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The argonaut shell: gas-mediated buoyancy control in a pelagic octopus

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Argonauts (Cephalopoda: Argonautidae) are a group of rarely encountered open-ocean pelagic octopuses with benthic ancestry. Female argonauts inhabit a brittle 'paper nautilus' shell, the role of which has puzzled naturalists for millennia. The primary role attributed to the shell has been as a receptacle for egg deposition and brooding. Our observations of wild argonauts have revealed that the thin calcareous shell also functions as a hydrostatic structure, employed by the female argonaut to precisely control buoyancy at varying depths. Female argonauts use the shell to 'gulp' a measured volume of air at the sea surface, seal off the captured gas using flanged arms and forcefully dive to a depth where the compressed gas buoyancy counteracts body weight. This process allows the female argonaut to attain neutral buoyancy at depth and potentially adjust buoyancy to counter the increased (and significant) weight of eggs during reproductive periods. Evolution of this air-capture strategy enables this negatively buoyant octopus to survive free of the sea floor. This major shift in life mode from benthic to pelagic shows strong evolutionary parallels with the origins of all cephalopods, which attained gas-mediated buoyancy via the closed-chambered shells of the true nautiluses and their relatives.

Keywords: gas-mediated buoyancy; cephalopod; argonaut; *Argonauta*; paper nautilus; shell

1. INTRODUCTION

The argonauts (family Argonautidae) are free-swimming octopuses of open ocean habitats (figures 1*a* and 2*a*–*d*). Female argonauts produce and occupy a brittle white shell commonly known as a 'paper nautilus', while dwarf males lack a shell. Females of some species attain total lengths of up to 50 cm, which are up to eight times the length and 600 times the weight of the minute males (Finn 2009). The role of the female argonaut shell has been a source of speculation for over 2000 years. In 300 BC Aristotle proposed that the shell functioned as a boat, allowing the female argonaut to row and sail (using flanged dorsal arms) on the water surface (Thompson 1910). Since the study of Naef (1923), the shell has primarily been considered a receptacle for attachment and brooding of egg strings.

One of the key challenges for animals with a pelagic existence is the ability to control and maintain their vertical position within the water column. Many pelagic animals obtain energetic advantage from being neutrally buoyant, as energy is not continually expended to counteract body weight (Denton *et al.* 1969). Cephalopods use a range of mechanisms to counter their body mass and maintain vertical position in the water column, including the use of: fins; water jets directed through the funnel; shells with partially evacuated closed chambers (e.g. *Nautilus*, *Spirula* and *Sepia*); and/or low-density aqueous solutions in various body tissues or organs (e.g. 'ammoniacal squids'; see Voight *et al.* 1994). To date, the process by which the pelagic argonauts control their vertical position in the water column has never been demonstrated.

Past studies have observed pockets of air trapped in the apex of female argonaut shells, both in wild and captive animals (Naef 1923; Young 1960; Nishimura 1968; Zeiller & Compton 1970; Nesis 1977; Boletzky 1983; Bello & Rizzi 1990; Sukhsangchan *et al.* 2008). The presence of air in the shells of wild female argonauts was proposed to be detrimental to their survival, trapping them at the sea surface (Naef 1923) and ultimately resulting in their demise in large-scale mass strandings (Nishimura 1968). In contrast, this trapped air was speculated by others as a temporary misfortune—a negative consequence of life near the ocean surface from which the female argonaut could instinctively free itself (Nesis 1977).

Observations of female argonauts in aquaria also led to diverse speculation. Captive female argonauts displayed various degrees of buoyancy as a result of air trapped in the apex of their shells, from being upright on the substrate to being trapped at the water surface (Young 1960; Zeiller & Compton 1970; Boletzky 1983; Bello & Rizzi 1990). However, the source of the air was never demonstrated. The presence of aquarium aeration devices led to the suggestion that trapped air may simply have been an artefact of aquarium captivity (Young 1960).

Despite a lack of supporting evidence, the assumption that female argonauts may attain neutral buoyancy by way of pockets of air in their shells has since gained popular acceptance in the literature (Stephens 1965; Voss & Williamson 1971; Nixon & Young 2003; Bizikov 2004; Martill & Barker 2006). To date, however, the means by which argonauts obtain, manage and use such gas has not been demonstrated (Saul & Stadum 2005).

In this study, underwater observations and experimental manipulations of individual female argonauts in the wild reveal the role of the argonaut shell as a precise and unique system for gas-mediated buoyancy control.

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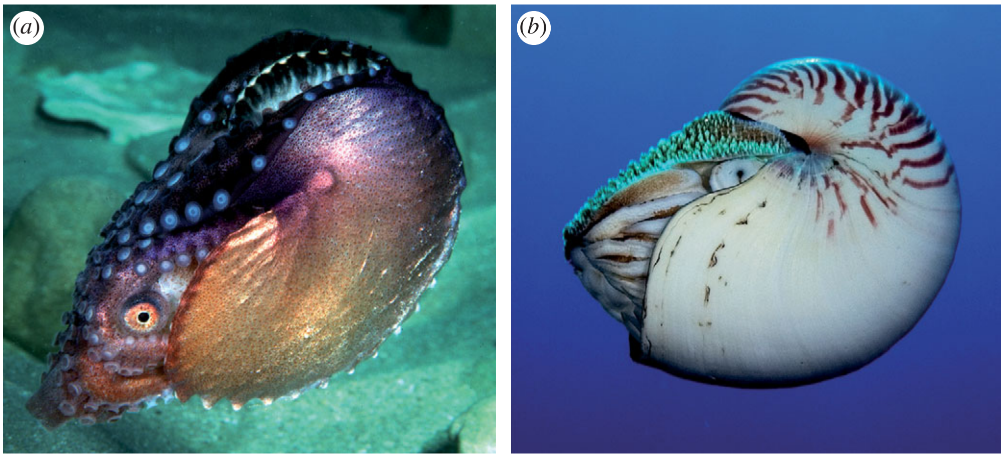

Figure 1. Comparison between a female argonaut and a chambered nautilus: (*a*) female argonaut (*Argonauta nodosus*), Port Phillip Bay, Victoria, Australia; (*b*) chambered nautilus (*Nautilus pompilius*), Osprey Reef, Coral Sea, Australia. Photos: (*a*) Rudie Kuiter and (*b*) Julian Finn.

The method by which female *Argonauta argo* purposely capture air from the water surface and expertly force it to depth is described.

2. MATERIAL AND METHODS

In January 2006, three female *A. argo* were collected live from commercial set-nets off Shimane Peninsula, Sea of Japan. The argonauts were transported live to Okidomari Harbour where they were housed in a 1200 l opaque vessel containing regularly changed sea water. The sea water was aerated using a purpose-made system that ensured that the argonauts could not come into direct contact with air bubbles from the aquarium aeration system. The containing vessel was covered with a matching opaque lid and only removed for feeding and changes of water. While in captivity, the argonauts were fed a combination of fresh squid and fish held against their beaks. Individual argonauts were removed and released into Okidomari Harbour for short periods and observed, videoed and photographed underwater while scuba diving. Female argonauts were manipulated underwater prior to release so as to remove all air from their shells. Individuals were released 1 m above the seafloor at water depths of 2–7 m.

3. RESULTS

In the absence of air within the shell, released live argonauts were observed to be negatively buoyant. Argonauts lacking air in the shell appeared to have difficulty in maintaining the vertical orientation of the shell, which flailed from side-to-side as the animal jetted.

Soon after release, all individuals behaved in the same manner, performing the following five-step sequence (figure 2):

1. The argonaut immediately jetted towards the sea surface.
2. At the surface, the argonaut oriented the funnel dorsally and vigorously jetted against the water surface, causing the shell to bob above the water surface and rock forward, 'gulping' the maximum possible volume of air into the shell via the dorsal openings of the shell aperture (figure 2*a*). The captured air was then sealed within the shell using the second pair of arms.
3. The direction of the funnel jetting was then shifted ventrally, causing the shell to roll away from the water surface (figure 2*b*).
4. Using strong jets of water from the funnel, the now-buoyant shell was forced downward, with the excess air caught outside the sealed air volume being released as the argonaut dived (figure 2*c*).
5. The argonaut levelled out at the depth where buoyancy from the trapped (and now compressed) air volume cancelled the weight of the animal, thus attaining neutral buoyancy (figure 2*d*). Once neutrally buoyant, the argonaut was capable of rapid swimming parallel to the water surface, at a speed that exceeded that of a swimming diver.

At all stages, released argonauts maintained complete control of the air volume within their shells and, consequently, their buoyancy. Once the captured volume of air was 'sealed off' in the shell, complete 360° vertical rotation underwater by physical manipulation of the live argonaut resulted in no air loss.

The released argonauts showed considerable dexterity in the orientation of their shells as depth increased. In shallower waters (2–3 m) the shell was held vertically and away from the body so that the larger volume of air could not escape. At greater depths (7–8 m), the argonaut gradually rotated the shell towards horizontal and settled further into the shell as the air was compressed into the top of the shell by the increasing ambient pressure.

All captive female argonauts that were left neutrally or negatively buoyant for an evening in the holding tanks were found the following morning to be positively buoyant at the surface with air in their shells.

4. DISCUSSION

This study constitutes the first direct observations of a cephalopod manipulating air obtained from the water surface as a means of attaining neutral buoyancy. The method by which the female argonaut captures and manages air is a complex, multi-phase behavioural sequence. By rocking the shell at the surface to capture air and then sealing off the air with the arms, the female argonaut is capable of capturing a larger volume of air than would

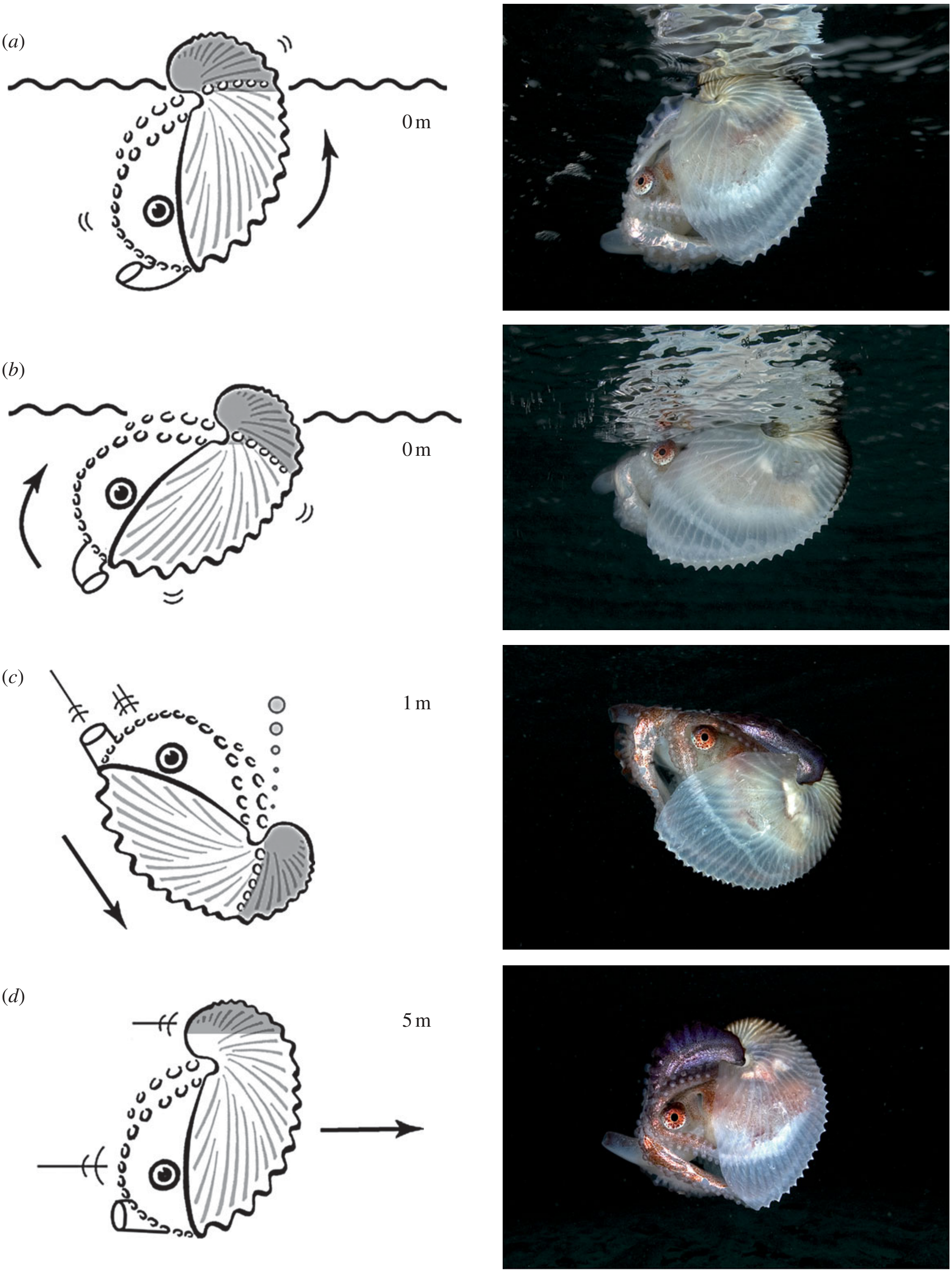

Figure 2. Behavioural stages (*a–d*) by which a female argonaut (*A. argo*) attains neutral buoyancy, Okidomari Harbour, Sea of Japan. Illustrations: Julian Finn/Kate Nolan. Photos: Julian Finn.

be possible with a passive shell at the surface. This larger volume of air allows argonauts to maximize the depth at which they attain neutral buoyancy. This increase in depth may allow the argonaut to avoid surface wave action and predation from above (i.e. from birds).

It is proposed here that previous captive observations may have failed to reveal the specific mechanism by which argonauts attain neutral buoyancy because the aquaria used to house the argonauts have been too shallow. Female argonauts attain neutral buoyancy by capturing a large volume of air at the surface and force it to a depth where the water pressure sufficiently compresses the air within the shell. At the targeted depth, the buoyancy of the captured air counteracts the submerged weight of the argonaut and neutral buoyancy is attained. Observations in the wild suggest that a depth of around 7–8 m is the target depth for the observed argonauts. In circumstances where an argonaut is incapable of diving to sufficient depth (e.g. captivity), the large air volume within the shell draws the animal back to the water surface.

Suggestions in the literature that air trapped in the shells of argonauts is a misfortune (Naef 1923;

Nesis 1977) or of detriment to the argonaut's survival (Nishimura 1968) are not supported by this study. Female argonauts were observed to have complete control of the volume of air in their shells. In the absence of air in their shells, female *A. argo* flailed from side-to-side, appearing to be unable to maintain the vertical orientation of the shell. Underwater observations in this study indicate that air in the shell is a necessity for maintaining the shell's vertical orientation and enabling fast directional locomotion.

Owing to superficial similarities in external shell shape, argonauts are often confused with their distant cephalopod relatives, the ancient chambered nautiluses (Subclass Nautiloidea). As a result they are often called 'paper nautiluses'. The live chambered nautilus (figure 1*b*) is permanently bound to its solid shell, which is laid down by the mantle. The shell is internally divided to form gas-filled chambers connected by a long tissue duct (the siphuncle). The siphuncle functions to add and remove fluid from the chambers (using osmotic gradients) in order to attain the correct ratios of fluid-to-gas required for neutral buoyancy. Gas pressures within the chambered nautilus shell are less than 1 atmosphere, with the rigid shell preventing implosion and enabling these cephalopods to attain maximum depths of around 750 m (Ward *et al.* 1980). Chambered nautiluses occupy the terminal open chamber of their shell.

By contrast, the female argonaut is an octopus that is not permanently bound to its simple open shell. The shell lacks internal chambers and is produced primarily by web flanges off the first arm pair (figure 1*a*). Air is captured from the water surface and neutral buoyancy is attained at relatively shallow depths, potentially less than 10 m.

These distantly related cephalopod groups represent evolutionary convergence in the use of an external shell and gas-mediated buoyancy. For both groups, the evolutionary context or selective advantages that led to departure from the benthos and adoption of a pelagic existence remain unknown. However, the dexterity and morphological plasticity of the female argonaut allows neutral buoyancy to be attained with far less morphological architecture or complexity than that of the true nautiluses.

While effective at providing buoyancy near the sea surface, use of air by the argonaut has limitations. In contrast to the chambered-shell cephalopods, the air held by the female argonaut is not entirely contained within a rigid structure. The volume of air within the female's shell is therefore directly influenced by water pressure and hence water depth. An increase in depth beyond a critical point results in the air being too compressed to provide the upward force required to counteract the argonaut's body mass. As such, energy would need to be expended to maintain vertical position. Conversely, a small rise towards the surface could significantly increase buoyancy of the air, thus pulling the argonaut towards the sea surface. As has been noted for fishes with soft swim bladders, the neutrally buoyant argonaut is 'in a state of unstable equilibrium' (Denton 1962).

With no known method for directly producing gas, it is assumed that the argonaut's system would only be effective over a small vertical range (speculated here as being the upper 10 m). Below the depth at which neutral buoyancy is attained, the argonaut would become negatively buoyant. Adult female argonauts with shells are regularly encountered at the sea surface (Adams & Reeve 1848; Verrill 1884; Allan 1950; Akimushkin 1965; Roper & Young 1975; Rosa & Seibel in press). By contrast, the minute shell-less males and immature females (mantle lengths less than 9 mm) have been collected in closing nets between 50 and 200 m depth (Lu & Clarke 1975; Roper & Young 1975; Salman *et al.* 2003). Unhindered by surface-acquired gas as a source of buoyancy, minute males and small females appear capable of inhabiting a greater depth range and must employ alternative strategies to maintain vertical position in the water column.

The pelagic argonauts are believed to have arisen from benthic octopod ancestors, based on both morphology (Young 1977, 1989; Young *et al.* 1998; Messenger & Young 1999) and molecular evidence (Strugnell *et al.* 2005; Takumiya *et al.* 2005). It has been proposed that the evolution of a buoyant chambered shell allowed the original benthic ancestors of all cephalopods to free themselves from the sea floor and invade the pelagic realm (Young *et al.* 1998). For the argonauts, however, it is unlikely that their 'air-gulping' buoyancy control played a role in this transition. The shell buoyancy of argonauts could not have initiated at depth as the critical air is obtained from the sea surface. Instead, the argonaut's method of attaining buoyancy is more likely to have evolved after the argonaut's ancestors had already become pelagic, potentially via the pelagic paralarval or juvenile stages found in many benthic octopuses with small eggs. This neotonous route has been demonstrated for another group of pelagic octopuses: the ctenoglossans, which includes members of the families Vitreledonellidae, Amiphitretidae and Bolitaenidae (Strugnell *et al.* 2004).

Two related shell-less pelagic octopuses, *Ocythoe tuberculata* and *Haliphron atlanticus*, are the only cephalopods reported to possess true gas-filled swimbladders (Packard & Wurtz 1994; Bizikov 2004). The method by which gas is attained and controlled in these octopuses has never been demonstrated. It is possible that the novel behaviour of surface acquisition of air, described here, may also occur more broadly in the Superfamily Argonautoidea.

Evolutionary origin of the argonauts and their relatives (Superfamily Argonautoidea) is the subject of ongoing research.

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