regardless of the posture, the arm or tentacles can be *Relaxed* or *Stiff*, depending on the extent of muscle contraction within the arm.

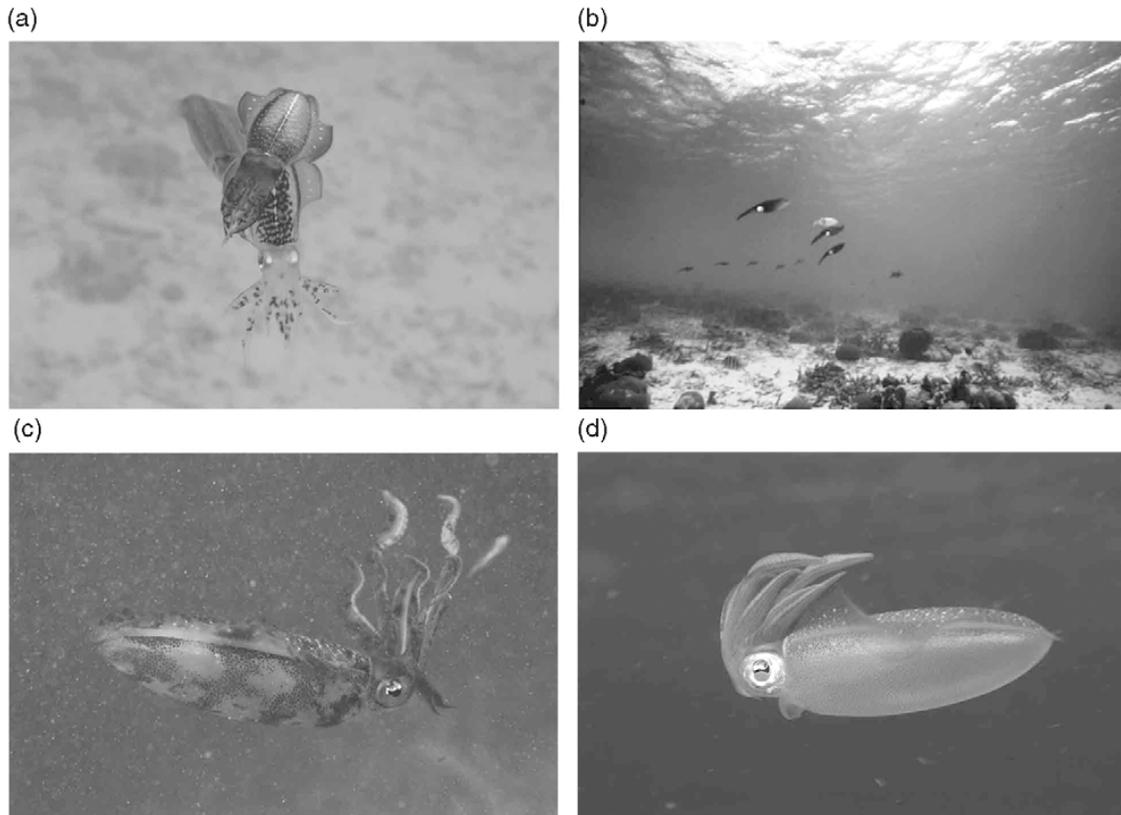
The clubs at the end of the paired tentacles present a special case. They can be *Facing*, close and with tentacles *Twisted* so the sucker-laden surfaces face each other or *Parallel* when not *Twisted*, or they can be *Bent* at the base of the club. Suckers line the ventral surface of arms and the distal tentacle clubs. During arm action they can *Adhere*, *Hold* or *Relinquish* objects or the substrate.

Figure 2. Combinations of arm and tentacle position units to produce the variety of postures of squid *Sepioteuthis sepioidea*.



These basic units of arm and tentacle postures combine in a finite number of ways to make more complex ones, many of which appear in combination with camouflage displays of juveniles (Figure 2). Tentacles are mostly *Tucked* inside the Linear Contracted arms in *Standard*, partly out of sight. When separated, arms can move to special cases of *Splayed*. One is *Belled*, *Splayed* at the proximal but not distal ends. Another is *Full-V*, when tentacles are extended far past the arms and *Splayed*, with the arms split and *Appressed*, four along each tentacle. *Full-V* can also combine with *Bend* upward and downward (Moynihan 1985, Figure 3). The two small dorsal arms can be *Bent* upward and separated by approximately 30° while all other appendages are *Linear*, to produce *Horns*. Arms and tentacles are *Extended*, somewhat *Splayed* and *Relaxed* in *Loose*. All the arms and tentacles are visibly separate in three complex postures. *Spread* (duration 8.6 s, SD=16.4, $n=19$) is the result of horizontal *Splay* with about 45° separation of each limb (Figure 3a). The arms and tentacles are *Bent* back towards the mantle at the proximal end and *Curled* along their length, this is seen in adult male *Formal Zebra* displays (a display indicating aggression) (Hanlon and Messenger 1996; Mather 2004). At maximum, the ventral pair of arms lies along the mantle, and the tentacles are next in line out from it. In *Crab* the tentacles and arms are *Splayed* a similar amount, but they are *Bent* downward proximally and back towards the body, making the squid look like a crab in mid-water. In combination with *Horns*, this produces Moynihan and Rodaniche's (1982) *Devilish*. In *Bad Hair*, also of small squid, the arms and tentacles are *Splayed* equally from one another, *Bent* back proximally towards the body without systematic spacing, held loosely and twisted (Figure 3c). There is some variability around the standard postures outlined here.²

Figure 3. (a) A pair of male squid in Over–Under with Zebra displays. The lower squid’s arms are in Spread and the upper one is in Belled; the fins of the upper one are in same-direction Undulate. (b) A group of squid in School, with several in Tilt; one female is in Rise Above with arms in down Curl and a Saddle display. (c) A juvenile squid with arms and tentacles in an upward-bent Bad Hair; note the arms in a combination of Spread, Splay and Twisted and the Plaid display. (d) A squid maintaining position as the fins Undulate and the funnel is aimed downward. The arms are Relaxed, Splayed and Bent upward.



Arm and tentacle movements (changes in position)

Squid have a variety of similar movements of several appendages. Actions which do not involve external items are considered first. *Sway* is produced when arms and tentacles are somewhat Extended and Relaxed, all arms but the dorsal two (which are often in Horns) are moved laterally at the proximal end and the rest of the arms loosely follow in a swaying motion, somewhat Bent. This movement appears preliminary to prey capture attempts and as camouflage during egg laying.

Two movements may be used for cleaning: one, *Shake*, results when arms and tentacles are somewhat Splayed and Extended in Loose, then irregular body or arm movements made at the proximal end due to a mantle-Jet. During the second, *Rub*, the arms are held loosely Appressed and Facing. They are Bent linearly so sucker surfaces pass along each other. The suckers do not Hold, and the arm movement is irregular and arms uncoordinated. Rub can also involve movement of an arm or two across the body surface or even into the mantle cavity for grooming. This is similar to Grooming by octopus arms (Mather 1998). There is no fixed sequence of limb use or area of coverage for this action.³

Other arm–tentacle actions involve external items. In *Strike* (duration 51 s) the arms separate from Appressed about 30° to make room for tentacle extension, and are Contracted, Relaxed and Linear. At the same time the tentacles are held in Linear and rapidly Extended with tentacle clubs Facing (used for prey capture, see Messenger 1968 for *Sepia*). For *Touch*, one or many arms make contact via suckers adhering to an item, the substrate or a conspecific. Males use Touch to place spermatophores onto the female's arm bases at mating.⁴ The arms are usually in Extension, about 20–30° Splayed, somewhat Relaxed, with no large arm movement. For *Grasp*, the arms are Stiff and somewhat Extended and make contact, suckers facing inward and Adhering to an object which is retained by sucker Hold. Arms and tentacles cooperate, so the tentacles may have completed Strike and retracted with the item in Grasp or may have Extended and Bent to keep out of the way. In *Manipulate*, suckers of several to all arms Adhere to and Hold an item, and the arms move with relation to each other. Tentacles are held Extended, Bent and Relaxed, and separate from the arms. This occurs when squid move food, deposit spermatophores and lay eggs. In *Grapple*, all arms make contact with and suckers attempt to Hold the arms of a conspecific who is usually behaving similarly, a coordinated all-arm attempt to Grasp, with arms Stiff but somewhat Bent.

Locomotion

Locomotion of squid is a dual system of mantle-funnel jets that expend a great deal of energy (O'Dor and Webber 1986, 1991) and fin movement that expends little (Hoar et al. 1994). Mantle contraction forces water through the flexible funnel to move the squid by jet propulsion, but its intensity can be modulated. High-velocity Jets due to sudden intense mantle contraction usually occur when the funnel is pointed towards the anterior so the animal moves posterior-first (also see fin action in next paragraph), although lower velocity ones often result in anterior-first moves and precede Grasp. Squid can thus reverse directions simply by changing funnel placement. There can be a single escape jet moving the squid around 0.3–1 m, or a series of jets.⁵ Low amplitude mantle contractions serve for position maintenance and respiration. Funnel position, usually downward, always assists in the maintenance of position in the water column (Figure 3d). The funnel can also Aim water jets to move items out from the mantle cavity or to move items in the environment.

The paired fins are attached all along the lateral margin of the squid mantle and can only move vertically. They can be held extended from the body a little above horizontal, in *Wings*, which may aid in gliding (Figure 3a, lower squid). They can move simultaneously vertically along all the fin length in *Flap*, which often accompanies a high-velocity mantle-Jet. This often leads to *Tuck*, when the fins are held (usually upward) pressed close to the mantle, probably to reduce drag during jet propulsion. The most complex movement of the fins is *Undulate*, when a wave of vertical displacement passes along the fin length (Figure 3d).⁶ Undulate can vary in displacement amplitude and in speed of movement along the fin. The extent of fin displaced varies, all the way from the total fin to a 'ripple' along the outer quarter, and movement of an undulating wave is slower when more fin width is involved. Fin undulation can be anterior to posterior or posterior to anterior, and an undulation along the two fins can be in the same or opposite directions along their length. Opposite-direction fin undulation would produce a Turn (Figure 1 and next section). Fin movement is responsible for much of position maintenance by squid as well as fine manoeuvres.

Whole-body movement and positions

Body positions can be maintained with relation to the substrate and thus the pull of gravity, to objects or to another animal, especially a conspecific (Figure 1) while in mid-water. The default and normal position is to have the longitudinal axis parallel to the substrate in *Horizontal*, seen in 75% of 128 observations (squid have a three-dimensional balance system, see Budelmann 1995). Squid can pivot around their

longitudinal axis in *Rotate*, fast due to jet action or slowly with fin movement, either quickly 360° to Horizontal again (rarely) or less and maintained for up to minutes. Squid can move one end of this linear body axis up and down in *Tilt*, upward Tilt was true for 20% of the observations and downward Tilt for only 3%. Upward Tilt was held for 11.1 s (SD=9.2, $n=61$) and Downward Tilt for 7.3 s (SD=5.9, $n=26$). Tilt is often combined with arm–tentacle Curled, Bent or Full-V, see Figure 3b. Horizontal was held for 8.1 s (SD=7.5, $n=34$), upTilt for 11 s (SD=8, $n=25$) and downTilt for 8 s (SD=8, $n=12$). Squid can also pivot around the lateral axis by fin movement without any change of location in Turn (0.9 s, SD=0.5, $n=47$). The fin–jet combination flexibility produces quick position change.

Arm position tended to be linear regardless of the body posture, 77% of 189 instances. When the body was Horizontal, arms were held Linear in 83% of 146 observations, when it was tilted up, this was true for only 61% of 41 observations. Thus arm position was actively held but influenced by gravity. This is clearer in the set of observations of arm curl, where gravity would dictate a curl downward when the arm muscles relaxed. Again the head-down Tilt posture was unusual (2/189 instances) and the Horizontal less common (22%). As the upward angle of the body increased the likelihood of downward Curl did also, from 73% at 0–20° ($n=24$), 80% at 20–40° ($n=40$), 94% at 40–60° ($n=102$) and 88% at 60° ($n=21$).

Squid commonly form groups during the daytime (Boom et al. 2001). They maintain a similar distance from the substrate, usually about 2–3 body lengths from one another and nearly parallel, in *School* (Figure 3b). From the observations of the three groups, angle to nearest neighbor was 20°, to the second nearest was 25° and to the third nearest was 30°. Closer alignment, less than 0.3m distant and a minimal deviation from parallel between them is *Parallel*, found in adults in male–female consortships. Keeping parallel and close but with one squid 0.3–0.5m behind the other is *Diagonal*. Males preliminary to a mating attempt take up this position. When the squid are parallel to one another and about a body length apart, but displaced vertically rather than horizontally, that is *Over–Under* (Figure 3a), often seen when adult male–female pairs exchange Saddle-Stripe displays (patterns used as courtship displays) or male–male ones exchanged in Formal Zebra. These relative positions may depart from strictly parallel and from precisely above–below, but the juxtapositions are clear.

Positions with reference to items or conspecifics are important for squid and sometimes part of stereotyped reproductive actions (Table 1). Thus a squid can *Maintain* a constant distance between itself and some target as described in the previous paragraph, mostly by fin Undulate and low-velocity Jet. It can decrease this distance in *Approach* by increasing jet velocity. High-speed Approach is posterior-first, low-speed is anterior-first. A squid can *Retreat* from a target using much the same components. A Jerk involves a Retreat of about 0.3–1m by a single high-velocity jet and a subsequent Maintain, moving far enough from a source of disturbance but stopping to see what is going on. During *Hide*, squid Maintain a position near the substrate or an item in the water, often parallel to its surface, for long periods. At this time camouflaging arm postures such as Full-V or Bend and body Tilt, accompanied by displays such as Plaid (Figure 3c), are common, especially in young squid (Moynihan and Rodaniche 1982).

Relative position is often stereotyped in courtship. *Chase* involves maintenance of a fairly constant distance between oneself and a target but when both are moving fairly rapidly with high-velocity jets, and is often part of courtship. In *Rocking*, a male–female pair Maintain a distance of about 0.3m Parallel to each other, moving forward and back about 1m in unison several times. This action precedes attempted spermatophore transfer. In *Switch*, a squid maintains a constant distance of approximately 0.3m lateral to a target in Parallel but moves from one side to another, when an adult male mate guards a female. *Rise Above* happens as one member of a group moves vertically above the others, Maintaining up to 1m above them (Figure 3b). Females initiate courtship in this position with a Saddle display with arms in down Bend (Mather et al. in preparation), and males may move Under with a Stripe display. Male squid pairs display Zebra in Over–Under (held on average 8.3 s, SD=13.7, $n=43$), but may lose the parallel

position when the Under one does Downward Tilt or the Over one Upward Tilt. Either way this may result in contact by Push with posterior mantles, as part of the male–male Formal Zebra contest.⁷

Table 1. Relative positions of squid *Sepioteuthis sepioidea*, usually to conspecifics.

	School
Maintain same distance and position	Parallel
	Under–Over Diagonal
	Chase
	Hide
	Rocking
	Approach
Change distance	Retreat
	Jerk
	Switch
Maintain distance	Switch
Change position	Rise Above
Change relative posture	Push

Complex actions

Only a few combinations of behaviours seem to involve all of the effector units at once. The first is *Catch*, the classic prey capture described in *Sepia officinalis* by Messenger (1968). A squid makes an anterior-first Jerk or jets to the appropriate distance from a prey item, in down Tilt if the prey is on the substrate. Then it Maintains with fin Undulate and low-velocity Jets, sometimes using one or more components of Sway. Next the arms quickly Splay and tentacles Strike. They Contract and the arms can Grasp and the squid feed (note the approaching and selection before this stereotyped prey capture may be variable, see Hanlon and Messenger 1996).

The second major combination of effector action is *Place*. A male spermatophore or female egg string is moved from inside the mantle cavity to the arms by funnel Aim and is kept there by Hold and Manipulate: tentacles are Loose and Bend laterally. Then the squid moves to a location of interest by Jet and fin Undulate, the suckers Release and arms Splay, and the squid Retreats by fin and jet locomotion (Figure 3d). The duration of egg string placement by females is 4 s (SD=1 s, $n=21$). Place is very fast when males place spermatophores at the female’s arms bases, but slower in an atypical spermatophore transfer directly into her mantle cavity.

Principles in the establishment of this repertoire

1. **Posture matters.** Without a major constraint by gravity, postures vary and often function to aid camouflage, making the squid look like something other than an animal and definitely not a squid. These postures of arms and tentacles, often combined with non-linear body positions, are common especially in young squid. Juvenile squid do little during the daytime but wait for night, although squid opportunistically feed whenever prey is available. Thus, unlike the octopus that hides in dens, the squid hides in the open by maintaining displays and postures. Nevertheless, the combination of arm and body postures suggests that squid favor head-up postures, logically for the use of vision, and their arm and body combination are not only constrained by relaxing to allow gravity to pull the arms downward.

2. **Interdependence rather than independence.** Squid arms and tentacles often seem to be programmed to act interdependently. For example, Full-V is a careful postural combination of arms and tentacles, and some coordination involves separate actions of these appendages. If tentacles Shoot out for prey the arms must Splay, if arms Place egg strings on the substrate the tentacles Bend to get out of the way. Yet other postures such as Spread use the arms and tentacles as apparently similar units. Similarly, jets and fin actions are carefully coordinated.
3. **Bilateral rather than radial symmetry.** The postures and actions of arms and tentacles (which are radially arranged around the mouth) are mirror-image of one side to the other. Tentacles must shoot out in unison or the prey is lost, most actions reflect identical movements or positions on one side and the other. A few actions such as funnel position and fin undulation are not obligate bilaterally symmetrical, but most are.
4. **There are common action units across the coleoid cephalopods.** Simple units such as Twist are found in squid Full-V and young octopus' Flamboyant (Packard and Sanders 1971). Catch is similar across many squid species (Messenger 1968) and Grasp to the octopus' Oppose (Mather 1998). Most cephalopods Groom similarly. But besides being smaller than the eight arms of the octopus, the arms of the squid seem to have a reduced behavioural repertoire. This may be because the animal itself is mobile so arms can hold items while the squid moves to where it wants to go, rather than the arms extending as would those of an octopus or many vertebrates.
5. **Position matters.** A social animal is concerned with where other individuals are, and in the open water the relative position of squid towards each other is visually obvious and may follow rules. Nevertheless, relative position is also vital in terms of camouflage matching to a part of the substrate (Hanlon and Messenger 1996) and in stereotyped position components of reproductive behaviour.

Discussion

The movement units in squid reveal complexity in their use of multiple effectors and a surprisingly short duration for most of the postures and actions mentioned here. The number of motor units and their coordination by the brain (which is not known) allow squid to carry out actions with arms, tentacles, mantle, fins and funnel, sometimes all at once. The use of a muscular hydrostat skeletal system (Kier 1985; Kier and Smith 1985; Kier 1989) guarantees flexibility in not one but several of these effector units, but the combination are finely tuned. The positions and actions of the arms of squid appear less complex than that of octopuses (Mather 1998; Byrne et al. 2006), not surprisingly given all its other means of movement and the relative brain area allocated to control (Nixon and Young 2003). Perhaps this is because the less mobile benthic octopus uses its arms to bring items of interest to itself, whereas the mobile squid can move in three dimensions to carry out some action. Similarly, open-sea fish and marine mammals have little use of their limbs in prehension but much for locomotion.

The use of multiple effectors raised the question of control of stereotypy which can be examined by the neural control of interdependence of actions of arms, tentacles, fins and mantle. There is some research on the neural control system of the complex arms of octopuses (Rowell 1963, 1966; Matzner et al. 2000) but little on the movement of squid except on the jet propulsion (Hoar et al. 1994). Yet the interdependence of the units seen in the present combinations is obvious. Modal Action Patterns (Barlow 1977). Motor Primitives (Flash and Hochner 2005) thus seem more likely in squid than in octopuses, as several units must be closely coordinated. The combination of modules that Jing et al. (2004) found in *Aplysia* and Zullo et al. (2009) in octopuses seems also likely here. The cuttlefish *Sepia* (not a true squid but a sepiid) shows stereotyped sequential actions in sand-digging (Mather 1986) and tentacle extensions to capture prey (Messenger 1977, 1986), so flexibility may be more true of octopus movement.

Combinations of actions and displays are common in the courtship behavior of *S. sepioidea*, which represent the stereotyped Modal Action Patterns (sensu Barlow 1977) one would expect in reproductive behaviour. Position maintenance is an important component paired with visual displays (Table 1), which are also actions although of chromatophore muscles in the squid's skin (Packard 1995; Messenger 2001) and which again require integration of output from quite different brain areas. Examples are the male–female Saddle-Stripe exchange in Over–Under, the male Flicker signal of intent to mate in Diagonal and the ritualized male–male Over–Under Formal Zebra (Mather 2004). Other regularities such as the linkage of angular deviation of the fins to time and fin area will be found beneath the cephalopod variability (as for octopus arm control, Gutfreund et al. 1996) – but this description of units is a start in identifying them.

The importance of positions to interactions of squid and to their maintenance of location in the group may be common in mobile mid-water animals with a very sensitive tactile perceptual system. Fish have a Lateral Line system along the lateral margin of their bodies (Bleckmann 2006) and squid have what has been designated a Lateral Line Analogue (Budelmann 1995). Both these systems can perceive very small water displacements, and both squid (Hanlon and Messenger 1996) and fish use position and displacement in courtship. Such a system produces the fine tuning of relative position for squid in alignment with their nearest neighbors in the group. This alignment is also true for *I. illecebrosus* (Mather and O'Dor 1984) that gathers in schools and move quickly in and this may be a general principle for cephalopod group spacing. Differences in relative position are then taken advantage of by these groups for courtship. Such sensitivity might also explain why squid seldom touch. Marine mammals, which have secondarily returned to the marine environment, have a heavy skin and insulation to maintain temperature of their homeothermal body system and thus lack this ability (Supin et al. 2001).

Another function of the effector system of squid is the maintenance of the startling repertoire of spreading, bending and twisting arm postures first mentioned by Moynihan and Rodaniche (1982), whose systematic combinations are explored in this article. All cephalopods are at risk from vertebrate predators, mainly fish (Packard 1972), and their concealment is tuned to the receptor systems in the vertebrate eye (Messenger 2001). The octopus relies heavily on skin texture and pattern to match its benthic habitat (Messenger 2001), but is also able to move and maintain camouflage postures (Huffard 2006) or confuse predators by changing patterns in milliseconds (Hanlon et al. 1999), an ability also present in sepiids (Anderson and Mather 1996) and squid. Squid must 'hide in plain sight' (Ruxton et al. 2004). The diversity of postures, often accompanied by concealing patterns such as Plaid and Mottle (Moynihan 1985; Byrne et al. 2003) which is the result of combinations of units, matches varied environmental features such as floating algae, marine grasses and ropes near which young squid are often found. Yet the combination of particular actions can be systematized and described in units making up part of the ethogram. Stimulation of higher motor centres of the basal lobes of octopuses produces discrete sets of movements, and with increase in stimulus intensity more units are recruited giving complex patterns (Zullo et al. 2009). Such perception of current and objects must feed into central processing, leading to a motor output program combining position, postures and skin display patterns (Hanlon and Messenger 1996), a major brain accomplishment.

Another way in which the flexibility and interdependence of the squid movement system functions is the coordination of fin and jet-propulsion movement during displacement, common across the squid but with species-typical fins shapes. The dual jet–fin locomotion combination suggests a fast–slow movement dichotomy, yet their close coordination means the squid can move over a large range of velocities and also resist the pull of gravity in the water column. After many years of research on the jet-propulsion system, O'Dor and Webber (1986, 1991) emphasized that the jet system, while versatile in terms of movement directionality, is energetically inefficient compared to the propulsion system of fish. More recently, however, they have been able to obtain telemetry data about oxygen consumption by squid in

the wild (O'Dor et al. 2002), and have discovered that movement in three dimensions is more versatile with the jet–fin combination. This combination of two effector systems (Hoar et al. 1994) which are controlled in different areas of the brain (Nixon and Young 2003), as well as microhabitat choice in upwellings (Sauer et al. 1997) or near objects (O'Dor et al. 2002) may compensate for the physiological inadequacies of jetting. It can supply the slow–fast balance that is found in fish by a combination of slow and fast muscle fibre types (Bone 1978) for manoeuvrability. The details of its flexible programming by the squid brain, a contrast to the fixity of that of insects (Alexander 2002), need to be worked out.

The effector combinations emphasize a theme expressed in Hoar et al. (1995), that each coleoid cephalopod species has adapted the basic flexible muscle and shell-free body to produce the greatest efficiency in its particular ecological niche, in the same way that fish emphasize the use of different fin shapes in propulsion (Korsmeyer et al. 2002). Hoar et al. (1994) comment about the typical fin shape of loliginids as rhomboid and the group as typically without balistiform (named after the triggerfish which mostly use the caudal fin for propulsion) locomotion. But the near-shore *Sepioteuthis* is not a typical loliginid, and its long lateral fin and locomotion style is much like that of *Sepia*, which lives in a similar low-current and demersal habitat. In comparison, the octopus has long arms with much flexibility (Mather 1998) yet stereotypies within this (Yekutieli et al. 2005a, 2005b) as well as the large brachial lobe representation in the brain (Maddock and Young 1987) and is adapted for movement in its benthic habitat. *Sepioteuthis* squid have much less flexibility in arm movement, suited to their mid-water location. In exchange for this and still utilizing the muscular hydrostat (Kier and Smith 1985) that gives such effector variability, they can make concealing postures, move in any direction, turn in their own body length yet also jet almost instantly away at a predator's approach. In short, they have taken the design of the cephalopod muscular hydrostat in quite a different direction than the octopus has done (Mather 1998), yet one that is exceptionally well suited to the demersal niche (O'Dor et al. 2002) in which they live.

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Notes

1. At the time of publication the authors provided links showing video images of aspects of the behaviour of these animals on websites controlled by them. These video clips can be found at www.byrne.at/squiddances.
2. Examples for the arm positions Standard, Upcurl, Extended, Splayed, Belled, Spread, Horns, and straight Bad Hair (not Twisted) can be viewed in supplementary video clips at www.byrne.at/squiddances.
3. A video clip showing cleaning behavior can be viewed at www.byrne.at/squiddances.
4. See supplementary video material of a mating at www.byrne.at/squiddances.
5. See supplementary video material of a group of squid bolting from a barracuda at www.byrne.at/squiddances.
6. Supplementary video material at www.byrne.at/squiddances.
7. Examples for the body positions School, Parallel, Diagonal, Over/Under, Rocking, Switch, Rise-above, Chase can be viewed in supplementary video clips at www.byrne.at/squiddances.

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