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REVIEW

How to tag a jellyfish? A methodological review and guidelines to successful jellyfish tagging

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Jellyfish have become a topic of interest of many marine scientists and managers alike due to their conspicuous socio-economic and environmental impacts. However, our knowledge about their "everyday life" remains limited. While electronic tags (transmitters and loggers) have been extensively used to study marine vertebrates for the past 50 years, tagging is still in its infancy for marine invertebrates and jellyfish in particular. Progress has been hampered by the difficulty and limited knowledge of attaching tags to soft-bodied animals. We argue that there is huge potential to use tagging to gather basic information on the ecology and behaviour of these species. Here, we give an overview of what has been learned so far by deploying tags on jellyfish, and why tagging is an appropriate method to study their behaviour and ecology. We then describe different tagging techniques, their advantages, disadvantages and challenges, and the steps to ensure future successful jellyfish tagging studies.

KEYWORDS: jellyfish; zooplankton; tagging; tracking; behaviour; accelerometry

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INTRODUCTION

Considered as a gourmet delicacy (Hsieh *et al.*, 2001), a marine pest, or a threat to the tourism industry (Lucas *et al.*, 2014), jellyfish species (i.e. pelagic cnidarians and ctenophores) are numerous and widespread while historically poorly studied and understood (Gibbons and Richardson, 2013; Malej *et al.*, 2014). Jellyfish populations worldwide may have considerable impacts on the long-term health, functioning and productivity of the marine environment and may interfere with fisheries (Purcell *et al.*, 2007; Lucas *et al.*, 2014). Some jellyfish species are of particular concern to fisheries because they feed on eggs, larval and early juvenile stages of commercially important fish and, given their substantial biomass, can be significant predators and competitors of fish (Purcell and Sturdevant, 2001; Brodeur *et al.*, 2008; Hays *et al.*, 2012). Ultimately, large blooms of jellyfish may alter ecosystem energy pathways and can have significant impacts on the fisheries these ecosystems support (Brodeur *et al.*, 2011; Robinson *et al.*, 2014). For instance, in the northern Benguela Current off Namibia, gelatinous zooplankton seem to have replaced overfished planktivorous sardines and anchovies as the main predators in the ecosystem, resulting in major ecosystem changes (Lynam *et al.*, 2006; Roux *et al.*, 2013). Beaches and coastal areas awash with jellyfish are undoubtedly detrimental to tourist appeal and can result in serious financial losses for the tourism industry (Lucas *et al.*, 2014; Ghermandi *et al.*, 2015). However, not all impacts are negative, as jellyfish can play important roles in healthy marine ecosystems (Ruzicka *et al.*, 2007, 2012; Breitburg *et al.*, 2010; Doyle *et al.*, 2014). Some juvenile fish can enhance their survival by sheltering underneath jellyfish umbrellas (Lynam and Brierley, 2007), and more than a hundred species of fish including rockfish, crustaceans, as well as endangered sea turtles feed on jellyfish (Arai, 2005; Lee and Sampson, 2009; Jones *et al.*, 2012). While there is strong evidence of jellyfish having serious ecological and socio-economic impacts, they remain an understudied component of marine ecosystems and are rarely included in stock assessments and ecosystem fisheries models (Richardson *et al.*, 2009; Ruzicka *et al.*, 2012; Gibbons and Richardson, 2013). Compared with other marine species, relatively little is known about the ecology and behaviour of many jellyfish species mainly because appropriate research tools were lacking until recently.

It has been suggested that jellyfish blooms worldwide may be becoming more frequent and more severe, particularly in coastal waters (Brotz *et al.*, 2012; Purcell *et al.*, 2007; Purcell, 2012). However, a detailed meta-analysis has found conflicting evidence regarding the global increase in jellyfish: observing some positive trends in certain areas, some negative trends in others and some areas with no significant change since 1940 (Condon *et al.*, 2013). While this debate is obviously not settled, there is a consensus that regardless of global trends, jellyfish (i) are important components of marine ecosystems, (ii) can cause societally relevant negative impacts in coastal areas, and (iii) are largely understudied, which makes any demographic inference and forecast difficult. Therefore, there is a clear need to focus research efforts towards understanding the mechanisms driving jellyfish blooms, investigating jellyfish ecology and behaviour in their natural environment, developing better ecosystem models including jellyfish and generally making jellyfish research more rigorous. To achieve these goals, the development of proper research tools and techniques for studying jellyfish in their natural environment is a major priority.

JELLYFISH TAGGING—BEYOND TRADITIONAL METHODS

Animal tagging, i.e. the use of animal-attached miniaturized electronic sensors to log and/or relay data about the movements, behaviour and physiology of free-ranging animals and their environment (Rutz and Hays, 2009), has been used for the past five decades to study hundreds of marine, aerial, and terrestrial species. The data collected have been critical in our ability to conserve and manage these species (Cooke, 2008) and increase our understanding of ecosystem function. Over the years, tags have become smaller and lighter, allowing researchers to study increasingly smaller species, including bumblebees and sea scallops (Hagen *et al.*, 2011; Robson and Mansfield, 2014). However, it is only recently that researchers have started considering tagging as a realistic and promising technique to study large jellyfish (i.e. medusal stages of scyphozoan and cubozoan species).

Early studies of jellyfish in their natural environment started in the 1970s and 1980s have sought to address their behaviour and ecology using techniques such as net sampling, scuba gear and submersibles (Hamner *et al.*, 1975; Madin, 1988; Costello *et al.*, 1998), which were later supplemented by echo-sounders, i.e. ship-based acoustic systems (e.g. Lynam *et al.*, 2006; Kaartvedt *et al.*, 2011, 2015), remotely operated vehicles (ROVs, e.g. Robison 1992, 1999; Sørnes *et al.*, 2008) and video profilers (e.g. Graham *et al.*, 2003; Klevjer *et al.*, 2009). These later techniques have been used to measure jellyfish abundance, size and vertical distribution (Brierley *et al.*, 2001, 2005; Lynam *et al.*, 2006; Klevjer *et al.*, 2009) and to study the variation in

behaviour and swimming speeds amongst individuals throughout the water column (Kaartvedt *et al.*, 2007, 2011). For instance, a wide range of vertical migration behaviours in relation to the diel cycle has been unveiled by an acoustic study of the jellyfish *Periphylla periphylla* in Lurefjorden, Norway (Kaartvedt *et al.*, 2011). Studies of this species with ROVs have also revealed different swimming patterns depending on the depth and size of the individuals and time of day (Youngbluth and Båmstedt, 2001; Kaartvedt *et al.*, 2007; Sørnes *et al.*, 2008; Klevjer *et al.*, 2009). A recent study combining both acoustic data and video observations from ROVs has also documented apparent social behaviour in this species (Kaartvedt *et al.*, 2015). The successful use of ROVs and video profilers however depends on light, which restricts observations at depth under natural light regimes (Sørnes *et al.*, 2008) and these data-sets usually are of very short duration. Acoustic studies may be longer term, but they present other challenges linked in particular to the low target strength of most jellyfish species compared with other vertebrate species and/or the surrounding water (Båmstedt *et al.*, 2003; Alvarez-Colombo *et al.*, 2003; Klevjer *et al.*, 2009). They may be difficult to implement in shallow coastal environments and typically require coordinated net tows or physical sampling to verify the acoustic records. Finally, the vast majority of studies using these techniques have taken place at the population level, as following the movements of individual jellyfish is technically difficult (but see Kaartvedt *et al.*, 2015). In comparison, tagging may facilitate the detailed study of individual jellyfish movements and behaviours *in situ* and over protracted periods.

JELLYFISH TAGGING—RESULTS TO DATE

Tagging techniques have so far been used to investigate four main aspects of jellyfish ecology: (i) horizontal and (ii) vertical movements, (iii) behavioural comparisons with other pelagic predators and (iv) behavioural cues that contribute to the formation and dispersal of jellyfish blooms. The following sections highlight how different technologies have been used to address questions relating to the biology of jellyfish. For a detailed review on available tagging technologies, sensors and their uses, we refer the reader to the multiple excellent reviews on this topic (Cooke *et al.*, 2004; Ropert-Coudert and Wilson, 2005, see also Supplementary Table 1).

Acoustic transmitters have been used to investigate the horizontal movements of individual jellyfish and their relationship with time of day and/or state of the tide. The box jellyfish *Chironex fleckeri* was the first species equipped with small acoustic transmitters by Seymour *et al.* (2004) in Australian waters. The data collected revealed that *C. fleckeri* showed a marked diurnal behaviour. During the day, jellyfish moved in straight-line distances of ~200 m h^{-1} and actively hunted, while at night they lay motionless on the sea floor, presumably to conserve energy normally used for locomotion, potentially diverting it towards growth. The habitat, i.e. coastal or estuarine, in which the jellyfish was located, also affected their behaviour (Gordon and Seymour, 2009). In coastal habitats, *C. fleckeri* demonstrated similar rates of travel throughout all tidal states. In contrast, in estuarine habitats, their movements were closely linked with the tide. In particular, estuarine jellyfish travelled at significantly faster rates towards the middle of the tide than at the low and high ebbs. Similar results were subsequently found for two other species of jellyfish: the lion's mane jellyfish *Cyanea capillata* and the fried-egg jellyfish *Phacellophora camtschatica* (Moriarty *et al.*, 2012). Like *C. fleckeri*, both species appeared to change their horizontal swimming speeds with diel period and tidal stage when tracked throughout Hood Canal, Puget Sound, Washington, USA. *C. capillata* swam faster at night than during the day, whereas *P. camtschatica* showed the opposite pattern. Both species had the highest swimming speeds during flood tides and typically swam towards the mouth of Hood Canal, against incoming tides. These results suggest that these species of jellyfish are active swimmers able to maintain their lateral position and not just passive planktonic organisms. An important aspect of such studies is to be able to measure current speed and direction near the tagged jellyfish. Current models have been used in addition to satellite-tracked drogues released near the animals.

Acoustic transmitters as well as time-depth recorders (TDRs) have been used to describe the vertical movements of individual jellyfish, and revealed that jellyfish exhibit more advanced swimming behaviours than previously thought. In all six species that have been studied so far, extensive vertical movements throughout the water column have been recorded (Hays *et al.*, 2008, 2012; Honda *et al.*, 2009; Bastian, 2011; Moriarty *et al.*, 2012; R. Sherlock, this study). Vertical speeds measured in two species (the compass jellyfish, *Chrysaora hysoscella*, and *C. capillata*) varied from 0.29 to 3.98 m min^{-1} (Hays *et al.*, 2008; Bastian, 2011). Over the course of a day, a Pacific sea nettle, *Chrysaora fuscescens*, equipped with a TDR swam at an average depth of ~12 m but made one excursion to 38 m (R. Sherlock, this study, Supplementary Fig. 1). Twelve giant jellyfish, *Nemopilema nomurai*, equipped with pop-up archival transmitting tags and acoustic pingers were tracked to depths down to 176 m (Honda *et al.*, 2009). *N. nomurai* also showed a diel

pattern in their dive behaviour, with deeper dives at night than during the daytime, and remained shallower than 40 m in the relatively high-temperature surface layer. High variations in vertical movements both within and among individuals, and the ability to actively reposition themselves in the water column over small or long time-scales have been described in three other jellyfish species: *C. hysoscella* equipped with miniature TDRs, *C. capillata* and *P. camtschatica* equipped with acoustic transmitters (Hays *et al.*, 2008; Bastian, 2011; Moriarty *et al.*, 2012). In these latter species, individuals were also able to remain at a constant depth for long periods of time (i.e. days) to avoid crossing density gradients within the water column. In particular, they tended to always stay below the pycnocline but made numerous dives into the hypoxic layer (Moriarty *et al.*, 2012).

While the studies noted above clearly show that jellyfish actively undertook both vertical and horizontal movements, tagging has also been used to compare the behaviour of jellyfish to seemingly more active predators such as fish. In a study involving 25 barrel jellyfish, *Rhizostoma octopus*, equipped with TDRs, Hays *et al.* (2012) revealed that these animals were swimming on average 619.2 m d^{-1} throughout the water column and sometimes exhibited complex vertical search patterns, including Levy flight movement patterns, which were previously thought to be exclusive to marine vertebrates. These results suggest that jellyfish may compete with fish for their planktonic prey more efficiently than previously thought, which may have important consequences in terms of ecosystem and fisheries management.

Data collected from tagged jellyfish can also help address how the behaviour of individuals can contribute to the formation and dispersal of blooms. This has been the focus of four recent studies, which have developed numerical models considering jellyfish as virtual, positively buoyant, passive particles drifting with currents (Moon *et al.*, 2010; Berline *et al.*, 2013; Lee *et al.*, 2013; Fossette *et al.*, 2015) but could be improved with vertical movement data from tags. These models can simulate the trajectories of hundreds to thousands of particles in realistic environmental conditions, and their results subsequently can be compared with existing observational data to assess the quality of the model. For instance, Moon *et al.* (2010) developed a particle-tracking model to predict the distribution and movements of *N. nomurai* in the Sea of Japan. Using wind forcing and coastal currents, this particle-tracking simulation was able to predict jellyfish drift with reasonable accuracy. A similar experiment was performed in the Ligurian Sea, where the jellyfish, *Pelagia noctiluca*, detrimentally affects the tourism industry (Berline *et al.*, 2013). The goal of the model was to predict when and where jellyfish blooms would strand onshore and be potentially dangerous for swimmers.

However, most of these numerical models consider jellyfish as passive, positively buoyant drifters and do not take into account recent results showing that jellyfish can be active swimmers. Only one study so far has used empirical data on jellyfish behaviour and movements to inform a particle-tracking model. *In-situ* observations combined with deployment of accelerometers on *Rhizostoma octopus* allowed Fossette *et al.* (2015) to show that these jellyfish could actively swim against the tidal current at a mean speed of 5 cm s^{-1}. Using this information as an input to a particle-tracking model enabled the authors to compare the dispersal of "swimming" *vs.* "non-swimming" particles, which in turn demonstrated how the observed behaviour would lead to significantly higher rates of survival (i.e. reduced the rate of stranding) and increase bloom formation. Simulating this behaviour observed in the wild within a high-resolution, particle-tracking model also contributed to improved predictions of jellyfish blooms' movements in coastal waters.

Use of tri-axial acceleration data-loggers is a promising way to collect unique data on swimming effort (i.e. bell pulses), swimming speed and diving behaviour in free-ranging jellyfish (Fossette *et al.* 2015). Captive experiments on five moon jellyfish *Aurelia* sp. in Woods Hole, MA using a newly developed, Invertebrate-specific TAGging package (i.e. ITAG, a multi-sensor data-logger specially developed for soft-bodied invertebrates) revealed three distinct behaviours: remaining stationary, swimming in a straight line, and turning (Mooney *et al.*, 2015). The acceleration amplitude of ±0.003 g and swimming frequency of 2 Hz during straight swimming was consistent with other untagged, similarly sized *Aurelia* sp. (Mooney *et al.*, 2015).

Undeniably, tagging can uncover new aspects of the ecology and behaviour of jellyfish, which allows us to better understand and more reliably predict the impact of these species on marine ecosystems, fisheries and the tourism industry. A challenging question remains: how does one attach these devices to different species without impacting their swimming ability and behaviour while collecting high quality data?

JELLYFISH TAGGING—BEST PRACTICES

Tag attachment

In theory, there are a number of possibilities for attaching devices to jellyfish depending on the species' morphology. In practice, three attachment techniques have been successfully used to date to tag nine jellyfish

species (eight scyphozoan species and one cubozoan species, Fig. 1) varying in size from 10 cm up to 1.6 m bell diameter (Table I). These three techniques can be classed broadly as the "glue method", the "cable tie method" and the "suction cup method" and are described in detail below. Seymour *et al.* (2004) and R. Sherlock *et al.* (personal communication) both tested a fourth method using implantation of tags into the jellyfish's bell. Seymour *et al.* (2004) used an incision and sutures; however, sutures would not remain in the animal, thus the tag could not be adequately secured. R. Sherlock *et al.* (personal communication) first made an incision that was glued shut with cyanoacrylate glue; however, the hardened glue cut the surrounding mesoglea and the jellyfish shed the plug of mesoglea and glue in <24 h.

Regardless of the attachment method, before tagging, the bell diameter and overall condition of the animal should be noted. Jellyfish showing any external signs of injury or senescence should not be tagged. Also it is important to be extremely careful to avoid damaging the animal, or to trap air under its bell during the tagging procedure. After deployment, the jellyfish should immediately be released and observed to ensure continued swimming as prior to tagging.

Glue method

Tags can be glued on jellyfish with Histoacryl® topical skin adhesive, a non-toxic surgical glue (Figs 1 and 2). Researchers have tried to use other less expensive superglues but the results were poor: tags dropped off more rapidly and some glues turned out to be harmful to jellyfish (J. Seymour, http://www.abc.net.au/local/stories/2006/06/01/1652615.htm, R. Sherlock, personal

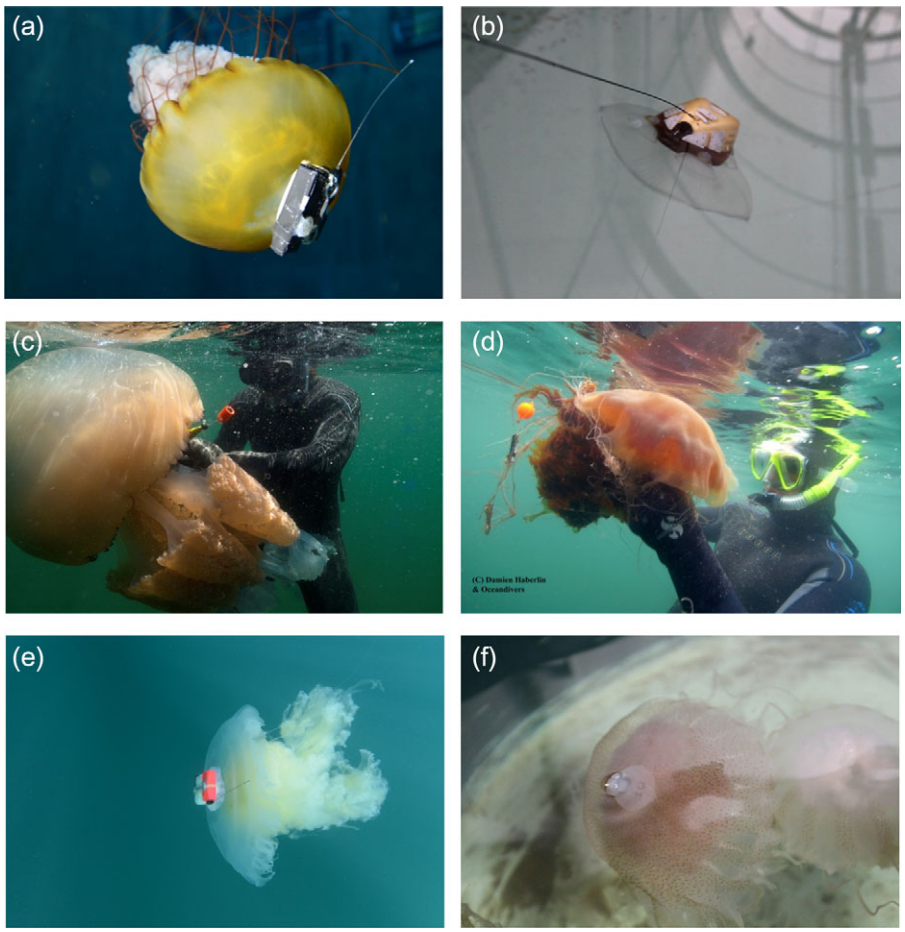

Fig. 1. Jellyfish equipped with data-loggers and/or transmitters. (**a**) Pacific sea nettle jellyfish (*Chrysaora fuscescens*) equipped with an accelerometer, an acoustic transmitter and a VHF radio-transmitter using the "glue" method (photo by S. Haddock). (**b**) Moon jellyfish (*Aurelia sp.*) equipped with the ITAG using the "suction cup" method (Mooney *et al.*, 2015). (**c**) Barrel jellyfish (*Rhizostoma octopus*) equipped with a tri-axial accelerometer using the "cable tie" method (Fossette *et al.*, 2015). Note the float used to make the tagging package neutrally buoyant. (**d**) Lion's mane jellyfish (*Cyanea capillata*) equipped with an acoustic transmitter using the "cable tie" method (Bastian, 2011, photo by D. Haberlin). (**e**) Fried-egg jellyfish (*Phacellophora camtschatica*) equipped with an accelerometer and acoustic and VHF transmitters (photo by S. Haddock). (**f**) Atlantic sea nettle (*Chrysaora quinquecirrha*) equipped with a suction cup in preparation for deployment of the ITAG (photo by K. Katija).

Table I: Summary of the type and characteristics of tags deployed on nine species of jellyfish and the type of attachment techniques used

Species	Tag type, Manufacturer	Tag dimensions	Tag weight	Attachment technique	Jellyfish size	Reference
Chironex fleckeri	Acoustic transmitter	*L*: 4 cm *D*: 1.2 cm	–	Glue	–	Seymour *et al.* (2004)
Chironex fleckeri	Coded acoustic transmitter Sonotronics©		<0.2% of the medusa's wet weigh	Glue	Interpedalia distance >8 cm	Gordon and Seymour (2009)
	Pico	*L*: 1.9 cm *D*: 0.7 cm	1.7 g in air 1 g in water			
	IBT 96-2	*L*: 2.6 cm *D*: 0.9 cm	2.5 g in air			
	IBDT 97-2	*L*: 4.9 cm *D*: 0.9 cm	3.0 g in air			
Chrysaora hysoscella	Time-Depth Recorder G5 CEFAS Technologies©	*L*: 3.1 cm *D*: 0.8 cm	2.7 g in air 1.3 g in seawater	Cable tie + tether	Bell diameter ~19–35 cm	Hays *et al.* (2008)
Nemopilema nomurai	Pop-up satellite archival tag PTT-100 Microwave Telemetry©	*L*: 16 cm *D*: 4 cm 16-cm antenna	65 g in air	Cable tie	Bell diameter ~0.8–1.6 m	Honda *et al.* (2009)
	Pop-up satellite archival tag PTMk10-PAT Wildlife Computers©	*L*: 16 cm *D*: 4 cm 16-cm antenna	65 g in air			
	Acoustic transmitter V13P VEMCO©	*L*: 4 cm *D*: 1.3 cm 16-cm antenna	6 g in air			
	Acoustic transmitter V16P VEMCO©	*L*: 6 cm *D*: 1.6 cm	10 g in air			
Cyanea capillata	Acoustic transmitter V9 VEMCO©	*L*: 4.5 cm *D*: 0.9 cm	3.5 g in seawater	Cable tie + tether	Bell diameter: ~25–48 cm	Bastian (2011)
Cyanea capillata	Acoustic transmitter with pressure sensors V9P-1L Vemco©	*L*: 4.2 cm *D*: 0.9 cm	2.7 g in seawater	Cable tie	Bell diameter ~20–35 cm	Moriarty *et al.* (2012)
Cyanea capillata	ITAG Woods Hole Oceanographic Institute	*L*: 10.8 cm *W*: 6.4 cm *H*: 2.9 cm	102.5 g in air 0 g in seawater	Suction cup	Bell diameter ~10–15 cm	Mooney *et al.* (2015)
Phacellophora camtschatica	Acoustic transmitter with pressure sensors V9P-1L Vemco©	*L*: 4.2 cm *D*: 0.9 cm	2.7 g in seawater	Cable tie	Bell diameter ~25–40 cm	Moriarty *et al.* (2012)
Phacellophora camtschatica	Tri-axial acceleration data-logger CATS©	*L*: 4.2 cm *W*: 2.5 cm *H*: 1.2 cm	14.2 g in air <1 g in seawater with float	Glue	Bell diameter ~17–27 cm	S. Fossette, this study
	Coded acoustic transmitter V9-6L VEMCO©	*L*: 2.1 cm *D*: 0.9 cm	2.9 g in air 1.6 g in seawater			
	VHF radio-transmitter V1G 102A SIRTRACK©	*L*: 1.5 cm *W*: 0.9 cm H: 0.6 cm	0.95 g in air			
Rhizostoma octopus	Time-Depth Recorder G5 CEFAS Technologies©	*L*: 3.1 cm *D*: 0.8 cm	2.7 g in air 1.3 g in seawater	Cable tie + tether	Bell diameter ~40–50 cm Wet weight 5–10 kg	Hays *et al.* (2012)
Rhizostoma octopus	Tri-axial acceleration data-logger G6a+ CEFAS Technologies©	*L*: 4.0 cm *W*: 2.8 cm *H*: 1.6 cm	18 g in air 4.3 g in seawater	Cable tie + tether	Bell diameter ~30–40 cm Wet weight 5–10 kg	Fossette *et al.* (2015)
Aurelia aurita	ITAG Woods Hole Oceanographic Institute	*L*: 10.8 cm *W*: 6.4 cm *H*: 2.9 cm	102.5 g in air 0 g in seawater	Suction cup	Bell diameter ~17–22 cm	Mooney *et al.* (2015)

Chrysaora quinquecirrha	ITAG Woods Hole Oceanographic Institute	*L*: 10.8 cm *W*: 6.4 cm *H*: 2.9 cm	102.5 g in air 0 g in seawater	Suction cup	Bell diameter ~20–25 cm	Mooney *et al.* (2015)
Chrysaora fuscescens	Tri-axial acceleration data-logger G6a+ CEFAS Technologies©	*L*: 4.0 cm *W*: 2.8 cm *H*: 1.6 cm	18 g in air 4.3 g in seawater	Glue	Bell diameter ~20–25 cm	S. Fossette, this study
	Tri-axial acceleration data-logger CATS©	*L*: 4.2 cm *W*: 2.5 cm *H*: 1.2 cm	14.2 g in air <1 g in seawater with float			
	Coded acoustic transmitter V9-6L VEMCO©	*L*: 2.1 cm *D*: 0.9 cm	2.9 g in air 1.6 g in seawater			
	VHF radio-transmitter V1G 102 A SIRTRACK©	*L*: 1.5 cm *W*: 0.9 cm *H*: 0.6 cm	0.95 g in air			
Chrysaora fuscescens	Coded acoustic transmitter VEMCO V8SC-6L	*L*: 2.0 cm *D*: 0.9 cm	4.0 g in air 2.0 g in seawater	Cable tie	Bell diameter ~20–25 cm	R. Sherlock, this study
	Time-Depth Recorder LOTEK LTD1110–50 m 32 K	*L*: 2.7 cm *W*: 1.6 cm *H*: 0.7 cm	4.6 g in air 2.1 g in seawater			

L, tag length; *D*, tag diameter; *W*, tag width; *H*, tag height. Details on the attachment techniques (i.e. Glue, Cable tie, Cable tie + tether, Suction cup) may be found in the main text.

communication). Histoacryl® has been successfully used in three species of jellyfish: *Chironex fleckeri* (Seymour *et al.*, 2004; Gordon and Seymour, 2009), *Chrysaora fuscescens* (Figs 1 and 2) and *Phacellophora camtschatica* (Fig. 1). The entire process of adhesion usually takes <5 min. First, the jellyfish is caught by hand or with a scoop net and brought close to the surface (Fig. 2). This is a delicate phase and great care must be taken to avoid damaging the jellyfish or trapping air underneath the bell, which would affect the jellyfish's ability to resume swimming below the surface. The area of the jellyfish where the tag will be attached is gently patted dry (with a simple paper towel in the case of *C. fuscescens* and *P. camtschatica*). The glue is then applied to the bottom of the tag, which is immediately placed on the aboral side of the jellyfish bell before it can be released. In *C. fuscescens* and *P. camtschatica*, the tag was gently pressed down onto the jellyfish bell for 1 min and allowed to dry for one additional minute (Fig. 2). In one trial on *C. fuscescens*, the tag was first glued to a foam mat (Poron Microcellular Urethane sheet), which was then glued to the jellyfish; however, this technique was not successful and the tag only remained on the jellyfish for a few hours. In captive trials, tags deployed on *C. fuscescens* ($n = 4$) remained firmly attached for an average of 17.3 ± 8.3 days and a maximum of 27 days (Fig. 2). On free-ranging *P. camtschatica* ($n = 4$), the tags remained attached for a shorter time, i.e. between 5 and 75 min. Tagged, free-ranging *C. fleckeri* were actively tracked for 10–38 h (Gordon and Seymour, 2009) but the tags may have remained attached for longer. Despite Histoacryl® theoretically polymerizing when exposed to water or water containing substances, our captive trials suggested that any water between the bell and the tag during deployment dramatically decreased deployment time to a few hours. In *C. fuscescens* and *P. camtschatica*, the tag was positioned near the centre of the bell (Figs 1 and 2). In *C. fleckeri*, the tag was positioned halfway between the top of the bell and the velarium, along the fold line that forms between the rounded shoulder that gives rise to the pedalia and the more flattened interpedalial face upon which the rhopalia are located (Seymour *et al.*, 2004; Gordon and Seymour, 2009).

Physical and behavioural impacts of this attachment method on the jellyfish could be assessed on *C. fuscescens* in captivity. The only apparent physical impact of the glued tag on the jellyfish was discoloration of the bell (loss of pigment, Fig. 2). Jellyfish that kept their tag on for a week or less showed a slight discoloration of the bell whereas the discoloration was more pronounced for those which kept their tags on for several weeks with, in one case, parts of the bell peeling off the jellyfish. In all cases, the jellyfish were actively swimming and feeding

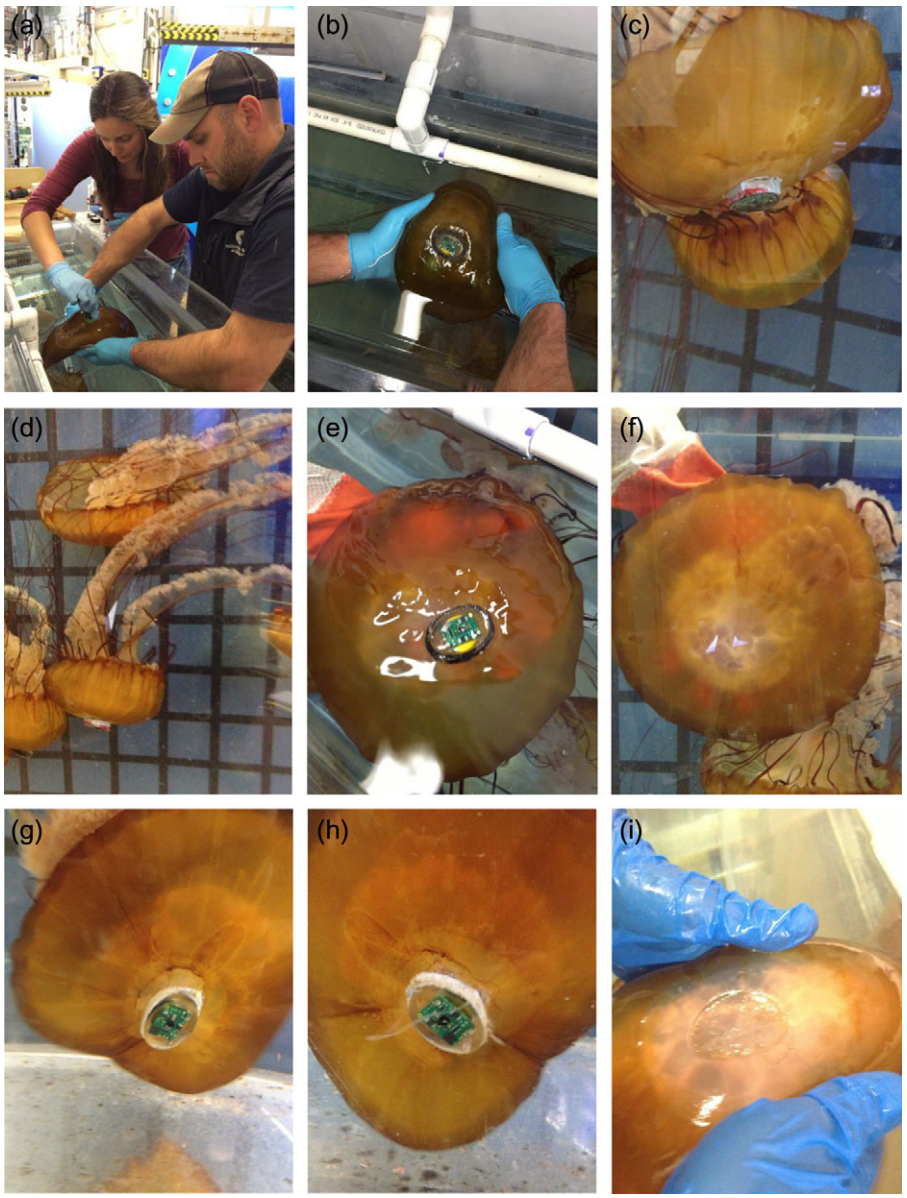

Fig. 2. Deployment of a tri-axial accelerometer on two Pacific sea nettle jellyfish *Chrysaora fuscescens* using the "glue" method. (**a**–**f**) Photos of a first individual on day 0 (a, b), day 6 (c), day 13 (d), day 22 (e), day 22 after tag was retrieved (f). A slight discoloration of the bell at and around the logger's previous location is apparent. (**g**–**i**) Photos of a second individual equipped on day 23 (g), day 27 (h), day 27 after logger fell (i). In this case, a discoloration and superficial peeling of the jellyfish bell were apparent.

both during and after deployment. All jellyfish survived, and healing processes (i.e. pigmentation began to return) at the tag attachment site were observed in 2–3 weeks for jellyfish that experienced short deployments (<7 days).

Cable tie method

Tags can be attached to certain jellyfish using plastic or nylon cable ties. This method has been successfully used in six species (Table I). The entire process usually takes <5 min. This technique usually requires snorkelers or divers to locate and equip jellyfish *in situ*. The logger can either (i) be directly attached to the cable tie with a loop of wire or (ii) be inserted first in a sheath of latex tubing or heat-shrink tubing and the cable tie is then inserted in between the tubing and the tag (Fig. 3, Supplementary Fig. 1). Using tubing is recommended to deploy accelerometers in this manner (i.e. motion-sensitive tags) as this will limit extrinsic movements of

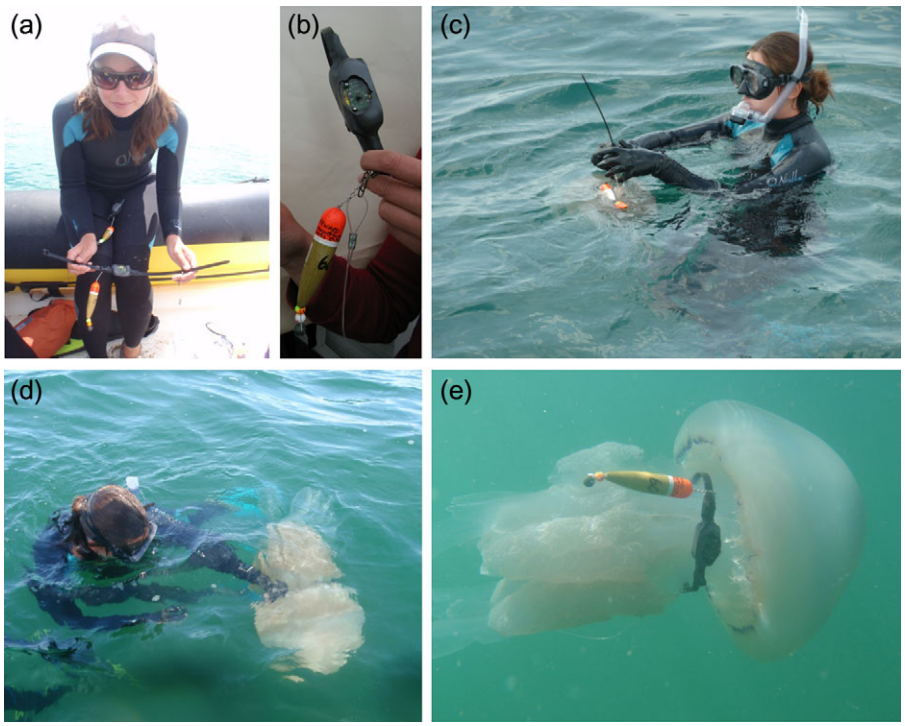

Fig. 3. Deployment of an accelerometer on barrel jellyfish using the "cable tie" method. (**A**) The logger is inserted first in heat-shrink tubing, and the cable tie is then inserted in between the tubing and the tag. A small float is added to the tagging package to ensure neutral buoyancy once deployed on the jellyfish. A monofilament tether is visible on the photo. (**B**) This tether is attached to the cable tie and a small fishing float is deployed at the other end of the tether in order to be able to visually follow the jellyfish during the deployment. At the end of the deployment, the jellyfish and the logger are retrieved by slowly pulling onto the tether and/or snorkelling to the jellyfish. (**C**) The nylon cable tie is tightly attached around the manubrium (which connects the swimming bell to the oral arms) without touching the jellyfish. (**D**) After deployment, the jellyfish should immediately be released and observed to ensure it continues to swim as prior to tagging. (**E**) The jellyfish appears to not be disturbed by the presence of the cable tie and continued swimming normally.

the logger that results in increased background noise in the data. In *C. hysoscella* and *R. octopus*, the nylon cable tie can be tightly attached around the manubrium connecting the bell to the oral arms, ideally without touching the jellyfish (Fig. 3, Supplementary video 2). In *C. capillata* and *P. camtschatica*, the jellyfish can gently be turned on its side or upside down and the cable tie is threaded around the coronal muscle in between two radial muscles, and loosely fastened (Moriarty *et al.*, 2012). In *C. fuscescens*, the cable tie can be attached to the oral pillars (Supplementary Fig. 1). One advantage of using cable ties is that the jellyfish do not have to be removed from the water. For jellyfish potentially harmful to humans, direct contact with the jellyfish should be avoided and tools to assist in the handling procedure can be used. For instance, Honda *et al.* (2009) equipped *N. nomurai* underwater using a pickup tool consisting of a 60-cm-long polyvinyl chloride pipe with a pre-set cable tie at the tip of the tool. The cable tie was attached to the jellyfish by first allowing the bell of the jellyfish to pass through the noose of the tie and then fastening the cable tie around the manubrium, under the bell.

The deployment duration with this technique varied between 50 and 240 min for *C. hysoscella*, 4–24 h for *C. fuscescens*, 2–21 days for *N. nomurai*, 1–15 days for *C. capillata*, 1–14 days for *P. camtschatica* and 2–28.5 days for *R. octopus* (see supplementary Table 1). These durations, however, stem from free-ranging individuals and it is difficult to ascertain whether attachments failed or whether the recording stopped for other reasons (e.g. death of the jellyfish, battery/tag failure) as jellyfish were usually not seen again at the end of the tracking period.

Based on the reports of divers or snorkelers who observed the jellyfish immediately after attaching the tags, jellyfish showed no signs of disturbance due to the presence of the cable tie. No major short-term behavioural and/or physical impacts, other than an initial rapid dive away from the person deploying the tag, were observed. In free-ranging *C. hysoscella*, the descent speeds during this initial phase ranged from 0.39 to 2.32 m min^{-1} (Hays *et al.*, 2008). It is less clear whether, in the long term (e.g. several weeks), the bodies of the jellyfish could become damaged from rubbing by the

cable ties or from excessive water flow resistance impeding the activity of the jellyfish.

The suction cup method

A surprising finding is that tag packages can be affixed to jellyfish using suction cups, which is a non-invasive mechanism commonly used for cetacean tagging packages (e.g. Johnson *et al.*, 2009). Initial investigations of suction cup attachment methods were conducted on captive *C. capillata* and the Atlantic sea nettle jellyfish *Chrysaora quinquecirrha* in Woods Hole, MA (n = 10; Mooney *et al.*, 2015). Thin-walled silicone suction cups were attached directly to the apex of the jellyfish bell and remained attached for durations up to 4 h. After suction cups detached from the bell, there was no observable tissue damage from the attachment technique. Subsequent deployments using suction cups with the ITAG were also conducted on captive *Aurelia* (n = 5, mean bell diameter of 15 cm; Mooney *et al.*, 2015, Fig. 1). Using veterinary-grade cyanoacrylate (3 M Vetbond™, which cures in water) with suction cups allowed tags to remain attached without any slippage on the dorsal surface of jellyfish bells for over 24 h, and suction cups eventually sloughed off ~1 week later (Mooney *et al.*, 2015). The application of suction cups with glue takes <2 min, and can be conducted in water with the apex of the bell lifted above the water's surface, thereby minimizing tissue damage to the jellyfish. The initial attachment pressure provided by the suction cups provides sufficient time and additional surface area for the glue to cure on the jellyfish's aboral (or exumbrella) surface.

Tag positioning

The position of a tag on a jellyfish is an aspect that needs to be carefully considered as it may impact both the jellyfish's behaviour and the quality of the data collected. Sometimes the position of the tag is simply dictated by the attachment method used. For instance, the cable tie method usually requires the tag to be located underneath the jellyfish bell. In contrast, the glue method and the suction cup methods give in theory more flexibility regarding the positioning of the tag. It is however important to note that a tag centrally placed on the exumbrella (i.e. apex of the bell) reduces flow separation along the surface of the bell (Mooney *et al.*, 2015). In addition, in this configuration bell pulses can be recorded with minimal background noise by an accelerometer (Fig. 4). In comparison, positioning within the subumbrellar cavity (used during the cable tie method) may result in measurement noise due to hydrodynamic interactions with the propulsive wake of the jellyfish. Finally, in the case of accelerometers, this configuration might also help analyse posture data as the logger is aligned with the longitudinal body axis of the jellyfish (e.g. Sato *et al.*, 2003; Gleiss *et al.*, 2011a). In any case, the position and orientation of the logger on the animal should always be precisely documented.

Experiment to quantify tagging's influence on jellyfish behaviour

Tagging may have a short-term influence on behaviour (see Supplementary video 1, Hays *et al.*, 2008). Usually, an initial rapid dive away from the person deploying the tag is observed in all tagged jellyfish regardless of the deployment method used (i.e. glue or cable tie). This pattern of fast descending through the water column is probably a reaction to handling. It is important to quantify the magnitude and the duration of this behavioural reaction in order to know when the animal starts behaving "naturally" and therefore when to start the data analysis. As there is limited data available in the literature documenting this short-term reaction, we performed an experiment to compare the behaviour of two captive *C. fuscescens* equipped with accelerometers to an animal that was neither tagged nor handled (control jellyfish). All three jellyfish were kept in the same tank at a temperature of 14°C. A three-axis accelerometer (G6A+, Cefas Technologies, *L*: 4.0 cm, *W*: 2.8 cm, *H*: 1.6 cm) was glued on the apex of each jellyfish bell following the method described above. Devices were set to record all three acceleration channels at a frequency of 15 Hz (12 bit resolution, range ±8 g, resolution 72 mg). Acceleration sensors were calibrated to g (9.8 m s^{-2}) by rotating devices through known angles in all three spatial planes. The analysis of accelerometry data is described in the legend of Fig. 4. A video camera was simultaneously used to record the jellyfish behaviour and interpret accelerometry data. The jellyfish were equipped and released 5 min apart. Using video observations, we counted the number of pulses in consecutive 20 s intervals for the first 5 min following deployment. The same procedure was repeated 15 min after tag deployment in order to compare behaviour imminently following handling to those later on. Accelerometer data combined with video observations revealed a "recovery" period for tagged jellyfish (Fig. 4). Just after deployment, equipped jellyfish were less active than before deployment when compared with a control animal. Their tentacles and oral arms were retracted, they dove towards the bottom of the tank, their bell pulses were irregular and their pulse rate was on average 0.38 ± 0.02 Hz (n = 2 jellyfish). After a minimum of 5 min, the jellyfish

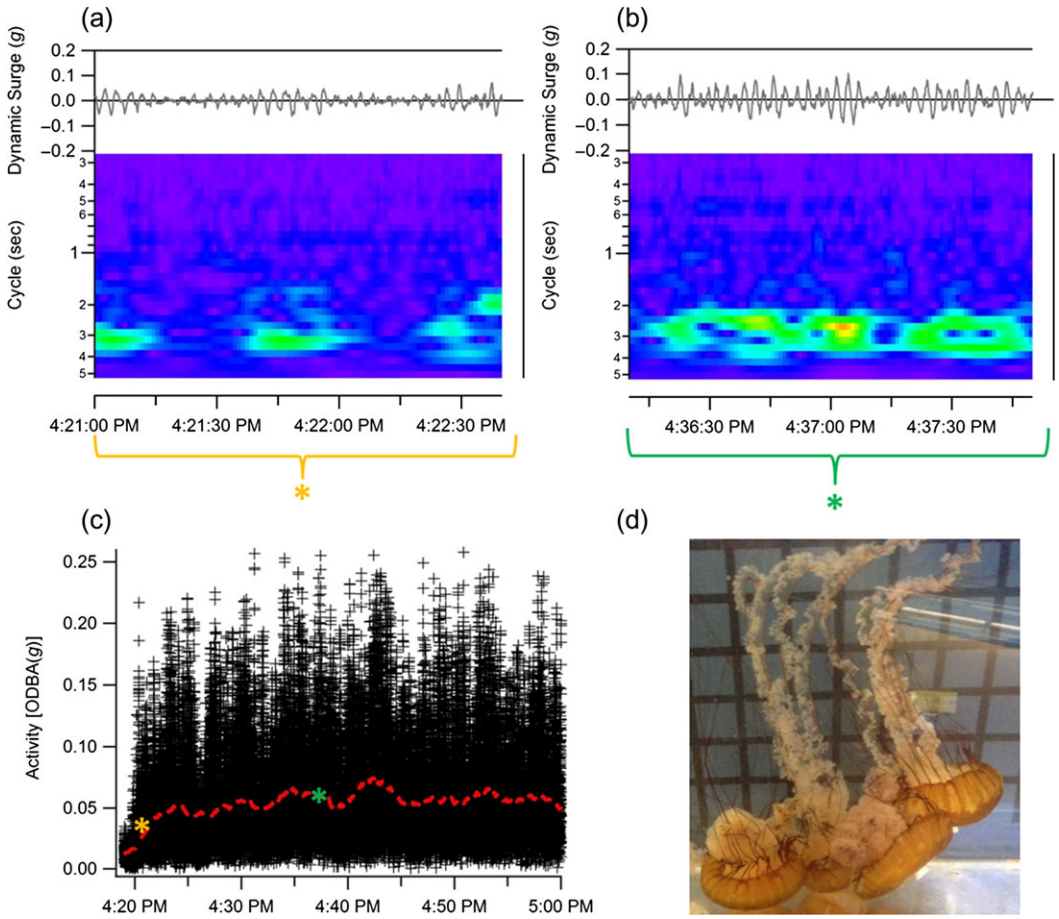

Fig. 4. Jellyfish behaviour and swimming activity following the deployment of a three-axis accelerometer on the apex of the jellyfish bell. The jellyfish was released at 16h21 (4:21 pm). (**A**) Surging acceleration (i.e. dynamic surge) recorded by the logger following handling of the jellyfish shows small and discontinuous bell pulses, as indicated by the irregular peaks in acceleration (top) and by the heat map (bottom) showing the continuous wavelet transform [green (light grey in the black and white version) indicates bell pulses]. (**B**) Surging acceleration (i.e. dynamic surge) recorded on the same individual 15 min after handling, displays more regular and vigorous bell pulsing as shown by the continuous peaks in acceleration (top) and by the heat map (bottom) showing the continuous wavelet transform [green (light grey in the black and white version) indicates bell pulses]. (**C**) Following handling, activity [ascertained through dynamic body acceleration (ODBA), a measure of activity derived from accelerometers, Gleiss *et al.*, 2011b] steadily increases until it reaches routine values after ~30 min post-handling. The red (grey in the black and white version) line represents a 5-min running mean. The yellow asterisk [(1) in the black and white version] shows the mean activity during the period displayed in (A). The green asterisk [(2) in the black and white version] shows the mean activity during the period displayed in (B). (**D**) The common response of jellyfish to handling and tagging coincides with the individual contracting its tentacles and oral arms into the bell and a disruption in bell pulsing. Here, two jellyfish have contracted their tentacles and oral arms following handling, whereas the other two individuals display regular swimming patterns with extended tentacles and oral arms.

behaviour started returning to normal, i.e. the bell pulse frequency increased (0.45 ± 0.05 Hz, $n = 2$) and the body posture of the two tagged jellyfish was comparable to the body posture (i.e. relaxed tentacles and oral arms) of the control jellyfish (Fig. 4). After 15 min, the bell pulses were more vigorous and regular and the activity level stabilized (see Fig. 4 for details).

Logger retrieval techniques

A challenge when deploying animal-borne data loggers is being able to retrieve them and access the data they recorded. Four logger retrieval techniques have been successfully described for jellyfish. The first consists of attaching a monofilament tether to the cable tie and deploying a small fishing float at the other end of the tether in order to be able to visually follow the jellyfish during the deployment. At the end of the deployment, the jellyfish and the logger are retrieved by slowly pulling onto the tether and/or snorkelling to the jellyfish. The tether length should exceed the water depth by at least 10 m in order to limit the risk of impeding the jellyfish's movements but may be problematic when in complex habitat (e.g. kelp forests). The second technique involves

deploying an acoustic transmitter in combination with a logger; the jellyfish can then be actively tracked and the logger manually retrieved by a diver/snorkeler at the end of the deployment. These two techniques require short-term deployments in relatively shallow waters.

For long-term deployments, retrieval options are currently limited. Hays *et al.*, (2012) deployed loggers on *R. octopus* using the cable tie technique and relied on surface currents and beach walkers to retrieve loggers washed ashore after they came off the jellyfish several weeks/months later. In this particular case, the logger would remain on the jellyfish until it senesced and started breaking apart, at which point the slightly positively buoyant logger could come off and float to the surface and finally strand ashore. However, this technique is completely dependent on local conditions and may not be applicable to many field sites. A final technique used in other marine species (e.g. Gleiss *et al.*, 2009) is a release mechanism combined with a VHF radio-transmitter (e.g. Mooney *et al.*, 2015; S. Fossette, this study). After a pre-set amount of time, a galvanic release mechanism allows the logger to detach and float to the surface where the radio-transmitter helps to locate and retrieve the logger. The main drawback of this technique is the size of the package to deploy on the jellyfish. This technique was successfully tested on free-ranging *P. camtschatica* (Fig. 1). Our tagging package was designed to be neutrally buoyant when deployed on the jellyfish. After a pre-set amount of time, the release mechanism allowed the positively buoyant logger to detach from the negatively buoyant baseplate glued on the jellyfish and float to the surface.

Separately, pop-up satellite tags are also programmed to detach at a set time and float to the surface, but then directly transmit their data through the ARGOS satellite system. There is therefore no need to retrieve the tag to access the data. However, because of their size and weight, the use of such tags has so far been limited to the "giant" jellyfish *Nemopilema nomurai* (Honda *et al.*, 2009). In addition, due to the limited bandwidth of ARGOS, the transmission and retrieval of high-resolution behavioural data (e.g. accelerometry data) is currently limited with such tags.

Size and buoyancy considerations

Size and buoyancy of tagging packages

Two important aspects that need to be considered when deploying a tag on a jellyfish are (i) the dimensions (shape/size), and (ii) the buoyancy of the tag relative to the jellyfish. The size, weight and shape of tags have been shown to impact the hydrodynamics and behaviour of marine animals (Ropert-Coudert *et al.*, 2000; Wilson and McMahon, 2006; Jones *et al.*, 2011, 2013) and it is now common practice to mitigate such negative effects. Most avian tagging studies follow the 5% rule, where tags mass must be within 5% of the bird's body mass (Barron *et al.*, 2010). However, this rule is less useful for marine organisms where buoyancy of the tag and increase in drag due to tag's shape and position on the animal are more important. Specific recommendations exist for marine birds and marine turtles (Jones *et al.*, 2011, 2013; Vandenabeele *et al.*, 2011, 2012). Here, we have tried to summarize information available for jellyfish.

Tagged scyphozoan jellyfish had a bell diameter varying from 10 cm (*C. capillata*) up to 1.6 m (*N. nomurai*) whereas *C. fleckeri* had a minimum interpedalia distance of 8 cm (Table I). The weights of the jellyfish were only estimated in three studies. The tags used were of different shapes. Most of them were cylinders varying in length from 1.9 to 16 cm and in diameter from 0.7 to 4 cm. Others were box-shaped varying in length from 2.7 to 10.8 cm, width from 1.6 to 6.4 cm and height from 0.7 to 2.9 cm. A tag's weight in air varied from 0.95 to 102.5 g; a tag's weight in water was not always reported (Table I).

In eight out of the nine published studies on jellyfish tracking, authors have mentioned the impact of tags on jellyfish buoyancy and how these were minimized. Moriarty *et al.* (2012) simply observed that in pilot trials conducted in large tanks and in shallow, nearshore waters, *C. capillata* and *P. camtschatica* with bell diameter ≥20 and ≥25 cm, respectively, were able to swim easily and maintain buoyancy when outfitted with tags attached with cable ties. In *C. fleckeri*, larger jellyfish with an interpedalia distance of 8 cm minimum were used in order to reduce potential confounding effects due to tag weight (Gordon and Seymour, 2009). In addition, the authors indicated that tag's weight in air was <0.2% of the medusa's estimated wet weight. In both studies, however, the buoyancy of the tags (i.e. tag's submerged weight) did not seem to have been adjusted nor considered (Gordon and Seymour, 2009; Moriarty *et al.*, 2012). In other studies on *N. nomurai*, *R. octopus*, *C. hysoscella* and *C. capillata*, small floats were added to the tagging package to achieve near-neutral buoyancy while attached to the jellyfish and slightly positive buoyancy when released from the jellyfish (Hays *et al.*, 2008, 2012; Honda *et al.*, 2009; Bastian, 2011; Fossette *et al.*, 2015). In captive *Aurelia*, the tagging package (logger + suction cup + release mechanism) was designed to be close to neutrally buoyant while deployed on the jellyfish; since the logger is positively buoyant, once detached the logger floats to the surface (Mooney *et al.*, 2015). In captive *C. fuscescens*, the buoyancy of the tagging package was

always adjusted with small floats to ensure the tag's weight in seawater was <0.1% of the jellyfish wet weight in air according to our experimental results (see below). In free-ranging *C. fuscescens*, the buoyancy of the tag was adjusted to near-neutral with hard-coated, incompressible styrofoam balls (Supplementary Fig. 1).

Experiment to estimate the maximum submerged weight of a logger

In theory, the deployed logger should be as close to neutrally buoyant as possible in order to limit any impact on jellyfish swimming ability and activity. In practice, however, this is a difficult undertaking since "neutral buoyancy" represents either a largely unachievable state or simply an arbitrarily set condition that may change with depth, salinity and temperature. We performed a simple experiment to obtain a first estimate of the maximum submerged weight of a logger that can be deployed on a jellyfish. We constructed dummy tags of different densities (i.e. of different buoyancies) and deployed them on 13 captive *C. fuscescens* (bell diameter between 20 and 25 cm and 1.1–1.8 kg wet weight). The jellyfish were kept in a tank at a temperature of 14°C. The loggers were moulded from an existing tag design (G6A+, Cefas Technologies, *L*: 4.0 cm, *W*: 2.8 cm, *H*: 1.6 cm). We cast 13 different dummies from epoxy resin, with Q-cell hollow spheres and lead weights to achieve a range of negative buoyancies between 0.5 and 6.4 g in seawater. Each dummy was randomly assigned to one jellyfish. The loggers were glued to the bell of the jellyfish, as previously described, and the animal's behaviour (i.e. actively swimming, passively sinking, position in the tank, pulsing) was recorded for the hour following release. We found dramatically different responses to the attachment of tags with a clear dichotomy of animals either resuming swimming after initially diving to the bottom of the tank or animals remaining near the bottom of the tank, despite vigorous bell pulsing. This experiment revealed that a tag's weight in seawater should be <0.1% of the jellyfish's wet weight in air to avoid impacting the jellyfish's swimming ability (Fig. 5). It is important to note that there may be other less obvious impacts, such as increasing drag, which may also hamper both swimming and feeding performance of the animals. Therefore, we suggest 0.1% of the jellyfish's wet weight in air to be considered a maximum for the in-water weight of tags. We also encourage replication of this experiment on other jellyfish species to derive a common set of criteria.

FUTURE DIRECTIONS AND CONCLUSION

Jellyfish tagging is still in its infancy, and our knowledge of free-ranging jellyfish's movements, behaviours and

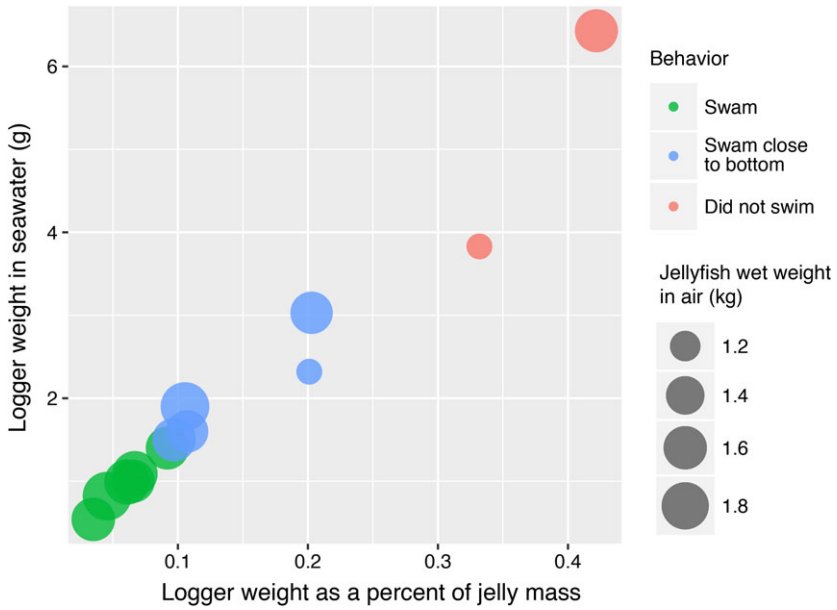

Fig. 5. Behaviour observed in 13 captive *C. fuscescens* equipped with dummy tags of different densities (i.e. of different buoyancies) and associated submerged weights. The loggers were glued to the apex of jellyfish bell and the animal's behaviour was recorded for the hour following release. The jellyfish were either swimming in the tank, swimming close to the bottom or not swimming. The behaviour of the animals changed (from swimming in the tank to swimming close to the bottom) when equipped with a logger with a weight in seawater >0.1% of the jellyfish wet weight in air.

physiology remains limited. Only 9 of ~220 species of scyphozoan and cubozoan jellyfish have been tagged so far. With the on-going miniaturization of data-loggers, we encourage the jellyfish community to consider using these new tools more frequently as an increasing number of jellyfish species will become viable candidates for tag deployment in the coming years. In addition, the development of specialized tags such as the ITAG (Mooney *et al.*, 2015) will allow for the routine collection of fine-scale and high-resolution behavioural and physiological data, and will expand the range of hypotheses to be tested under natural conditions.

In particular, tagging of free-ranging jellyfish now provides access to *in situ* measurements of an individual's behavioural and physiological responses to its environment (e.g. Moriarty *et al.*, 2012; Fossette *et al.*, 2015). Much work is focused on disentangling the environmental drivers that result in a perceived switch from fish- to jellyfish-dominated ecosystems (e.g. Brodeur *et al.*, 2002; Daskalov *et al.*, 2007). An important component of this effort seeks to understand the responses of individual organisms to environmental heterogeneity. Tagging studies on fish have long been used to identify physical drivers of abundance, movements and distribution (e.g. Simpfendorfer *et al.*, 2011; Hazen *et al.*, 2013), and similar work should focus on jellyfish. Future projects may also aim at quantifying the fine-scale movements and behaviour of predatory jellyfish foraging in a prey field or conversely, the escape behaviour of jellyfish when predators are present. Such data on predator–prey relationships may be important when refining ecosystem models to include jellyfish.

Tagging could also be combined with other techniques such as echo-sounders and/or ROVs to collect data on jellyfish populations at different spatio-temporal scales and resolutions. An interesting example may be the case of *Periphylla periphylla*, engaging in apparent social behaviour in Lurefjorden, Norway (Kaartvedt *et al.*, 2015). As these jellyfish may reach a body size of up to 30 cm, equipping a cohort with accelerometers could reveal for instance, how an individual's swimming speed, motion and direction relate before, during and after the "social" interactions with other individuals, and whether environmental factors such as temperature and/or light trigger these interactions.

Finally, particle-tracking models are increasingly being used to forecast the timing or the magnitude of harmful jellyfish blooms near major tourist areas, aquaculture facilities or power plants (Moon *et al.*, 2010; Berline *et al.*, 2013; Lee *et al.*, 2013; Fossette *et al.*, 2015). Including empirically derived behaviour of jellyfish in particle-tracking models has been shown to significantly modify predicted patterns of distribution and abundance (Fossette *et al.*, 2015). Collecting behavioural data on potentially harmful jellyfish species may therefore help achieve more realistic predictions of bloom formation and jellyfish dispersal. Tagging may provide such behavioural data and could be combined, for instance, with aerial drones or AUVs, which may help locate blooms.

The increasing miniaturization of tagging technologies will allow for tagging of increasingly small individuals and subsequently opening the doors to investigate more and more genera. One solution to reduce the size of tagging packages is to affix acoustic transmitters to the organism, which is then tracked by an autonomous underwater vehicle (AUV) equipped with environmental sensors (Clark *et al.*, 2013; Skomal *et al.*, 2015). Deploying an AUV with high-definition video capabilities will enable investigators to evaluate organismal behaviour. These deployments have already been successful with sharks (Clark *et al.*, 2013; Skomal *et al.*, 2015), are currently underway for turtles and could also be achieved with jellyfish. As we continue to move to fully autonomous systems that can track individuals and aggregate jellyfish using less-invasive methods (e.g. stereo imaging or high-resolution broadband acoustics) on board AUVs, tagging efforts will have provided baseline information on jellyfish swimming behaviour to develop and improve these autonomous tracking algorithms. Deployments like these will ultimately allow us to evaluate jellyfish energetics and mobility patterns in a dynamic fluid environment, evaluate whether individual or aggregate organismal behaviour is linked to varying prey fields, and whether "jellyfish oceanographers" can provide information on a changing ocean at finer spatial and temporal resolutions than can currently be achieved with existing technology.

While jellyfish tagging may at first seem technically challenging, and to some unfeasible, we hope the information and data presented in this review have demonstrated that it is a powerful and promising tool that will undoubtedly allow new hypotheses on jellyfish ecology and behaviour to be tested in the field. When important aspects of this method, such as tag buoyancy and attachment techniques, are carefully considered and designed, tagging success is high and collected data unique. Tagging should be considered as a new research tool in the jellyfish scientists' portfolio that will complement other, more established techniques, and help us to better understand this little studied component of marine ecosystems.

SUPPLEMENTARY DATA

Supplementary data can be found online at http://plankt.oxfordjournals.org

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