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Role of winds and tides in timing of beach strandings, occurrence, and significance of swarms of the jellyfish *Crambione mastigophora* Mass 1903 (Scyphozoa: Rhizostomeae: Catostylidae) in north-western Australia

John K. Keesing · Lisa-Ann Gershwin · Tim Trew ·
Joanna Strzelecki · Douglas Bearham · Dongyan Liu ·
Yueqi Wang · Wolfgang Zeidler · Kimberley Onton · Dirk Slawinski

Abstract Very large swarms of the red jellyfish *Crambione mastigophora* in north-western Australia disrupt swimming on tourist beaches causing economic impacts. In October 2012, jellyfish stranding on Cable Beach (density 2.20 ± 0.43 ind. m^{-2}) was estimated at 52.8 million individuals or 14,172 t wet weight along 15 km of beach. Reports of strandings after this period and up to 250 km south of this location indicate even larger swarm biomass. Strandings of jellyfish were significantly associated with a 2-day lag in conditions of small tidal ranges (<5 m). More than 90% of strandings occurred 2 days after winds were blowing onshore, but with the small number of days when satellite wind data were available during the study period, this result was not statistically significant. Dedicated instrument measurements of meteorological parameters, rather than the indirect measures used in this study (satellite winds and modelled currents) may improve the predictability of such events and help authorities to plan for and manage swimming activity on beaches. We also show a high incidence of predation by *C. mastigophora* on bivalve larvae which may have a significant impact on the reproductive output of pearl oyster broodstock in the region.

Keywords Jellyfish · Bloom · Wind · Tide · Diet · Bivalve larvae

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Introduction

Jellyfish are a ubiquitous and readily observed component of marine plankton. They may exist in high

densities as swarms (aggregations from local or distant sources usually brought together by oceanographic or behavioural processes) or blooms (high density, locally derived population). The different manifestations of high densities of jellyfish and how they are formed have been reviewed previously (Graham et al., 2001; Hamner & Dawson, 2009). However, there has been recent interest in using and understanding oceanographic processes to develop predictive capacity to forecast when jellyfish might swarm near the shore bring them into contact with swimmers (Pontin et al., 2009; Gershwin et al., 2014). The extent to which jellyfish biology and behaviour can affect swarming and beach stranding (Fossette et al., 2015) has also gained recent attention. Jellyfish swarms at the coast cause other problems such as clogging power and desalination plant seawater intakes (Daryanabard & Dawson, 2008; Dong et al., 2010) and fish mortality in aquaculture farms (Doyle et al., 2008), and predictive capacity would assist in preparing for or preventing harmful and damaging effects of jellyfish swarms.

Jellyfish swarms and blooms are natural phenomena, but their occurrence is increasingly being associated with anthropogenic disturbance and modification of the world's oceans and coastal seas. Climate change, overfishing and coastal development have all been suggested as contributing to jellyfish swarms and blooms, although the evidence is often equivocal (Mills, 2001; Purcell et al., 2007; Richardson et al., 2009; Dong et al., 2010; Lilley et al., 2011; Duarte et al., 2012; Purcell, 2012; Gibbons & Richardson, 2013), and the evidence of a world-wide trend in jellyfish swarms and blooms is debated (Condon et al., 2012, 2013). The jellyfish swarms described in this study occurred in the remote north-western Australia, where anthropogenic impacts are regarded as being very low on a global scale (Halpern et al., 2008) offering an opportunity to examine the drivers of swarms as well as their ecological, social and economic significance.

The jellyfish *Crambione mastigophora* Maas 1903 is recorded from the eastern Indian Ocean and western Pacific (Kramp, 1961; Omori & Nakano, 2001; Kitamura & Omori, 2010). Despite its apparently common and sometimes abundant occurrence in north-western Australia (this study), Indonesia (Omori & Nakano, 2001), the "Malayan Archipelago", Sri Lanka and the "Truk Islands" (Micronesia) (Kramp, 1961), there is little published information on *C. mastigophora* beyond the taxonomic texts of Kramp (1961) and Stiansy (1929). *C. mastigophora* is capable of forming large swarms in north-western Australia where they are a nuisance due to stinging swimmers (Marsh & Slack-Smith, 2010). Hamner & Dawson (2009) categorised it as a putative bloomer on the basis that if they are fished commercially (Omori & Nakano, 2001), they must be very abundant, at least seasonally. However, there have been no previous studies anywhere describing the nature, extent, and time course of *C. mastigophora* swarms. Similarly, there are no published studies on any aspect of the biology of *C. mastigophora*.

This study resulted from an unplanned opportunity which arose when very large swarms of *C. mastigophora* washed ashore in a small population centre on the only regularly lifeguard patrolled beach in what is a very remote part of Australia in 2012. The purpose of the paper is to record the incidence and scale of these, and earlier *C. mastigophora* swarms off the western coast of Australia, determine whether wind, currents and tides play an influential and predictable role in beach stranding events of these jellyfish and outline the likely socioeconomic and ecological implications of swarms of this species.

Materials and methods

Occurrence of swarms

Details on the occurrence of *C. mastigophora* swarms in 1976, 2000, 2006, 2007, 2010, 2011, 2012, and 2013 were collated from a series of eye witness accounts by the authors and their associates: JK, TT, DB, JS, LG in 2010, 2012 and 2013, TT, KO in 2011 and TT in 2006 and others as well as reports to the Western Australian Museum (Marsh & Slack-Smith, 2010), the Western Australian Department of the Environment, the Broome Shire Council (Cable Beach life guard logbooks), the Eighty Mile Beach Caravan Park and from news reports. For the period of detailed investigation on Cable Beach (Fig. 1iii) in 2012, daily records of jellyfish strandings were made by TT and other Cable Beach life guards, for the period from 12 August to 31 October.

Biomass of stranded jellyfish

To determine the biomass of jellyfish washed up on Cable Beach, we first sampled jellyfish offshore to determine the size and weight distribution of the jellyfish population. We then compared the size distribution of jellyfish on the beach with those offshore using a Mann–Whitney U test (see Results section), and finding no difference, we applied the average weight of the jellyfish sampled offshore to counts of jellyfish washed ashore. A total of 159 individuals of *C. mastigophora* were collected with a dip net offshore of Gantheaume Point on 19 September 2012 at 17.977614°S, 122.173300°E from a 6-m boat taking care to collect all individuals that could be reached from the boat in the top 500 cm of water to ensure no bias in size selection. These were collected into buckets and then measured on shore for maximum

bell width (diameter) and weighed (whole wet weight) to the nearest 1 gramme on an Accura ACC2070RD electronic scale. A further 186 individuals washed up on Cable Beach were measured for maximum bell width on 5 October 2012 by collecting all jellyfish from an area 4 by 8 m quadrat at 17.933556°S, 122.208500°E. Biomass in terms of wet weight to size was determined as above, and dry weight and ash-free dry weight (AFDW) were determined by drying samples of jellyfish tissue (principally from the bell) of known wet weight in a Labconco Freezone 2.5 freeze dryer at −40°C until constant weight was achieved and then reweighing before ashing at 450°C for 4.5 h and reweighing (Larson, 1986). Jellyfish tissue was not rinsed in freshwater before drying, so some residual salt may have remained when dried. The mean ratios of wet to dry and wet to AFDW were then used to calculate biomass for the full-size range of
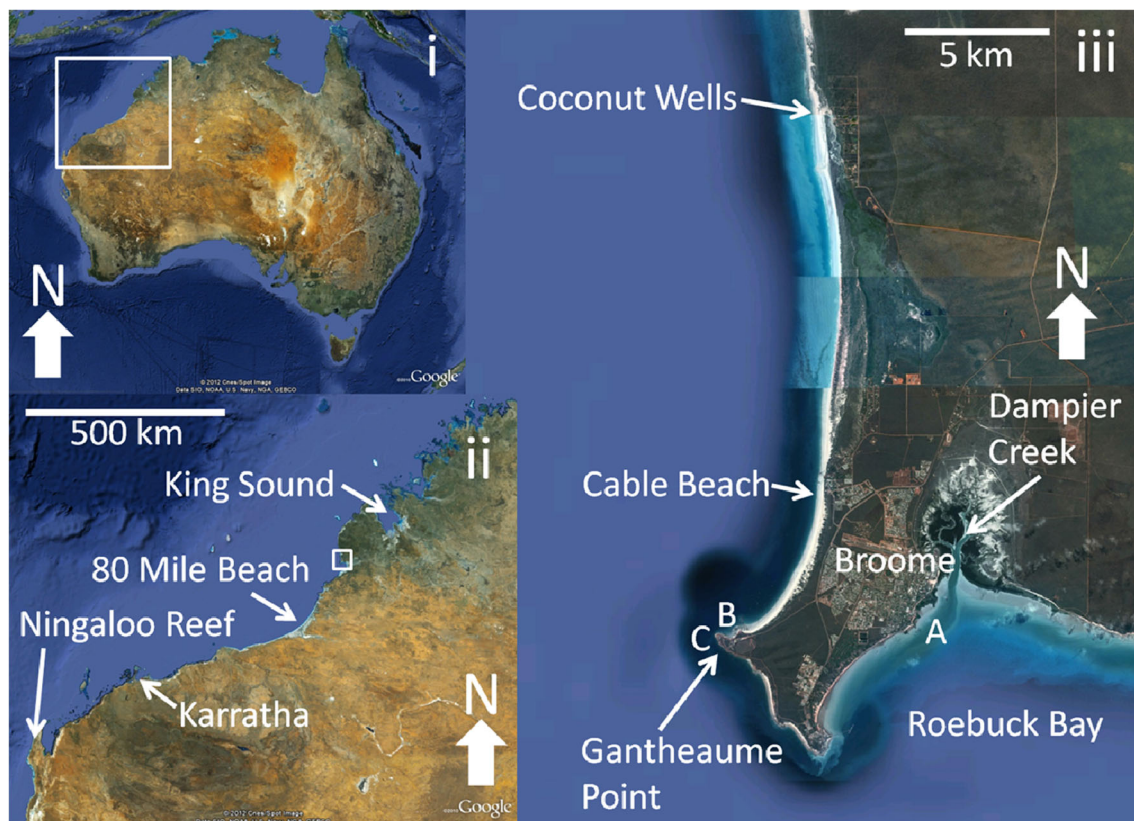
Fig. 1 **i** Map showing Kimberley region in northern Australia and location of study area; **ii** Study area showing locations of observed *Crambione mastigophora* swarms and strandings (*top right*, *lower left* positions of panel **ii** are 13.67°S, 127.00°E and 24.30°S and 113.25°E respectively) and; **iii** sites sampled on 19 September 2012. Sites *A* and *B* were sampled for prey species, Site *C* was sampled for medusa size frequency (*top right* and *lower left* positions of panel **iii** are 17.79°S, 122.30°E and 18.03°S and 122.12°E, respectively)

jellyfish sampled. Total organic carbon, total nitrogen content and stable isotopes (^{13}C and ^{15}N) were assessed using freeze-dried tissue. Samples were analysed for δ^{15}N and δ^{13}C, using a continuous flow system consisting of a Delta V Plus mass spectrometer connected with a Thermo Flush 1112 via Conflo IV (Thermo-Finnigan/Germany) following the methods of Paul et al. (2007) and Skrzypek et al. (2010).

To determine the biomass of jellyfish washed up on the Cable Beach (Fig. 1iii), we counted all jellyfish in twelve 20-by-1 m transects at six sites on 8 October 2012. The transects were set out in pairs along 2.5 km of beach heading south from a site seaward of the Broome Surf Life Saving Club (BSLSC). The location of the first transect was at 17.932639°S, 122.208833°E. The sites were 500 m apart along the beach, and at each site, two transects were conducted parallel to the shoreline. One transect was near the water's edge, and one transect was near the high-water mark so as to capture the range of densities at each site across the width of the beach. Figure 2iii shows the apparently even distribution of jellyfish across the beach on the day of sampling. The density of jellyfish from both high and low transects was calculated. To calculate total average biomass on the beach, the mean density was calculated from all 12 transects, and this density was converted to wet weight based on the size distribution measured on the same beach 3 days earlier and the relationship between size and wet weight. To enable the density of jellyfish on the full width of beach to be estimated, we used a conservative estimate of 100-m width based in two measurements made from aerial photographs (averaging 115.5 m) of the width of the beach adjacent to the BSLSC (127.5 m) and 3 km to the south (103.5 m). These measurements were made between the high (6.85 m) and low (3.32 m) tide points for 8 October 2012. A more extensive visual survey of jellyfish on the beach was made by driving a 4WD vehicle south from the BSLSC for 5 km to Gantheaume Point (17.970083°S, 122.191000°E) and north for 10 km to Coconut Wells (17.838611°S, 122.209028°E) (Fig. 1ii). This 15 km survey recorded the southern extent of the strandings, but they may have extended further north as the beach extends a further 7 km to a creek and then a further 13 km north after that. At one-km intervals along with this 15 km section of beach, a visual assessment and photograph along with the GPS position were recorded. This survey confirmed that densities measured over the 2.5 km

stretch south of the BSLSC were representative of the entire beach.

Diet

To examine for diet, samples of live *C. mastigophora* were collected (as per the description above) from two locations on 19 September 2012: Offshore of Gantheaume Point at 17.966944°S, 122.178989°E and near Dampier Creek in Roebuck Bay at 17.967536°S, 122.243281°E. The jellyfish were measured (as per above) and placed in plastic bags and then on ice. The method of determining prey items followed that of Browne & Kingsford (2005) except it was necessary to freeze the samples in order to transport them to the laboratory where 14 individuals were thawed over 1–2 h in seawater filtered through Whatman® glass microfiber filters (0.6–0.8 μm) and then washed in the container to dislodge any prey items adhering to oral arms. Much of the jellyfish disintegrated during this process but otherwise large pieces of intact jellyfish were removed and washed with a wash bottle containing filtered seawater before all the remaining liquid was filtered through 1 mm and 63 μm sieves. The filtrate was fixed in 5% formalin before later being searched under a dissection microscope Leica M 205 C, magnification 6.3, objective 10x. Prey items were identified to the lowest taxonomic unit possible by an experienced zooplankton biologist (JS). The method used does not permit gelatinous prey items to be identified.

Wind, tide, sea-surface temperature, chlorophyll-*a*, and modelled surface currents

The satellite-derived sea-surface chlorophyll-*a* (Chl-*a*) concentration data are 8-day composited Level-3 global standard mapped images (SMI) derived from the moderate resolution imaging spectroradiometer (MODIS) aboard the Aqua satellite. The sea-surface temperature (SST) data were derived from long-wave (11 μm) SST algorithm (Franz, 2006). Only night-time data were used to avoid any surface skin created by diurnal warming. The satellite-derived sea-surface wind data are from a daily near-real-time (NRT) product derived from WindSat Polarimetric Radiometer instrument. These satellite images were downloaded from the Remote Sensing Systems under the sponsorship of NASA (http://www.remss.com/). The

Fig. 2 **i** *Crambione mastigophora* swarm washed ashore on Cable Beach, Broome 12 September 2012, **ii** close-up of specimen immediately after capture, **iii** swarm washed ashore on Cable Beach, 8 October 2012 (**ii**) and **iv** on 80 Mile Beach 11 November 2012
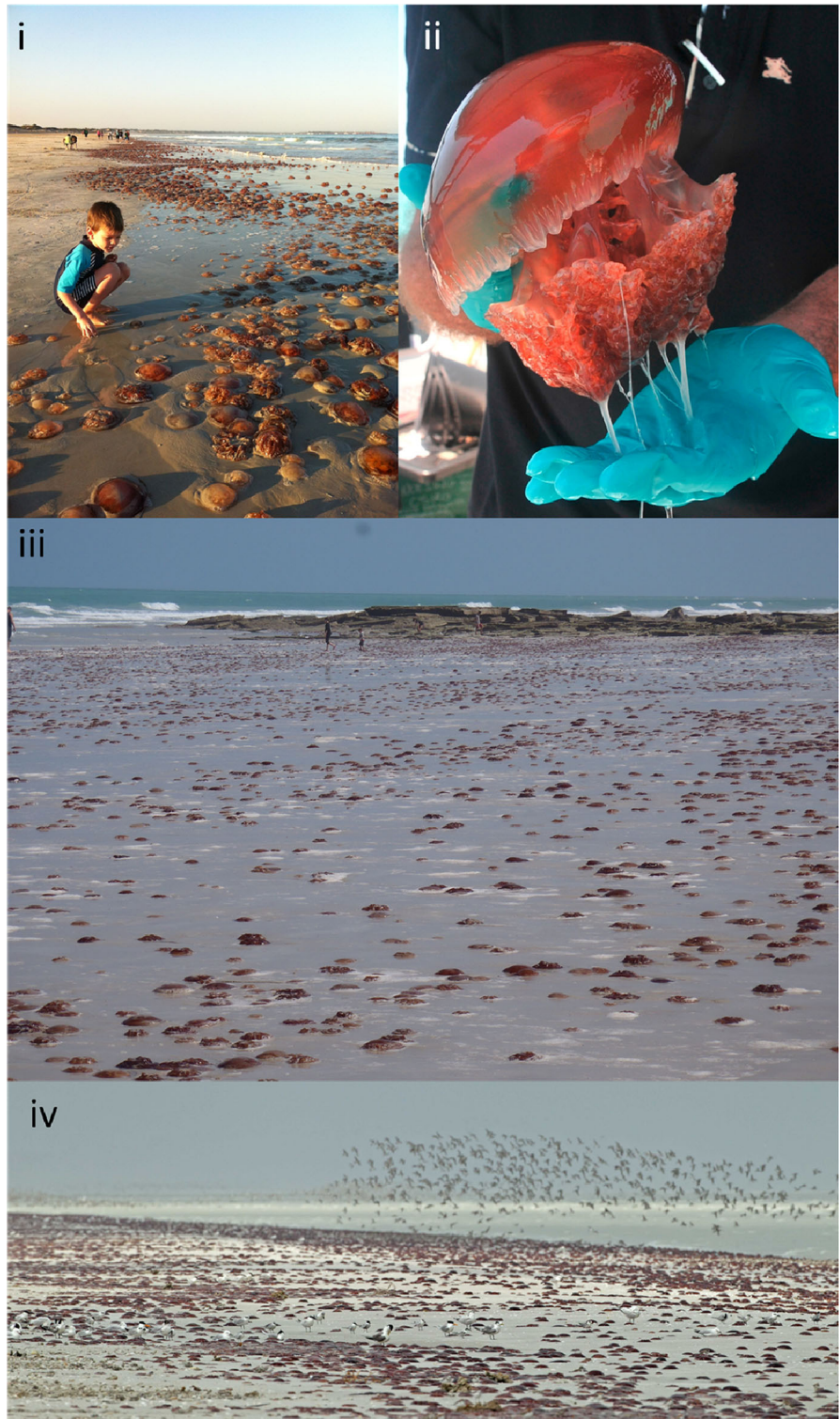
time span of the MODIS images is from 4th August, 2012 to 30th October, 2012, and the geographic area covers in 121–123°N and 17–19°S, with a resolution of 4 km × 4 km. The satellite wind data are from the same area and time period but with a resolution of 0.25° × 0.25°. For statistical analysis of daily satellite wind data, an average of only the 16 data points comprising a 1° square (17.5°S–18.5°S and 121.0°E–122.0°E) immediately off Cable Beach was used. The depth in the area of this grid is 0–108 m, with three quarters of the area between 30 and 100 m deep. Additional wind speed and direction data (daily averages of anemometer and wind vane) along with tide data were obtained from the land-based Broome station of the Australian Bureau of Meteorology (BOM) http://www.bom.gov.au (which is within 10 km of all our study sites). The land-based wind data are more readily available than satellite data (which have data gaps) but are less relevant to affecting sea conditions in the offshore location of the jellyfish swarms. In addition, the land-based wind data can be influenced by factors such as the daily land/sea breeze cycle, which sometimes occurs. Modelled surface current data were derived from BOM's OceanMAPS http://wp.csiro.au/bluelink/global/oceanmaps/ model using the analysis phase data. Model data are available on a 0.1° × 0.1° grid with 51 layers; the surface layer represents the top 5 m and does not take into account tides. Daily surface velocities for the region bounded by 17.5°S–18.5°S and 121.0°E–122.0°E were extracted and spatially averaged to produce a daily time series of current velocity and direction relative to north and magnitude in m.s^{-1} for 24 August 2012 to 20 October 2012 inclusive. Comparisons of swarm occurrence and the Southern Oscillation Index were made using data reported by the National Oceanic and Atmospheric Administration at https://www.ncdc.noaa.gov/teleconnections/enso/indicators/soi/.

Predictors of beach stranding events

In order to test the hypothesis that the incidence of beach strandings was independent of local wind, current and tide conditions we sought to compare the incidence of jellyfish strandings (19 out of 58 days) with the prevailing offshore oceanographic and weather conditions. We compared the conditions on days with strandings to conditions on days without strandings for the 58 day period from 24 August to 20

October (3 days before the first and 3 days after the last major stranding) using the χ^2 statistic. As Cable Beach is oriented north–south, we were interested in the influence of onshore (north-west through to south-west) and offshore winds and currents (northeast through to south-east). Thus for wind and current, we used the satellite wind/current direction to determine for each day whether the wind/current was predominantly blowing/flowing from each of the NW (e.g., 270°–360°), SW, NE, or SE quarters. On days where both a morning (around 6 a.m.) and an evening (around 6 p.m.) wind reading was available and they were not the same (onshore vs offshore), we used the wind direction from the observation with the highest wind speed. This only occurred on three occasions and it made no difference to the result of the χ^2 hypothesis testing whether we chose the wind direction with the slowest speed or omitted these three data points altogether. When the satellite did not provide any wind data (23 of 58 days), these days were not included in the analyses. For tides, we compared tidal ranges of <5 or ≥5 m (approximately half the maximum range of 9.82 m observed in this period). To calculate the tidal range, we used the difference between the highest and lowest of the semi-diurnal tides for that day. The reason we chose to do the likelihood test on wind direction and tide as categorical variables, in addition to the more dynamical multivariate approach described below, was to attempt to have a easy to use decision tool for lifeguards patrolling what is a popular tourist beach.

Logistic regression analysis has previously been used (Decker et al., 2007) to relate jellyfish presence/absence data to environmental variables. We used a similar approach using the LOGIT module in SYSTAT (Systat Software Inc., San Jose, USA) to determine which predictor variable contributed the best fit to the regression, and which combination of environmental variables best described the relationship between the occurrence of jellyfish strandings and the potential environmental predictor variables of tide range, model current direction and speed, wind speed and wind direction at Broome. We used only environmental variables for which we had data over all the jellyfish sampling dates. For this reason, chlorophyll-a, sea-surface temperature and satellite wind data obtained were not used because of gaps resulting from intermittent cloud cover. A total dataset of 58 days including 19 days when jellyfish strandings took place

(stranding events) was analysed. We used a two-staged approach, first modelling the presence/absence of jellyfish strandings with individual environmental variables, and then we applied a backward and forward stepwise regression in SYSTAT to choose the best set of predictive variables. Descriptive measures of goodness of fit provided from the analysis for each variable (log likelihood, receiver operating characteristic (ROC) analysis, McFadden's ρ^2, Cox and Snell R^2 and Nagelkerke R^2) were used to determine the variables which provided the highest level of prediction. The models with multiple predictors were compared using log likelihood, Aikaike's information criterion (AIC) and Bayesian information criterion (BIC) to determine the best model selection. The use of AIC and BIC is considered more rigorous that likelihood analysis alone in evaluating logistic regression models and their use is described by Neath & Cavanaugh (2012). We have had to ignore the possibility of autocorrelation in the daily observations of stranding events, and we did not account for the circular nature of wind and current direction data (e.g., $5°$ is closer to $355°$ than is $340°$). However, we do not think this would have had a large bearing on the analyses, at least for the wind direction as just two values were from the northeast direction (i.e., between $0°$ and $90°$). Current directions were more uniformly distributed around the compass.

Results

Location, occurrence and timing of swarms and beach strandings

Observations and locations of known swarms and beach strandings of *C. mastigophora* are shown in Fig. 1ii and summarised in Electronic Supplementary Material (ESM) Table 1. The earliest swarm recorded in the region was in August 1976 when the power plant at Cape Lambert (near Karratha, see Fig. 1ii) was forced into an emergency shutdown when the intake pipes became clogged with red jellyfish (Marsh & Slack-Smith, 2010) (see also ESM Table 1). The largest swarm is likely to have been in April 2000 when high densities of *C. mastigophora* were observed from the air stretching over 1,200 km from Ningaloo (Fig. 1ii) south to Rottnest Island (Marsh & Slack-Smith, 2010, see also ESM Table 1). Photographs of

the recent swarms, at Cable Beach (Fig. 2iii) and 80 Mile Beach (Fig. 2iv) in 2012 and in the water column at Ningaloo in 2013 (Fig. 3), are shown. With the exception of the 1976 swarm, the swarms were recorded from two regions: near Broome on the Dampier Peninsula and elsewhere in the southern Kimberley region in 2006 (September/October), 2010 (April), 2011 (September to November) and 2012 (late August to November) and further south of Exmouth and Ningaloo in 1987, 2000, 2007, 2010, and 2013 (always in April/May for these large swarms). Except for the observation of high densities of *C. mastigophora* offshore of the Dampier Peninsula in April 2010, all swarms in the northern region have been in the late August/September to November period and those in the more southern region occur in April and May. Some non-serious stings to swimmers on Cable Beach in 2011 and 2012 were treated by one of us (TT; see ESM Table 1). It is difficult to compare the size and significance of swarms between years; however, observations recorded in daily log books by life guards at Cable Beach show 2006 and 2012 as the largest strandings, with swarms in the intervening years not of comparable size.

During 2012, numbers of *C. mastigophora* built up from 12 August with the first significant strandings on 27–29 August, becoming more dense from 12 to 15 September (Fig. 2i). The beach was closed to swimmers on 12 September. On subsequent days, when jellyfish were present in large numbers, although the beach was not closed, life guards continued to patrol and advised visitors of the hazard of swimming with the jellyfish. Life guards treated 396 minor stings in September and 336 in October. The last significant stranding was on 17 October, and *C. mastigophora* were uncommon by 23 October. The jellyfish were present throughout this period, but the very large strandings of many thousands of individuals occurred on 12, 13, 14, 15, 28, 29 September and 1, 4, 5, 8, 9, 10, 12, 15, 16, 17 October (Fig. 4). On days in-between, there were fewer jellyfish washed up but very high densities were being seen offshore. Log book records of the Broome Shire Life Guards and our own observations confirmed very high densities offshore of Cable Beach on 3 September and at the mouth of Dampier Creek in Roebuck Bay on 17 September; jellyfish were still very abundant offshore of Gantheaume Point on 19 September and another large influx was observed offshore of Cable Beach observed on 28 September. In the days following 12 September

Fig. 3 *Crambione mastigophora* bloom photographed underwater off Ningaloo Reef 12 April 2013

Fig. 4 Timeline of 2012 showing dates of jellyfish beach strandings (jellyfish icon), tide range (*vertical bars*) and satellite wind direction (*down arrow* is southerly wind, *up* northerly, *right* westerly, *left* easterly)
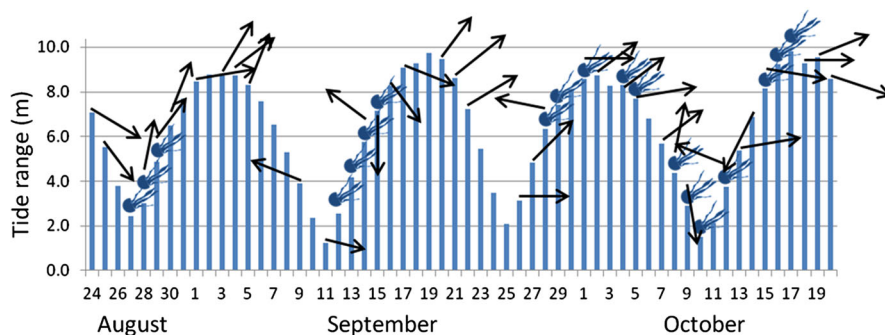
and as late as 20 September, when we (JK, DB) used a vehicle to visit beaches along the coastline to about 60 km north of Broome, small numbers of jellyfish could be observed along the Dampier Peninsula but campers and tourists we interviewed reported no large strandings. We (TT) found jellyfish stranded in large numbers from Gantheaume Point as far north as Coconut Wells on 8 October. They may have occurred further north as this was as far as observations were made at that time.

Oceanographic information in relation to jellyfish strandings in 2012

Tide range varied from 1.25 m to 9.82 m during the period 24 August to 20 October. Of the 19 days with significant jellyfish strandings, there were 9 days (47.4%) that occurred when the tidal range was <5 m although only 18 days (31.0%) of all days during the same period had tidal ranges <5 m. This association was not significant ($P = 0.061$, χ^2 statistic = 3.522, 1 *d.f.*). However, tide range <5 m that occurred 1 and 2 days prior to the stranding days were both significantly associated with stranding events ($P = 0.013$, χ^2 statistic = 6.158, 1 *d.f.* for both 1 and 2 day lags). This result indicates that strandings were significantly more likely to follow days of small tidal range than those of larger tidal ranges. However, as shown in Fig. 4, not all stranding events occurred on days which followed smaller than average tide ranges.

Water temperature increased from 20.5 to 28.5°C over the two-month period from early August until late October (ESM Fig. 1). The most significant change was during September water temperatures of Cable Beach increasing from 24°C to 27°C between 28 August and 29 September. Chlorophyll-a levels of Cable Beach were low (0.4–0.5 mg m^{-3}) from 4 August to 4 September and then increased to 1.3–1.5 mg m^{-3} as chlorophyll-a levels increased first in Roebuck Bay and south and north to Cable Beach and beyond (ESM Fig. 2). Winds

were easterly on average from 4 to 19 August before shifting south-westerly to westerly between 20 August and 4 September (Fig. 5). Winds were again easterly from 4 to 12 September before shifting westerly to south-westerly between 13 September and 6 October. From 7 October, winds were variable but predominantly southerly and south-westerly before turning westerly again from 15 to 22 October. From 23 to 30 October, winds were again variable from the south and west (Fig. 5). Among the 35 days that satellite wind data were available during the 58-day period analysed (24 August to 20 October), 7 of 11 (63.6%) of strandings occurred when winds were blowing onshore (north-west through to southwest). However, the direction of the wind (all four quadrants compared) was not significantly associated with jellyfish strandings on the days they occurred ($P = 0.432$, χ^2 statistic $= 2.751$, 3 $d.f.$). Neither was it significantly associated with wind direction one or 2 days prior to strandings ($P = 0.921$, χ^2 statistic $= 0.491$, 3 $d.f.$ and ($P = 0.413$, χ^2 statistic $= 2.867$, 3 $d.f.$ respectively) despite 90.9% of strandings occurring when winds were blowing onshore (north-west through to south-west) with a 2-day time lag. It is likely that the small sample size which was affected by the absence of wind data from 23 of the days during the period of observation during which time there were 8 stranding events. During the 58 days, 12 of 19 (63.2%) of strandings occurred when currents flowed onshore. However, current direction (all four quadrants compared) was not significantly associated with jellyfish strandings on the days they occurred ($P = 0.863$, χ^2 statistic $= 0.741$, 3 $d.f.$) or one or 2 days prior to strandings ($P = 0.290$, χ^2 statistic $= 3.748$, 3 $d.f.$ and ($P = 0.501$, χ^2 statistic $= 2.363$, 3 $d.f.$ respectively). Logistic regression analysis reinforced the importance of tide range as a predictor of strandings. The strongest individual predictor was tide range 2 days before strandings ($P = 0.009$, see Table 1), and the next best was current direction, also with a 2-day lag. Wind direction was a worse predictor than either tide or current. The best logistic regression model which combined the two predictors of tide range (2 day lag) and wind speed (2 day lag) provided only slight improvement in the fit over tide range alone according to Aikaike's Information Criteria (AIC) (Table 1). The Bayesian Information Criteria (Shwartz's BIC) did not show any improvement in the model fit when tide range and wind speed were combined (Table 1).

This difference in model selection is easily explained by the way that Shwartz's BIC penalises attempts to improve model fit simply by an exhaustive exercise of adding more parameters and in analyses with small sample sizes such as ours. For this reason, Shwartz's BIC is favoured by some statisticians (Neath & Cavanaugh, 2012). Nevertheless, the improvement gained by the inclusion of current direction ($P = 0.018$) or wind speed with tide range in the model ($P = 0.008$) was slight, and the difference in wind speed between jellyfish stranding days (with a 2 day lag) and other days was negligible (means of 11.7 km h^{-1}, SD $= 3.6$ and 12.8 km h^{-1}, SD $= 3.2$, respectively). Both the univariate and multivariate approaches reinforced the importance of tide range as an important predictor of strandings. Neither of the two approaches found wind or current direction as a significant predictor of strandings.

Size frequency and individual biomass

Diameter of *C. mastigophora* collected offshore of Gantheaume Point on 19 September ranged from 3.5 to 18.0 cm in diameter with size frequency greatest at 5.0–5.9 cm and 11.0–11.9 cm (Fig. 6). Individuals between 10.0 and 12.9 cm made up 34.6% of the population and those <6.0 cm made up 17.0%. Diameter of jellyfish collected from Cable Beach on 5 October ranged from 4.3 to 21.5 cm in diameter with a peak in abundance at 10.0–10.9 cm. This sample had fewer small jellyfish (7.5% <6.0 cm), but there was no significant difference in mean size of medusa collected on 19 September and 5 October between the two samples (9.9 cm (SD $= 3.5$) and 10.1 cm (SD $= 3.0$) respectively), Mann–Whitney U test, $U = 14,076$, $P = 0.442$. Despite having equal variances (F test: $F_{(158,185)} = 1.298$, $P = 0.087$), the samples were non-normally distributed (Shapiro–Wilk test, $W = 0.979$, $P = 0.015$ and $W = 0.983$, $P = 0.025$ respectively) and could not be satisfactorily transformed, so the non-parametric test was applied instead of a *t* test. Biomass of *C. mastigophora* collected offshore of Gantheaume Point increased exponentially with diameter (Fig. 7), as estimated from the equation $W = 0.2665 \times D^{2.8943}$ (Fig. 7) where W is whole wet weight in grammes and D is bell diameter in cm. The linear regression of $\log_{10}$ W against D was highly significant with $R^2 = 0.844$, $P < 0.0001$. In the population, sampled
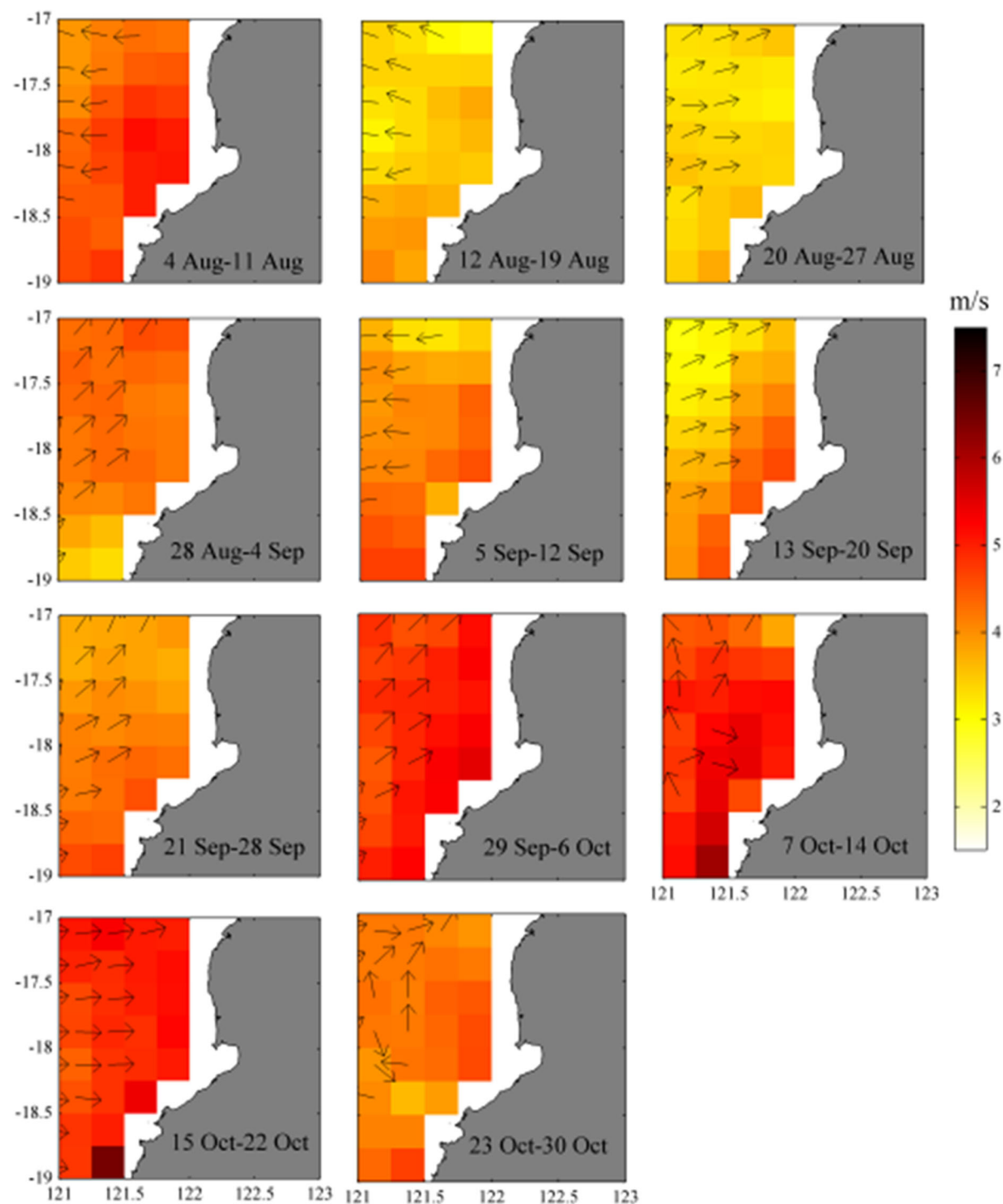
Fig. 5 Satellite-derived sea-surface wind speed and direction (WindSat Polarimetric Radiometer $0.25^0 \times 0.25^0$). instrument for the period from 4th August, 2012 to 30th October, 2012

Table 1 Summary of logistic regression analysis using predictor variables of wind speed, wind direction and tide range (J = the day of a mass jellyfish stranding event, J-1 = 1 day before stranding, J-2 = 2 days before stranding)

Predictor variable and combined variable models	ROC proportion	McFadden's ρ^2	Cox and Snell R^2	Naglerke's R^2	Log likelihood	AIC	Schwarz's BIC	P value for variable or combined model
Tide range/J (day of Jellyfish stranding)	0.601	0.022	0.028	0.039	−33.385	70.771	74.673	0.221
Wind speed/J	0.604	0.014	0.018	0.025	−33.655	71.310	75.213	0.327
Wind direction (dir.)/J	0.580	0.010	0.013	0.017	−33.804	71.608	75.511	0.415
Current direction/J	0.527	0.000	0.000	0.000	−34.135	72.270	76.172	0.968
Current speed/J	0.484	0.000	0.000	0.000	−34.128	72.255	76.158	0.900
Tide range/J-1 (1 day before Jellyfish stranding)	**0.679**	**0.067**	**0.084**	**0.115**	**−31.852**	**67.704**	**71.607**	**0.033**
Wind speed/J-1	0.565	0.008	0.011	0.014	−33.859	71.717	75.620	0.457
Wind direction/J-1	0.537	0.007	0.010	0.013	−33.880	71.761	75.663	0.475
Current direction/J-1	0.519	0.002	0.003	0.003	−34.069	72.138	76.041	0.716
Current speed/J-1	0.509	0.002	0.003	0.003	−34.080	72.160	76.062	0.739
Tide range/J-2 (2 days before Jellyfish stranding)	**0.715**	**0.100**	**0.123**	**0.168**	**−30.731**	**65.463**	**<u>69.365</u>**	**<u>0.009</u>**
Current direction/J-2	0.681	0.055	0.069	0.095	−32.267	68.535	72.437	0.053
Wind speed/J-2	0.589	0.027	0.035	0.047	−33.219	70.438	74.340	0.176
Wind direction/J-2	0.555	0.001	0.002	0.002	−34.090	72.180	76.082	0.762
Current speed/J-2	0.545	0.005	0.006	0.008	−33.982	71.964	75.866	0.930
Tide range/J-2, wind speed/J-2	<u>0.825</u>	<u>0.142</u>	<u>0.170</u>	<u>0.232</u>	<u>−29.305</u>	<u>64.609</u>	70.463	**0.008**
Tide range/J-2, current direction/J-2	**0.746**	**0.118**	**0.144**	**0.196**	**−30.105**	**66.210**	**72.064**	**<u>0.018</u>**

Descriptive measures of goodness of fit are provided for each variable by log likelihood, McFadden's ρ^2, Cox and Snell R^2, Nagelkerke R^2 and receiver operating characteristic (ROC) analysis. Models with combined variables were evaluated using Aikaike's information criterion (AIC) and Bayesian information criterion (BIC). The best parameter or model determined by each statistic is underlined and those that were significant ($p < 0.05$) are bolded

individuals ≥ 13 cm made up 46.6% of the biomass but only 17.6% of the abundance. The mean water content of the jellyfish after drying was 95.8% (SE = 1.25, $n = 21$), and after ashing, the mean percentage of dry weight that was found to be organic matter was 34.0% (SE = 1.26, $n = 10$). The mean organic carbon and total nitrogen content of the dried tissue were 7.5% (SE = 0.4, $n = 21$) and 2.0% (SE = 0.1, $n = 21$), respectively. The tissue of the jellyfish had carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotopic signatures of −20.79 (SE = 0.06, $n = 21$) and 8.14 $\delta^{15}N$ (SE = 0.08, $n = 21$), respectively. Mean C:N ratio was 3.9 ($\pm$ 0.02 SE, $n = 21$).

### Abundance and biomass of *C. mastigophora* stranded on Cable Beach

The average wet weight of 168 *C. mastigophora* washed ashore on Cable Beach on 5 October 2012 (as predicted from mean bell diameter) was 268.4 g. The mean density (ind. per $m^2 \pm 1$ standard error) of *C. mastigophora* washed ashore on Cable Beach on 8 October 2012 was 2.65 ± 0.64 (range 0.6–5.4) for the six high-water transects and 1.74 ± 0.58 (range 0.5–3.9) for the six low-water transects. The average was 2.20 ± 0.43 ind. per m^2 for all 12 transects along the whole beach. This was used as an estimate of density

Fig. 6 Size (bell diameter)-Frequency plots of *Crambione mastigophora* sampled off Gantheaume Point 19 September 2012 and Cable Beach 8 October 2012
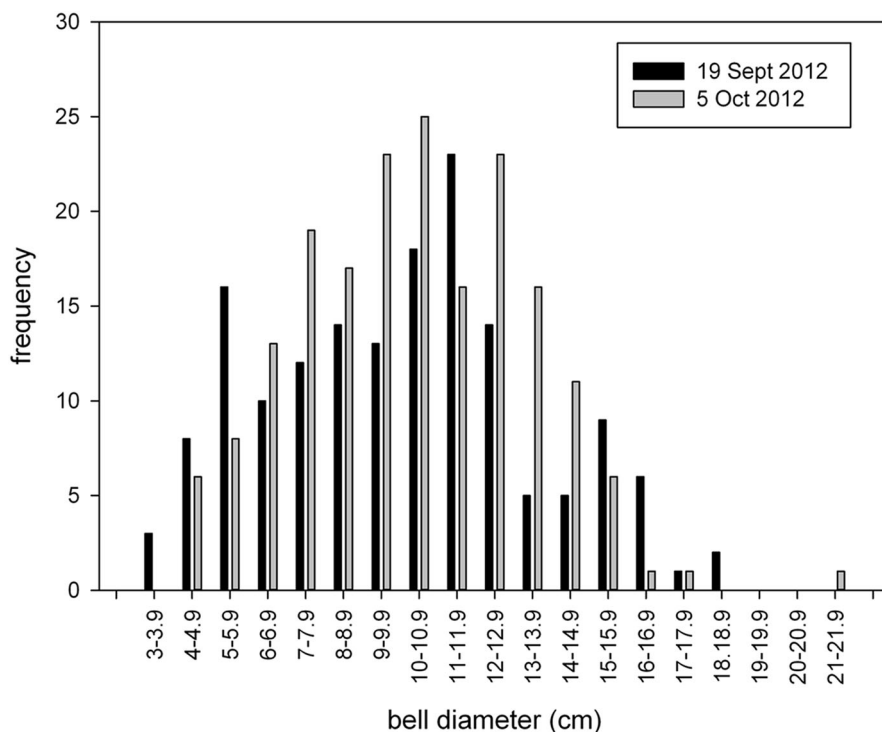
Fig. 7 Plot of bell diameter against whole wet weight for *Crambione mastigophora* sampled off Gantheaume Point 19 September 2012. Power curve fitted by least-square best fit

$$y = 0.2665x^{2.8943}$$
$$R^2 = 0.9717$$
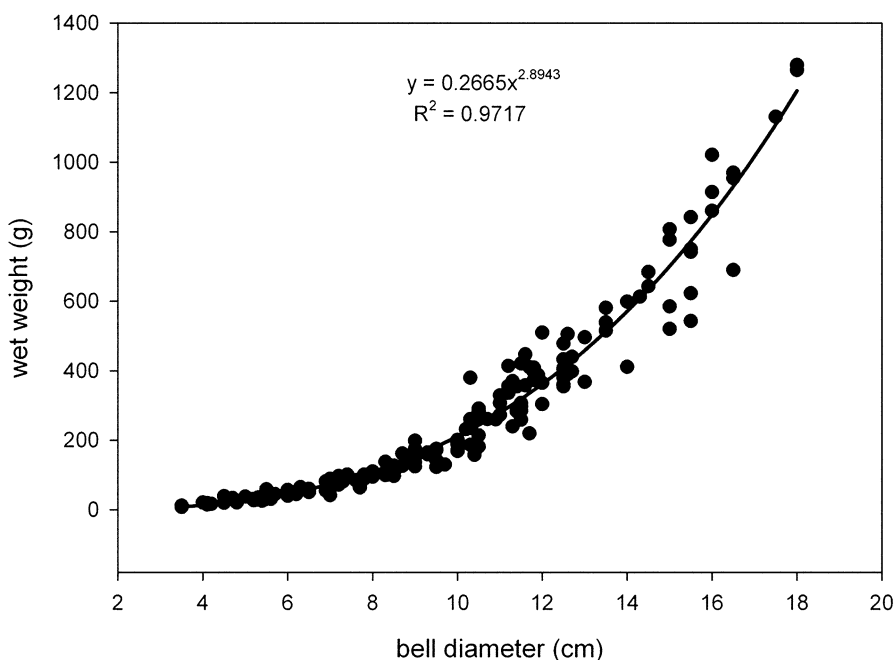
for the whole beach and corresponded to a wet weight of 590.6 ± 115.4 g per m². Using a conservative estimate of beach width of 100 m (measured average was 115.5 m, see Materials and Methods section) along the 2.5 km of beach where the density data were collected, means that the area of beach surveyed was 250,000 m². Accordingly it can be calculated that along this stretch of beach, 147.6 ± 28.9 tonnes of jellyfish was deposited

by the tide. This is equivalent to 59.0 ± 11.5 tonnes per linear kilometre of beach. The survey by vehicle of the extent of the swarm south and north of Cable Beach revealed that the jellyfish were washed up in similar numbers between Gantheaume Point and Coconut Wells, a distance of 15 km (Fig. 1iii). If the density and size distribution of *C. mastigophora* along this section of coastline were similar to that measured on Cable Beach as suggested by the photographic record obtained in our survey, then this would equate to a biomass of 886 ± 173 tonnes (3.30 million ± 0.64 million jellyfish) being deposited along the coast on 8 October 2012. Strandings of similar scale were observed on a total of 16 days between 12 September and 17 October 2012 meaning a total of 52.8 million ± 10.3 million (14,172 ± 2,770 tonnes) jellyfish may have washed ashore during this time. The estimate is

conservative given on each of these 16 days that there were two tidal cycles each depositing jellyfish on the beach and there were smaller (but significant) numbers washed up on each of the other 57 days between 12 August and 23 October (see ESM Table 1).

Diet and commensal organisms

The prey items recovered from the tentacles of 14 *C. mastigophora* are shown in Fig. 8. On average, 220 organisms were recovered from tentacles (±68 SE). The taxonomic composition included small copepods, copepod fragments and other crustaceans, bivalves, invertebrate eggs, phytoplankton and microzooplankton (Fig. 8). All medusae had invertebrate eggs, and the majority had bivalves, pteropods, amphipods and copepods (Fig. 8). Proportionately bivalves,

Fig. 8 Relative frequency of organisms recovered from arms of 14 *Crambione mastigophora* as a proportion of all items on arms. Percentages given after each prey type in the legend are the percentage of jellyfish that had captured that prey item
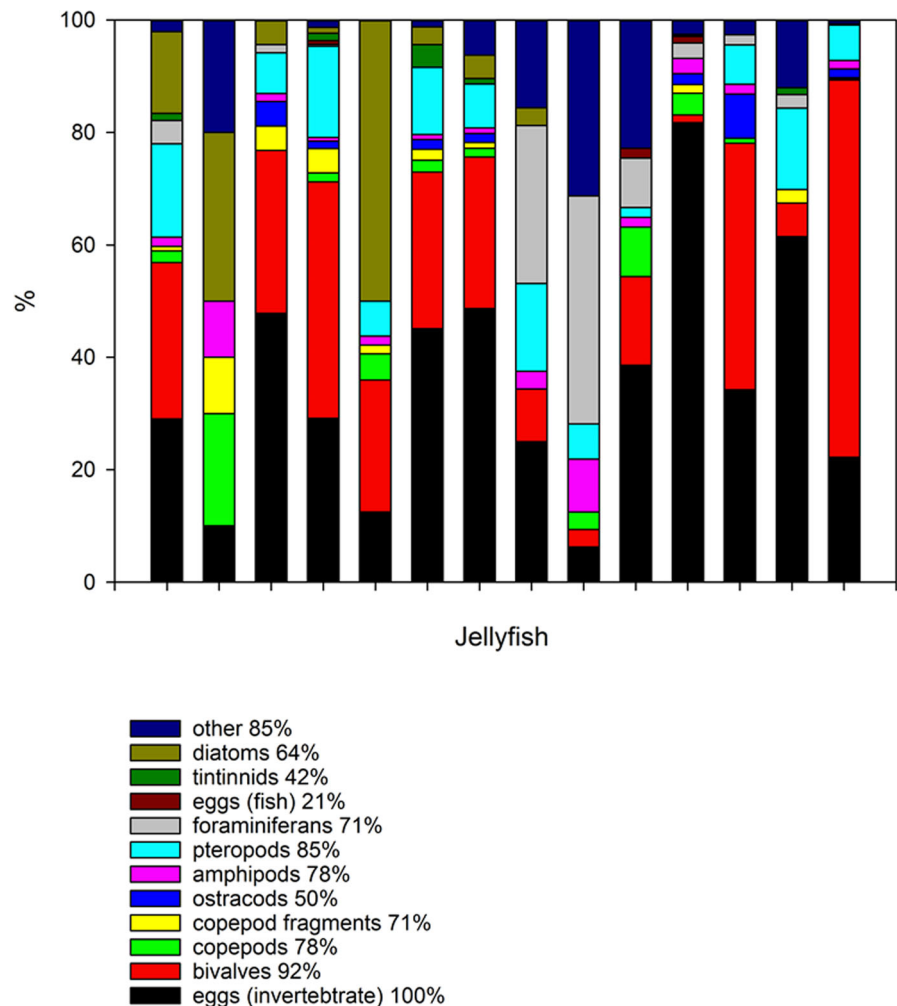
pteropods and invertebrate eggs dominated the prey captured (Fig. 8). There was no difference in organisms found in tentacles of medusae collected from Dampier Creek or Gantheaume Point (Permanova Pseudo-F = 079, $P = 0.6$). Two jellyfish from Gantheaume Point harboured small (2 cm) carangid fishes as associate/commensal organisms.

Discussion

Distribution and occurrence of swarms

This study found that significant jellyfish stranding events were associated with smaller than average tide range, with a time lag of 2 days. Using the same time lag, more than 90% of all strandings occurred when winds (as measured by satellite out over the oceans to the west of the beach) were blowing onshore, but this result was not statistically significant. Modelled currents flowing onshore were associated with 63–68% of strandings depending on the time lag used. Combining these three factors in a logistic regression model failed to provide a better prediction of stranding events than tide range on its own (but see comment on use of circular data in methods section). The influence of tide alone on *meso*-scale physical processes affecting jellyfish distribution would explain why days with significant beach strandings were interspersed with days of absent or minimal stranding. However, we expect that some combination of influence of wind or currents acting to bring the jellyfish close to the shore and the small tides preventing significant advection away from the beach is taking place. Tides, winds and currents are known to influence distribution of jellyfish and cause them to concentrate or "swarm" near to the shore (Zavodnik, 1987; Graham et al., 2001). The time lags account for the period between when physical processes are enacted and when their consequences (jellyfish on beach) are observed. The use of time lags in wind data has previously been shown (Pontin et al., 2009) to be important in predicting jellyfish distribution in *Physalia* (which have "sails"). Our study shows that the use of time lags in tide range may be a useful predictor of rhizostome jellyfish distribution, at least, in areas where large tide ranges exist, such as in the north-west of Australia (Short, 2011). Tidal influence has been shown to be the dominant onshore–offshore current transport mechanism in this region (Condie

et al., 2006). The element of predictability of jellyfish strandings may provide beach management authorities to plan for and manage beach use and swimming activity when jellyfish swarms are brought close to shore by tides and onshore winds. This has previously been emphasised by Gershwin et al. (2014) who show how changes in wind patterns can be responsible for onshore transport of cubozoan jellyfish and can be used to predict when irukandji jellyfish stings are most likely to occur. Although our results show tide as a significant predictor of strandings, our results did not reveal wind or modelled current direction as significant predictors. It is possible that for the χ^2 analyses which relied on wind measurements from satellite made out to sea, we had an insufficient sample size to find an effect because the satellite did not provide any data during 23 of the 58 days over which the strandings occurred. For the logistic regression, we used wind measurements taken at a weather station on land to avoid missing values; however, these data are less relevant to where the jellyfish are located offshore before stranding, and thus, those winds will have less influence on the onshore transport of jellyfish. It is possible that direct measurements of wind and current related to jellyfish occurrence would yield better results than the satellite wind and modelled current data used here. Thus for the purposes of prediction and to be routinely applied, a method of more reliably obtaining current speed and direction and wind direction, from out over the ocean, west of the beach where the jellyfish are swarming, needs to be found. This could be in the form of moored weather stations and current metres. Another factor that could be important in confounding attempts to match stranding events to environmental conditions is that some scyphozoan jellyfish have been shown to exhibit swimming behaviour including prey searching and diel vertical migrations (Hays et al., 2011; Moriarty et al., 2012) which will influence the extent to which ocean conditions and currents will influence onshore directional movement of jellyfish. Moreover, recent novel research (Fossette et al., 2015) using jellyfish tagged with accelerometers has shown how jellyfish can actively orient themselves to swim with or against a tidal current and that this behaviour can act to both maintain swarms and avoid beach strandings.

The observations of Marsh & Slack-Smith (2010) and those from our study suggest that *C. mastigophora* can be seasonally abundant in tropical north-western Australia. However, the observed strandings may

represent a small fraction of those that have occurred due to the remoteness and sparse human population (<100,000) in this region. The areas where it has been observed to be washed up in large numbers are popular tourist areas and strandings in more remote areas are unlikely to be recorded, especially given our observations of rapid disintegration of stranded jellyfish and their subsequent removal by large tidal ranges in the region. Any link between interannual variability in the timing and scale of observed swarms in relation to ocean climate variability is not evident. The swarm in 2012 coincided with an increase in both water temperature and chlorophyll-*a*, but it is not possible to say the swarm event is related to either as these are likely to be seasonal events. The large swarms in Broome in the latter months of 2006 and 2012 were during or at the end of El Niño conditions; however, other large swarms observed further south in April 2000 and 2013 were during La Niña conditions; the swarm in April 2007 was during neutral or slight El Niño conditions and the 2010 swarm was neutral but right on the transition between the strong 2009 El Niño and 2010 La Niña conditions.

Economic and ecological significance of *C. mastigophora* swarms

Large swarms, especially those that occur over protracted periods such as was the 2012 swarm, result in numerous stings on swimming beaches and also deter swimmers from beaches and from areas where tourism is of great economic importance (e.g., Cable Beach, Broome). Other significant impacts of the swarms have included blocking the water cooling intakes of the power station in Karratha in 1976 (Marsh & Slack-Smith, 2010) (see also ESM Table 1).

C. mastigophora is an edible jellyfish species, and a fishery has been established in Indonesia (Java south coast) based on export to Japan (Omori & Nakano, 2001; Kitamura & Omori, 2010). To avoid confusion, it is worth noting here, that Rumpet (1991) provides an excellent description of another sea-east Asian fishery for "red" jellyfish, but it is unlikely that this is *C. mastigophora*. Rumpet's (1991) report from the South China Sea (Sarawak, Malaysia) almost certainly refers to *Rhopilema esculentum* Kishinouye 1891 based on the description of fisheries for this species and *Rhopilema hispidum* (Vanhöffen 1888) (white) elsewhere in the South China Sea (Vietnam) by Nishikawa

et al. (2008). The economic feasibility of a fishery for *C. mastigophora* has not been evaluated in Australia and maybe worthy of examination especially if swarms continue to have detrimental economic impacts.

Bivalve larvae, pteropods and invertebrate eggs dominated the prey items we found on *C. mastigophora* arms and 26% of all observed prey items were bivalve larvae. Nothing is known of the feeding rates of *C. mastigophora*; however, at the population sizes we recorded the potential for them to deplete plankton from the water column must be considered. Some jellyfish species feed predominantly and selectively on bivalve mollusc larvae including other rhizostome jellyfish. For example, Larson (1991) found very high feeding rates by *Stomolophus meleagris* Agassiz 1862 on oyster larvae which made up 56% of prey items and Ballard & Myers (1997) found bivalve larvae made up more than 80% of the diet of *Proboscidactyla stellata* (Forbes 1846). In the southern Kimberley region where we observed significant swarms in 2006, 2010, 2011, and 2012, the silver lipped pearl oyster *Pinctada maxima* (Jameson 1901) forms the basis of Australia's pearl industry valued at A\$120 million per year (Hart & Joll, 2006). *P. maxima* spawn in the spring beginning in September when the peak spawning occurs although the spawning season can extend through to April (Rose et al., 1990). The peak spawning period coincides with the same period that *C. mastigophora* swarms have occurred near Broome and Eighty Mile Beach which is the most important area for pearl oyster broodstock in north-western Australia (Condie et al., 2006), meaning that when they are dense, *C. mastigophora* might be a significant predator of pearl oyster larvae. Condie et al. (2006) showed how tidal currents dominate pearl oyster larval transport in the Eighty Mile Beach region meaning larvae are retained in the area. This would make them vulnerable to large swarms of *C. mastigophora* which would be subject to the same transport patterns. Larson (1991) measured the feeding rate of the closely related *S. meleagris* and found a 325 g jellyfish would consume 6,000 prey items per day over half of which were oyster larvae. Based on these feeding rates, the population numbers of *C. mastigophora* estimated in this study ($>50 \times 10^6$ million, 1.4×10^4 tonnes) could consume upwards of 3×10^{11} oyster larvae per day. It is important that a more in-depth study of the diet and feeding rate of *C. mastigophora* be

undertaken to determine its significance as a predator of *P. maxima* and other bivalve larvae as our data on diet represent just a snapshot in time.

Studies on the planktonic system are also required to determine the relative abundance of oyster larvae and other plankton in the water column as well as in the diet of *C. mastigophora.* The low C:N ratio (3.9:1) and δC^{13} (-20.8) of *C. mastigophora* tissue indicate a dependence on marine derived sources of carbon in its diet (Meyers, 1997). The C:N ratio is similar to that found in other jellyfish: 4.0:1 (Faganeli et al., 1988) and 3.1:1 to 4:2:1 (Cui et al., 2012). The δC^{13}(-20.8) and δN^{15} (8.1) isotopic signatures of *C. mastigophora* are similar to that recorded for another catostylid jellyfish (*Catostylus mosaicus* (Quoy and Gaimard 1824), $\delta C^{13} = -20.9$ to -22.2) (Pitt et al., 2008) and a rhizostome jellyfish ($\delta C^{13} = -22.0$ to -17.4, $\delta N^{15} = 4.8$ to 10.6 by Cui et al. (2012) but lower than in *Pelagia noctiluca* ($\delta C^{13} = -18.8$) (Faganeli et al., 1988; Malej et al., 1993). Pitt et al. (2008) found that copepods and mysids were the most important components of the diet of *C. mosaicus* based on comparative analysis of jellyfish and prey item stable isotope values. The use of stable isotopes can be used to infer the importance of particular food sources integrated over time as opposed to a snapshot in time in the case of prey items sampled from jellyfish arms (Pitt et al., 2009a). However, we can conclude little about the importance of different components of the diet of *C. mastigophora* over the longer term given we lack stable isotope data for the prey items we found and the difficulties interpreting diet from jellyfish tissue isotopic signatures without adequate temporal, spatial, ontogenetic and between organ sampling (Pitt et al., 2009a).

C. mastigophora have a water content on 95.8% which is almost identical to other species studied (Doyle et al., 2007). Dead jellyfish decay quickly (2–3 days) on tropical beaches (personal observations, see ESM Table 1) meaning that the organic carbon and nitrogen in their bodies indirectly derived from primary and secondary production offshore are made available in the nearshore coastal zone. Using our measurements of density of jellyfish in strandings, frequency of strandings and biomass of jellyfish, it can be calculated that this contribution was of the order of 44 tonnes of carbon and 11 tonnes of nitrogen in 2012. However, although we were able to provide some data on the biomass of stranded jellyfish that this is only a reflection of the total biomass as we do not know what percentage of the population is stranded at any one time. Other jellyfish species which undergo swarms have been shown to be important in delivering significant quantities of organic matter into coastal food webs (Pitt et al., 2009b; West et al., 2009).

Kramp (1961) records *C. mastigophora* as reaching 400 mm in diameter, but our specimens were almost all less than half this size. There is no information on growth rates of *C. mastigophora,* and it is not known if *C. mastigophora* in Australian waters grow to the size stated by Kramp (1961) whose records drew on studies in Malaysia. Extensive further study of the biology (especially growth and feeding and swarm size) along with better resolution of spatial and temporal occurrence of *C. mastigophora* is needed to evaluate the ecological and socioeconomic significance of this phenomenon and whether the frequency or intensity of swarms has changed recently.

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