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Submersible observations on the daytime vertical distribution of *Aequorea ?forskalea* off the west coast of southern Africa

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The vertical distribution of the hydromedusa *Aequorea ?forskalea* was investigated using observations from the research submersible 'Jago' collected during 36 dives off the west coast of southern Africa during November 1997 and April 1999. The mean population depth of *Aequorea ?forskalea* deepened with increasing sea surface temperature. We suggest that this behaviour enables individuals to avoid offshore advection, to minimize spatial overlap with other large medusae and to maintain their position over the middle of the shelf.

INTRODUCTION

A number of factors influence the vertical distribution of pelagic organisms including light levels (e.g. Russell, 1926; Forward, 1988), the thermal and haline structure of the water column (Gallager et al., 2004) and the distribution of food (e.g. Sameoto, 1976; Hamner et al., 1987), predators (e.g. Bollens & Frost, 1989), competitors (e.g. McGowan & Walker, 1979) and nutrients (e.g. Pitcher et al., 1992). It also varies with gender and developmental stage or age (e.g. Verheye & Field, 1992). The occupational depth of a pelagic organism is rarely fixed, and many species will change their position on a seasonal (Goy, 1987) or diel basis (Russell, 1925).

Much of our understanding of the vertical distribution of pelagic organisms has been derived from studies of crustacean zooplankton, and we are comparatively ignorant about the factors responsible for this pattern in other taxa, such as medusae (but see Graham et al., 2001). Medusae can be important components of coastal and oceanic zooplankton, and although they are known to change their vertical position through time (Russell, 1926; Graham et al., 2001) patterns even within species are often contradictory (Buecher & Gibbons, 2003). Part of the reason for this contradiction must lie in the comparative paucity of the present database. The intent of this study is to augment the baseline data for one species of hydromedusa, *Aequorea ?forskalea*, in the Benguela region using novel observations from a research submersible (see also Mackie & Mills, 1983). The data set is significant because unlike that generated from other studies of plankton using submersibles (e.g. Vinogradov, 2005) it is based on a fairly large number of dives.

Aequorea forskalea (previously identified in the region as *A. aequorea*) is one of two common species of large jellyfish in the northern Benguela upwelling system (Fearon et al., 1991; Brierley et al., 2001, 2004; Buecher et al., 2001). It is found in greatest abundance at the edge of the shelf off central Namibia and gives way to the scyphozoan *Chrysaora hysoscella* closer inshore (Sparks et al., 2001).

MATERIALS AND METHODS

The vertical distribution of *Aequorea ?forskalea* was studied from the research submersible 'Jago' during two separate dive expeditions for De Beers Marine (Pty) Ltd (see e.g. Gibbons et al., 2002). The first was conducted in November 1997 between 28°15'S and 29°40'S at a bottom depth of ~130 m (13 dives), whilst the second was conducted between 27°59'S and 28°59'S at a bottom depth of between 54–184 m (23 dives) in April 1999.

Observations on *Aequorea ?forskalea* were made through the bow window of the submersible by a single observer during descent to, and ascent from, the seabed. Although the bow window of the 'Jago' is slightly convex (700 mm diameter), only conspicuous (large) medusae seen immediately in front of the window were counted (i.e. the width of the field of view was 700 mm). The depth of observational field is obviously turbidity-dependent but 'Jago' was only deployed in calm weather, when visibility was ~3 m. Medusae were counted on a continuous basis with reference to depths reported by hull mounted instruments, and counts were summed over 5-m depth bins: temperature too was monitored from hull-mounted instruments. All observations were made between 0800 and 1845 hours.

The mean vertical position (weighted mean depth, WMD) of *Aequorea ?forskalea* in the water column was determined using the method of Pearre (1973):

$$\mathrm{WMD} = \Sigma n_i d_i / \Sigma n_i \quad (1)$$

where n_i is the total number of individuals recorded over depth range i, and d_i is the mid-point of depth-range i.

RESULTS AND DISCUSSION

Unfortunately, no specimens of the *Aequorea* that were observed from the 'Jago' were actually collected and this prevents us from making a definitive identification. Five species of *Aequorea* have been reported from the south-east Atlantic Ocean (Bouillon, 1999): *Aequorea forskalea* Péron & Lesueur, 1810, *A. coerulescens* (Brandt, 1838), *A. conica* Browne, 1905, *A. pensilis* (Eschscholtz, 1829) and *A. macrodactyla* (Brandt, 1834). The latter three of these attain a relatively small size (Bouillon, 1999) and are uncommon in the region (Pagès et al., 1992): they are unlikely to have been that observed here. Although *A. forskalea* and *A. coerulescens* can both attain a large size (Bouillon, 1999), *A. coerulescens* has only been reported from a few specimens in the region (Pagès et al., 1992), whilst *A. forskalea* is both abundant and common (Fearon et al., 1991; Pagès et al., 1992): hence our tentative identification of the present material as *A. ?forskalea*.

A total of 318 *Aequorea ?forskalea* was recorded during the 36 dives conducted during 1997 and 1999. The relationship between WMD and sea surface temperature (SST) was positive (r=0.39, P<0.05): in other words the mean population depth of *Aequorea ?forskalea* increased significantly with increasing SST (Figure 1).

We suggest that this behaviour represents a strategy whereby individuals can maintain themselves in the mid-shelf region along the west coast of southern Africa. *Aequorea forskalea* has been noted by a number of previous authors to occupy the middle region of the Namibian shelf, and to occur offshore of the other large medusa present in the system, *Chrysaora hysoscella* (Fearon et al., 1991; Brierley et al., 2001). Such a consistent pattern of distribution has been tentatively ascribed to niche-partitioning (Sparks et al., 2001), and requires some sort of maintenance mechanism. By remaining close to the surface at low temperatures *Aequorea ?forskalea* ensures that it will be advected offshore in the initially cool surface waters of the Ekman layer. Cool surface water is typically encountered close to shore in an upwelling region such as the Benguela, and such a behaviour would take it out of the zone occupied by *C. hysoscella*. By moving into deeper water when the SST is high, *Aequorea ?forskalea* ensures that it is not lost to oceanic waters and that it is able to take advantage of the onshore compensation currents that exist at depth. The warmer the SST the deeper the depth of occupation—a reflection of the fact that warmest waters are found towards the edge of the shelf and that therefore the depth of movement required to effect shoreward movement in the compensation current will be greater.

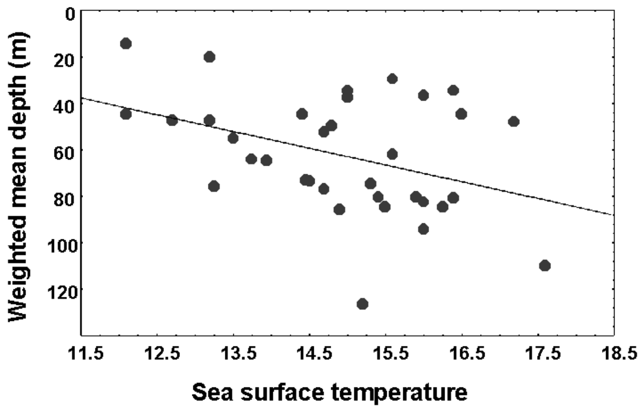

Figure 1. Relationship between the weighted mean depth (m) of *Aequorea ?forskalea* and sea surface temperature (°C).

This hypothesis is partially supported by data that were collected during a separate field survey conducted over the Namibian shelf in 1999, the methods and some results of which have been reported on by Brierley et al. (2001), Buecher et al. (2001) and Sparks et al. (2001). During that study, stratified jellyfish samples were collected from an inshore (~100 m depth), mid-shelf (~160 m) and offshore (~230 m) station along a survey transect at 22°S off Walvis Bay, using a modified Åkrehamn trawl fitted with a multi-sampler. The results indicated that the WMD of *Aequorea forskalea* (note that specimens were in this instance collected and identified) were 23.1 m (±8.8 m SE), 42.8 m

(±14.1 m SE) and 41.8 m (±15.8 m SE), respectively, for these three stations. Data are too few to conduct meaningful tests of significance, but they suggest that *A. forskalea* was located mostly in the surface waters close to shore but occurred at a greater range of depths at the offshore station.

The shuttling of individuals between different water layers that move in different directions has been proposed as a means of maintaining populations close to shore for a number of other taxa in the region (Verheye et al., 1991; Pillar et al., 1992; Gibbons & Stuart, 1994). Such studies have tended to demonstrate a cross-shelf size distribution of individuals (big inshore, small offshore) where size is linked to migratory ability.

In proposing this putative explanation for the observed behaviour, we also need to take cognisance of other arguments that could be advanced to explain the patterns. Firstly, although irradiance at any depth obviously varies with time of day, and zooplankton typically respond to light intensity by displaying diel vertical migration (DVM) (e.g. Russell, 1926) there was no relationship between time of day and WMD in the data collected here (P>0.05).

Secondly, although different developmental stages of holo-zooplankton will frequently occupy different depths (Verheye et al., 1991; Pillar et al., 1992), it should be remembered that *Aequorea* is meroplanktic: it is the sexually active and dispersive phase of an organism with a benthic component to its life history. Other species of *Aequorea* are thought to mature at between 35–60 mm (Mayer, 1910), which would mean that all individuals noted here would have been 'large' and sexually mature. Unless sexually mature individuals of (presumed, but not measured) different size (and age?) occupy different depths, developmental stage cannot be accepted as an explanation for the observed pattern.

Thirdly, although predators are known to influence the behaviour of crustacean zooplankton through kairomones (Folt & Burns, 1999), hydromedusae are strictly carnivorous and, when large, have few common natural predators, except perhaps other medusae (e.g. Purcell, 1991; Purcell & Decker, 2005; but see Ates, 1988). Such predators were not observed during the course of underwater observations and are unlikely to account for the observed results.

Unfortunately ambient food concentration was not measured during the course of this study. Although Scyphozoa might track prey migrations (Graham et al., 2001), and are known to behave in such a way that would allow them to stay within high-density food patches (Bailey & Batty, 1983; Matanoski et al., 2001), the result observed here (interpreted in this way) would imply that an increase in SST is associated with a deepening of the food-rich layer. We cannot discount this explanation for the relationship, as a deepening of the thermocline is associated with sub-surface phytoplankton blooms (e.g. Pitcher et al., 1992), which in turn might reflect the occupational depth of herbivorous zooplankton (e.g. Sameoto, 1976). However, most species of crustacean zooplankton in the Benguela ecosystem display pronounced DVM and are uncommon in the surface waters during the day (Verheye & Hutchings, 1988).

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