

# Hidden Components in Tropical Seascapes: Deep-Estuary Habitats Support Unique Fish Assemblages

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**Abstract** Tropical coastal seascapes are biodiverse and highly productive systems composed of an interacting mix of habitats. They provide crucial ecosystem services that support people's livelihoods, yet key components of these seascapes remain unstudied. We know little about the deep (>2 m) subtidal areas of tropical estuaries, because, due to gear restrictions, there have been no detailed studies of the habitats they contain and the fish that use them. Consequently, potentially important functions and linkages with surrounding habitats remain unknown. Using unbaited videos, an approach capable of sampling the full breadth of benthic habitats and whole fish assemblages, we investigated patterns of fish occupancy of the deep subtidal habitats (2–20 m) in one of Australia's largest tropical estuaries. We identified 19 taxa not previously recorded from estuaries of tropical eastern Australia, along with 36 previously identified estuary taxa. Three recognisable fish assemblages were associated with distinct benthic habitat types: open bottom fine sediment, seagrass and structurally complex rocky areas. In deep water, habitats often overlooked in shallow water become important, and there are sharp differences in habitat function. Deep subtidal habitats are potentially an important zone for direct interaction between estuary and marine fauna, with a range of consequences for intertidal habitat use and nursery ground functioning. The interface between marine areas and the shallow-water estuary may be richer and more complex than previously recognised.

**Keywords** Fish habitat · Subtidal · Seascape · Underwater video

## Introduction

A complex mosaic of estuarine and near-shore habitats interlink to form the highly productive and biodiverse coastal seascapes of the tropics (Igulu et al. 2013; Nagelkerken and Van der Velde 2004). The life histories of a multitude of organisms are embedded within this mosaic (Nagelkerken et al. 2015) as they move among different habitats in the realisation of both their daily functions and their life cycle strategies. This movement of organisms leads to complex functional webs integrated across space and time, and together, these functional webs interlink habitats in ways that engender substantial interdependence (Gillis et al. 2014; Sheaves 2009). The loss or damage of one habitat can affect entire coastal systems, which are threatened by intensifying development globally. In turn, even small habitat-level changes can have far-reaching consequences because of the countless services provided by coastal ecosystems.

Many components of the coastal seascape mosaic remain poorly studied leaving our understanding of habitat linkages and seascape functioning restricted and incomplete. While much attention has been given to the nursery values of structurally complex intertidal vegetated habitats (Minello et al. 2003; Skilleter et al. 2005), these areas are only available to nekton when inundated (Baker et al. 2015; Minello et al. 2012), so fish must spend a large proportion of their time in estuaries and near-shore coastal habitats occupying subtidal areas (Laegdsgaard and Johnson 1995; Sheaves 2005, 2009). Thus, the habitats used at these times must be as important for nursery functioning as the better studied intertidal areas (Johnston and Sheaves 2007). This is emphasised by the absence of records of the early life-history stages of a large

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range of species, which suggests that many important nursery functions are likely to occur in habitats outside of commonly surveyed areas. Consequently, unsurveyed areas are likely to provide critical functions and linkages not supplied by better-studied seascape components (Nagelkerken et al. 2015).

Globally, the deep waters (>2-m subtidal) of tropical estuaries have rarely been comprehensively surveyed for fish utilisation. This is due to the unique challenges that estuarine environments present. While some studies, and even fisheries, have targeted these areas with beam trawl and other netting techniques (Blaber et al. 1989), these gears are restricted to smooth bottom habitats (Rozas and Minello 1997); therefore, they are unable to represent the full breadth of structurally complex habitats in these areas. The presence of estuarine crocodiles (Caldicott et al. 2005) coupled with typically high turbidity (Blaber 2008; Uncles et al. 1994) renders approaches such as underwater visual census unviable. As a result, there has been very little sampling of complex subtidal habitats in the tropics (Sheaves 1998) and little advance in knowledge of deep estuary habitats globally in the past decade (as reviewed in Blaber 2013). Recent advances in underwater video technology now allow us to remotely survey previously inaccessible areas and do so in a much less selective way (Cappo et al. 2003), and so have opened new methodological pathways for understanding inaccessible areas.

To begin addressing this gap in our knowledge of coastal environments, and advance our understanding of an otherwise well-studied local seascape, a detailed investigation of habitat variation was carried out in the previously unexamined deep (>2 m) waters of an estuary complex in north-eastern Australia. These areas contain features such as extensive permanently submerged cobble and boulder fields, as well as unique habitats such as sponge gardens, gorgonian corals and other biogenic benthic habitats that are absent from shallow estuarine waters (unpublished data). The aim of the study was to understand what fish species are associated with the different deep subtidal habitats, by examining how fish occurrence varied according to a range of habitat characteristics.

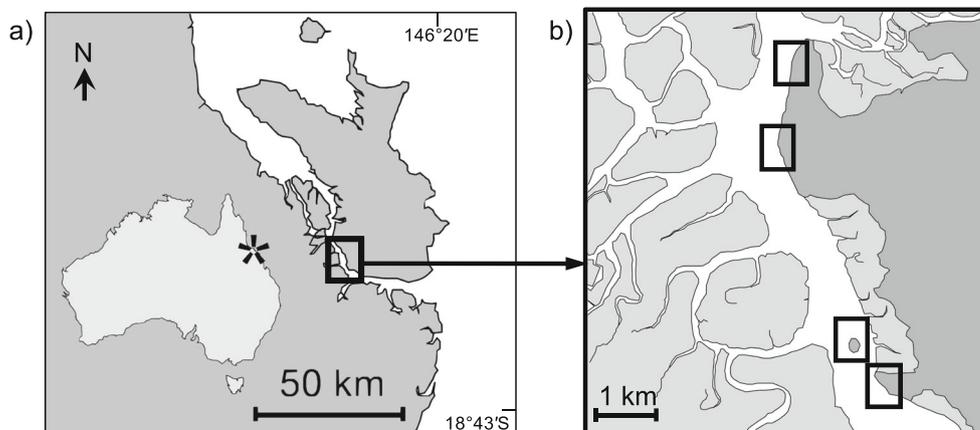
This is a critical starting point needed to underpin a more holistic understanding of the role of these deep estuarine areas within coastal seascapes.

## Materials and Methods

### Study Site

Sampling was carried out in Hinchinbrook Channel (18°20' S, 146°10' E), a semi-enclosed delta (Alongi et al. 1998) in the wet tropics of north-eastern Australia (Fig. 1), during November and December 2012, preceding the North Australian Monsoon. This tropical delta is a 'giant mangrove swamp' (Clough 1998; Wolanski et al. 1990) defined as an estuary based on freshwater inflow from two rivers and many smaller creeks, clear gradients in salinity and clearly defined mouths to the ocean. We used side scan sonar to identify the broad habitat types present in subtidal waters and a Remotely Operated Underwater Vehicle (ROV) to ground truth these observations. Based on this habitat mapping, four sites were selected for fish surveys; (from north to south) Wilkin Hill, Leefe Peak, Haycock Island and Reese Point (Fig. 1). We selected sites that encompassed the major variation in subtidal benthic features present throughout the estuary and maximised the spread of this benthic variation across the greatest range of depths possible. Details of the habitat mapping by side scan sonar and ROV are to be published elsewhere. Sites began from 0.5-m subtidal near the water's edge to include the depths commonly studied in other parts of the estuary and extended down the channel slope to the floor of the channel which sat at depths between 10 and 20 m. The shallow (<2 m) habitats of the Hinchinbrook Channel have been the focus of many previous studies, so information exists on the assemblage composition of these areas (e.g. Sheaves and Johnston 2009). In addition, there are numerous published studies of various aspects of the fish assemblage of the fringing reefs of Orpheus Island (e.g. Ackerman and Bellwood

**Fig. 1** Subtidal estuarine study sites in NE Australia: **a** location of Hinchinbrook channel estuary and **b** study sites within the estuary indicated by rectangles. In **b**, dark grey depicts terrestrial areas, light grey depicts areas of intertidal flats and mangrove forest, and white depicts subtidal areas, of which the majority are beyond the depth range comprehensively surveyed in previous studies >2-m subtidal



2000) that lies 15 km offshore from the southern end of the channel. Combined, these previous studies allow us to make direct and detailed comparisons between our study sites and these better-understood areas of the local seascape.

### Fish Survey Design

We surveyed the fish assemblages of subtidal areas using unbaited video point census. Video cameras were deployed remotely from a boat by slowly lowering the units until they landed on the substrate below. We used unbaited cameras because baited cameras would attract fish from adjacent habitats thereby biasing our results. Surveys were conducted in the daytime during periods of low tidal movement (<1.5-m run), in order to ensure light and visibility conditions appropriate for video sampling. To represent the depth range and variation in substrates and biological features within each site, parallel transects were carried out along the full length of each site, working down the channel slope at randomised depth intervals. To ensure sampling independence, cameras were spaced >20 m apart.

After inspection of the initial metadata, we conducted additional video sampling to target specific combinations of site, depth and habitat that were poorly replicated in the initial round of sampling. Not all combinations of depth and biotic habitat were possible because nearly all biotic features were restricted to particular depth zones (e.g. seagrass 0–3 m; gorgonian corals >4 m). The resulting 260 video samples, while not orthogonal, encompassed the major variation in substrate across all depths in all sites as comprehensively as possible.

Each sample consisted of 15 min of continuous video recording and provided a point census of fish taxa present, as well as biological and structural habitat characteristics. This approach is suitable for broad-scale studies of fish distribution and habitat relationships because both dependent and predictor variables are measured within the same spatial and temporal window and high replication is possible (Hannah and Blume 2012). Although many authors record abundance (e.g. Harvey et al. 2007), we recorded presence, to reduce biases caused by differences in water clarity. Reliable presence-absence data can provide a proxy for abundance, because abundant species tend to occur more frequently (i.e. in more videos) than less abundant species (Royle and Nichols 2003). Present data are robust because, although there are still issues of visibility bias, the biases are minimised by excluding the numeric component of count data. This bias was further reduced by only including videos where water clarity was above a minimum threshold (0.5 m) determined by the ability to see the distal end of a flexible, 3-mm diameter, 0.5 m long rod fixed centrally within the camera's field of view. Even under the best visibility conditions during our study, fish could rarely be reliably identified beyond approximately 2 m. Hence, the effective sampling range was between 0.5 and 2 m.

We identified fish to the finest taxonomic resolution possible, and taxa were only recorded as present if identification was made with total confidence. Several taxa could only be identified to genus or family level because the features that distinguish some closely related species (e.g. fin ray counts) were not visible on camera or could not be distinguished due to a lack of water clarity or colour definition. Accordingly, for detailed analysis, we grouped taxa to genus level when none or only some individuals were positively identified to species. We grouped Leigonathids to family level because genera could not be differentiated reliably. Where we were able to differentiate juveniles, classification as juveniles was based on juvenile markings and patterns of shading, rather than size. Identifications were reviewed by at least two additional experts to ensure consistent identification.

We categorised habitat attributes for each video sample based on the range of characteristics visible in the field of view. Our classification scheme followed that of Ball et al. (2006), with a reduced number of modifiers for simplicity (Table 1). Two attributes were used—substrate texture and dominant biota—and we assigned each video sample into one category for each attribute. When the substrate was mixed, we assigned the sample to the largest substrate size present. The depth of each video sample location was recorded during deployment using an acoustic depth sounder.

### Statistical Analysis

Rather than imposing predetermined 'habitats' onto the data and analysing for differences in fish species composition among them, we used analyses that do not employ a priori grouping, specifically Classification and Regression Tree (CART) analyses. This approach allowed differences in fish presence and species composition to drive the identification of the habitat characteristics that are important to fish and to define the typological boundaries of these habitat units empirically.

First, we determined which attributes drove the presence of any fish. Each sample (replicate video) was categorised with a single binary variable for either fishes present or fishes absent. Univariate classification tree analysis was carried out using the 'party' package in R (Hothorn et al. 2010), with dominant biota, substrate texture, location, depth and tidal movement as predictor variables.

Second, to determine which variables drove differences in species composition, we used multivariate regression tree analysis. Because the univariate tree described above identified that few fish occurred in bare substrate samples, these samples were excluded to allow the analysis to focus on patterns of fish presence rather than being unduly influenced by absences. Accordingly, we also excluded from the remaining data set videos where no fish was present and considered only taxa that occurred in five or more samples. This left a data set

**Table 1** Simple classification scheme used for determining habitat attributes

Variable	Category	Definition
<i>Substrate texture</i>	Solid	Consolidated/unbroken rock pavement
	Large boulder	Grain size >630 mm
	Boulder	Grain size 200–630 mm
	Cobble	Grain size 63–200 mm
	Gravel	Grain size 2–63 mm
	Shells	Grain size 2–63 mm, composed of shells
	Fine sediment	Silt and sand, grain size 0.002–2 mm
<i>Dominant biota</i>	Bare	No visually obvious biota
	Bioturbated	Substrate physically altered by biotic activity—e.g. burrows and castings
	Algae	Visually obvious filamentous algae
	Seagrass	Members of the following seagrasses genera: <i>Cymodocea</i> , <i>Halophila</i> , <i>Halodule</i> , <i>Thalassia</i> and <i>Zostera</i>
	Macro algae	Members of the phyla Ochrophyta and Chlorophyta
	Sessile invertebrates	Branching cnidarian structures, encrusting hard coral, barnacles, soft coral, sponges of the family Tetillidae and other unidentified sponges

of 19 taxa across 124 samples. The multivariate regression tree analyses were run using the *mvpart* package in R (De'ath 2007; Ouellette and Legendre 2012).

Third, based on the combinations of predictor variables that were most important in driving both fish presence and assemblage composition, we determined a set of ecologically meaningful habitat categories appropriate for deep-water estuary areas. Using this new classification scheme, we calculated the probability of encountering a fish in each of these new habitats based on all data. Predictor variables were habitat type (defined by the analyses described above) and location (sample site). Finally, the individual probabilities of encounter for each of the 19 common taxa in each of these habitats were calculated.

## Results

We identified a total of 55 taxa from 28 families (Table 2). The level of taxonomic resolution varied; the 55 taxa we identified were composed of 39 identified to species, 11 to genera and 6 to family level. Twelve species were present only as juveniles (based on patterns of colouration and shading). The subtidal fish fauna identified in this study differed markedly from that of adjacent habitats; 19 taxa were not previously recorded in shallow areas of north-eastern Australian estuaries (Blaber 1980; Robertson and Duke 1990 and Sheaves' complete database of published and unpublished fish surveys) including the intertidal and shallow subtidal areas of Hinchinbrook channel (Abrantes and Sheaves 2009; Johnston and Sheaves 2007; Sheaves 2006; Sheaves and Johnston 2009). The

remaining 36 taxa comprised a subset of common shallow-water fauna (Table 2).

## Defining Ecologically Meaningful Habitats

Habitat attributes were the main drivers of both fish presence and assemblage composition. Substrate texture had the greatest influence on the probability of encountering a fish (Fig. 2); at least one fish was encountered in 95 % of video samples from coarse textured substrates (gravel, cobble, boulder, large boulder). Encounters were much lower in fine sediment and depended on sediment structure, with fish occurring in 49 % of video samples on seagrass, algae or bioturbated sediment but on 10 % of video samples from bare areas. Most of the taxa (7/11) observed on bare sediments were also found over other substrates. Additionally, we found very little consistency in species over bare fine sediment areas; no taxa were observed in more than two videos. Based on these results, samples from bare fine sediment were excluded from the following multivariate analysis because they contributed many zeros to the data matrix without providing substantive information.

Even with bare fine sediment excluded, substrate texture and dominant biota drove assemblage composition (Fig. 3). The coarsest substrates observed—cobble, boulder and large boulder—contained an almost entirely different set of taxa than finer substrates (silt, sand and gravel). Fish composition on finer substrates differed based on the presence of seagrass, which was dominated by early juveniles of the Lethrinid *Lethrinus genivittatus* and the Terapontid *Helotes sexlineatus*. In the absence of seagrass, fine sediments contained few

**Table 2** Fish taxa identified in subtidal video surveys 0.5–10-m depth in the Hinchinbrook Channel Estuary, North Queensland, Australia

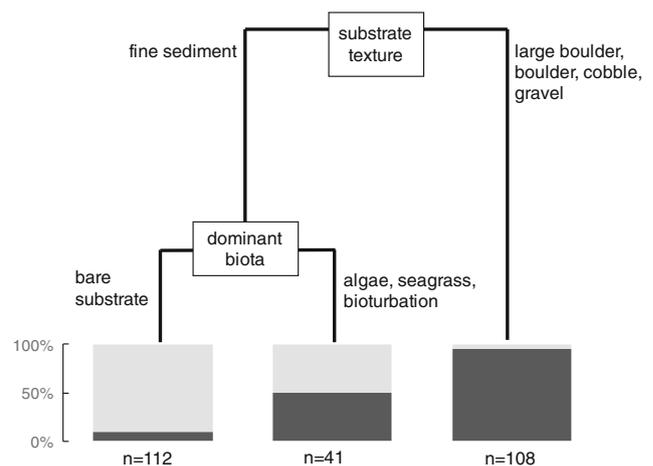
Family	Taxon
Acanthuridae	$\Delta$ <i>Acanthurus auranticavus</i>
Apogonidae	<i>Apogon spp.</i>
Carragidae	<i>Caranx ignobilis</i> <i>Scomberoides</i>
Chaetodontidae	$\Delta$ <i>Chelmon muelleri</i> $\Delta$ <i>Parachaetodon ocellatus</i>
Clupeidae	<i>Herklotsichthys spp.</i>
Dasyatididae	Dasyatididae
Drepaneidae	<i>Drepane punctata</i>
Engraulidae	Engraulidae
Ephippidae	<i>Platax sp.</i>
Gerreidae	<i>Gerres filamentosus</i> <i>Gerres oyena</i>
Gobiidae	<i>Acentrogobius</i> $\Delta$ <i>Istigobius sp.</i> <i>Redigobius balteatus</i>
Haemulidae	<i>Pomadasys argenteus</i> <i>Plectorhinchus gibbosus</i> $\Delta$ <i>Diagramma pictum</i>
Labridae	$\Delta$ <i>Halichoeres nigrescens</i> $\Delta$ <i>Halichoeres kneri</i> $\Delta$ <i>Choerodon sp.</i>
Latidae	<i>Psammoperca waigiensis</i> <i>Lates calcarifer</i>
Leiognathidae	<i>Nuchequula gerreoides</i> <i>Gazza spp.</i> <i>Leiognathus equulus</i> <i>Secutor ruconius</i>
Lethrinidae	<i>Lethrinus lentjan</i> * <i>Lethrinus genivittatus</i>
Lutjanidae	<i>Lutjanus argentimaculatus</i> * <i>Lutjanus fulviflamma</i> * $\Delta$ <i>Lutjanus fulvus</i> * <i>Lutjanus johnii</i> * $\Delta$ <i>Lutjanus rivulatus</i> * <i>Lutjanus russellii</i> *
Monacanthidae	$\Delta$ Monacanthidae
Monodactylidae	<i>Monodactylus argenteus</i>
Mugilidae	Mugilidae
Mullidae	Mullidae
Nemipteridae	$\Delta$ <i>Pentapodus sp.</i>
Platycephalidae	Platycephalidae
Pomacentridae	<i>Neopomacentrus bankieri</i> $\Delta$ <i>Neopomacentrus tenuis</i> $\Delta$ <i>Abudefduf bengalensis</i> $\Delta$ <i>Pomacentrus sp.</i>
Scaridae	$\Delta$ <i>Scarus sp.</i> *
Serranidae	<i>Epinephelus coioides</i> *

**Table 2** (continued)

Family	Taxon
	<i>Epinephelus malabaricus</i> *
	<i>Epinephelus coeruleopunctatus</i> *
Siganidae	$\Delta$ <i>Siganus javus</i> <i>Siganus lineatus</i> <i>Siganus spinus</i> $\Delta$ <i>Siganus virgatus</i>
Sparidae	<i>Acanthopagrus pacificus</i>
Terapontidae	<i>Helotes sexlineatus</i>

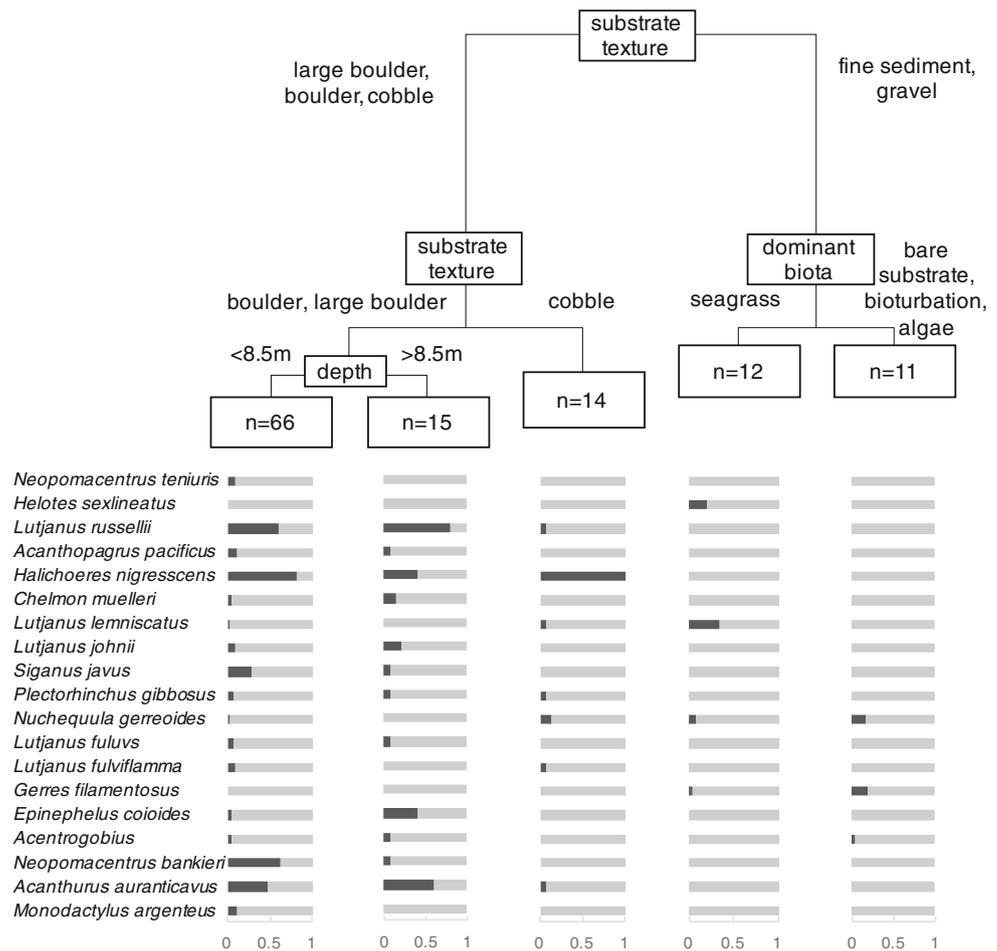
$\Delta$  = species not previously recorded as estuary fauna in North Queensland, \* = species present as juveniles only

species. A recognisable assemblage occurred throughout rocky areas, typified by the snapper *Lutjanus russellii*, the surgeon fish *Acanthurus auranticavus* and the wrasse *Halichoeres nigrescens*. Of the 19 ‘new species’ recorded in this study, 17 were found in the rocky habitat and are almost entirely reef-associated taxa (Randall et al. 1997). The other taxa found in this habitat comprise many of the most common estuarine predators, such as groupers, *Epinephelus coioides* and *Epinephelus malabaricus*, and snappers, *L. russellii*, *Lutjanus argentimaculatus* and *Lutjanus johnii* that occur in estuaries throughout the region as juveniles (Russell and McDougall 2005; Sheaves 1995). In areas of cobble, the balance of this assemblage was dominated by *H. nigrescens*, with other taxa occurring less frequently and a lower overall diversity. Areas of boulders (and large boulders) contained a diverse assemblage that differed according to depth. Shallow boulder areas contained the pomacentrid planktivore *Neopomacentrus bankieri* more frequently, whereas the



**Fig. 2** Univariate classification tree based on the presence or absence of fish, performed on all samples  $n = 260$ . Each of the two splits are labelled with the variable that determined the split and the categories separated by the split. Black bars indicate the percentage of samples where fish were present in each terminal tree node

**Fig. 3** Multivariate regression tree showing the major divisions in the data based on assemblage composition. Each of the splits are labelled with the variable that determined the split and the categories separated by the split. The length of descending branches is proportional to divergence between groups. *Bar plots* show proportion of each taxa in all samples in the data set sharing the attributes identified for each terminal node. Sample size for each bar plot is the same as that displayed for each terminal node except for ‘seagrass’  $n = 26$  and ‘all else’  $n = 31$  which encompass samples with 0 presences excluded from the multivariate tree analysis



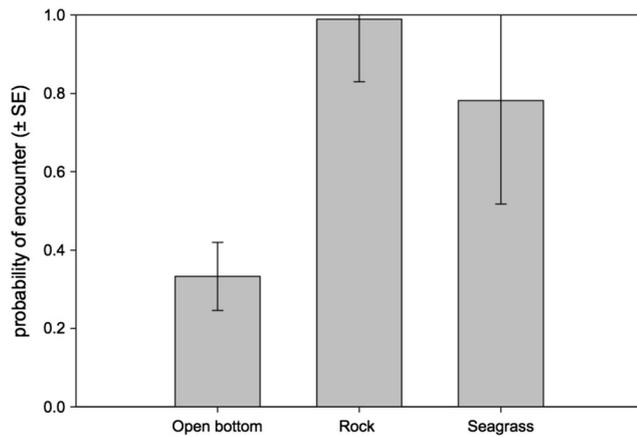
Serranid *E. coioides* was encountered more frequently in areas deeper than 8.5 m.

The distinct assemblages identified in our analyses relate strongly to just a few specific habitat attributes. Substrate texture formed the initial, strongest bifurcation in both trees. Dominant biota was important in distinguishing between seagrass and non-seagrass localities. Thus, the major variation in fish assemblages in the deep-water estuarine areas studied can be accounted for by three habitat categories, seagrass, open bottom and rock; each of which features a variety of substrate types and sessile biota (Table 3). Looking across our entire dataset, we used stepwise logistic regression to predict probability of encounter with an estimate of error around that prediction. This demonstrated clear differences in probability of encounter among the

three major habitat categories (Fig. 4), but no effect of differences among locations. Based on the entire data set (including videos with no fish, and taxa with few occurrences), the probability of encounter modelled by logistic regression was highest in the rocky habitat (99 %), followed by seagrass (78 %), and quite low in the open bottom habitat (33 %). The individual probabilities of encounter of the 32 most common subtidal taxa across each of these habitat units (Fig. 5) indicated that most species were largely restricted to a single habitat type—invariably either rock or seagrass, with very few habitat generalists present. The three generalist taxa (*Leiognathidae*, *Gerres filamentosus* and *Drepane punctata*) were the only fish commonly encountered in open bottom areas, suggesting that few species are solely dependent on those areas as habitat.

**Table 3** The three habitat categories defined in this paper and the habitat variables that denote each

Category	Open bottom	Rock	Seagrass
Substrate texture	Gravel, shells, fine sediment	Large boulders, boulders, cobble	Gravel, shells, fine sediment
Dominant biota	Bare, bioturbated, algae,	Bare, algae, macro algae, sessile invertebrates	Seagrass



**Fig. 4** Probability of encountering any fish in the three distinct habitat units identified based on logistic three-habitat model of binary fish presence-absence for all 260 samples. Deviance 120.44, degrees of freedom 2,  $p = 0.0025$

## Discussion

Although Hinchinbrook Channel is one of the most thoroughly studied large tropical estuaries, our surveys of previously unstudied deep waters detected many taxa not previously recorded from estuaries in the region. Additionally, the way taxa are distributed does not simply mirror adjacent shallow areas of the estuary. In fact, the categorisation of fish habitat into rock, seagrass and open bottom in deep estuary waters is different from a typical shallow water estuary habitat classification for the region, which usually contains sandy and muddy bottoms, depositional and erosional banks, mangrove flats and mangrove drains (e.g. Blaber et al. 1989; Johnston and Sheaves 2007). This deviation is due to both the identification of previously missing components and sharp differences in fauna-habitat relationships, discussed below. Clearly, our understanding of tropical estuarine seascapes is incomplete. Basing assumptions about habitat values and functional roles of deep estuarine areas on understanding derived from adjacent shallow water areas risks overlooking important attributes and functional relationships. Rather, where no data exist, it seems safer to assume substantial faunal differences in deep-estuary areas.

### Missing Components Identified

The unique habitat categories and novel deep estuary fish communities uncovered in this study allow for the critical examination of assumptions commonly employed in coastal zone science and management. By using novel sampling gear, we were not constrained (as most previous studies have been) to shallow tidal creeks and so were able to sample in parts of the estuary where different habitats dominate. Seagrass has been poorly represented as fish habitat in tropical estuaries because of its limited extent in shallow tidal creeks, where it

occurs mainly as intertidal beds. Seagrass can cover large areas of the estuary subtidally (Lee Long et al. 1996) and has long been recognised as habitat for herbivorous megafauna like turtles and dugongs (Carruthers et al. 2002; GBRMPA 2004). Likewise, areas of rock are present in the small tidal creeks where most sampling has occurred, yet due to their limited extent, they have rarely been sampled. In our study, taxa commonly encountered in shallow water surveys demonstrated strong relationships with both of these habitats. Despite being poorly characterised in the tropics as fish habitat in areas previously surveyed (M. Sheaves pers. Obs.), structurally complex habitats such as rock and seagrass are potentially important for coastal fish wherever they occur in the estuary.

### Predictable Habitat Relationships

In some senses, the fish-habitat relationships in subtidal areas were predictable from a generalised understanding of relationships from previous fish habitat studies, both locally and globally. Complex structured habitat was of overriding importance to fish habitat relationships in subtidal areas; the highest taxonomic diversity and the highest probability of encountering a fish occurred in rock habitats. This aligns with previous studies of shallow estuarine areas where the dominant complex structure is fallen timber, which also supports a diverse and abundant assemblage (Sheaves 1992). It also aligns with wider concepts of the general importance of complex structure for fish (Gratwicke and Speight 2005; Heck et al. 2003; Laegdsgaard and Johnson 2001). In line with these notions, diversity dropped off sharply in areas within this habitat where rock size was smallest, highlighting the importance of large structure. Moreover, the species found to associate with fallen timber in shallow estuaries (Sheaves 1992) were associated with rock habitat in our study, illustrating their fidelity to complex structure. However, despite these similarities, habitat relationships did differ markedly from those in shallow waters.

### Shallow Water Habitat Relationships That Are not Found Subtidally

Most of the taxa that commonly use both open bottom and seagrass habitats locally in shallow water were missing from these same habitats in deep water, suggesting that open bottom and seagrass habitats do not fulfil the same functions when they occur in subtidal areas. The subtidal seagrass assemblage of the estuary differed from those of seagrass beds elsewhere, which are known to harbour many species as juveniles (Coles et al. 1993; Kwak and Klumpp 2004). While deep seagrass contained some fish species commonly found in coastal seagrass beds such as *Helotes sexlineatus* and *Lethrinus genivittatus*, other seagrass-associated taxa, such as *Sillago*, *Mullidae*, *Labridae* and *Acanthopagrus* (Coles et al. 1993), were absent, despite being common in local estuarine and

**Fig. 5** Probability of encounter for the 32 taxa commonly encountered in deep subtidal waters 2–20 m of the Hinchinbrook Channel, according to the three habitat categories determined by CART analyses



coastal systems (Abrantes and Sheaves 2009; Johnston and Sheaves 2007; Sheaves and Johnston 2009). Similarly, the assemblage of open bottom areas lacked many of the taxa that dominate this habitat in shallower areas. Intertidal and

immediate subtidal open bottoms contain a rich and specialised fauna including families such as Sillaginidae and Ambassidae (e.g. Sheaves 2006) that were not observed in our study of deep open bottoms. Apparently, open bottom and seagrass habitats

lose a substantial component of their functional value when subtidal rather than intertidal. The composition of seagrass fish assemblages can be strongly driven by proximity to mangroves or coral reefs (Dorenbosch et al. 2007; Jelbart et al. 2007; Unsworth et al. 2008). For both habitats then, this loss of functionality may be the result of seascape effects, whereby distance from other habitat types renders them less useful to many fish species. Also, benthic invertebrate abundance and diversity has been observed to peak in intertidal habitats and taper off significantly in subtidal habitats both locally (Sheaves et al. 2016) and elsewhere (França et al. 2009). Hence, these areas likely do not function as important feeding grounds as they do in shallow areas.

### Undocumented Functions

The results of our study also point to other, undocumented habitat functions of deep estuary habitats. These functions are likely to effect the surrounding seascape, and so the presence or absence of the deep-water habitats studied here is likely to be important in structuring seascape level processes.

### Nursery Functions

The deep-estuary habitats we surveyed may provide important nursery habitat that influences the supply of juveniles to surrounding areas of the seascape. That 12 species (22 % of all species observed) were present as juveniles suggest that deep areas may have some nursery ground value. Small-scale habitat structure can provide early settlement and recruitment sites (Diaz et al. 2003; Tupper 2007), a critical component in nursery function (Fodrie et al. 2009; Nagelkerken et al. 2015), while large-scale habitat structure can provide ‘stepping stones’ to adult areas for larger juveniles (e.g. Grol et al. 2014). A nursery ground can in fact be a chain of different habitats that a juvenile utilises as its requirements change through ontogeny (Nagelkerken et al. 2015). Deep water habitats may be an undocumented link in this chain and may fulfil previously unidentified roles for particular species. These indications of nursery value are compelling yet incomplete. Due to prohibitively low water clarity at other times of the year, this study was conducted during a single season. These habitats could have been used by other life stages and by other species outside our sampling window, such as during the immediate post-wet season recruitment period (Sheaves et al. 2010).

### Undocumented Subtidal Refuge Functions

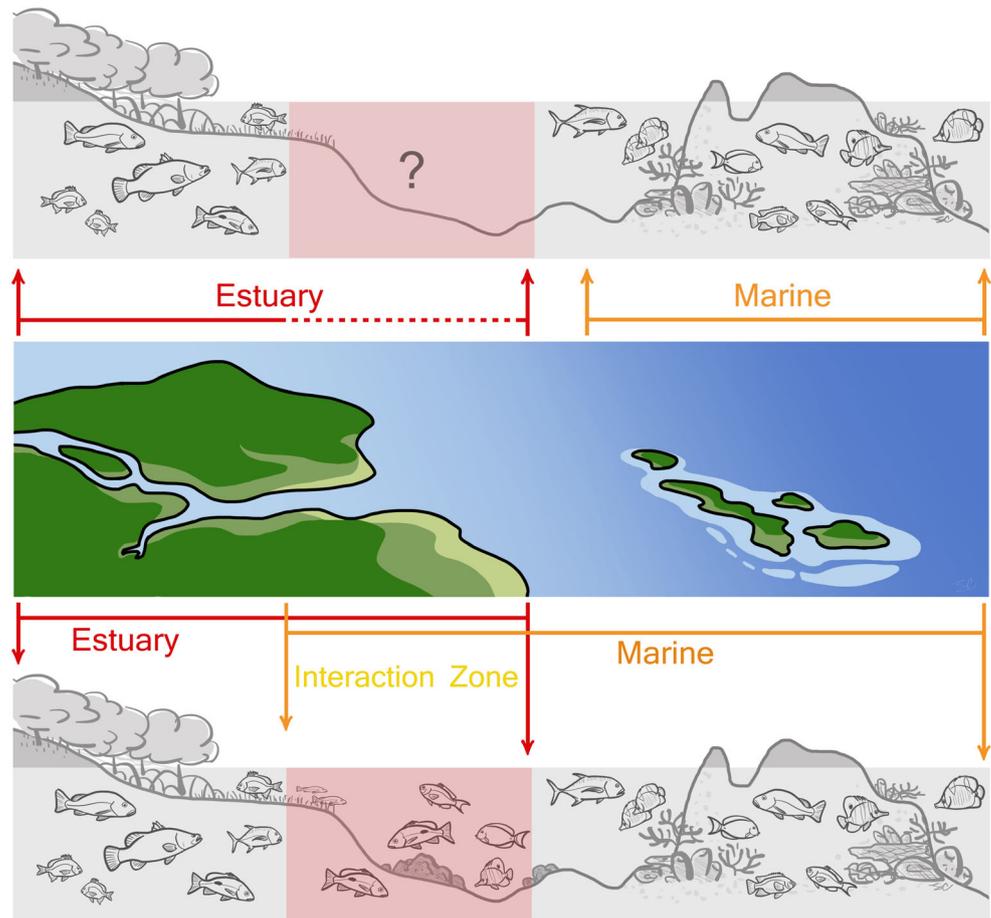
The structurally complex subtidal habitats identified in this study have the potential to facilitate the utilisation of adjacent habitats, interacting with, and modifying, processes in those habitats. Fish in similar coastal seascapes, such as in the Caribbean, routinely move from refuge to foraging habitats

(Hitt et al. 2011; Nagelkerken et al. 2001), connecting these areas on a daily basis. In areas where tidal range plays an important role in access to available habitats, fish migrate between intertidal and subtidal habitat (e.g. Dorenbosch et al. 2004) leading to a system where habitat value is a dynamic rather than a static property. The implication is that the absence of suitable subtidal structured habitat is likely to preclude the use of particular intertidal areas for some fish (Irlandi and Crawford 1997; Sheaves 2005), regulating the extent of predation on invertebrate prey in these intertidal areas, in turn modifying the structure of the intertidal invertebrate communities (Rilov and Schiel 2006). Three fish species of the rocky habitat in particular (*E. coioides*, *E. malabaricus* and *L. argentimaculatus*) are known to specialise in consuming sesarmid crabs, which only occur in mangrove forests, so these species link mangrove forests to their low tide refuges through the export of biomass and productivity (Sheaves and Molony 2000).

### The Coastal Interaction Zone

Our ‘first look’ at the assemblage composition of deep estuary habitats provides compelling evidence for approaching these areas as interaction zones (Fig. 6), which in many landscapes are known to play a critical role in controlling or modifying flows of organisms, materials and energy between ecosystems (e.g. transition zones sensu Yarrow and Marín 2007). Interaction zones for open bottom habitats have been found in inshore coastal areas (Blaber et al. 1995) that contain characteristic fish communities which partly resemble those found in this study. Similarly, the particular mix of species found using rock habitat is not a predictable extension of shallow water habitat relationships and appears to represent a previously unrecognised inshore structure-associated fauna. This assemblage is composed of a characteristic mixture of species found in adjacent estuarine habitats (Russell and McDougall 2005; Sheaves 1995), such as fallen timber (Sheaves 1992) and on nearby coral reefs (Ackerman and Bellwood 2000). The assemblage represents the spatial coincidence of what would usually be considered two separate faunas. This means firstly that the range of functionally ‘marine habitat’ can extend into large, deep estuary systems. Secondly, given the significant functional roles, these areas may play as outlined above, structuring processes that occur within these unique ‘interaction zone’ assemblages that could connect estuarine and marine systems in previously undescribed ways. For instance, they may regulate the supply of recruits or adults to the surrounding seascape (Caddy 2008; Juanes 2007). The fish that occur in deep estuary habitats may prey on new recruits (sensu Baker and Sheaves 2009) and exert a structuring force in arguably the most significant population bottleneck in a fish’s life-history (Chambers and Trippel 2012; Searcy and Sponaugle 2001). Similarly, if low tide refuge habitats are

**Fig. 6** Current conceptualisations assume estuary and marine habitats to be spatially and faunally distinct top panel. Our focal deep-estuary habitats extend marine habitat into the estuary, leading to overlap with estuary fauna and the presence of a unique interaction zone bottom panel. Figure artwork by C. Trave



indeed a limiting factor for coastal fish, competition and other density-dependent processes that occur in deep areas could regulate the species composition and abundance of assemblages in the surrounding seascape. The extent of connectivity between these newly explored subtidal habitats and the surrounding seascape requires further investigation to facilitate a full understanding of the functioning of these ecosystems.

## Conclusions

An increased understanding of deep-estuary areas requires a subtle but important shift in the way we conceptualise coastal seascapes. Habitats for estuary and marine fish are not spatially segregated and clearly overlap in some places (Blaber et al. 1995). Deep-estuary habitats appear to support ecosystem functions distinct from those of shallow water habitats, suggesting the need to broaden the range of habitats included in our conceptualisation of seascapes. The typical three-component seascape model composed of seagrass, mangroves and coral reefs (Berkström et al. 2012) is likely to require careful adaptation for use in

different parts of the world (Barnes et al. 2012; Williams 1991). The inclusion of deep-estuary components could markedly improve the explanatory power of shallow-water seascape models (e.g. Whaley et al. 2007) by replacing unmapped space with potentially important drivers of fish assemblage composition. Deep-estuary habitats are likely a widespread feature of tropical seascapes. For instance, they appear to perform the same functions along the east African coast (Blaber 2008; e.g. Kimani et al. 1996). Finding and describing important but under-represented components of the seascape (e.g. Fitzpatrick et al. 2012) should go hand in hand with the continuing endeavour to apply landscape ecology principles to the marine environment.

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## Compliance with Ethical Standards

**Conflict of Interest** The authors declare that they have no conflict of interest.

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