# Use of mangroves by fish: new insights from in-forest videos

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ABSTRACT: Even in some of the best-studied areas, there has been little direct evaluation of how extensively mangroves are used by fish, or the extent of their penetration through mangrove forests. As a result, paradigms about the utilisation and value of mangroves have not been fully tested. We used an array of unbaited underwater videos to investigate the extent to which fish used mangroves in north-eastern Australian estuaries. Only a small subset of estuarine species were observed entering the mangroves, and patterns of utilisation differed from those expected based on standard paradigms. In particular, trophic groups such as planktivores occurred rarely even 1 m inside the seaward mangrove margin, with utilisation dominated by a few species known to specialise on mangrove-associated prey. Of the species that did enter the mangroves, only a few penetrated through to the landward edge. The limited use of mangroves by fish in these systems suggests a need to reconsider the ways in which mangroves provide refuge and the extent to which they are used as foraging sites. The fact that mangrove use was more restricted than expected implies that the nursery value of these systems is likely to be conferred at a whole-ecosystem scale, and emphasises the need for a detailed, region-specific understanding of the specific values of the different components of mangrove ecosystems.

KEY WORDS:  Mangrove · Refuge · Tropical estuary · Fish · Underwater video

## INTRODUCTION

Mangroves provide important habitats for fish (Morton 1990, Robertson & Duke 1990a, Nagelkerken et al. 2002); there are clearly demonstrated links between mangroves and the health, diversity and community structure of nearshore fish populations (Nagelkerken et al. 2001, Mumby et al. 2004), and indeed the health of nearshore ecosystems (Mumby & Hastings 2008). It is also widely accepted that mangroves provide substantial fisheries value (Costanza et al. 1997, Kathiresan & Bingham 2001, Creighton et al. 2015), although the extent of that value has rarely been definitively assessed (Manson et al. 2005).

Substantial variations in mangrove flooding dynamics in different parts of the world suggest that patterns of mangrove habitat use by fish may also vary considerably among locations (Igulu et al. 2014,

Baker et al. 2015). While underwater visual censuses have facilitated detailed studies of mangrove utilisation by fish in a number of areas of the world (e.g. Nagelkerken et al. 2001, Mumby et al. 2004), quantifying direct use of tropical Indo-Pacific estuarine mangroves has been hampered by substantial populations of estuarine crocodiles. Consequently, studies have been mainly restricted to netting techniques that are limited in their effectiveness in dense mangrove forests. The most successful method to determine which fish use mangroves is block netting; however to our knowledge, only 2 studies (Morton 1990, Halliday & Young 1996) used this approach in a way that assured that all fish sampled had actually entered the mangrove forest (i.e. they used block nets deployed directly along the front edge of the mangroves). Other studies used methodologies that included adjacent mud banks (Blaber et al. 1989) or

blocked mangrove drainage channels (Robertson & Duke 1990a), both of which are habitats known to harbour substantial numbers of fish (Johnston & Sheaves 2007), and therefore likely included fish that had not entered the flooded mangrove forest itself. Both the Morton (1990) and Halliday & Young (1996) studies sampled single sites, and both recorded a total of 42 species, only 6 of which comprised >55% of the total numbers. In addition, while Morton (1990) reported high fish densities, Halliday & Young (1996) found that densities were low, highlighting site-specificity in mangrove utilisation.

The use of underwater video overcomes many of the problems associated with sampling in mangroves, and provides the opportunity to collect data from within flooded meso- and macrotidal mangrove forests at a level of detail not previously possible. Until now, there have been few video studies conducted in estuaries (Meynecke et al. 2008, Kimball & Able 2012). However, video has proved successful at detailing movements in and out of seaward mangrove margins (Ellis & Bell 2008), suggesting the potential for more detailed investigations of mangrove use. Although not without limitations (Kimball & Able 2012) (e.g. only sampling small areas, being limited to areas with sufficient water clarity, and only being employed during the day), underwater video provides the opportunity to determine which species use the forests, their temporal patterns of use, and their behaviours while in the forest; information not available from traditional capture sampling (Becker et al. 2010).

To develop a more detailed understanding of how fish use tropical Indo-Pacific mangrove forests, we used an array of replicate, unbaited underwater video cameras in the mangrove forests of tropical north-eastern Australia to address 3 questions: (1) What component of the available fish fauna enters mangrove? (2) How extensive is penetration into the forest by those species? (3) What are the temporal patterns of mangrove use by those species?

## MATERIALS AND METHODS

### Study sites

During 2012 and 2013, we deployed underwater video cameras (UVCs) in fringing mangrove forests at 7 sites in 4 macrotidal estuaries in north-eastern Australia: Deluge Inlet (3 sites), Mulligan Creek (1 site), Victoria Creek (2 sites) and Cassady Creek (1 site) (Fig. 1). Forest widths at the study sites

ranged from narrow (~5 m) to wide (>150 m) fringes, and vegetation structure varied among and within sites from *Rhizophora* spp. stands, through mixed stands of *Rhizophora* spp. and *Avicennia marina*, to multi-species stands with various mixtures of *Rhizophora* spp., *A. marina*, *Bruguiera* spp., *Osbornia octodonta*, *Aegiceras corniculatum*, *Aegialitis annualata* and *Sonneratia alba*. The maximum tide range in the region is 4 m, and the lower mangrove edge is flooded approximately 70% of the time (Baker et al. 2015).

### Field methods

We used unbaited UVCs (Model ATC9K, Oregon Scientific; camera dimensions: 9.8 × 6.2 × 7.3 cm; field of view: ~49 cm wide × 24 cm high at 50 cm from the lens), mounted on stable bases (20 × 14 cm; max. height with camera: 13 cm) to record fish using mangrove forests. Unbaited videos were preferred because baiting techniques can produce biased esti-
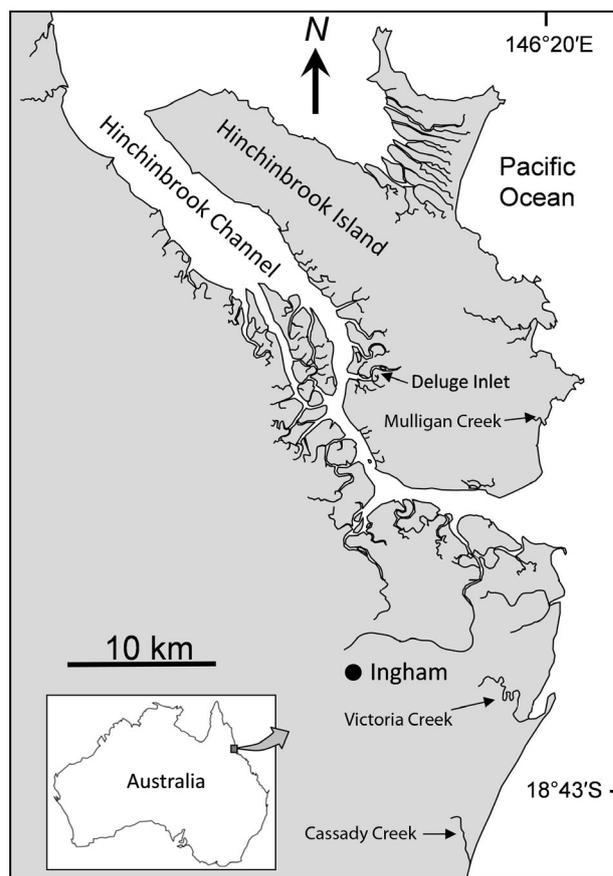


Fig. 1. Location of estuarine mangrove study sites in north-eastern Australia

mates of small-scale habitat use by drawing fish in from adjacent habitats (Bassett & Montgomery 2011). The cameras were set to record high definition images at 30 frames s$^{-1}$. At each site, 9 cameras were positioned 1 to 2 m inside the seaward edge of the forest ('seaward zone'), at the edge adjacent to the estuary main channel, and in an area of the forest first flooded by incoming tides. The forest edge was defined as having essentially continuous mangrove root structure, such as beds of *A. marina* pneumatophores or *Rhizophora* spp. prop roots. A second set of 9 cameras was deployed the same distance inside the landward edge ('landward zone') of the forest. The logistical difficulty in deploying cameras at the landward edge of mangrove forests backed by natural terrestrial forest meant that there were limits to how far apart the cameras could be placed; thus, cameras were positioned haphazardly, most >50 m apart, and at a minimum of at least 20 m apart. This spacing did not appear to compromise sample independence since the faunal composition recorded by adjacent cameras was no more similar than that between the 2 most distant cameras at a given site.

UVCs were placed in small gaps among the roots/pneumatophores with no obstructions to the field of view within at least 50 cm of the camera lens, and were directed towards the interiors of the forests to prevent sighting of fish outside forest edges. Cameras were deployed so that their horizontal orientation was parallel with the substrate, the lower edge of the lens was 7 cm above the substrate, and the substrate horizon was two-thirds of the way down the field of view. UVCs were deployed and left to record during flood tides. Seaward zone cameras were deployed as the water first entered the mangrove forest at depths less than 8 cm (the depth at which camera lenses were fully submerged), were left to record until the camera batteries were discharged (2 to 3 h, depending on light conditions), and retrieved at the commencement of the ebb tide. Seaward zone cameras were deployed from a small dinghy and landward cameras from the shore following the same protocols as seaward cameras. Information about mangrove species, substrate type and forest width was recorded at each camera position.

Sampling was confined to spring tides to ensure there was sufficient tidal flooding for fish to utilise mangroves. Video recording was not attempted if secchi depth was <1 m (which was always the case when spring high tides exceeded 3 m, and occurred at other times due to the presence of suspended sediment caused by wave action). Maximum water depths over the cameras at the 7 sites were: Cassady Creek, 1.15 m; Deluge 1, 1.50 m; Deluge 2, 1.79 m; Deluge 3, 1.10 m; Mulligan Creek, 0.85 m; Victoria Creek 1, 0.59 m; Victoria Creek 2, 0.85 m. Wet and post-wet season conditions were generally too turbid for video sampling; therefore, sampling was undertaken through the pre-wet period. This is a period of high recruitment in Australia's tropical estuaries, when fish densities and species richness are greatest (Robertson & Duke 1990a, Sheaves et al. 2010), thus providing the greatest potential to determine mangrove utilisation.

## Data extraction from videos

Of 126 videos collected, 27 were omitted due to poor visibility, resulting in a total of 50 seaward and 49 landward videos used in the analysis. Useable videos had visibilities ranging from 50 to 210 cm, with the majority around 100 cm; visibility in the unusable videos was <50 cm and caused by conditions such as unfavourable patterns of shade, turbidity caused by the activities of stingrays or the wash of passing boats, or unacceptable restrictions to the field of view such as floating debris lodging across the camera lens.

Videos were viewed in media players (e.g. VLC player) capable of slow speed replay and image optimisation (contrast, brightness, colour saturation) to aid in fish identification. For data extraction, videos were subdivided into 1 min intervals commencing once the camera lens was first fully submerged (8 cm); the occurrence of each fish taxon present in each 1 min of video was recorded. Data extraction was limited to recording presences because such data are usually more robust than fully quantitative approaches (Manley et al. 2004), particularly where indices of abundance are likely to be unstable (Legendre & Legendre 2003), and because they treat species with different patterns of behaviour (e.g. schooling versus non-schooling) in equivalent ways (Sheaves & Johnston 2009). Identification of fish was undertaken by 2 researchers experienced in local fish identification and validated by exchanging videos between recorders and cross-referencing results. When fish were too indistinct to be identified, or if discrepancies in identification could not be resolved, those occurrences were recorded as 'fish'. Some fish (particularly blenniids and many gobiids) were allocated to species-level morphotypes even though their species could not be determined from video examination. None of these were common faunal components (only 148 records out of >23 000).

Ontogenetic stage was recorded where it could be determined from colour or morphology. For most species, almost all individuals were in a single onto-genetic group so the information was not utilised in analyses. However, although *Acanthopagrus* spp. juveniles did not possess characteristics that would enable them to be allocated to species and thus were only identified to genus, they did have distinct pat-terning which allowed them to be reliably distin-guished from more mature individuals. Most larger *Acanthopagrus* spp. individuals could be reliably identified as either *A. australis* or *A. pacificus.* Un-identifiable larger *Acanthopagrus* spp. were only included in analyses of total fish occurrences.

## Data analysis

A ranking procedure was used to develop an index of the extent of mangrove utilisation by the different fish. This comprised all identified taxa, including species and species-level morphotypes. Species were ranked for each site based on the proportion of 1 min intervals in which that species occurred, summed across all videos at each site, and the mean rank cal-culated for the top 10 species at any site.

## Fish composition

Fish composition was compared among sites, zones (seaward vs. landward), substrate type (rock, sand, silt, mud) and dominant mangrove vegetation type (*Rhizophora* spp., *A. marina, Bruguiera* spp., *O. octo-donta, A. corniculatum*), using a multivariate classifi-cation and regression tree (mvCART) (De'ath 2002) based on Bray-Curtis dissimilarities. Dependent vari-ables were the proportion of 1 min intervals each species was present in each video. Only species that occurred in >5% of videos were included. Data were 4th root transformed to reduce the impact of extreme values, and row-standardised to convert the data into proportions for each video. This focussed interpreta-tion on a definition of 'composition' such that videos with similar profiles of species proportions were interpreted as having similar compositions. The mvCART analysis was conducted using the 'mvpart' routine (De'ath 2007) in R, and fitted using 10-fold cross validation. Tree selection was based on min-imising cross validation error, with the final mvCART tree selected as the most common 1-SE tree (i.e. the smallest tree within 1 standard error of the tree with minimum cross validation error) from 100 replicate runs. Species richness was analysed using a univari-ate classification and regression tree (uvCART) on the same explanatory variables and using the same tree-fitting procedure.

## Pattern of mangrove forest use

The extent of the fishes' penetration into the man-groves over time during the rising tide was investi-gated for the most commonly occurring taxa (spe-cies/morphotypes) in the mangrove videos (i.e. those occurring in >25% of videos), again employing uvCARTs with the fitting procedure described above. The base data were taxon presence min$^{-1}$ of video. Dependent variables were calculated as the propor-tion of presences min$^{-1}$ for each 10 min segment of video for each taxon. These data were arcsine trans-formed before analysis. Explanatory variables were site, zone, substrate type, dominant mangrove vege-tation and maximum water depth (at video retrieval). To investigate temporal patterns in occurrence dur-ing tidal flooding, the analyses were re-run with the addition of the variable 'minutes since flooding'. The analyses were also re-run using only the landward samples and the variables forest width and site, to investigate the extent to which the occurrence of dif-ferent species in landward mangroves was influ-enced by mangrove forest width.

Patterns of mangrove use over the rising tide for commonly occurring taxa were investigated graphi-cally. The large number of profiles (i.e. individual videos) were summarised by calculating the mean number of videos in which each taxon occurred for each minute across all videos (keeping landward and seaward videos separate). The resulting profiles were smoothed using locally weighted regression (LOESS, 1st degree polynomial, sampling proportion 0.25; Cleveland & Devlin 1988) to display major pat-terns of fish occurrence over time. The videos were of different durations because the landward edge of the mangroves is flooded for a shorter amount of time than the seaward edge; therefore, to ensure that the same number of observations contributed to mean numbers, only videos with durations of ≥110 min for seaward videos (42 of 50 videos; 84%) and ≥90 min for landward videos (39 of 49 videos; 80%) were ana-lysed. Videos of shorter durations were omitted, and those of longer durations were truncated at the spec-ified time cut-offs. Only videos in which a species or morphotype was present were included. Conse-quently, these estimates cannot be related to total probability of encounter per minute but rather are

focussed on understanding patterns of utilisation when the taxon was present in the mangrove forest. Patterns of use were also investigated for barramundi *Lates calcarifer*, a species of high commercial and recreational value that is widely reported to use northern Australia's estuaries as nurseries, but that occurred in only 7% of videos. Information on its use of mangroves was analysed due to its high economic value, but should be interpreted with caution due to the small sample size.

## RESULTS

### Faunal compositional

Approximately 96.6% of fish observed in the mangrove videos (23 765 total records) could be confidently identified to at least genus level, and comprised 67 taxa (see Table S1 in the Supplement at www.int-res.com/articles/suppl/m549p167_supp. pdf). However, a few species occurred in a high percentage of the videos (Table 1). The sparid *Acantho-*

*pagrus pacificus* made the most extensive use of mangroves, occurring in 89% of videos and ranking in the top 10 of proportional duration observed at all 7 sites (Table 1). Juvenile *Acanthopagrus* spp. exhibited similar use, occurring in 81% of videos and also ranking in the top 10 at all sites. Although identified at all sites, a second sparid, *A. australis*, showed a lower level of utilisation, occurring in only 47% of videos and ranking in the top 10 in only 5 sites. Other fish species that used mangroves extensively included *Gerres filamentosus*, *G. oyena*, *Pseudomugil signifer*, and *Lutjanus argentimaculatus.*

Fish composition varied greatly among sites, with distinct assemblages differentiating 4 groups: Cassady Creek and Victoria Creek 2, Deluge 3 and Victoria Creek 1, Mulligan Creek, and Deluge 1 and 2 (Fig. 2). Cassady Creek and Victoria Creek 2 were particularly distinct, with substantial contributions from most of the common species. Each of the other sites was dominated by a smaller group of species. Deluge 3 and Victoria Creek 1 were further differentiated on the basis of substrate type, with high occurrences of *P. signifer* over mud and silt substrates ver-

Table 1. Species identified by underwater video cameras that used mangroves most extensively during this study. All species that ranked in the top 10 at any site are shown; sites (D1: Deluge 1; D2: Deluge 2; D3: Deluge 3; M: Mulligan Creek; V1: Victoria Creek 1; V2: Victoria Creek 2; C: Cassady Creek ) are listed in order from north to south as per Fig. 1. The ranks (when in top 10) at each site are displayed for each site; the percentage of videos in which a species was present, number of sites present, mean rank, and number of sites at which a species ranked in the top 10 are also provided. Blank cells indicate the species that did not rank in the top 10 at that site. Note: at Site D2, only 9 taxa were observed, hence rankings are from 1–9

| Species | D1 | D2 | D3 | M | V1 | V2 | C | % of videos | No. of sites present | Mean ranking | No. of sites in top 10 |
|---|---|---|---|---|---|---|---|---|---|---|---|
| *Acanthopagrus pacificus* | 1 | 2 | 4 | 2 | 2 | 6 | 5 | 89 | 7 | 1 | 7 |
| *Acanthopagrus* spp. juveniles | 3 | 1 | 2 | 7 | 7 | 3 | 1 | 81 | 7 | 2 | 7 |
| *Gerres filamentosus* | 4 | 3 | 6 | 4 | | 9 | | 63 | 7 | 3 | 5 |
| *Gerres oyena* | 7 | 5 | 9 | 9 | | 2 | 4 | 58 | 6 | 4 | 6 |
| *Pseudomugil signifer* | 2 | 4 | 1 | 5 | 6 | | 8 | 54 | 6 | 5 | 6 |
| *Lutjanus argentimaculatus* | 6 | 7 | | 5 | | | 7 | 51 | 7 | 7 | 4 |
| *Acanthopagrus australis* | 8 | 8 | | 8 | 9 | | 6 | 47 | 7 | 6 | 5 |
| *Toxotes chatareus* | | | 10 | 3 | | 7 | | 44 | 6 | 8 | 3 |
| *Chelonodon patoca* | | | | | 4 | | 3 | 40 | 4 | 14 | 2 |
| *Siganus lineatus* | | | 7 | | | 8 | | 37 | 6 | 10 | 2 |
| *Lutjanus russellii* | | | | | | 4 | 9 | 34 | 6 | 9 | 2 |
| *Ambassis vachellii* | | | | | 3 | 1 | 2 | 31 | 6 | 11 | 3 |
| *Lutjanus fulviflamma* | | | | | | 5 | | 28 | 5 | 13 | 1 |
| Goby sp. 9 (pelagic, spot) | 8 | 9 | 3 | | 1 | | | 22 | 4 | 12 | 4 |
| *Chelon subviridis* | | | | 10 | 8 | | | 17 | 6 | 15 | 2 |
| Goby sp. 10 (pelagic, line) | | | 1 | 4 | | | | 15 | 3 | 18 | 2 |
| *Terapon jarbua* | | | | | 10 | | | 13 | 3 | 22 | 1 |
| Redigobius balteatus | 5 | | | | | | | 12 | 3 | 25 | 1 |
| *Zenarchopterus buffonis* | | | 8 | | | | | 10 | 5 | 19 | 1 |
| *Neoarius graeffei* | | | | | | 10 | | 8 | 2 | 30 | 1 |
| Lates calcarifer | | | | | | | 10 | 7 | 4 | 17 | 1 |
| Goby sp. 7 | | | 5 | | | | | 3 | 2 | 28 | 1 |
| *Psammogobius* sp. | 10 | | | | | | | 3 | 2 | 31 | 1 |
| *Gerres oblongus* | | 6 | | | | | | 2 | 1 | 40 | 1 |
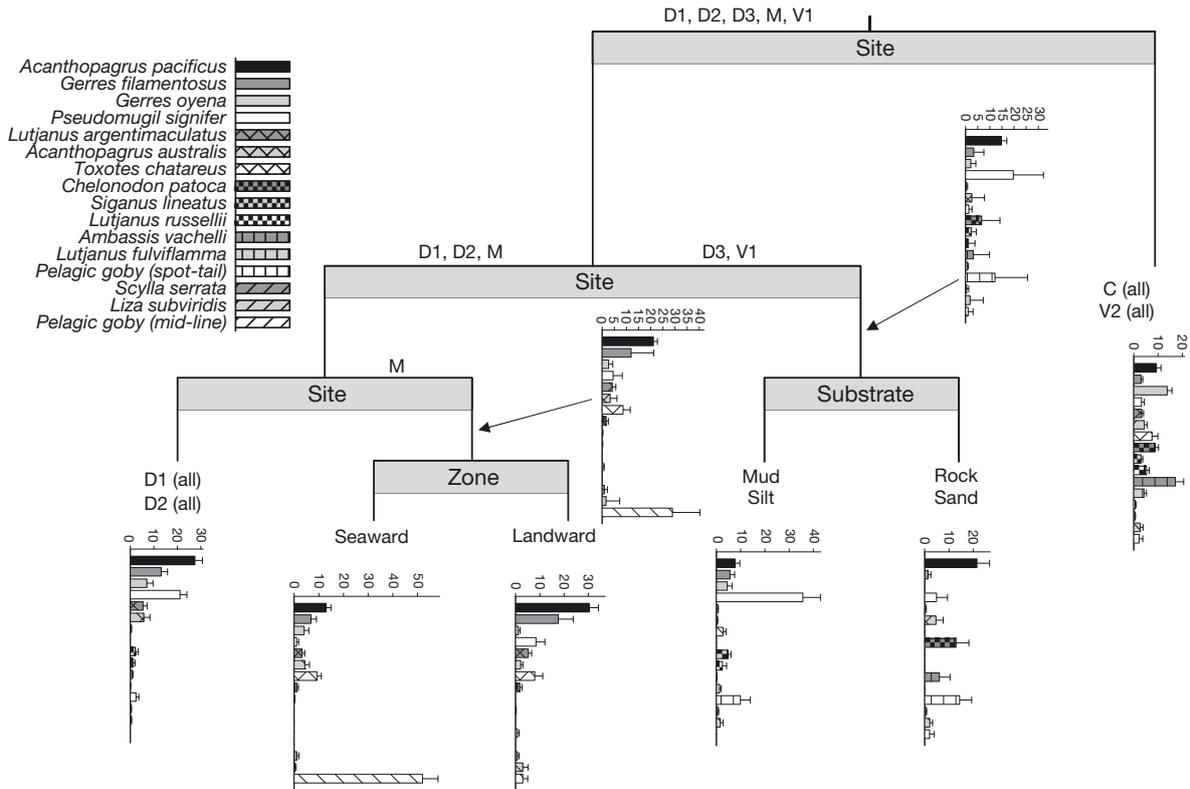
Fig. 2. Fish use of mangrove sites in north-eastern Australia (see Table 1 for definitions of site abbreviations). Multivariate classification and regression tree (mvCART) analysis was based on Bray-Curtis dissimilarities, and dependent variables were the percentage of minutes that each species seen in >5% of videos occurred in each video. Data were 4th root transformed to reduce the impact of extreme values and row standardised to convert to proportions for each video. Explanatory variables were compared among sites, zones (seaward vs. landward), substrate type (rock, sand, silt, mud) and dominant mangrove vegetation type (*Rhizophora* spp., *Avicennia marina*, *Bruguiera* spp., *Osbornia octodonta*, *Aegiceras corniculatum*). Bar plots under each terminal node and adjacent to non-terminal site nodes indicate mean (±SE) % of minutes present for each species. Species in each bar plot from left to right are shown from top to bottom in the key
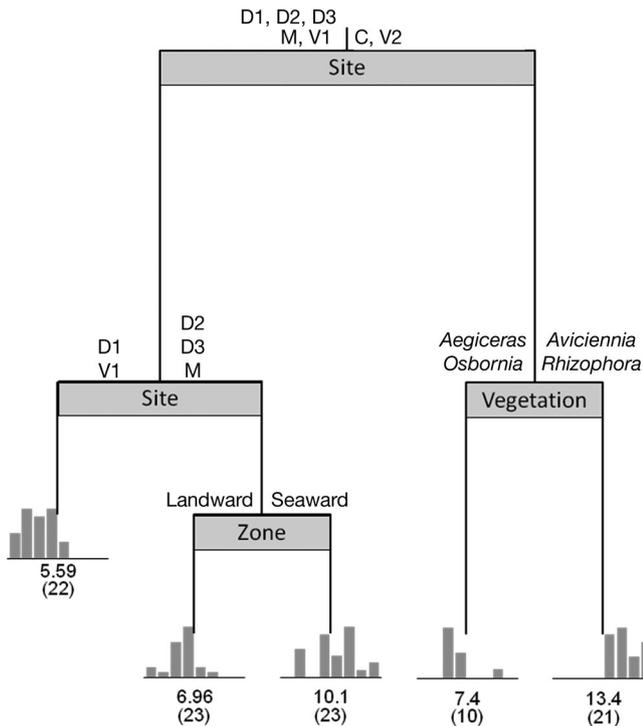


sus dominance of *A. pacificus* and *Chelonodon patoca* on sand and rock substrates. The only differentiation in overall assemblage composition between the seaward and landward zones of the mangrove forest occurred at Mulligan Creek, and was almost entirely attributable to a very high occurrence of an unidentified pelagic goby that was confined mainly to the seaward part of the site. Species richness also varied substantially among sites (Fig. 3), although site grouping was somewhat different. Vegetation type influenced species richness at Cassady Creek and Victoria Creek, with substantially more species in sites with *Avicennia marina* or *Rhizophora* spp. than those with *Aegiceras corniculatum* or *Osbornia*

Fig. 3. Univariate regression tree for species richness of mangrove fauna in north-eastern Australia. Explanatory variables are the same as in Fig. 2. Bar graphs below the terminal branches indicate the distribution of species richness values at that node. Numbers below bars are estimates of mean species richness for each node; numbers in brackets indicate the number of samples in each node

*octodonta*. More species were found in the seaward fringe of the mangroves in Deluge 2, Deluge 3 and Mulligan Creek than in Deluge 1 or Victoria Creek 1.

## Estuary fauna that use mangroves

Eleven studies from north-east Queensland encompassing 48 different estuaries provided data enabling the ranking of fish catches based on some measure of catch per unit effort (CPUE) from a specified gear type for 234 named species. The 25 species that ranked highest in occurrence on our videos were all reported from at least one of those previous stud-

ies (Fig. 4), with the exception of *Redigobius balteatus*, which was probably not identified to species in previous studies (*Parvigobius* spp., a synonym for *Redigobius*, was reported from seine net catches in a study from Trinity Inlet; Blaber 1980). Despite similarities with previously reported fauna, the rankings from our mangrove videos differed substantially from those made using fishing gears that sampled the main estuaries. The characteristics of gill nets and fish traps (Fig. 4c,e) result in the targeting of particular components of the fish assemblage, at least partly explaining the differences in rankings. In particular, the ability of the fish to escape through mesh netting means that many of these gears most probably
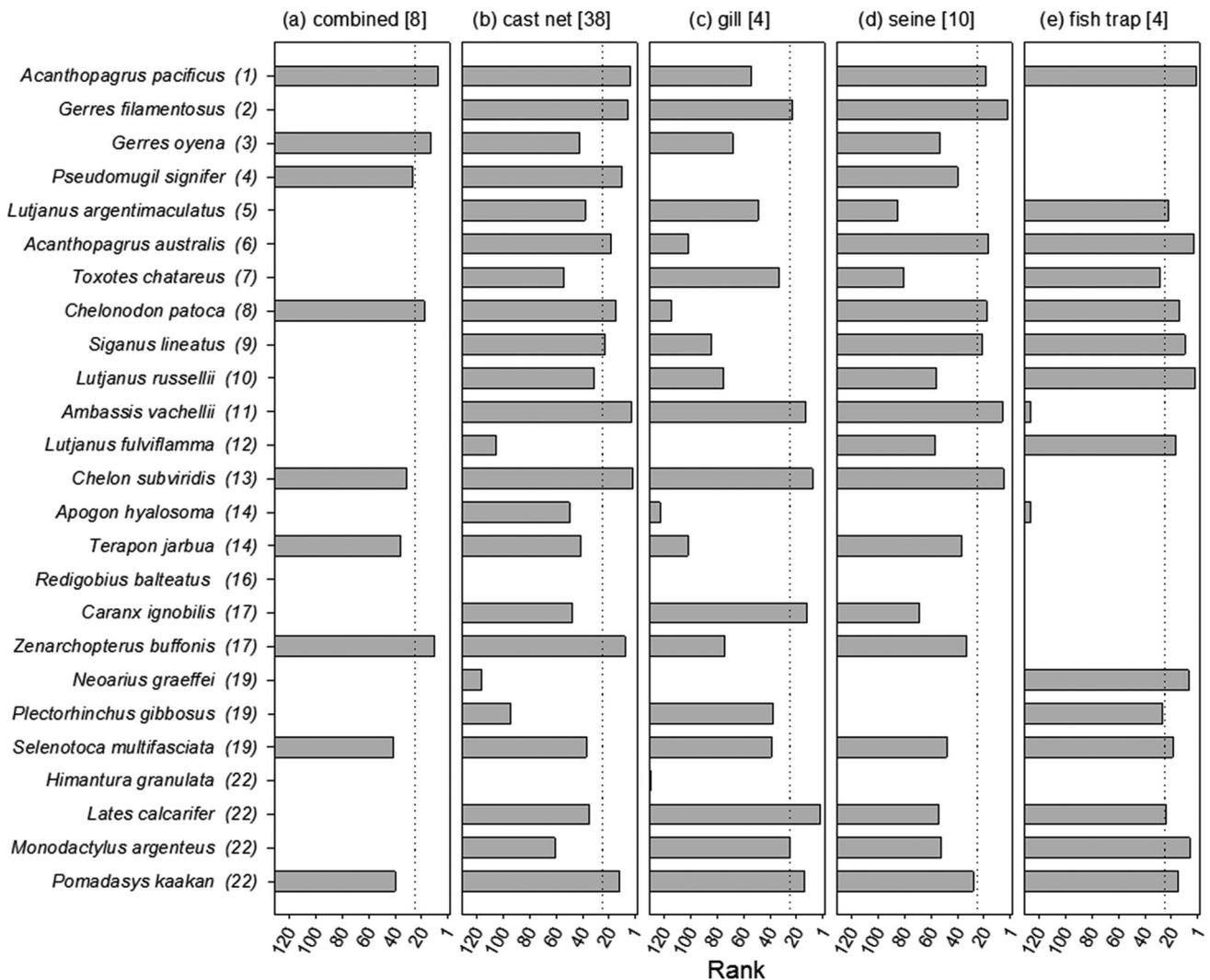


Fig. 4. Comparisons of species rankings in mangrove videos to rankings in previous north-east Queensland estuarine studies. Bars indicate ranks determined by (a) combined gears, (b) cast nets, (c) gill nets, (d) seine nets and (e) fish traps of the top 25 ranked species in the mangrove videos. Numbers in brackets next to species names indicate rankings in videos; numbers in square brackets indicate the number of estuaries that contribute to the estimates for each gear type. The 8 estuaries contributing to estimates for (a) all included gill nets plus at least 1 other gear

underestimate small species and juveniles that likely use mangroves extensively. However, this does not explain the divergent rankings between the videos and cast and seine nets (Fig. 4b,d), which use mesh sizes small enough to catch most small fish (cast nets: 5 to 6 mm mesh; seine nets: all except 1 case, 2 to 12 mm mesh). Rather, it suggests that some species make extensive use of mangroves, while other common estuarine species tend to remain in the estuary main channel. This is clearly demonstrated by the number of species that ranked highly in samples collected from the main estuaries, but were absent or lowly ranked in mangrove videos (Fig. 5). Of particular note:

• Only 2 sightings of *Epinephelus malabaricus* were recorded in mangrove videos, even though *E. malabaricus* and its congener *E. coioides* are common components of fish trap catches along steep mangrove banks

• Planktivores (such as *Herklotsichthys castelnaui* and *Escualosa thoractata*) that ranked highly in net catches were rarely seen in mangrove videos

• Benthopelagic micro-invertebrate feeders, such as *Leiognathus equulus* and *Nuchequula gerreoides*, which comprise a large part of net catches in northeast Queensland estuaries, were rarely encountered in mangroves

• Although a number of species of Mugilidae rank highly in estuarine net catches, there were relatively few occurrences in mangrove videos, and those did not rank highly. Other detritivores that are common in the regions estuaries, such as *Anodontostoma chacunda*, *Nematalosa come* and *Chanos chanos*, were never seen in mangrove videos

• Shallow water predators (such as *Platycephalus fuscus*) that might be expected to enter shallow mangrove waters to feed were absent from mangrove videos

• Although cursorial piscivores such as the carangids *Caranx* spp. and *Scomberoides* spp. were common in studies of the main estuary body, they were absent or low ranking in videos

• While 4 species of Sillaginidae are common components of the fauna of shallow estuarine banks in north-eastern Australia, only 1 species, *S. ciliata*, was identified in the videos, and then only at 1 site.

## Extent of fish penetration through the mangroves

In line with the results of the mvCART and the analysis of species richness, the species-by-species univariate analyses of occurrences per 10 min block

reflected a high level of variation in the presence of commonly occurring mangrove fish between sites, with a primary site split for all taxa (Table 2). For all fish combined, and for 6 of the 13 taxa occurring in >25% of videos, there was a greater proportion of occurrences in seaward versus landward videos, although this effect was generally only apparent for sites with the highest proportion of occurrences. This trend of higher abundance in seaward videos is reflected in the overall percentage of videos in which these taxa occurred; of the 13 commonly occurring mangrove fish, only the 2 *Gerres* species occurred in more landward than seaward videos.

In line with the full data set, when landward samples were analysed separately the primary effects were differences among sites. Width of mangrove forest was only important for 2 species: *C. patoca* and *Siganus lineatus*, both of which occurred more often in videos from narrow (<12 m) mangrove forests (Table 3). Other species showed no differences in the proportion of time they were present in relation to mangrove forest width.

## Temporal patterns of mangrove use

When the variable 'minutes since flooding' was included, uvCART analysis indicated variations in occurrence over time for all commonly occurring fish except *S. lineatus* and *Toxotes chatareus* (Table 2). For most variables, the addition of minutes only produced subsidiary splits — meaning variation over time was not always detectable in all sites or zones. However, for *P. signifer* the model was modified substantially, with minutes forming the primary split, indicating a general difference in presence over time with occurrences greatest in the first 20 min of mangrove flooding regardless of site or location of the camera (seaward or landward). The pattern of highest occurrences early in the flooding period (20 to 30 min) was also apparent for juvenile *Acanthopagrus* spp. and *C. patoca*. Most other species delayed arrival until flooding was more extensive, and thus were generally not common in the first 10 to 20 min.

The smoothed profiles of most fish followed one of 2 patterns of occurrence over the tide. One group remained at relatively constant numbers once they entered the mangroves during the first 20 min of flooding, with similar patterns in both seaward and landward zones (Fig. 6a, Fig. S1 in the Supplement). This group was designated 'foragers', because most are known to feed extensively on prey found in man-
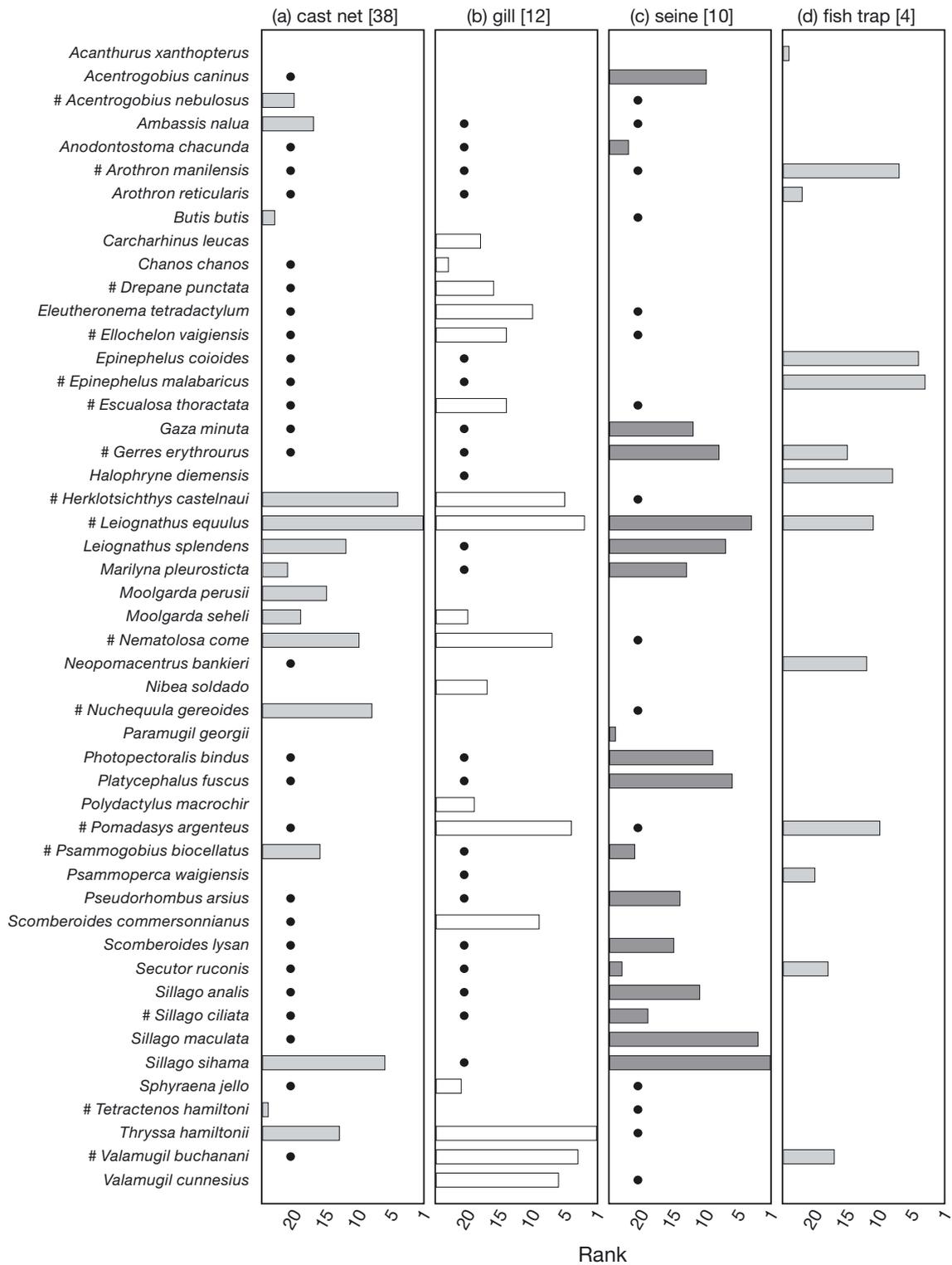
Fig. 5. Species that ranked highly in previous north-east Queensland estuarine studies but that were absent or lowly ranked in mangrove videos. Bars: ranking of the top 25 species in (a) cast net, (b) gill net, (c) seine net and (d) fish traps; numbers in square brackets: number of estuaries that contributed to the estimates for each gear type. ●: species occurring in a gear but not ranked in the top 25 in that gear; #: species seen but not ranked in the top 25 in videos. Studies used were: Blaber (1980), Robertson & Duke (1987, 1990a), Ley et al. (2002), Ley (2005), Sheaves (2006), Johnston & Sheaves (2007, 2008), Ley & Halliday (2007), Sheaves & Johnston (2009), Sheaves et al. (2010)

Table 2. Univariate classification and regression tree (uvCART) analyses of fish presence inside mangrove forests in north-east Queensland, showing the proportion of presences per 10 min of video for species/groups occurring in >25% of videos. For each analysis, uvCART includes site (see Table 1 for site abbreviations) and zone (seaward or landward) as explanatory variables. Numbers in brackets after species indicate regression tree size (i.e. number of terminal branches). Site always formed the primary split in each tree; columns 2 and 3 indicate the proportion of videos in each zone that each species group was present. When a zone split occurred, the sites at which the split occurred and the mean proportion of minutes the species group was present in each zone is shown. For example, 'All fish' indicates a split among zones at Sites C and V2, with fish present 79% of the time in the seaward and 44% in the landward zone. The CARTs were re-run after adding minutes as an explanatory variable; when this formed a split, the time factor levels leading to the terminal branch with highest proportion of presences is indicated (note some variables have 2 'minute' splits); e.g. *Acanthopagrus* spp. juveniles formed 2 splits based on minutes, indicating greater occurrence in the first 45 min of videos, especially high in the first 25 min. –: models where there were no zone splits

| Species | % of videos present | | Primary split (always 'site') | Zone split | Minutes |
|---|---|---|---|---|---|
| | Seaward | Landward | | | |
| All fish (7) | 100 | 100 | C, D2, D3, V2 > D1, M, V1 | For C, V2: seaward (0.79) > landward (0.44) | >15 |
| *Acanthopagrus* spp. juveniles (5) | 82 | 79 | C, D1, D2, D3, V2 > M, V1 | – | <45 particularly <25 |
| *Acanthopagrus australis* (3) | 64 | 30 | C > D1, D2, D3, M, V1, V2 | For C: seaward (0.05) > landward (0.001) | – |
| *Acanthopagrus pacificus* (8) | 94 | 83 | C, D1, D2, M, V2 > D3, V1 | For C, D1, D2, M, V2: seaward (0.04) > landward (0.01) | >25 |
| *Ambassis vachellii* (4) | 36 | 26 | V2 > C, D1, D2, D3, M, V1 | For C, V2: seaward (0.49) > landward (0.01) | >15 |
| *Chelonodon patoca* (3) | 48 | 32 | C > D1, D2, D3, M, V1, V2 | – | <35 |
| *Gerres filamentosus* (5) | 58 | 67 | D2 > C, D1, D3, M, V1, V2 | – | <35 but >5 |
| *Gerres oyena* (6) | 54 | 61 | C, V2 > D1, D2, D3, M, V1 | For C, V2: seaward (0.08) > landward (0.02) | >15 |
| *Lutjanus argentimaculatus* (3) | 60 | 40 | C > D1, D2, D3, M, V1, V2 | – | >35 |
| *Lutjanus fulviflamma* (4) | 42 | 14 | V2 > C, D1, D2, D3, M, V1 | For V2: seaward (0.06) > landward (0.003) | >15 |
| *Lutjanus russellii* (5) | 50 | 18 | C, V2 > D1, D2, D3, M, V1 | For C, V2: seaward (0.04) > landward (0.001) | >25 |
| *Pseudomugil signifer* (6) | 56 | 51 | D3 > C, D1, D2, M, V1, V2 | – | <25[a] |
| *Siganus lineatus* (2) | 46 | 28 | C, D3, V2 > D1, D2, M, V1 | – | – |
| *Toxotes chatareus* (2) | 52 | 36 | M, V2 > C, D1, D2, D3, V1 | – | – |

[a] In contrast to the other models where it formed additional subsidiary splits, 'minutes' formed the primary split for *P. signifer*, taking primacy over location splits

groves (*A. australis*, *A. pacificus*, *L. argentimaculatus*, *T. chatareus*) or were observed spending a large part of their time in mangroves picking from the substrate surface (*G. filamentosus*, *G. oyena*) or mangrove pneumatophores and roots (*S. lineatus*). Consequently, this profile appears to be characteristic of species dispersing to feed throughout the mangrove forest. In contrast to most other foragers, *A. pacificus* had a consistently lower presence in landward zones, suggesting it spent more time in the forest proper rather than penetrating through to higher intertidal levels. *G. filamentosus* exhibited a slight variation, with initially high occurrences in both seaward and landward zones, suggesting an initial mass arrival followed by dispersal as more intertidal area became available. The forager pattern was generally underpinned by a substantial number of videos ranging from 17–37 for seaward zones and 10–30 for landward zones.

A second group, 'early arrivers' (Fig. 6b, Fig. S2), comprising juvenile *Acanthopagrus* spp., *P. signifer* and *C. patoca*, arrived as soon as the water was deep enough to cover the camera lens (i.e. 8 cm), then declined over time. These were all small fish (maximum length of *P. signifer*: 7 cm; Froese & Pauly 2014), juveniles in the case of *Acanthopagrus* spp., and all individuals that had marking patterns consistent with small size in the case of *C. patoca*. The details of the patterns of occurrence varied for the 3 early arrivers. Although the number of juvenile *Acanthopagrus* spp. declined substantially in both seaward and landward zones, they still occurred in both areas throughout the flood tide (Fig. S2). However, the decline in landward zones was much less than in seaward zones, to the extent that mean presences were consistently twice as high in landward zones from 40 min on-

Table 3. Univariate classification and regression tree (uvCART) analyses of site and forest width effects on fish presence in the landward zone of mangrove forests in north-east Queensland. Data are the proportion of minutes present per video for species occurring in >25% of landward videos. Numbers in brackets following species names indicate regression tree size; numbers in brackets in 'Site splits' column indicate the number of splits ('site' always formed the primary split). See Table 1 for site abbreviations. When present, splits based on forest width are described

| Species | Site splits | Forest width split |
|---|---|---|
| All fish | No effects | |
| *Acanthopagrus* spp. (small) (3) | (2) C, D1, D3, V2 > D2, M, V1<br>D2 > M, V1 | |
| *Acanthopagrus australis* (2) | (1) C, D2, M > D1, D3, V1, V2 | |
| *Acanthopagrus pacificus* (2) | (1) D1, D2, V2 > C, D3, M, V1 | |
| *Ambassis vachellii* (2) | (1) C, V1, V2 > D1, D2, D3, M | |
| *Chelonodon patoca* (3) | (1) C, V2 > D1, D2, D3, M, V1 | Greatest occurrences in <10.5 m |
| *Gerres filamentosus* (2) | (1) D1, D2, D3 > C, M, V1, | |
| *Gerres oyena* | No effects | |
| *Lutjanus argentimaculatus* | No effects | |
| *Pseudomugil signifer* (4) | (3) D1, D2, D3 > C, M, V1, V2 D3 > D1, D2<br>C > M, V1, V2 | |
| *Siganus lineatus* (4) | (2) C, D1 > D2, D3, M, V2, V1<br>D3, V2 > D2, M, V1 | Greatest occurrences in <11.5 m |
| *Toxotes chatareus* (2) | (1) M, V2 > C, D1, D2, D3, V1 | |
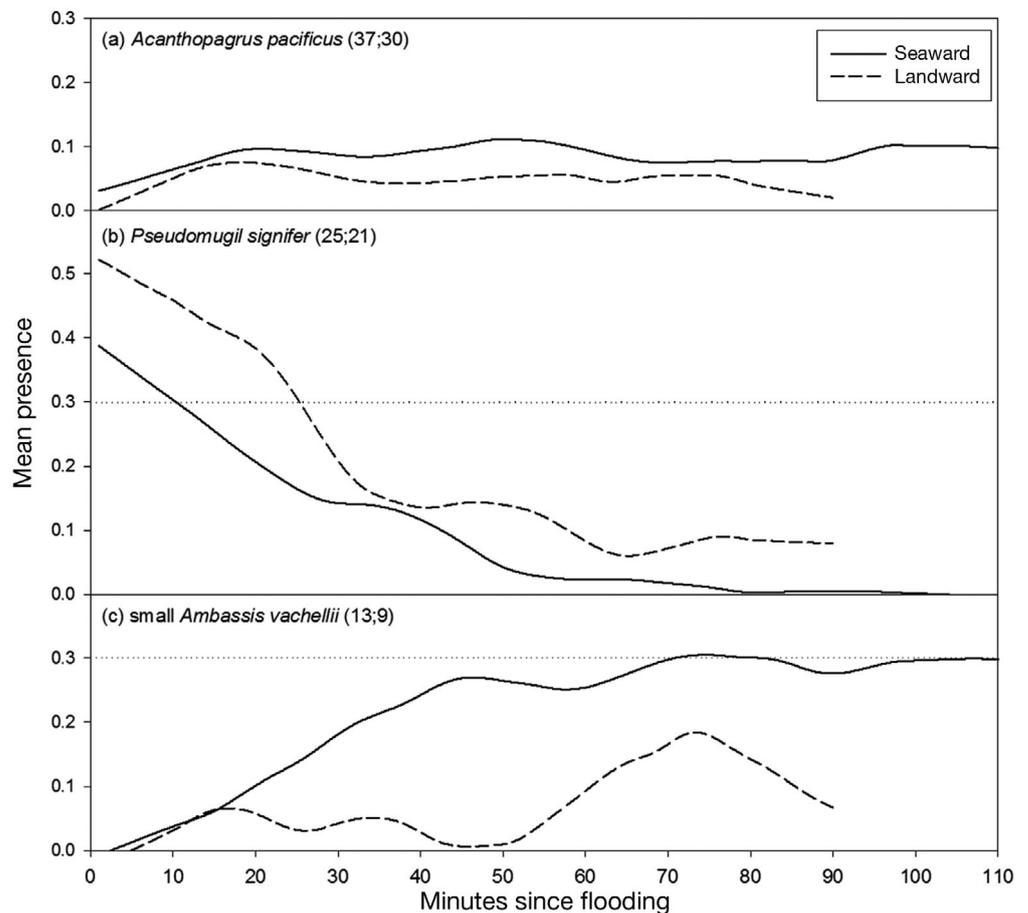


Fig. 6. Representative LOESS-smoothed profiles of mangrove utilisation for each of 3 groups of species: (a) foragers, (b) early arrivers, and (c) variants. LOESS fits are 1st degree polynomials with a sampling proportion of 0.25. Note: only videos where a species or species group was present are included in these analyses. Numbers in brackets: number of videos contributing to the profile (first number: seaward zones; second: landward). Profiles for each of the 7 forager species are presented in Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m549p167_supp.pdf, the 3 early arrivers in Fig. S2, and the 3 variants in Fig. S3

wards. This pattern suggests that juvenile *Acantho-pagrus* spp. moved into mangroves early in the tide and spread throughout the forest, but compared to their larger conspecifics and congeners, made more extensive use of landward than seaward zones as the duration of flooding increased. *P. signifer* (Fig. 6b) exhibited a more extreme pattern, with higher early occurrences in both landward and seaward zones followed by a more precipitous decline, with numbers dropping to essentially zero at seaward sites after about 1 h but remaining at low levels in landward zones. *P. signifer* appeared to pass through the forest rapidly, following the advancing tide and continuing to the extreme landward fringe of the mangroves above our landward cameras, or further on to shallow, high intertidal areas landward of the mangroves while still using the landward fringe to some extent. *C. patoca* (Fig. S2) demonstrated a similar pattern as *P. signifer*, but with a lower rate of occurrence and no indication of remaining in landward mangrove edges higher in the tide, suggesting that few fish remained in the mangroves once water was deep enough for them to move to higher intertidal areas. The early arriver pattern was generally underpinned by a substantial number of videos ranging from 15–32 for seaward zones and 13–26 for landward zones.

A number of profiles did not align with either the forager or early arriver patterns. These 'variants' (Fig. 6c, Fig. S3) included 2 species that occurred in >25% of videos as well as *Lates calcarifer*. Variant profiles were generally based on a smaller number of videos than those of foragers and early arrivers, particularly for landward sites. *Ambassis vachellii* (Fig. 6c) showed a progressive increase in occurrence in seaward zones over the first hour following flooding, then stabilised at a high level. This pattern can be interpreted as fish slowly moving into the front edge of the mangrove forest and then remaining at that location. *A. vachellii* penetrated to landward zones in some cases, but for the most part arrived very late in the tide. The number of *Lutjanus russellii* (Fig. S3) steadily increased at seaward sites over time but there was little activity at the landward edge. This pattern suggests gradual entry of fish into the seaward part of the mangrove forest but with little penetration to the back of the forest. *L. calcarifer* (Fig. S3) was rarely seen in videos, and then only at seaward sites, late in the tide when water depths were greatest. This was also the case for many other species such as *Caranx* spp., *Pomadasys* spp., *Drepane punctata*, *Selenotoca multifasciata* and *Plectorhinchus gibbosus*.

## DISCUSSION

### Complexity of estuarine mangrove use by fish

Only a small number of species used the mangrove forests extensively; these were primarily sparids, lutjanids, gerreids and pseudomugilids. Important tropical estuary species such as barramundi were rarely detected in the mangroves, at least during the day while the UVCs were operating. The species that did enter the mangroves represent a restricted subset of the species found in tropical estuary habitats in the region (Blaber 1980, Robertson & Duke 1990a, Ley 2005, Sheaves & Johnston 2009). This contrasts with the commonly held belief that many or most tropical estuarine fish use mangroves extensively (Faunce & Serafy 2006). Our rankings of species' importance based on this video study were very different from those obtained from previous studies using gill, seine or cast nets that focussed on the main body of the estuary (predominantly at low tide), with many species common in net catches apparently making little use of mangroves. Previous netting surveys, conducted in the same estuaries investigated here, have shown that many species track the shallow edge on the rising tide and then disappear from net catches in open waters once the mangrove forest floods (Johnston & Sheaves 2008), suggesting use of the mangrove forest by these species. It is possible that some estuarine species do use mangroves more often during those times when our video method could not be used (e.g. during larger spring tides, at night). However, the previous netting surveys (Johnston & Sheaves 2008) showed similar patterns of fish movement across a wide range of conditions, including equivalent conditions to the current sampling, yet few of these fish were seen even 1 m inside the mangrove edge during the present study. This suggests that these species probably remain along the outside edge of the mangrove fringe over the top of the tide.

### Mangroves as feeding and refuge sites

A number of the absences and near absences of fish from mangroves seem counterintuitive, and suggests the need to reconsider the role of mangroves as feeding or refuge sites. For instance, there were only 2 sightings of *Epinephelus malabaricus* in our mangrove videos and none of its congener *E. coioides*, even though both are among the most common species in tropical estuary fish trap catches (Sheaves 1996), and are known to feed extensively on man-

grove-associated sesarmid crabs (Sheaves & Molony 2000). This discrepancy may be explained by an unexplored linkage to mangrove forests. *Epinephelus* spp. are most common along steep mangrove banks (Sheaves 1996) where sesarmid burrow entrances are exposed by bankside erosion. Moreover, the diets of *Epinephelus* spp. include more non-sesarmid crabs (e.g. Xanthidae, Ocypodidae) than other mangrove crab feeders (Sheaves & Molony 2000). Consequently, it seems likely that *Epinephelus* spp. capture the sesarmid crabs they consume from the exposed burrows that are common along steep erosional banks, without actually entering the mangrove forest. In contrast, *Lutjanus argentimaculatus*, another mangrove crab feeder (Sheaves & Molony 2000) that focuses more specifically on sesarmid crabs, was common in the mangrove videos. It seems likely that *Epinephelus* spp. could benefit from mangroves, not by entering them to feed but by feeding outside the mangrove forest proper on crabs deriving their nutrition from mangrove forests.

Other taxa with unusually low occurrences within mangroves reinforce the importance of understanding the small-scale detail in the way fish use mangrove systems. Planktivores, such as *Herklotsichthys castelnaui* and *Escualosa thoracta* that consistently rank highly in net catches (Robertson & Duke 1990a, Sheaves & Johnston 2009), were rarely seen in mangrove videos. These are extremely abundant members of north-eastern Australian estuarine fauna. Although these species are found at highest densities in the main body of the estuary they do occur along mangrove margins (Johnston & Sheaves 2008) so were expected to be common, at least in seaward zone videos. Similarly, benthopelagic micro-invertebrate feeders such as *Leiognathus equulus and Nuchequula gerreoides,* which comprise a large part of net catches in north-east Queensland estuaries (Robertson & Duke 1990a, Sheaves & Johnston 2009), were rarely encountered in mangroves even though they congregate along edges at low tide when the mangroves are not flooded (Johnston & Sheaves 2008). It may be that these species entered mangroves late in the tide and remained in surface waters out of the video field of view, although the almost complete lack of detection argues against this explanation since these species tend to be distributed throughout the water column. Apparently, neither group of micro-invertebrate feeders enter mangroves to feed, possibly in response to low prey availability; plankton densities are highest in the main body of the estuary (Robertson et al. 1988) and other small invertebrate benthic prey occur in highest abun-

dances in mid intertidal areas outside the mangrove fringe (Dittmann 2000). However, there may be substantial temporal effects at play. Many plankton feeding fish forage extensively on crab larvae when they are available (Robertson & Duke 1990b), and they may enter mangroves at these times. On the other hand, it may be more profitable for them to remain outside the forest and feed on the outwelling of mangrove crab larvae originating from the forest, again providing a connectivity link to the mangrove forest and mangrove productivity without necessarily entering the forest itself.

Other groups that are common in the main part of the estuary but occurred relatively rarely in mangrove videos support the idea of more complex linkages between fish, mangroves and mangrove estuaries. Although Mugilidae rank highly in estuarine net catches (Ley 2005), relatively few individuals were detected in mangrove videos, while other common detritivores (e.g. *Anodontostoma chacunda*, *Nematalosa come* and *Chanos chanos*) were not seen at all. This suggests that there is little acquisition of detritus by fish within these north-eastern Australian mangroves. Similarly, Sillaginidae (shallow water benthos-feeding specialists) (Wilson & Sheaves 2001) were rarely observed in mangrove videos, suggesting that they remained in intertidal areas outside the mangroves where benthic prey abundances are highest (Dittmann 2000) during high tide. The situation in tropical north-eastern Australia is quite different from that of sub-tropical Australia, where both mugilids and sillaginids are among the most abundant mangrove fish (Morton 1990, Halliday & Young 1996), emphasising spatial differences in patterns of utilisation by fish, and potentially in ecological functioning.

Not only does the role for mangroves as direct feeding sites appear much less important than previously thought, but the nature of the species that are absent implies that we may need to reconsider the way in which mangroves provide refuge. Many of the species that were most common along mangrove edges at low tide (e.g. Leiognathidae, Clupeidae) (Johnston & Sheaves 2008) did not make regular use of mangroves at high tide. Similarly, juvenile snappers (such as *L. russellii*) that are common components of the areas' estuary nursery fauna (Sheaves 1995) seemed to make much less use of mangroves — appearing at relatively few sites, entering late in the tide and showing little penetration into the forest. These small and juvenile fish are precisely those thought to rely on mangroves as refuges (Blaber 1980). So, rather than moving in to mangroves when they are available in order to seek refuge (Nanjo et al. 2014), it seems

that many such species may use a different refuge strategy — staying close to the mangrove line but only retreating into them when danger threatens (Laegdsgaard & Johnson 2001). This is supported by the observation made repeatedly during the present study that most small fish responded to the approach of a large predator by moving away rather than by retreating into the cover of the mangrove root complex.

## Patterns of mangrove forest utilisation

Not only did relatively few species make extensive use of mangrove forests, but those that did used them in quite different ways and, by implication, for different reasons. The overall composition of the fish assemblage using seaward and landward parts of mangrove forests was similar; however, for many species there were higher rates of occurrence in the seaward fringe, as well as evidence that the width of the mangrove stand influenced penetration to landward zones for at least 2 species: *Chelonodon patoca* and *Siganus lineatus*. At a more detailed level, there were clear differences in the patterns of use of the mangrove forest.

Most of the species that were common in the mangroves followed 1 of 2 patterns over time. The first featured similar rates of occurrence once they had entered the mangroves, and displayed broadly similar patterns in both seaward and landward zones. This profile was termed 'forager' because it appears to be characteristic of species dispersing to feed throughout the mangrove forest; the foragers were composed of species known to feed extensively on prey found in mangroves — sesarmid crabs: *Acanthopagrus australis*, *A. pacificus* (Sheaves et al. 2014); *L. argentimaculatus* (Sheaves & Molony 2000); insects and small crabs: *Toxotes chatareus* (Allen 1991, Allen et al. 2002) — or species that spent a large part of their time in mangroves picking from the substrate surface (*Gerres filamentosus*, *G. oyena*) or from mangrove pneumatophores and roots (*S. lineatus*). Variations among the foragers' patterns of occurrence indicated subtle differences in the mode and timing of entry and dispersal. In contrast to most other foragers, large individuals of *A. pacificus* were consistently less abundant in landward zones, suggesting that they spent more time in the forest proper than penetrating through to higher intertidal levels. *G. filamentosus* had initially high occurrences in both seaward and landward zones, suggesting an initial mass arrival followed by dispersal as more of the intertidal became available.

A second group (termed 'early arrivers') entered the mangroves as soon as flooding began then declined markedly over time. This pattern was displayed by small fish (including juvenile *Acanthopagrus* spp., *Pseudomugil signifer* and *C. patoca*) and is broadly consistent with fish following the rising tide in order to remain in shallow water, although the 3 early arrivers seemed to use the strategy in slightly different ways. Juvenile *Acanthopagrus* spp. made greater use of the landward mangrove zone than their larger conspecifics, indicating that they spread through the forest less extensively and suggesting a greater tendency to remain in shallow water, perhaps because of a greater need for refuge from aquatic predators than their larger conspecifics. In contrast to juvenile *Acanthopagrus* spp., *P. signifer* and *C. patoca* appeared to follow the shallow water edge, passing through the mangrove forest into higher intertidal areas. Notably, *C. patoca* was one of the species more likely to be found in narrow rather than wide mangrove areas. Their preference for narrow forests, together with their rapid passage through the forest, suggests that they may principally use mangroves as a conduit to access higher intertidal areas.

The variant profile was assigned to those species that did not align well with either the forager or early arriver patterns. These variants included 2 species (*Ambassis vachellii* and *Lutjanus russellii*) that occurred in >25% of videos, along with *Lates calcarifer*. *A. vachellii* exhibited a pattern whereby its numbers increased progressively in seaward zones over the first hour following flooding, then stabilised and remained at a high level, indicating a slow movement to the front edge of the mangrove forest, where they remained over time. *A. vachellii* is largely planktivorous, and this pattern is consistent with movement into the mangrove fringe to utilize the refuge or hydrodynamic advantage provided by the complex root structures, while remaining close to the main body of the estuary where the supply of plankton is likely to be greatest (Robertson et al. 1988). Similarly, occurrences of *L. russellii* increased steadily in seaward sites over time but few fish penetrated to the landward edge, suggesting gradual entry of fish into the seaward part of the mangrove forest over time but little utilisation of the inner parts of the forest. Apparently, whatever value the species gained from entering the forest was afforded by the seaward mangrove fringe. *L. calcarifer* was rarely observed in the mangrove videos, and when it was detected, it was only in the seaward videos late in the tide when water was deepest (and most small potential prey fish had passed through to landward areas),

a pattern also seen for *Caranx* spp. and large *Pomadasys* spp. Apparently, these species did not enter the mangroves to feed (in fact, no feeding activity was observed). This later arrival contrasts with larger *Acanthopagrus* spp., which were of similar body depth as most of the *L. calcarifer*, *Caranx* spp. and *Pomadasys* spp., and entered the mangroves early in the tide, apparently to forage.

## CONCLUSIONS

Only a small subset of the species found across tropical estuary habitats made extensive use of the mangrove forests, and those that did enter the mangroves used them in a variety of ways and presumably for a variety of reasons. This limited use and complex mix of patterns suggest a need to reconsider the extent and ways in which fish use mangroves. Although direct utilisation of the mangrove forest seems to be much more restricted than in other areas (Nagelkerken et al. 2001, Mumby et al. 2004, Faunce & Serafy 2006), the complexity of mangrove use supports the idea of more intricate links between fish, mangroves and mangrove estuaries (Nagelkerken et al. 2015, Sheaves et al. 2015). As is the case in other estuarine ecosystems (e.g. Weinstein et al. 2005, Wasserman & Strydom 2011), many of the advantages provided by mangroves are probably derived at an ecosystem scale, with mangroves part of a complex, life-supporting habitat mosaic (Nagelkerken et al. 2015). This, in turn, emphasises the need for a whole-ecosystem approach to management and restoration, as has been successful in temperate estuaries (Weinstein et al. 2005, 2014, Weinstein & Litvin 2016).

Many of the species that did enter mangroves remained near the seaward edge, with very few penetrating through to landward margins despite the relatively narrow width (5 to 150 m) of the mangrove forests studied. This suggests substantial variation in the value of the mangrove forest to fish, and indicates the need for more emphasis on evaluating the specific components of mangrove forests. This is particularly important given the proliferation of anthropogenic modification of estuaries across the tropics (Waltham & Connolly 2011) that has modified the extent and nature of mangrove habitats available to fish. Clearly, more specific research, gathered from many more locations is necessary if we are to truly understand the function and importance of mangrove systems and their component parts (Sheridan & Hays 2003, Faunce & Serafy 2006).

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