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PRIMARY RESEARCH PAPER

Geographic variation in mangrove flooding and accessibility for fishes and nektonic crustaceans

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Abstract Intertidal habitats are only available to most nekton when inundated by tides. We assessed the variability of access to mangrove habitats for aquatic organisms over 3500 km of Australia's east coast. After determining the elevation of the lower mangrove edge across 19 locations, we used 6 years of historic hourly tide gauge readings to estimate wetland edge flooding frequency, duration, and depth at each location. Although mangrove edges broadly tracked mean sea level along the east coast, deviations in edge elevation corresponded to substantial geographic variation in flooding dynamics. Mangrove edges were flooded from as little as 20% of the time in central Queensland sites, to as much as 90% of the time during some seasons in northern New South Wales. Flooding frequency and depth were also highly variable, with some mangrove edges flooding and draining almost twice as frequently as others. Flooding depth profiles revealed dynamic patterns of flooding of mangrove habitat. The variability in flooding dynamics demonstrates that the availability of mangrove habitat to aquatic organisms varies significantly among locations. This variability in flooding patterns suggests the nature of mangrove use and the functional value of these habitats for fishes and nektonic crustaceans may differ substantially among regions.

Keywords Tidal wetland · Nursery ground · Refuge · Foraging migrations · Mangrove restoration

Introduction

Vegetated tidal wetlands are critical nursery habitats for many fishes and crustaceans of economic importance (Beck et al., 2001), providing rich foraging grounds (Rozas & LaSalle, 1990; Kneib, 2000), shelter from adverse conditions (Rountree & Able, 2007), and refuge from predation (Minello et al., 2003). While the precise functionality of these intertidal habitats and the mechanisms driving their use remain key areas of research (Sheridan & Hays, 2003; Faunce & Serafy, 2006; Sheaves et al., 2015), whatever values or functions they provide to aquatic fauna must be mediated by flooding patterns that regulate direct access and the transfer of materials between intertidal and subtidal areas (Kneib & Wanger, 1994; Rozas, 1995; Ennis & Peterson,

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2014). Little consideration has been given to the role of hydrology in regulating ecological functioning in mangrove wetlands (but see Faunce & Layman, 2009; Igulu et al., 2014). In contrast, the role of hydrology in salt marsh ecology is more broadly recognised (Turner & Lewis, 1997; Connolly, 1999; Rountree & Able, 2007; Weinstein et al., 2014). Even so, few studies have explicitly quantified variations in marsh flooding (Minello et al., 2012) or directly assessed the implications of these variations in flooding for ecosystem function or value (Baker et al., 2013).

Flooding patterns of tidal wetlands depend on the interaction of tides, rainfall, and meteorological conditions (Rozas, 1995). In turn, flooding patterns are vital determinants of biological pattern and process. For instance, tides are particularly important in determining the vertical distribution of intertidal plants. Lewis (2005) stated that most mangrove forests occur above mean sea level (MSL) and are flooded for 30% of the time or less because mangrove plants are unable to survive longer durations of flooding. The more general consensus is that the lower limit of dominant wetland plants including mangroves and *Spartina alterniflora* (Loisel) is around mean sea level (MSL) (Chapman, 1960; Duke, 2006). If this is the case, then the wetland edges would be flooded 50% of the time and thus equally available to aquatic organisms regardless of the hydrological regime in any particular area. This may account for the implicit assumption in the literature that vegetated tidal wetlands everywhere provide similar functional benefits for aquatic species (Baker et al., 2013). However, Minello et al. (2012) found that flooding patterns in *S. alterniflora* salt marshes in south-eastern USA show substantial geographic and temporal variation, with annual flooding durations ranging from less than 50% of the time at some tidal wetlands to over 90% at others. A recent meta-analysis indicated the importance of regional variations in tidal regime in regulating fish use of mangrove habitats (Igulu et al., 2014). Such findings highlight that the flooding dynamics of tidal wetlands is by no means consistent in space and time.

Australia's eastern seaboard spans over 28° of latitude with tidal wetlands occurring across a broad spectrum of climatic and tidal regimes, from temperate to tropical, from micro- to macro-tidal, and from semi-arid coastlines to high rainfall areas, making it the ideal setting to examine broad scale patterns in mangrove flooding dynamics. The tide range varies from less than 1 m at Lakes Entrance in Victoria to over 9 m at Broad Sound in central Queensland (between Port Alma and Mackay, Fig. 1). Portions of the dry tropics coast around Bowen and Gladstone receive only about 900 mm of rainfall per year, while the wet tropics coastal catchment in northern Queensland has the highest rainfall in Australia, receiving in places over 8000 mm annually (Australian Bureau of Statistics, 2012). Although tidal wetlands occur over a broader range of conditions around the world, few regions encompass such a wide range of hydrological conditions with the potential to produce an array of different patterns of tidal wetland flooding. Eastern Australia's tidal wetlands are dominated by mangrove forests, from the world's southern-most and highest latitude stand of mangroves (*Avicennia marina* Forsskal) at Corner Inlet in the south, to mixed forests dominated at

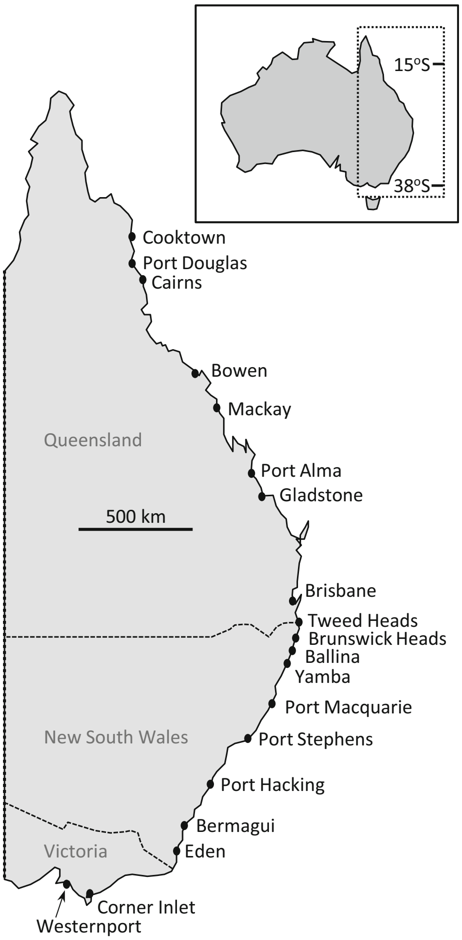


Fig. 1 Mangrove wetland study locations along the east coast of Australia

the lower intertidal edge by *A. marina* and *Rhizophora stylosa* (Griffith) in the north (Duke, 2006).

The aim of this study was to assess geographic variations in the availability of tidal wetlands for aquatic organisms along the entire east coast of Australia. This was achieved by determining the elevation of the lower edge of mangrove wetlands at 19 locations along 3500 km of Australia's east coast, and then quantifying variability in flooding patterns of the mangrove edge. Any geographic variations in flooding patterns would provide the potential for variation in the functional relationships between aquatic fauna and mangrove wetlands.

Materials and methods

Study sites

Wetland edge elevations were measured at 19 locations (estuaries) spanning 23° of latitude from Cooktown (15°S) to Corner Inlet (38°S) (Fig. 1). Study locations were chosen in the lower parts of estuaries where mangroves occurred in close proximity (mostly <1.5 km, maximum 5.6 km; Table 1) to active tide gauges with freely available data. There were no free tide data for gauges between Cairns and Bowen, or Gladstone and Brisbane. Tide gauge data were available for Lakes Entrance in Victoria (between Eden and Corner Inlet), however the nearest mangroves at this location were upstream in a narrow inlet resulting in a significant lag in tide level between the mangroves and the gauge, and this location was excluded from analyses. Three replicate sites were sampled at each location. Each site was a 100 m section of non-eroding shoreline with mangroves at the lowest elevations of the wetland edge accessible for sampling. Hence, as far as was practical, the sites encompassed the first structurally complex intertidal wetland habitat to flood at each location. Sampling was conducted between Westernport Bay and Tweed Heads during May 2010, and at locations north of Tweed Heads between March and October 2010.

Flooding measurements

Metrics of mangrove flooding duration, frequency, and depth were derived by relating the elevation of the lower edge of mangrove vegetation at each site to the local tide gauge, then using historic hourly water level readings from the gauge to calculate flooding metrics (Minello et al., 2012). We defined the lower mangrove edge as the boundary between living plant structures (pneumatophores, prop roots, and stems) and bare substrate lower in the intertidal zone, which at all sites was a clearly defined boundary. The edge elevation at each site was related to the local tide gauge by measuring the time at which the edge flooded, and determining the corresponding water level on the gauge. This approach assumed no significant lag or difference in water level between each site and the local tide gauge. Consequently, sites had been selected as close to the gauge as possible to minimise any such effects. We defined the mangrove edge as "flooded" when 90% of the waters edge at each site encroached on plant structure and 10% was still below the level of the lowest vegetative structure (Fig. 2). We chose 90% flooded as our standard to avoid outlying low structures (e.g. a single line of *Avicennia* pneumatophores reaching lower into the intertidal) or small gaps in structure along the shoreline from unduly biased comparisons. We considered at 90% flooded that aquatic fauna had access to at least some vegetated structure at each site.

Wherever possible we took a series of photographs of the mangrove edge at each site spanning the timeframe from fully drained (the entire waterline below any structure) to fully flooded. Preliminary analyses of data from these sites ($n = 13$ sites) showed that the timing of edge flooding to 0 and 100% were highly correlated (Pearson $R = 0.97$) indicating that spatial patterns in flooding were similar regardless of how we defined edge flooding. At sites that were already flooded when sampling commenced, and were safely accessible by foot (saltwater crocodiles occur at sites from Gladstone north), at least 10 depth measurements were recorded at random points along the lower edge of the vegetation, along with the time they were taken. The corresponding depth on the tide gauge at which 90% of the sampled points would be flooded represented the elevation at which the edge was considered 90% flooded. Sites that did not flood to 90%, or were fully flooded and not accessible by foot were excluded from analyses. This meant that the final analysis included less than 3 replicate sites at some locations (Table 1).

Analysis

We obtained hourly water level data from each tide gauge for the 6 years from 2005 to 2010. The tide

Table 1 Details of the mangrove wetland sampling locations along the east coast of Australia

Location	Lat	Long	Gauge name (number)	Replicate sites[a]	Distance site-gauge (km)	Dominant mangrove	Tide range (m)	Data completeness		
								% Total 2005–10[b]	% Seasons >80%[c]	% Seasons >95%[c]
Cooktown	15°27′S	145°15′E	Cooktown Storm Surge (066003A)	3	0.3–0.6	*R. stylosa*	3.24	94	92	88
Port Douglas	16°28′S	145°28′E	Port Douglas Marina Mirage (041015A)	3	0.1-0.6	*R. stylosa*	3.36	94	92	92
Cairns	16°55′S	145°46′E	Cairns Storm Surge (056012A)	2	0.6–1.5	*R. stylosa*	3.47	94	92	92
Bowen	20°01′S	148°15′E	Bowen Storm Surge (061007A)	3	0.7–0.8	*R. stylosa*	3.70	87	83	83
Mackay	21°06′S	149°13′E	Outer Harbour Storm Surge (100084)	2	1.5–3.2	*R. stylosa*	6.44	87	83	83
Port Alma	23°34′S	150°52′E	Port Alma Storm Surge (050008A)	3	0–0.8	*A. marina*	5.39	87	83	83
Gladstone	23°49′S	151°15′E	Auckland Point (052027A)	3	0.4–4.5	*R. stylosa*	4.62	85	79	67
Brisbane	27°22′S	153°09′E	F1 Grain Terminal	2	0	*A. marina*	2.77	75	67	33
Tweed Heads	28°10′S	153°33′E	Tweed River	1	0.1	*A. marina*	2.11	89	83	71
Brunswick Heads	28°33′S	153°33′E	Brunswick River	3	0.6–0.8	*A. marina*	2.14	83	67	54
Ballina	28°53′S	153°35′E	Ballina Breakwall	2	1.0–1.2	*A. marina*	1.97	87	75	75
Yamba	29°26′S	153°21′E	Yamba Tide Gauge	3	1.7–2.6	*A. marina*	2.08	91	88	83
Port Macquarie	31°25′S	152°54′E	Hastings River	2	1.4–1.6	*A. marina*	1.94	90	88	75
Port Stephens	32°41′S	152°09′E	Tomaree	3	5.2–5.6	*A. marina*	2.20	93	92	92
Port Hacking	34°05′S	151°08′E	Port Hacking Tide Gauge	3	1.2–1.4	*A. marina*	2.12	90	83	79
Bermagui	36°25′S	150°04′E	Bermagui Boat Harbour	2	0.5–0.7	*A. marina*	2.06	92	92	83
Eden	37°05′S	149°52′E	Eden Tide Gauge	2	3.5–3.7	*A. marina*	2.26	89	88	79
Corner Inlet	38°42′S	146°27′E	Port Welshpool Wharf	3	0–0.2	*A. marina*	3.18	15	13	13
Westernport	38°22′S	145°13′E	Stony Point	2	0.3–0.4	*A. marina*	3.51	98	96	92

[a] Number of sites in final analysis

[b] Percent of valid hourly readings from 2005 to 2010

[c] Percent of seasons from 2005 to 2010 (out of total of 24 seasons) with >80 or >95% complete hourly water level records

Fig. 2 Examples of study sites showing 90% of the mangrove edge flooded. **a** *Avicennia marina* site at Yamba, the rising tide has already flooded into pneumatophores along most of the edge at this site, except for a section of bare substrate in the foreground; **b** *Rhizophora stylosa* site at Port Douglas, with a short section of the waters edge covering unstructured bare substrate at the *left end* of the image

gauges were referenced to a variety of datums. Consequently, we standardised our estimate of the elevation of the mangrove edge relative to mean sea level (MSL) by calculating MSL for each location from the gauge data. We computed MSL according to the widely used Intergovernmental Committee on Surveying and Mapping standard (ICSM, 2011), being the mean of hourly water level readings over all available data for each gauge for the years 2005–2010. Our estimates of MSL were used only to examine the relationship between edge elevation and MSL among locations. All site edge elevations were determined relative to the local gauge regardless of the datum for each gauge, therefore our flooding metrics (described below) are unrelated to our estimates of MSL.

Based on the edge elevations of each site, we determined whether each hourly water level reading corresponded to the mangrove edge being flooded or drained and from this derived the metrics of flooding duration, depth, and frequency. Flooding duration estimates were the proportion of hourly readings that the edge would be flooded. Flooding frequency was the number of times each day that the edge transitioned from drained to flooded. We developed flooding depth profiles by calculating the duration of flooding of the mangrove edge for each depth from 0 m (i.e. edge 90% flooded as defined above) to maximum depth in 0.1 m increments.

To summarise flooding metrics for each location, the historic water level data were grouped by season; summer (Dec–Feb), autumn (Mar–May), winter (Jun–Aug), and spring (Sep–Nov). Data completeness varied among gauges; most had >85% valid hourly readings from 2005 to 2010, while the Corner Inlet gauge was only operational from winter 2009 onwards, resulting in only 15% complete records. We initially compared flooding duration among locations during summer 2009/10, when most locations had complete water level data, to all seasons with <20% of hourly water level readings missing (Online Resource 1). Because there was little difference in spatial patterns of flooding duration between the two data sets (Pearson $R = 0.99$), we used the larger data set comprising all locations and seasons with <20% missing data (Online Resource 2) for all subsequent flooding duration comparisons because this provided a more representative indication of regional trends in flooding patterns. Flooding frequency is an absolute measure and is thus affected to a greater extent by missing data than estimates of flooding duration.

Fig. 3 Variation in the tide range and the elevation of the lower edge of mangrove wetlands along the east coast of Australia. *Data* are mean elevations at each location relative to mean sea level (MSL) such that a value of zero indicates the edge at MSL. *Bars* indicate range among replicate sites. Locations mentioned in results section are indicated

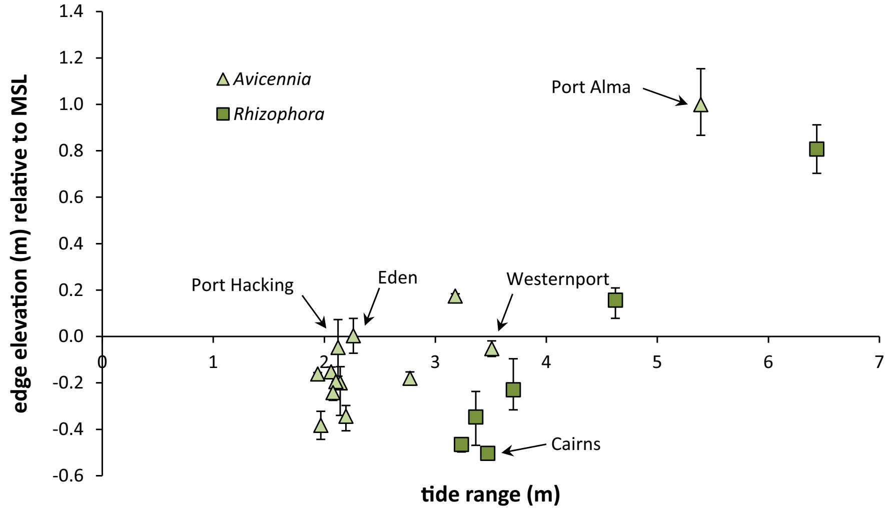
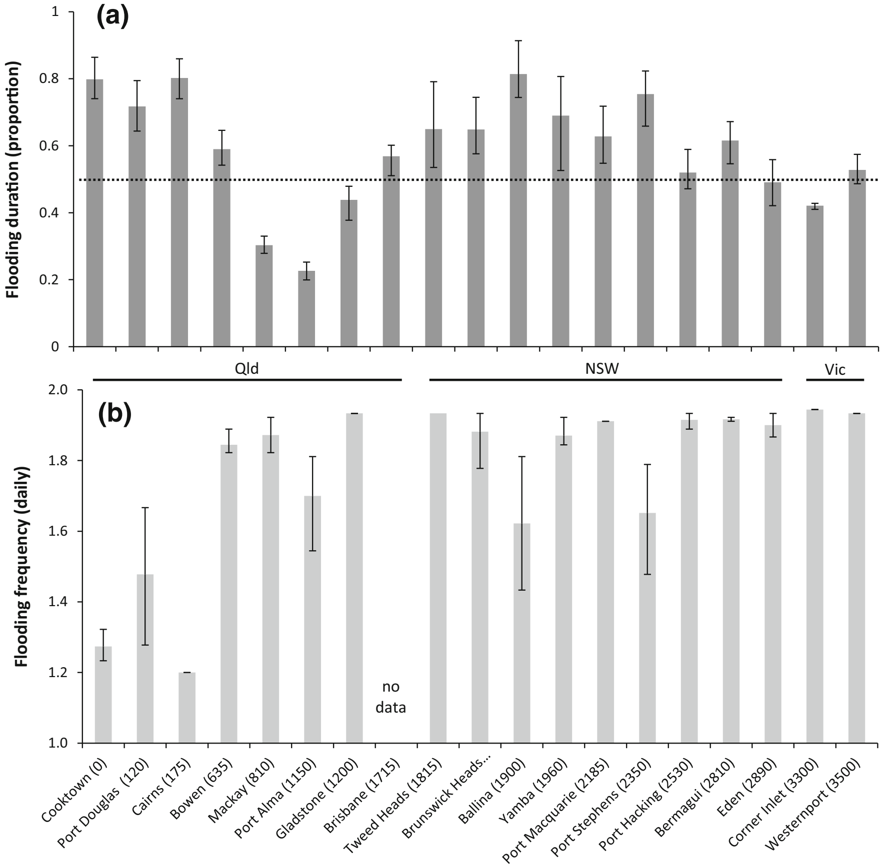
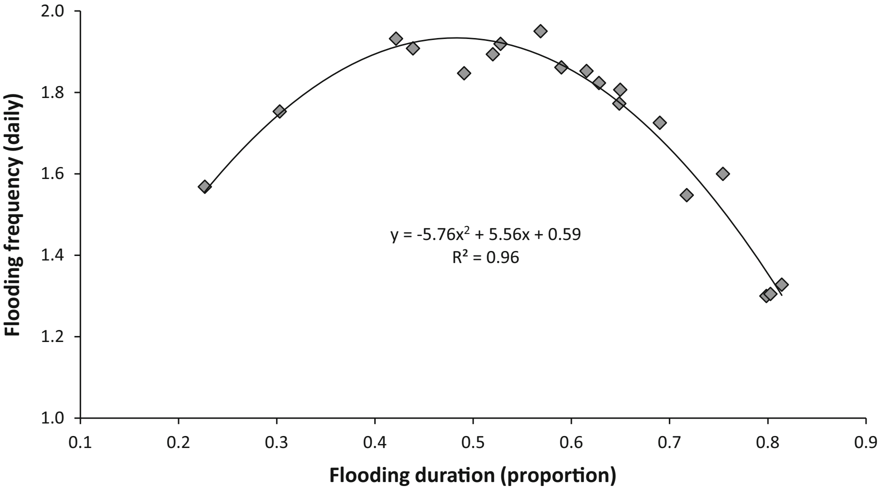


Fig. 4 Geographic variation in flooding of intertidal wetland edges along the east coast of Australia. **a** mean flooding duration, bars indicate range among seasons from 2005 to 2010. *Horizontal line* at 0.5 indicates predicted flooding duration if wetland edge was at Mean Sea Level; **b** mean daily flooding frequency, during summer 2009/2010 (Dec–Feb), *bars* indicate range among replicate sites. This was the season with the most complete gauge data, but no data were available from Brisbane (see Appendix Table 1 in ESM). *Values* in parenthesis after each location name on x-axis indicate approximate coastal distance (km) south from Cooktown. The state in which each location is situated is indicated by the *bars* between (**a**) and (**b**): Qld, Queensland; NSW, New South Wales; Vic, Victoria



Therefore, we compared flooding frequency among locations during summer 2009/2010, the season with the most complete data across locations. Likewise, we used data from summer 2009/2010 to produce edge flooding depth profiles. For this period, 17 of the gauges had complete water level records, Cairns was missing 3.7% of the hourly readings, and the Brisbane gauge had no data available (Online Resource 2).

Fig. 5 Relationship between the duration and frequency of mangrove edge flooding along the east coast of Australia. Flooding duration values are mean duration for each location among all seasons between 2005 and 2010 with <20% missing data, while flooding frequency data are for all seasons during the same period with <5% missing data (see Online Resource 2)



Hence, spatial comparisons of flooding frequencies and depth profiles excluded Brisbane.

Results

Edge elevation

Although the lower mangrove edge broadly tracked mean sea level (MSL) along the east coast of Australia (Online Resource 3a), deviations in edge elevation from MSL (Fig. 3) corresponded to significant geographic variability in wetland flooding (Figs. 4, 5, 6). Edge elevations of individual replicate sites ranged from 0.5 m below MSL at Cairns to 1.15 m above MSL at Port Alma (Fig. 3). The range of edge elevations among replicate sites within locations spanned MSL at only 2 locations: Port Hacking and Eden. The replicate sites at Westernport were close to MSL; just 0.02–0.09 m below. Edge elevations at remaining locations had greater deviations from MSL. There was a positive relationship between edge elevation relative to MSL and tide range, such that locations with the smallest tide ranges tended to have edge elevations below MSL, while those with the largest tide range had edges well above MSL (Fig. 3).

Flooding duration

The lower edges of mangrove wetlands were flooded from an average of 23% of the time in Port Alma (20–25% among seasons) to over 80% of the time in Ballina (74–91% among seasons) (Fig. 4a). The macro-tidal regions of central Queensland (Mackay and Port Alma) had the shortest flooding durations, while the far northern locations and locations in northern NSW tended to have the longest durations. Flooding duration varied widely even between some nearby locations; Port Alma and Gladstone are separated by only 50 km, yet the mangrove edge in Gladstone was flooded for approximately twice as long as the edge in Port Alma. Larger geographic variations in flooding duration mean that some sites were flooded for up to 4 times longer than others.

Flooding frequency

Flooding frequency was also highly variable. During summer 2009/2010, the mangrove edge in Cairns flooded on average little more than once a day, while several locations flooded and drained almost twice daily (Fig. 4b). The large error bars for some locations (e.g. Port Douglas, Ballina, and Port Stephens, Fig. 4b) indicate that variation in edge elevation among sites within a location can result in substantial small-scale differences in the frequency of mangrove flooding. At the broad scale, the flooding frequency data show that, at some locations, most aquatic organisms must be forced to leave the mangroves almost twice as often as at other locations.

There was a strong relationship between flooding frequency and duration (Fig. 5). To examine this relationship, we used flooding frequency estimates from all seasons between 2005 and 2010 that had <5% missing data (Online Resource 2) so that the frequency and duration data represented the same time period. The locations with the highest flooding frequency (average of almost twice daily) were flooded for around 50% of the time. Longer or shorter flooding durations at other locations corresponded with lower flooding frequencies.

Flooding depth

The flooding depth profiles for summer 2009/2010 highlight further complexity in geographic patterns of mangrove edge flooding along the east coast of Australia (Fig. 6). Despite a wide range of durations of mangrove edge flooding to > 0 m, the flooding depth profiles for Queensland (Qld) locations converge as flooding depth increases (Fig. 6a). The duration of edge flooding to >0 m was not closely linked to the maximum flooding depth at these locations. For example, while Port Alma had the shortest edge flooding duration of all locations (26%), and the shallowest maximum depth in Qld (2 m), Mackay had the second shortest edge flooding duration (32%) but the greatest maximum depth (2.7 m) (Fig. 6a). The locations in New South Wales (NSW) showed a different pattern, with lower durations of edge flooding corresponding to lower maximum depths. Edge flooding durations ranged from 45% at Eden to 75% at Ballina and Port Stephens, while maximum depths ranged from 1.1 m at Eden and three other locations, to 1.5 m at Port Stephens (Fig. 6b). The two Victorian (Vic) locations at the southern end of the transect had similar flooding profiles, with the edge flooded from between 41 and 49% of the time, and maximum depths between 1.1 and 1.4 m (Fig. 6c). Comparing these regional depth flooding profiles reveals that geographic patterns in edge flooding duration vary considerably for different flooding depths (Fig. 6d). For example, the mangrove edge at Gladstone was flooded to >0 m for 47% of the time (Fig. 6a); around the middle of the range of edge flooding durations across all locations and close to the minimum duration among NSW locations (Fig. 6d). However, the mangrove edge at Gladstone flooded to a depth of 0.8 m for longer (21%) than any NSW location (2–16%).

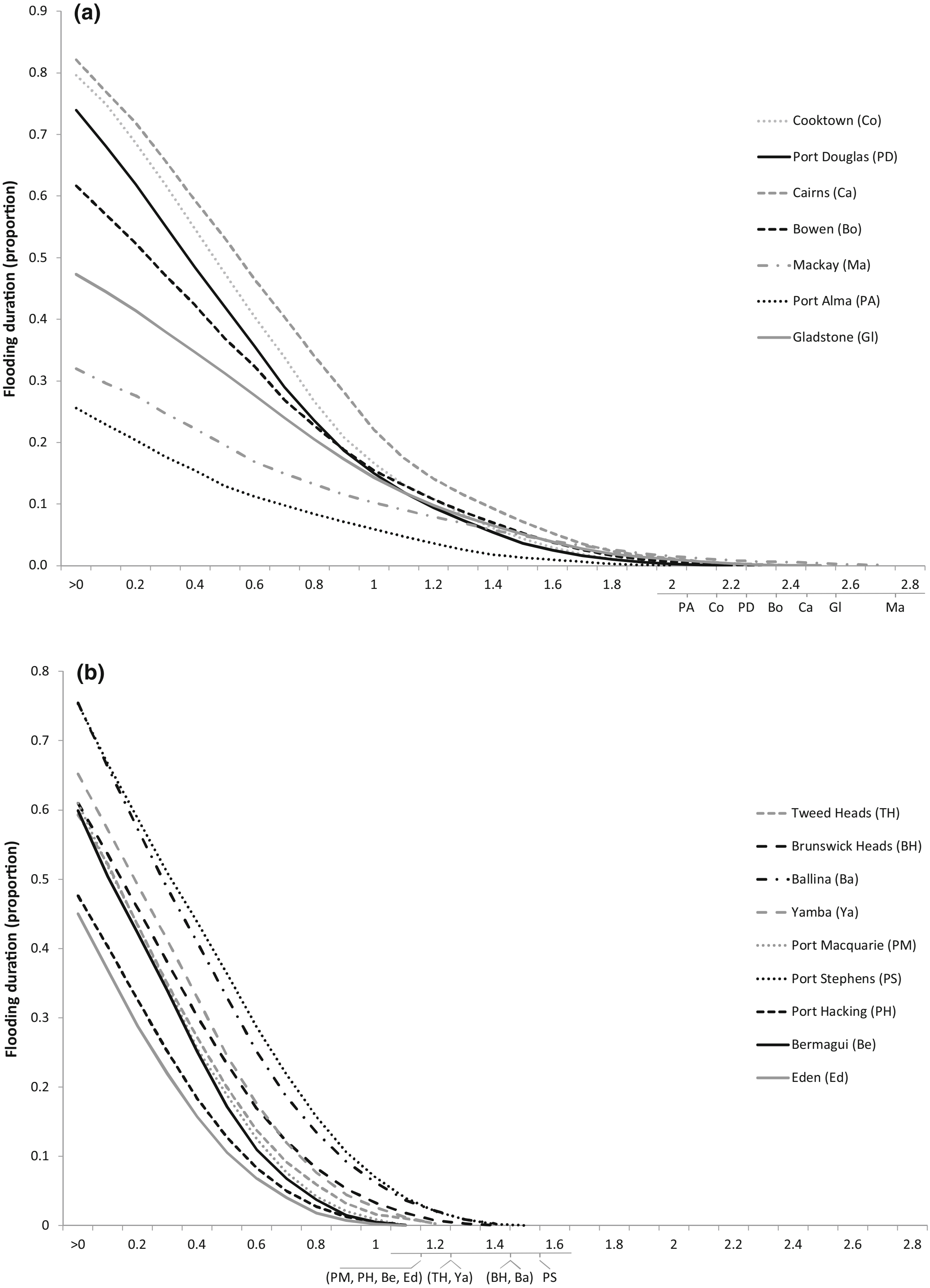
Discussion

Variability in tidal wetland flooding

The elevation of the lower mangrove edges broadly track mean sea level (MSL). However, the deviations from MSL were significant enough to show substantial variation in mangrove flooding patterns. Deviations in edge elevations from MSL of up to 1.15 m corresponded to flooding durations ranging from approximately 20 to 90% of the time among locations. The interaction of variable edge elevations and tidal regimes also resulted in variable flooding frequencies, with some locations flooding almost twice as frequently as others. Maximum flooding depths were also variable, yet all 19 mangrove locations had at least 1 m (and up to 2.7 m) of water over the lower edge on some tides. The interaction between tidal amplitude and the shape of the tidal profile at each location gave rise to highly variable edge flooding durations to different depths, as indicated by the flooding depth profiles. So despite the general relationship between mangrove edge elevation and MSL, tidal wetland flooding patterns are far from consistent among regions, with high variability in flooding frequency, duration, and depth.

Along with a range of interacting physical, chemical, and biological factors, flooding duration is an important determinant of wetland plant distribution (Krauss et al., 2008; Feller et al., 2010), primarily through the influence of soil waterlogging on oxygen availability (Curran, 1985; Ball, 1988; Colmer & Flowers, 2008). Oxygen conditions in soils directly affect plant physiology and metabolic processes (Ungar, 1991; Youssef & Saenger, 1998; Chen & Ye, 2013), and regulate the form and availability of nutrients such as nitrogen and phosphorus (Ball, 1988). Soil oxygen content is modified by flooding duration and interactions with flooding frequency, sediment type, salinity, organic content, and bioturbation (Ball, 1988; Ungar, 1991; Colmer & Flowers, 2008). Although the lower edge of mangrove forests have been broadly considered to occupy relatively fixed positions in the intertidal zone (Lewis, 2005;

Fig. 6 Comparisons of relationships between flooding duration ▶ and depth along the east coast of Australia in summer 2009/2010. Shown from north to south; **a** Queensland locations; **b** New South Wales locations; **c** Victorian locations; **d** all locations combined to allow comparison of flooding profiles among regions. Second x-axis in **a** and **b** indicate maximum water depth over the mangrove edge at each location based on depth profile calculations in 0.1 m increments. E.g. the mangrove edge at Port Alma (PA in *top panel*) was flooded for >0% of the time to 2 m depth, but 0% at 2.1 m. >0 m on the x-axis indicates the initial edge flooding as defined in the methods, and shown in Fig. 4a


(a)
Flooding duration (proportion)
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
>0
0.2
0.4
0.6
0.8
1
1.2
1.4
1.6
1.8
2
2.2
2.4
2.6
2.8
PA
Co
PD
Bo
Ca
Gl
Ma
Cooktown (Co)
Port Douglas (PD)
Cairns (Ca)
Bowen (Bo)
Mackay (Ma)
Port Alma (PA)
Gladstone (Gl)
(b)
Flooding duration (proportion)
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
>0
0.2
0.4
0.6
0.8
1
1.2
1.4
1.6
1.8
2
2.2
2.4
2.6
2.8
(PM, PH, Be, Ed)
(TH, Ya)
(BH, Ba)
PS
Tweed Heads (TH)
Brunswick Heads (BH)
Ballina (Ba)
Yamba (Ya)
Port Macquarie (PM)
Port Stephens (PS)
Port Hacking (PH)
Bermagui (Be)
Eden (Ed)

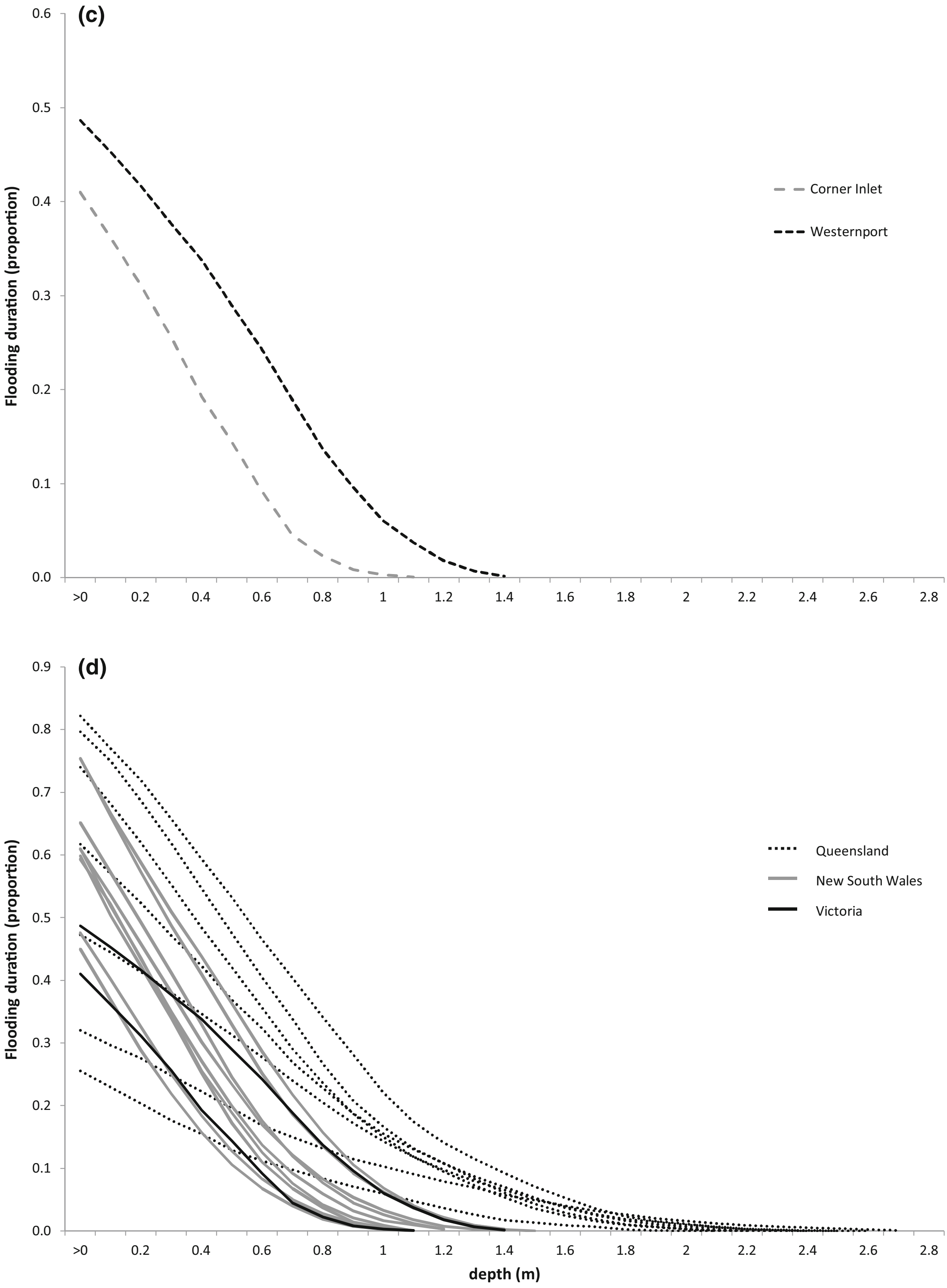


Fig. 6 continued

Duke, 2006), the precise drivers of mangrove distribution remain contentious and key areas of research (Krauss et al., 2008; Crase et al., 2013; Clarke, 2014). From the viewpoint of aquatic organisms that utilise these habitats, variations in the elevation of the lower wetland edge reflect significant differences in accessibility of mangrove habitat among regions (Minello et al., 2012).

Functional values for aquatic fauna

The dynamic and spatially variable nature of access to mangrove habitat must translate into variable functional values of these habitats for aquatic organisms (Igulu et al., 2014). Salt marshes in the southeast of the USA (Minello et al., 2012) show similar levels of variability in flooding patterns to the mangrove systems in eastern Australia. Variable marsh flooding appears to drive selection of the marsh surface by fishery species (Minello et al., 2012) and the significance of wetland production in the food webs supporting them (Baker et al., 2013). Similarly, tidal flooding patterns appear to regulate fish density (Igulu et al., 2014) and foraging (Lugendo et al., 2007) within mangrove habitats. While clear understanding of the functional values of mangrove wetlands for fish and mobile crustaceans remains elusive in many regions (Faunce & Layman, 2009), whatever values these habitats have must be regulated by flooding dynamics that in turn determine patterns of access and occupation (Connolly, 1999; Minello et al., 2012).

Vegetated tidal wetlands are widely considered to provide fish and mobile crustaceans with benefits including increased foraging opportunities and refuge from predation (Sasekumar et al., 1992; Rountree & Able, 2007; Nagelkerken et al., 2008). If access to these habitats is beneficial for aquatic fauna, then time spent outside the wetlands at lower tidal levels logically represents a period of disadvantage through reduced foraging opportunities or increased predation risk (Sheaves, 2005). The costs and benefits of the occupation of vegetated wetlands and adjacent subtidal habitats are unlikely to be a simple linear function of time (i.e. flooding duration), since foraging in tidal systems is often focused during particular parts of the tidal cycle (Gibson, 2003) or at transition zones between different habitats (Hammerschlag et al., 2010). For example, small fish that find refuge in the complex habitat of mangrove roots may be particularly vulnerable to predation as they are forced from the mangroves by ebbing tides (Sheaves, 2005; Hammerschlag et al., 2010). So while our simple metrics of mangrove flooding duration, frequency, and depth serve to highlight the substantial geographic variation in accessibility of mangroves, these factors may interact in complex ways to regulate the functional values of tidal wetlands for aquatic fauna.

The geographic patterns in mangrove edge flooding duration are quite variable for different water depths. For instance, several locations in Qld and NSW have similar edge flooding durations, meaning that access for small nekton that move into mangrove structure as soon as it floods is similar among these locations. However, the durations of flooding to greater depths rapidly diverge such that the geographic patterns of accessibility for fish that require or prefer greater water depths differ from the geographic patterns of accessibility for fish able to access mangrove at shallower depths. Interactions between different sized individuals, or groups of nekton that move into mangrove habitats at specific depths (Ellis & Bell, 2008; Meynecke et al., 2008), are further complicated by these dynamic flooding profiles. Thus, values such as refuge are likely to vary due to complex interactions between flooding dynamics, patterns of habitat use, and local assemblage composition.

We developed simple flooding metrics to highlight variability in factors that may regulate important ecological functions. The development of more sophisticated and detailed metrics may provide greater insights into the specific functional values. For example, the relationship between topography of the wetland surface and tidal flooding adds further complexity to the availability of shallow wetland habitat beyond the lower edge (Minello et al., 2012; Ennis et al., 2014). The physical structure provided by different mangroves (cf. *Rhizophora* prop roots and *Avicennia* pneumatophores) offers refuge opportunities at different scales. The interaction between habitat complexity and water depth means that any refuge provided by mangroves is likely to be highly dynamic, changing rapidly in nature and extent through time and space. Despite the obvious complexities in understanding the functioning of these systems (Rozas, 1995; Rountree & Able, 2007), our simple metrics serve to highlight the potential for significant geographic variability in wetland function.

Implications for research and management

The objective of this study was to assess geographic variability in tidal wetland flooding and thus potential access for aquatic organisms. Our sampling sites were chosen to represent mangrove wetlands in the lower reaches of estuaries in each region. However, mangrove community composition and forest structure changes longitudinally along the length of an estuary (Duke, 2006), as do the relationships between tidal forces and other factors such as river flow and geomorphology (Krauss et al., 2008). Consequently flooding patterns measured in mangroves in our lower estuary sites were unlikely to represent flooding dynamics farther upstream. Regional or location-to-location differences in the extent of longitudinal change in flooding dynamics introduce yet another layer of complexity for understanding mangrove ecosystem function. For example, while Minello et al. (2012) reported similar broad geographic patterns in *Spartina* salt marsh flooding in lower estuary sites of south-eastern USA to those reported here for mangroves, Rozas & Zimmerman (2000) found considerable variation in *Spartina* marsh flooding across sites within a single large estuary (Galveston Bay, Texas, USA). Thus, while our findings represent the broad geographic patterns in mangrove flooding dynamics in eastern Australia, flooding patterns are likely to show significant variations at smaller spatial scales (e.g. within estuarine systems). Connolly (1999) called for the reporting of flooding durations in salt marsh studies to facilitate meaningful comparisons among studies, however reports of flooding duration remain rare. Our findings further emphasise the importance of understanding geographic differences when drawing on information from studies in other regions, and the need for caution in extrapolating understanding from one region to another.

Regional variation in wetland function has further implications for assessments of habitat value, guiding coastal developments, identifying appropriate offsets, and for wetland restoration (Sheaves et al., 2015). For example, many restoration projects that involve replanting mangroves fail completely (Lewis, 2009). Our findings suggest that the appropriate elevation for successful wetland restoration may be site-specific, and restoring natural hydrological regimes and sedimentation processes to facilitate recolonisation is increasingly recognised as more effective than direct planting (Lewis, 2009; Schmitt et al., 2013).

Beyond variability in tidal wetland flooding dynamics, other factors are likely to contribute regional variability in wetland function and value. Climate variability (e.g. Staunton-Smith et al., 2004), ecosystem productivity and catchment processes (e.g. Abrantes et al., 2013), floristic composition and vegetation structure (Duke, 2006), and faunal composition (Sheaves, 2012) all vary over different spatial and temporal scales, and interact to add further complexity to the functioning of tidal wetlands (Faunce & Layman, 2009). The precise mechanisms and processes driving the use and value of tidal wetlands remain key areas of further research (Sheridan & Hays, 2003). The current findings highlight that whatever benefits aquatic organisms gain from accessing wetlands, these benefits must show substantial variation among regions and through time. Examination of wetland function at broad spatial and temporal scales will enhance our understanding of geographic variations in tidal wetland value and help to identify the general properties of these systems that transcend regional variations.

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