

Diving behaviour of jellyfish equipped with electronic tags

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*Jellyfish are one of the most abundant and conspicuous members of our coastal marine fauna and are now known to play major trophic roles in marine systems. However, little is known about the movements and behaviour of individuals. We equipped individual compass jellyfish (*Chrysaora hysoscella*) ($n = 15$) off the Dingle coast, Ireland, with miniature time-depth recorders to log their depth over periods of a few hours. Vertical movements were extensive, with all jellyfish changing their depth during tracking. A range of vertical movements were seen including initial diving from the surface down to a maximum of 29.6 m after device attachment, some jellyfish remaining near the bottom, some moving up and down in mid-water and some moving back near the surface. These results show that jellyfish actively reposition themselves in the water column over small time-scales and open the way for more extensive studies equipping jellyfish with electronic tags.*

INTRODUCTION

Over the last few decades, a range of tracking devices have transformed our knowledge of the behaviour and physiological ecology of a huge range of terrestrial, aerial and aquatic species. In marine environments, for example, data-loggers and transmitters are now routinely deployed on marine mammals, fish, turtles and birds to record their fine-scale movements over periods of hours or days, their broad scale movements over months or even years as well as their diving behaviour (e.g. Sims *et al.*, 2005; Watwood *et al.*, 2006; Bradshaw *et al.*, 2007). However, some important taxa have remained fairly intractable as far as instrument deployments are concerned, with a case in point being gelatinous zooplankton.

Gelatinous zooplankton have historically been a little studied component of marine ecosystems with even basic aspects of the biology of most species, such as their levels of abundance, seasonal population changes and depth distribution remaining enigmatic (Mills, 2001). There is evidence to suggest that rather than

being weak swimmers that passively drift with the water currents, many scyphozoan jellyfish can display sophisticated interactions with their biological, chemical and physical environment (Hamner and Hauri, 1981; Hamner *et al.*, 1994; Albert, 2007). There is also an increasing realization that jellyfish can play major trophic roles in marine systems as well as having many important socio-economic effects (CIESM, 2001; Sommer *et al.*, 2002; Coll *et al.*, 2007). For example, there is growing concern that jellyfish may be replacing fish as the dominant higher predators in marine systems, with this pattern being recently described in the Benguela upwelling ecosystem off south west Africa where fish have been heavily exploited and where jellyfish biomass now, but did not previously, exceeds the biomass of fish (Lynam *et al.*, 2006). Other examples of increases in jellyfish abundance include the Bering Sea (Brodeur *et al.*, 1999) and the Black Sea (Kideys, 2002; Daskalov *et al.*, 2007) and more recently Attrill *et al.* (2007) have suggested a more gelatinous future for the North Sea at the expense of commercial fin fisheries,

although a lack of understanding means such predictions remain highly speculative. Yet despite the profound effects of jellyfish, historically a lack of research tools has limited scientific advances in our understanding of the group.

In the 1970s and 1980s, pioneering studies using SCUBA gear and submersibles began to address this gap in our knowledge (Hamner *et al.*, 1975; Madin, 1988) and painted a dramatic picture of gelatinous zooplankton interactions, abundance and diversity (Haddock, 2004). More recently, a range of new methods have been developed. Ship-based acoustic systems have allowed broad scale mapping of jellyfish distribution (both horizontal and vertical) and abundance (Brierley *et al.*, 2001), while aerial surveys have been used to map the distribution of large surface dwelling species (Purcell *et al.*, 2000; Graham *et al.*, 2003; Houghton *et al.*, 2006a). Generally, these methods provide information about populations. To supplement these techniques, in theory, the range of data-logging and transmitting devices now available to the wildlife telemetry community might be deployed onto jellyfish to learn more about the behaviour of individuals. However, to date this potentially fruitful area of research has not been extensively developed although there are a few exceptions. In a pioneering study in Australia, Seymour *et al.* (Seymour *et al.*, 2004) attached time-depth recorders (TDRs) to box jellyfish (Class Cubozoa, *Chironex fleckeri*) to record their vertical movements. To each individual, a TDR was glued to the swimming bell with quick setting glue. These devices revealed how box jellyfish remain on the seabed at night and then actively hunt in the water column during the day (Seymour *et al.*, 2004). Given this success of TDR attachments to box jellyfish, we set out to conduct a proof-of-concept study of attaching TDRs to the scyphozoan compass jellyfish (*Chrysaora hysoscella*) which has been widely reported in coastal areas of the NE Atlantic (Barz and Hirche, 2007; Doyle *et al.*, 2007) and so presumably plays an important ecosystem role.

METHOD

Fieldwork was conducted between 8 and 23 August 2007 on the Dingle peninsula on the west coast of Ireland. Sampling was performed from one of two rigid inflatable boats (lengths 5.5 and 6.5 m) at three sites around the peninsula, Sauce Creek (52.28°N, 10.21°W), Smerwick Harbour (52.22°N, 10.38°W) and Ventry Bay (52.12°N, 10.35°W) (Table I). Compass jellyfish were located visually near the surface and then approached by a snorkeller. Sometimes upon approach,

Table I: Details of the TDR deployments onto individual jellyfish

Date	Location	Bell diameter (cm)	Duration (min)	Tag id
8 August	Sauce Creek	33	53	1028
10 August	Ventry Bay	29	240	1028
10 August	Ventry Bay	25	214	1015
10 August	Ventry Bay	22	134	942
10 August	Ventry Bay	31	76	942
10 August	Ventry Bay	35	75	941
11 August	Ventry Bay	20	139	941
11 August	Ventry Bay	–	65	1028
11 August	Ventry Bay	26	95	1028
11 August	Ventry Bay	19	137	1015
11 August	Ventry Bay	28	175	942
13 August	Smerwick Harbour	22	79	1015
19 August	Smerwick Harbour	26	207	1028
23 August	Smerwick Harbour	20	135	942
23 August	Smerwick Harbour	32	122	1015

Where no bell width was recorded, the tether was felt to break free of the jellyfish.

the jellyfish moved slightly deeper and were then gently brought to the surface with a fishermen's landing net. A nylon cable tie was then attached around the peduncle which connects the swimming bell to the oral arms (Fig. 1). To the cable tie a 10 kg breaking strain monofilament tether was attached with a small loop. A small TDR was attached with a loop of wire to the monofilament loop. Connected to the other end of the monofilament tether was a small fishing float and depending on the water depth the length of the tether was either 20 or 40 m, so that the tether length exceeded the water depth by at least 10 m.

We used the CEFAS G5 TDR (CEFAS Technology Ltd, Lowestoft, UK). The G5 is a cylindrical TDR (31 mm length by 8 mm diameter) that weighs 2.7 g in air and < 1 g in seawater, and is the most powerful TDR of its size available. The G5 is capable of storing 693 000 data points: depth with a nominal 0.03 m resolution and a full recording range of 100 m; temperature with a precision of 0.03°C and an accuracy of 0.1°C (see Hays *et al.*, 2007a for a full description).

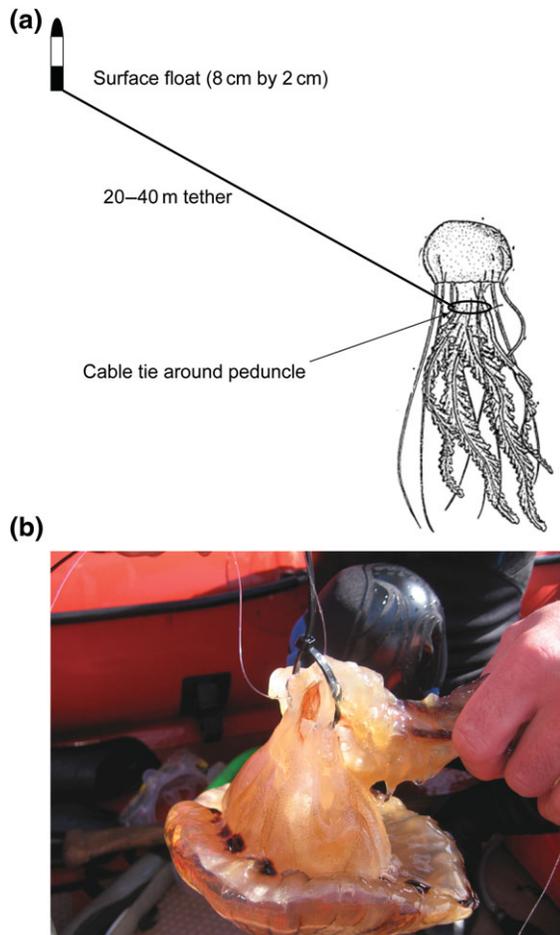


Fig. 1. (a) A schematic of the system for attaching TDRs to compass jellyfish. (b) A retrieved jellyfish hanging upside down showed the cable tie loosely fitted around the peduncle. Drawing of compass jellyfish modified after Ford *et al.* (1997).

When each tether was deployed on a jellyfish, we generally deployed a drogue to measure help maintain visual contact with the tethered jellyfish. Drogues consisted of a 20 cm float beneath which was suspended a 50 cm line connected to 1.5 m by 0.7 m rectangular sail made of clothe fibre, weighed with a metal tube along its lower edge so that the sail unfurled fully.

Periodically (generally every 15–30 min), we approached the float attached to each jellyfish and recorded the water depth (depending on the sampling date and boat, using either a Garmin GPSmap Z38 sounder or a Navman Fish 4350). Sometimes we also swam down the tether to examine each jellyfish if it was within snorkelling depth. To retrieve the TDR, the tether was gently pulled, although in some cases we felt the TDR pull free of the jellyfish upon retrieval. Retrieved jellyfish were brought onboard and their bell diameter measured prior to release.

RESULTS

A total of 15 jellyfish were equipped with TDRs (Table I). Total tracking duration ranged from 53 to 240 min. Upon initial attachment of TDRs, all the jellyfish showed a similar pattern of descending through the water column ($n = 15$ out of 15 deployments) (Fig. 2a). On all these initial descents, there was always a linear increase in depth with time and we used the gradient of this relationship to define the descent speed. Descent speeds ranged from 0.39 to 2.32 m min^{-1} ($n = 15$, mean 1.14 m min^{-1} , $\text{SD} = 0.64$). The maximum depth attained by each jellyfish ranged from 4.2 to 29.6 m and increased with water depth (Fig. 2b). The implication is that dive depth was constrained by the local bathymetry. However, initial decent speed was not related to water depth ($F_{1,13} = 0.1$, $P = 0.7$) nor to jellyfish size ($F_{1,12} = 0.1$, $P = 0.8$). We visually observed several jellyfish as they descended.

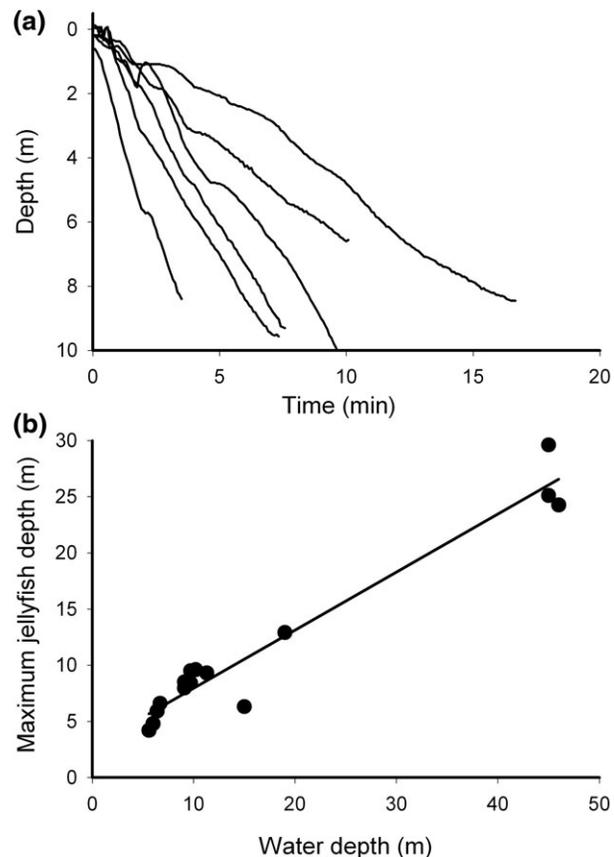


Fig. 2. (a) Examples of the initial descent through the water column of jellyfish equipped with TDRs. Data from six jellyfish are shown. The period of linear increase in depth is shown, which always started within a few minutes of instrument attachment. All tagged jellyfish showed an initial descent after equipment attachment. (b) The relationship between the maximum depth attained by individual jellyfish and the water depth. Maximum jellyfish depth (m) = 2.78 + 0.517 water depth (m) ($r^2 = 0.95$, $F_{1,13} = 232$, $P < 0.001$).

They maintained a vertical orientation while continuing to pulse their swimming bell. Presumably, they had reduced their pulse frequency to the point that their active swimming no longer overrode their negative buoyancy. The jellyfish did not invert and actively swim downwards.

Subsequent to this initial descent, we saw a range of vertical movements. Some jellyfish made a series of both upward and downward vertical excursions after the initial descent (Fig. 3a). In other cases, repeated vertical excursions were less marked but jellyfish gradually ascended through the water column until they were near the surface (Fig. 3b). In several instances, jellyfish continued to remain relatively deep, close to the seabed (Fig. 3c). For some of these jellyfish, a snorkeller was able to make visual contact with the jellyfish and see that they were just above (within ~ 1 m) of the seabed, but still in a normal vertical orientation and swimming, as evidence by pulsing of the bell. When we were also able to directly observe tethered jellyfish near the surface and in mid-water and they were always swimming as evidenced by the pulsing swimming bell. From these direct observations, the tether did not seem to impede the jellyfish as it angled away from the bell towards the surface and was not under tension (Fig. 1). However, for those jellyfish that dived deepest (>25 m), the tether was under tension when retrieved suggesting that it might have limited the dive depth.

This range of behaviours that we saw in TDR equipped jellyfish was also reflected in observations of unequipped free-swimming jellyfish that we encountered while snorkelling to observe tethered jellyfish. For example, while snorkelling, we also saw unequipped jellyfish close (within 50 cm) of the seabed, some swimming in midwater and others near (within 2 m) of the surface. Ambient water temperature measured by the TDRs attached to the jellyfish ranged from 12 to 15°C.

DISCUSSION

We have shown here for the first time that it is feasible to attach devices to scyphozoan jellyfish, which opens the way for a new era of tracking studies to learn more about the behaviour and ecology of this group. This development can be likened to the first attachment of data-loggers to seals and other air-breathing vertebrates in the 1970s (Gentry and Kooyman, 1986). As with the evolution of device attachment to marine vertebrates, we can now envisage ever more elegant ways of attaching devices to jellyfish as well as longer deployments and an increase in the parameters that are measured. While our study is clearly limited in scope, it paves the way for these future developments.

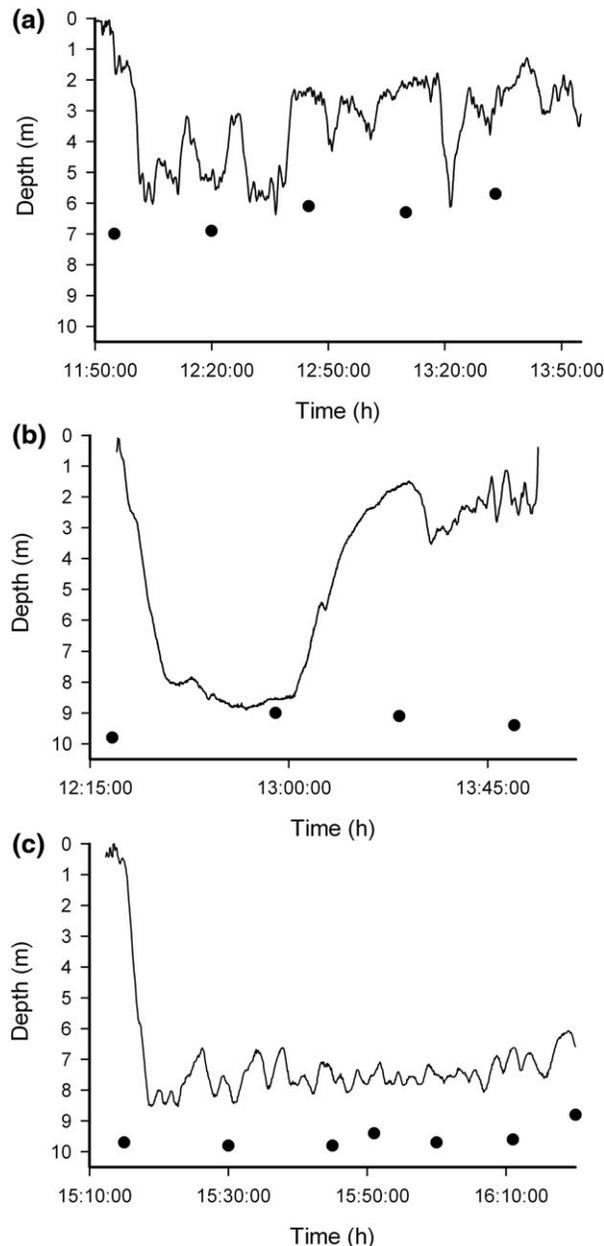


Fig. 3. Examples of the time-depth records for different jellyfish. After an initial descent, a range of patterns were seen. **(a)** An example of a jellyfish that conducted repeated vertical excursions, in this case between ~ 2 m and 6 m. **(b)** An example of a jellyfish that ascended gradually through the water column from ~ 9 m to 2 m. **(c)** An example of jellyfish that remained closely associated with the seabed. Lines without symbols show the jellyfish depth. Filled symbols show seabed depths.

The attachment system we employed, with a cable tie around the peduncle, appeared robust with most attachments remaining intact even when jellyfish were forcibly retrieved by pulling in tethers. Hence, we are confident that the attachment system would have remained intact indefinitely. Seymour *et al.* (Seymour *et al.*, 2004) recently

attached electronic tags to box jellyfish by using quick setting glue to secure the tags directly to the swimming bell. Clearly, there are a number of possibilities that can be considered for attaching devices to jellyfish depending on the specifics of the structure of the species at hand. Future studies could consider attaching acoustic transmitters so that jellyfish can be followed without the need for a surface tether along with pop-off systems that allow instrument detachment and hence recovery. Long deployments onto jellyfish would clearly be useful and electronic tags, like the G5s we used, are capable of recording diving behaviour for many months or even years. In well populated areas, recovery after long deployments might simply be through the return of tags washed ashore on beaches, which has worked surprisingly well for equipment attached to a range of diving vertebrates such as fish (e.g. Hays *et al.*, 2007b).

TDR attachments to jellyfish give us the opportunity of examining just how plastic vertical movement behaviour can be for individual animals. Information on the vertical movements of jellyfish might also have utility in efforts to quantify patterns of abundance. Surface observations, for example from boats and aircraft, have been used to map the distribution of jellyfish (Sparks *et al.*, 2001; Graham *et al.*, 2003; Doyle *et al.*, 2007). Knowledge of the vertical distribution of jellyfish during such surveys might allow informed extrapolation from surface densities to water column integrated abundance.

Certainly, vertical movement and active swimming play central roles in the lives of many jellyfish species (Hamner and Hauri, 1981; Seymour *et al.*, 2004; Kaartvedt *et al.*, 2007). There is strong evidence for vertical repositioning in the water column by a wide range of free-living zooplankton taxa, including jellyfish (Hamner *et al.*, 1982). For example, many species of zooplankton travel up and down through the water column over the diel cycle, with the most widely described pattern, termed normal diel vertical migration, being for zooplankton to be deeper in the water column during the day and shallower at night (Hays, 2003). In an elegant study, Kaartvedt *et al.* (Kaartvedt *et al.*, 2007) were recently able to track individual jellyfish (*Periphylla periphylla*) acoustically in a Norwegian fjord and recorded mean vertical velocities associated with diel vertical migration that were very similar to those we found: *Periphylla* mean vertical velocity 1.2 m min^{-1} , *Chrysaora* mean initial descent speed 1.1 m min^{-1} . Although compass jellyfish have not been the subject of studies on individual movement, their sibling species *Chrysaora quinquecirrha*, have attracted considerable attention. In controlled laboratory conditions, there have been elegant observations revealing the complexity of jellyfish movements. Pioneering studies with *Chrysaora*

quinquecirrha and some other species of jellyfish have involved detailed video recordings in aquaria and have shown complex movements that change in line with prey density, i.e. they can perceive prey and change their behaviour accordingly (Costello and Colin, 1995; Ford *et al.*, 1997; Matanoski *et al.*, 2001). In 2.3 m deep tanks, *Chrysaora quinquecirrha* were observed to vary their depth over a range of up to 153 cm within a few minutes, presumably in search of prey (Matanoski *et al.*, 2001). *Chrysaora quinquecirrha* has also been the subject of direct *in-situ* observations by SCUBA divers that have revealed almost continuous swimming and hence the suggestion that the species should be considered a cruising predator whose foraging patterns are inherently bound to swimming (Costello *et al.*, 1998). Given these previous studies showing the importance of movement in *Chrysaora*, we might predict *a priori* that free-living compass jellyfish might reposition themselves in the water column. Our results clearly confirm this prediction with compass jellyfish actively changing their depth over small time-scales. Clearly, there was a reaction of the jellyfish to handling and/or equipment attachment with an initial descent through the water column. Handling and device effects are a recurring issue within all telemetry studies, with a general aim being for researchers to reduce device effects regardless of the study animal (e.g. Bannasch *et al.*, 1994, Wilson and McMahon, 2006). However, it appeared that jellyfish often initiated their descent simply by being lightly handled in the water, rather than due specifically to the attachment system itself. This consistent initial descent of jellyfish clearly showed how compass jellyfish react to external stimuli within their physical environment.

In common with the conclusions of Matsumoto and Harbison (Matsumoto and Harbison, 1993), it is hard to imagine that the relatively slow descent by a *Chrysaora* might allow escape from fast moving predators such as the leatherback turtle (*Dermochelys coriacea*) and the oceanic sunfish (*Mola mola*) that have been observed off the coast of Ireland (Houghton *et al.*, 2006b). Alternatively, the descent by jellyfish that we observed might reflect a reaction to physical disturbance that might be experienced in rough seas where breaking waves might cause physical damage. Certainly aerial surveys seem to show that for some jellyfish species (e.g. *Rhizostoma octopus*), fewer individuals are seen on rough days and more on calm days (Houghton *et al.*, 2006c), which implies they avoid the surface in rough conditions. Indeed, turbulence causes another Rhizostomeae species, *Stomolophus meleagris*, to sound in the coastal waters of North Carolina (Graham *et al.*, 2001). We found that jellyfish descended further when the water was deeper. This might simply be because

physical disturbance in rough seas will be less at increased depth and so jellyfish descend further when they are able to.

After the initial descent, the continuous vertical repositioning that we observed by jellyfish suggests that they move through the water column with purpose, possibly in search of high concentrations of prey as reported in aquaria (Matanoski *et al.*, 2001). Clearly, this idea is speculative without synoptic measurements of prey concentration. However, our results suggest that jellyfish might be a tractable group for examining predator search strategies.

In conclusion, we have shown it is possible to record the diving behaviour of free-living scyphozoan jellyfish and the stage is now set for refinements to methodologies and deployments of electronic tags for longer periods on an extended range of species.

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