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Environmental conditions constrain nursery habitat value in Australian sub-tropical estuaries

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Abstract

High quality nursery grounds are important for species success and the long-term sustainability of fish stocks. However, even for important fisheries species, what constitutes nursery habitats is only coarsely defined, and details of specific requirements are often lacking. In this study we investigated upstream estuarine areas in central Queensland, Australia, to identify the environmental factors that constrain nursery ground utilisation for important fisheries species. We used unbaited underwater video cameras to assess fish presence, and used a range of water quality sensors to record fluctuations in environmental conditions, likely to influence juveniles, over several months (e.g. tidal connection patterns, temperature, salinity and dissolved oxygen). We found that juveniles of three fisheries target species (*Lutjanus argentimaculatus, Lutjanus russellii* and *Acanthopagrus australis*) were common in the upstream sections of the estuaries. For each species, only a subset of the factors assessed were influential in determining nursery ground utilisation, and their importance varied among species, even among the closely related *L. argentimaculatus* and *L. russellii.* Overall, tidal connectivity and the availability of complex structure, were the most influential factors. The reasons for the importance of connectivity are complex; as well as allowing access, tidal connectivity influences water levels, water temperature and dissolved oxygen – all important physiological requirements for successful occupation. The impact of variation in juvenile access to food and refuge in nursery habitat was not directly assessed. While crucial, these factors are likely to be subordinate to the suite of environmental characteristics necessary for the presence and persistence of juveniles in these locations. These results suggest that detailed environmental and biological knowledge is necessary to define the nuanced constraints of nursery ground value among species, and this detailed knowledge is vital for informed management of early life-history stages.

Keywords:

Nursery ground, Constraint map, *Lutjanus argentimaculatus,* ecosystem-based management, Transitional zones

Highlight:

- Identifying nursery grounds is necessary for the long-term sustainability of fish stocks
- Tidal connectivity patterns and habitat structure are strong predictors of juvenile presence
- Knowledge of species-specific constraints can assist management of early life-history stages

Introduction

Managing fisheries requires striking a balance between preserving social and economic interests, while ensuring the long-term sustainability of fish populations. Traditional approaches have mostly focused on harvest restrictions, such as size, gear and catch limits. However, in recent years it has become increasingly clear that such approaches are not always optimally effective in supporting fisheries sustainability (Pikitch et al., 2004; Link and Browman, 2017), because concentrating on the exploited component of fish stocks ignores factors outside the direct effect of fishing. This has led to an increasing emphasis on ecosystem-based management (Hilborn, 2011), and focus on the importance of ensuring quality outcomes across the whole life-cycle of fisheries species. However, including early life-history stages in management considerations is often difficult because the data needed for such assessments are often sparse. In fact, despite their obvious importance, for many species nursery ground utilisation and value are often poorly understood (Levin and Stunz, 2005;

Sheaves, 2006; Litvin et al., 2018), or assumed to be known based on circumstantial evidence (Sheaves, 2017; Sheaves et al., 2020a). A large part of the problem is that, although nursery grounds are often defined as areas that provide resources (e.g. food) and protection for juveniles at a greater rate than any other available habitats (Beck et al., 2001; Sheaves et al., 2006; Nagelkerken et al., 2015), differences in specific resource requirements mean that the details of nursery use vary from species to species. To further complicate the matter, exactly how habitats provide values to species and how the utilization of particular areas is influenced by contextual factors, such as proximity to other key habitats (Cocheret de la Morinière et al., 2002; Dorenbosch et al., 2004) or food availability (Davis et al., 2014b; Tableau et al., 2016), is complex and usually poorly understood. Consequently, even among habitats in apparently similar settings, nursery values differ depending on a range of contextual factors (Bradley et al., 2019; Bradley et al., 2021). Without well-designed studies aimed at the stage-specific requirements of specific species, it is hard to be sure the extent to which an area provides a valuable, or even a viable, nursery. Additionally, habitat value is often associated with a structural feature, like mangrove trees or seagrass beds, which are believed to be the catalyst for enhanced protection and/or food. However, the value of a nursery is also dependent on other factors, such as water quality dynamics (e.g. patterns of change in salinity, temperature, dissolved oxygen), and connectivity among habitat components (Sheaves, 2009), that influence how, when and how often an area can be used as a nursery (Amorim et al., 2016). These last aspects are often overlooked, but the need to understand the components of habitat value is particularly relevant for species that use coastal and estuarine nurseries, because the nursery stage often represents a bottleneck for species success (Sheaves et al., 2015) and coastal and estuarine nurseries incorporate a range of habitats with diverse characteristics (Davis et al., 2014a). Moreover, the catchments of coastal nurseries are often among the areas most extensively affected by human activities

(Bugnot et al., 2019), with both water quality and connectivity at risk of degradation because of the constructions of barriers, such as roads, weirs and dams (Sheaves et al., 2008; Sheaves et al., 2014; Kroon and Phillips, 2016), and pollutants and sedimentation from human activities.

Recognition of these issues has focused increasing attention on preserving coastal and upper tidal systems and their function (Bayraktarov et al., 2016), and fostered policies aimed at restoring ecological functions (Tempest et al., 2015). However, many restoration projects are initiated without comprehensive knowledge of the characteristics necessary for nursery ground use by the species of interest (Gilby et al., 2020). Such projects are often unsuccessful because of a mismatch between the restoration actions and the features that need to be restored (Elliott et al., 2016). More specifically, instead of simply identifying the general types of habitats that a species occupies and restoring the physical structure of degraded areas of habitat of that type, it is necessary to understand the physical, chemical and contextual features of the system and how they interact with connected components to support healthy populations of juveniles (Sheaves et al., 2021). For instance, restoring of an area of mangroves to support fish populations is likely to fail in a mesotidal area if attention is not paid to ensuring the availability of suitable low tide structural refuges necessary during periods when mangroves are unavailable to fish.

Estuaries and coastal wetlands of Australia’s Great Barrier Reef (GBR) catchment are nurseries for important reef associated (Sheaves, 1995) and coastal (Laegdsgaard and Johnson, 1995; Curley et al., 2013) fisheries species. While upstream estuarine and transitional habitats are utilised extensively by marine juveniles (Sheaves et al., 2007a; Davis et al., 2012), human-imposed barriers such as bund walls, weirs, culverts or causeways (Sheaves et al., 2007b; Sheaves et al., 2007c; Kroon and Phillips, 2016) has seen marine fish excluded from substantial areas of upstream estuarine and coastal wetland habitat (Sheaves et al., 2014). This has led to a focus on prioritising the removal of human-made barriers to fish passage (Kroon and Phillips, 2016). However, it is unlikely that all upstream areas are equivalent. Consequently, prioritisation is inhibited by the lack of a nuanced understanding of the factors that constrain the use of upper estuary and coastal wetland habitats by marine-associated fishes.

There are proxies that are used to estimate the amount of refuge and/or food a juvenile fish has available (e.g. structure in water, invertebrate abundance, shallow water). However, areas can experience large variations in physical conditions that will affect juveniles in different ways based on their species and life stage. If the environmental conditions are unfavourable to the fish, even if just for a few hours (e.g. at low tide), they are likely to actively avoid an area (Dubuc et al 2021), even if it might have other favourable features (e.g. food and shelter).

This aspect of understanding how environmental conditions affects nursery ground value to juveniles is often overlooked.

We considered the Baffle region, an area of the GBR catchment that features one of the lowest percentages of tidal wetland loss (Sheaves et al., 2014), and investigated the characteristics of estuarine areas likely to host juvenile marine fish species and how fish assemblages varied in response to changes in environmental characteristics. The relatively unimpacted nature of the region provides the opportunity to develop a nuanced understanding of the environmental conditions that limit the utilisation of upstream tidal wetland nurseries; information that can be used in prioritising actions for restoring or retaining nursery function in this or other locations.

Materials and Methods

Study location

The study was conducted in the Baffle Drainage Basin (BDB) located on Queensland's central coast (23.94°S-24.67°S). The drainage basin contains extensive estuarine areas surrounded by 135 km^2 of estuarine mangroves, saltpans and saltmarshes. While much of the catchment has been cleared for agricultural activities, the waterways of the BDB are in near pristine conditions, with fish excluded by human-imposed barriers from <1% of the Basin's 329 km^2 tidal wetlands (Sheaves et al., 2014). Because of the low intensity of modification, low population density and low intensity of development (BMRG, 2011), there is little anthropogenic degradation of water quality. The major historical impact in the area is grazing from hard-hoofed mammals. The geomorphological structure of these tidal systems and estuaries varies from many other areas of north-eastern tropical Australia. Many estuaries along the GBR coastline occur as meandering channels, mainly confined to sedimentary flood plains and bordered by extensive mangrove forests. In contrast, in the BDB, estuaries feature linear tidal channels, with only part of their total length on the floodplain, and the majority comprising a channel incised through terrestrial sedimentary rock substrate. While downstream areas are bordered by extensive mangrove forests, upstream areas have only sparse, intermittent mangrove fringes, interspersed with overhanging terrestrial forest. In-stream rock bars are common in upstream areas, often resulting in the formation of a series of rocky pools disconnected to a greater or lesser extent at low tide (Figure 1).

Figure 1: Images of some channel structures in the Baffle Basin, downstream areas regularly connected by the tide in a) Deepwater Creek and b) Eurimbula Creek, and less frequently connected upstream areas that still receive monthly tidal connections in (c) Worthington Creek and (d) Scrubby Creek.

Study Sites

The upstream areas of five estuaries in the BDB were investigated: Scrubby, Worthington, Eurimbula, Deep Water and Baffle Creeks (Figure 2).

Scrubby Creek (Figure 2a) receives seasonal freshwater flows, and extensive mangrove forests surround downstream parts of the estuary. The extent of the tidal ingress is about 10 km and the mangroves become sparse in upstream areas, with the most upstream mangrove found at pool SC3. The systems have high banks covered with extensive terrestrial vegetation and upstream of pool SC2 most of the creek is under constant shade from riparian vegetation. The substrate is mostly sand over bedrock that is exposed in some areas of the creek, leading to the formation of isolated pools during period of low tide when freshwater flushes are absent. With the exception of a culvert positioned between SC1 and SC2, direct human impacts on the creek are minimal.

Worthington Creek (Figure 2b) is a more complex system comprising several tributaries with about 14 km of tidal ingress. Upstream areas are characterised by high rock or earth banks (> 5 m), and sediment within the streambed is mostly coarse sand, rock or rubble. During low tide, most areas upstream of pool W1 form pools isolated by rock or sand bars. These pools are either completely disconnected or have only shallow (< 10 cm) drains between pools. Many of these low tide pools are confined to the centre of a broad rubble and bolder strewn channel with little overhang by terrestrial forests. Worthington Creek is subject to episodic freshwater flows during periods of high rainfall, however permanent freshwater pools occur upstream of the estuary. Most of Worthington Creek is located within a National Park and so receives relatively little human impact.

Eurimbula Creek (Figure 2c) receives only seasonal freshwater flows but retains permanent freshwater pools in upstream areas. The creek has about 14km of tidal ingress and it is characterized by a series of natural rock bars that form distinct pools in upper tidal reaches during periods of low tide, but, unlike Worthington Creek, pools extend to the forested banks at low tide. Pools up to E5 receive some degree of tidal connection, but beyond this point remnant pools are permanently freshwater. This separation in connectivity aligns with the presence of intermittent mangroves along the bank of the waterway, which extend upstream as far as pool E4. Eurimbula Creek has a mix of sediment types, with substantial areas of sand and smooth bedrock, as well as fallen trees and organic litter derived from the extensive overhanging vegetation. The system and its catchment are all within National Park boundaries, meaning human impact is minimal.

Deepwater Creek (Figure 2e) and Baffle Creek (Figure 2d) are both permanently connected systems that do not form distinct pools during low tide. The tidal ingress for baffle is more than 35 km, while Deepwater is about 14 km, however tidal incursion in Deepwater Creek is limited by a weir, meaning that natural intrusion could have been longer. Their banks are diverse in character, with more extensive mangrove fringes in upper estuarine areas than the other systems. Sediment are also diverse, with sand interspersed with areas of exposed bedrock. Baffle Creek has a constant freshwater flow, while areas upstream of the weir in Deepwater Creek are permanently fresh (See supplementary material for full description).

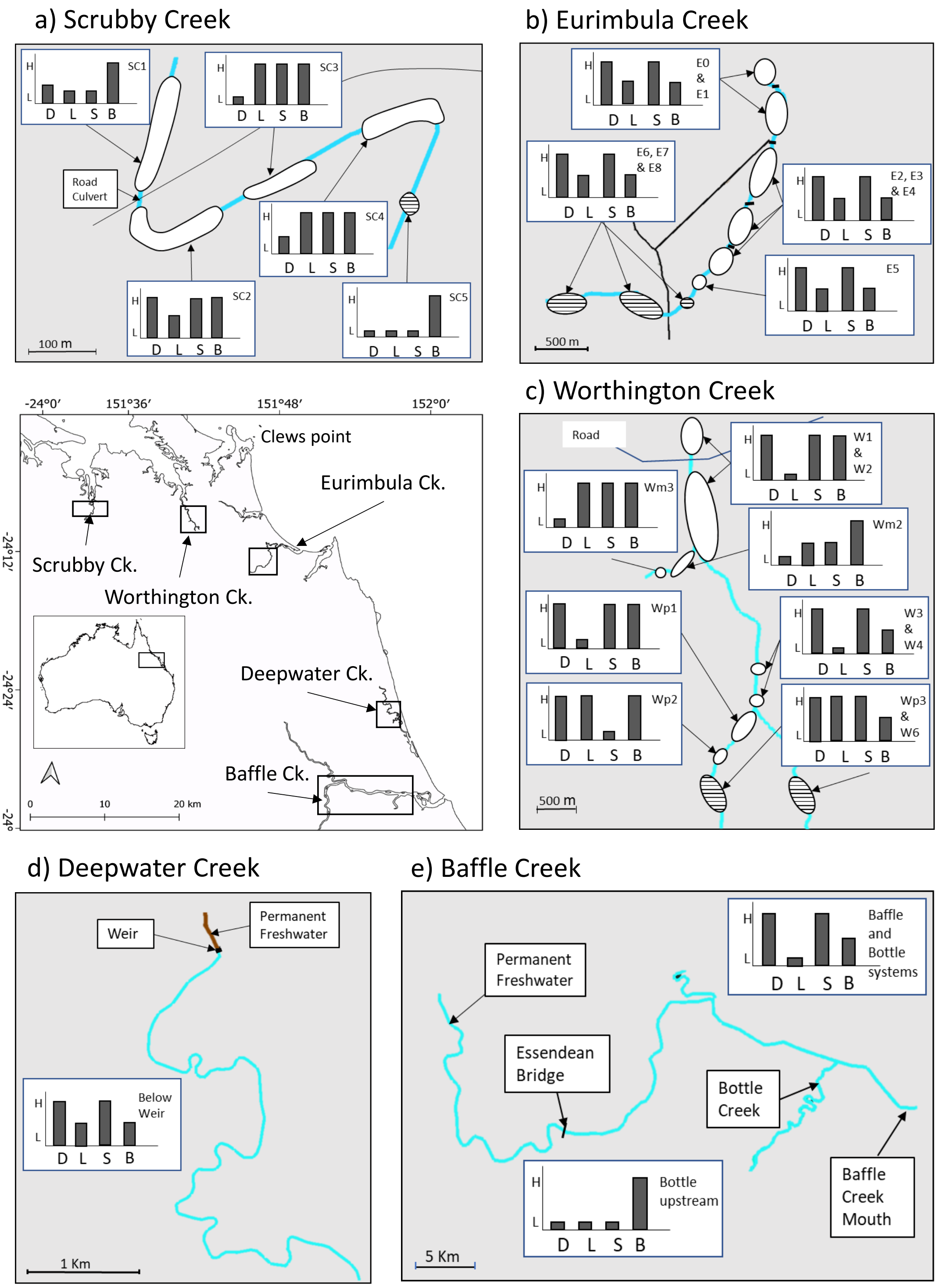


Figure 2: Map of study area and research sites; a) Scrubby, b) Worthington, c) Eurimbula, d) Deepwater, and e) Baffle Creeks. Scrubby, Eurimbula and Worthington Creeks feature identifiable pools in upstream areas, and these are indicated by expanded ovoid areas (not to scale). The ovoid areas with horizontal bars indicate permanent freshwater areas. Bar graphs provide a qualitative description of 4 key variables for each study site; D= Depth, L = Leaf litter, S= presence of complex structure in water, B= Bank height), going from Low (L) to High (H) (vertical axes).

Sampling

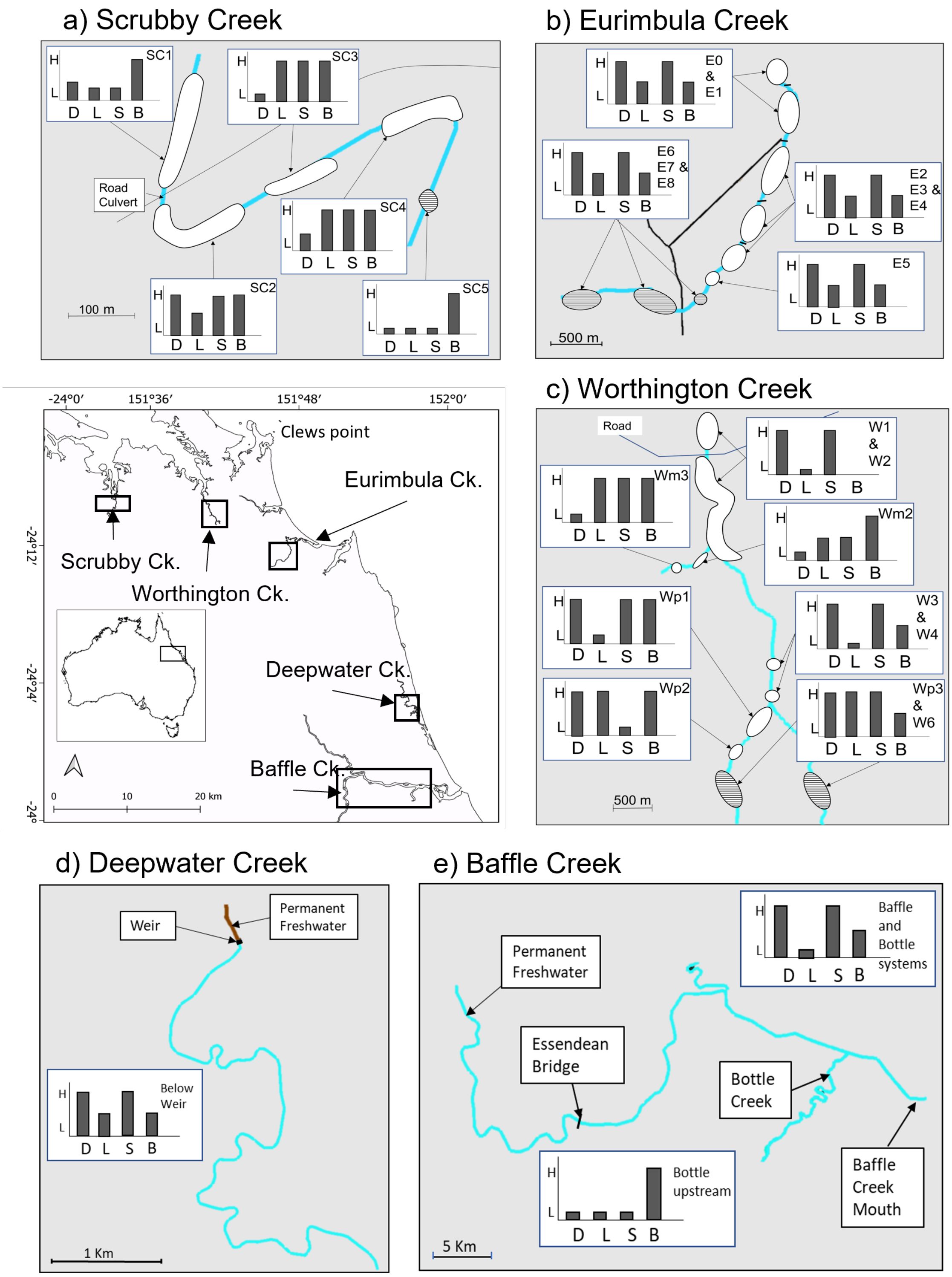
Sampling was conducted in June and September 2017, and July and November 2018. During these periods, tidal connection patterns, temperature, salinity and dissolved oxygen (DO) were recorded. These physical factors, while not inclusive of all possible environmental parameters, were chosen because they were most likely to have direct effects on the nursery value of these systems (Sheaves et al., 2015). Water quality loggers and meters were placed in strategic positions along the five systems to allow a representative coverage of areas that receive daily tidal connections and those that are more intermittently or rarely connected. HOBO U20L pressure loggers were used to recorded pressure and temperature at 10 minutes intervals, to determine the frequency with which each upstream pool was tidally connected. These data were cross-referenced with predicted tide levels at the nearest tide gauge (Clews Point, Australian Bureau of Meteorology tides tables (AusTides, 2018), to determine the tide levels that provided connectivity at each site (See supplementary material for full results). YSI proODO oxygen meters were used to gain an initial understanding of dissolved oxygen dynamics across the five systems. The meters were used both to collect initial immediate readings and left to log at five minutes intervals over a 24-hour cycle. This information allowed prediction of the likely variability in DO among sites and assisted the placement of long-term loggers across the systems. HOBO U26 dissolved oxygen loggers were placed 5cm above the sediment surface in pools identified as of representative of the area, including locations along upstream gradients, and locations with variable levels of algae and decomposing matter. The loggers were calibrated before deployment and cross-validated with individual meter readings collected at the time of deployment and retrieval. They were left in place for at least three months (logging at 10 minutes intervals) to gain an in-depth understanding of oxygen dynamics, within each system. More than 20 HOBO pressure loggers and 10 HOBO dissolved oxygen loggers were placed throughout the BDB, with loggers providing long-term information on tidal connections and freshwater flooding patterns for nearly one year. DO fluctuations beyond the first six weeks following deployment need to be interpreted with caution because biofouling increasingly affected readings from some loggers during long deployment (See supplementary material for full details).

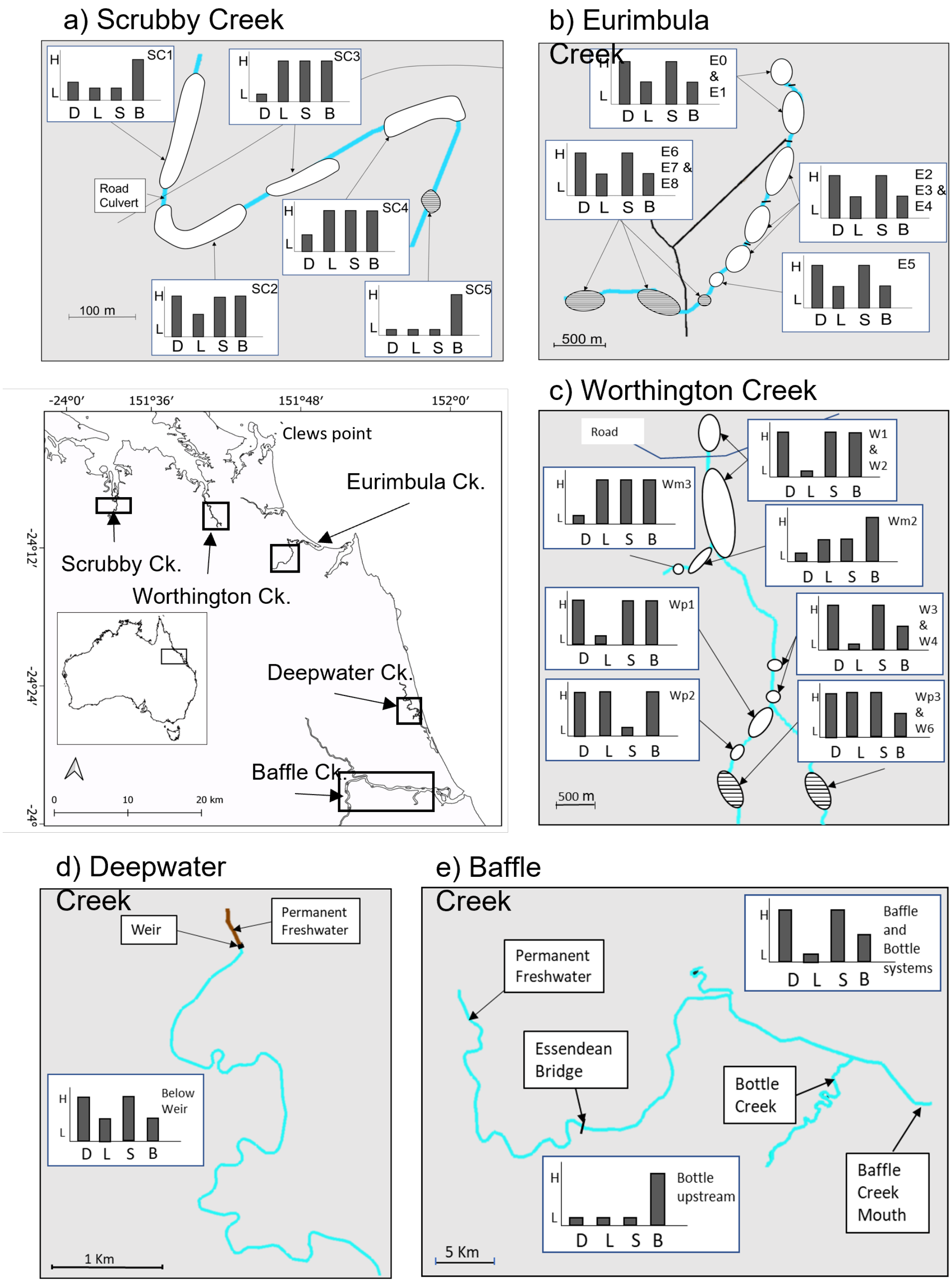
Nekton surveys were conducted using Garmin XE underwater video cameras mounted on aluminium bases and left to record for 15 minutes (see Bradley et al., (2019) for detailed information on deployment and operation). The cameras were unbaited to avoid attracting organisms from surrounding areas, because the aim was to assess fish habitat utilization (Sheaves et al., 2020b). To minimize the bias associated with variable visibility, cameras were deployed only if the visibility was greater than 50 cm when tested using a Secchi tube. Camera were placed haphazardly and spaced at least 20 m apart to reduce the chance of inter-dependency among samples. As a result, although we attempted to deploy at least five replicate videos per pool, in instances where the pool area was too limited, we used lower replication.

Site selection was designed to represent the range of situations, including tidal connection, , system size, bank elevation, substrate type, river morphology, freshwater influx, to further assess the range of environmental factors that could constrain nursery ground value. All video sampling was conducted when pools were completely disconnected, or in the instance of permanently connected parts of the systems, during low tide. Cameras placements were chosen to cover the range of habitat types available.

253 videos were viewed by nekton experts who identified each individual to the lowest taxonomic level possible (species in most cases). When this was not possible taxa were grouped up to the Genus or Family level. The approximate size class and life stage of fish

was also recorded when possible. It is not possible to determine the actual size of a fish using single underwater videos, however, many taxa have distinctive features and patterns during their early juvenile phase that allows confident identification of juveniles from post-settlement stage to late juvenile stage. Additionally, during video processing, information on the local habitat in the background of the video was recorded to identify fine scale species-habitat relationships. Fish species presence, rather than abundance, was recorded, to minimize bias associated with variable visibility (Sheaves et al., 2020b) and allow comparison between species with different schooling behaviours (Sheaves and Johnston, 2010). Additionally, videos were processed using a convolutional neural network (CNN) to identify and extract frames where juvenile *L. argentimaculatus* were observed (for details see (Konovalov et al., 2019; Sheaves et al., 2020b). This was done to validate human consistency detection, as well as CNN's accuracy in finding juveniles. Overall, the humans and the CNN's detection ability were comparable with the CNN detecting 61 out of the 65 videos where early juvenile *L. argentimaculatus* were detected (93% accuracy). However, the CNN substantially reduced the amount of time required by human experts with only 8 hrs required to examine and validate the frames extracted by CNN, compared with the 63.25 hours of recording available which a fish expert would have to visually assess.


a) Scrubby Creek
SC1
SC2
SC3
SC4
SC5
Road Culvert
100 m
H
L
D L S B
b) Eurimbula Creek
E0 & E1
E6 E7 & E8
E2 E3 & E4
E5
500 m
c) Worthington Creek
Road
W1 & W2
Wm3
Wm2
Wp1
W3 & W4
Wp2
Wp3 & W6
500 m
-24°0′
151°36′
151°48′
152°0′
-24°12′
-24°24′
-24°
Clews point
Eurimbula Ck.
Scrubby Ck.
Worthington Ck.
Deepwater Ck.
Baffle Ck.
0
10
20 km
d) Deepwater Creek
Weir
Permanent Freshwater
Below Weir
1 Km
e) Baffle Creek
Permanent Freshwater
Essendean Bridge
Bottle Creek
Baffle Creek Mouth
Baffle and Bottle systems
Bottle upstream
5 Km


a) Scrubby Creek
SC1
SC2
SC3
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Road Culvert
100 m
b) Eurimbula Creek
E0 & E1
E6 E7 & E8
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Clews point
Eurimbula Ck.
Scrubby Ck.
Worthington Ck.
Deepwater Ck.
Baffle Ck.
0
10
20 km
c) Worthington Creek
Road
W1 & W2
Wm3
Wm2
Wp1
W3 & W4
Wp2
Wp3 & W6
500 m
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Weir
Permanent Freshwater
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Bottle upstream
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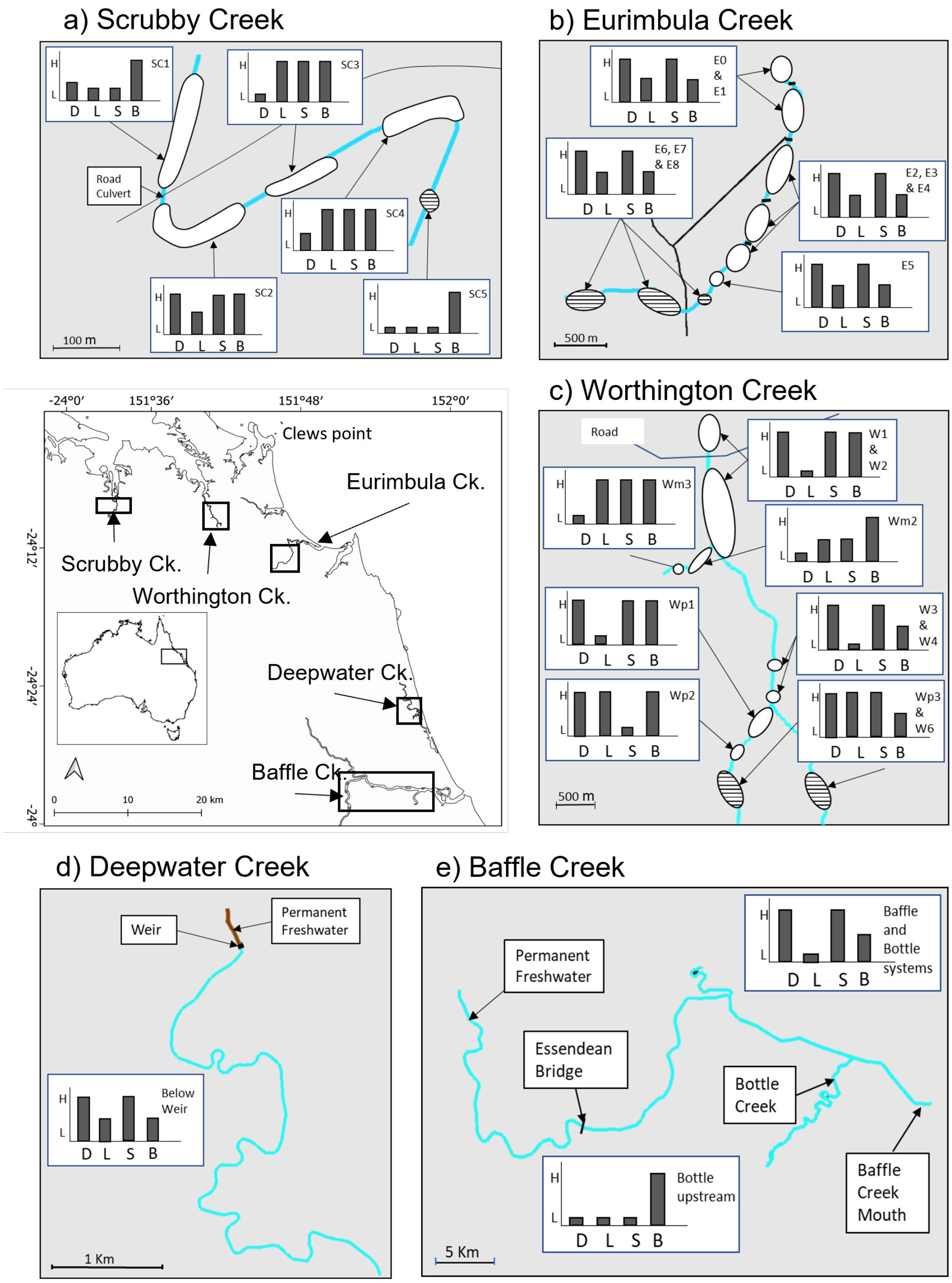

Data analysis

Differences in fish composition (proportion of cameras in which each species occurred) at the study sites were investigated using non-metric Multidimensional Scaling (nMDS) based on Bray-Curtis dissimilarities on row standardized data using Primer-E (Clarke and Gorley, 2006). Only species that occurred at more than 5 sites were included in the nMDS.

Multivariate regression trees were used to explore the relationships between the fish community and environmental factors using R open-source software (RCoreTeam 2019) employing the 'mvpart' routine for mCARTs (De'ath 2007). Predictor variables were: size of the pool (categorical: 3 levels), connectivity in days per year (numerical), substrate type (categorical: 5 Levels), structure in water (categorical: 5 levels), salinity during dry periods (numerical: 10 values), Dissolved oxygen pattern classification (Categorical; 3 levels) (see supplementary material for details). All replicate videos were included in analyses.

Juveniles of three fish of commercial and recreational value (*Acanthopagrus australis, Lutjanus argentimaculatus* and *Lutjanus russellii*) were common in Baffle Catchment videos. Univariate classification and regression trees (uCART) were used to determine the extent to which sites within the systems were used by juveniles of these species, using probability of encounter (PoE, Sheaves et al., 2012) per pool as the dependent variable and Pool Identity (Categorical; 29 levels) as the predictor. The final CART model was selected based on ± 1 standard error selection criteria (Breiman et al. 1984; De'ath and Fabricius 2000). All replicate videos were included in the analyses. Contrasts in the physio-chemical, geomorphological and biological characteristics of the pools with high probabilities of encounter versus those with low probabilities of encounter were used to assess the characteristics that appeared to determine juvenile occurrence.

To investigate the influence of in-pool factors on juvenile occurrence, uCARTs were conducted on species PoE data for pools with high juvenile occurrence. Predictor variables were those identified at the time of sampling: DO (numerical: 0-100), salinity (numerical), substrate (categorical: 5 levels), structure in water (Categorical: 5 levels), size of the pool (Categorical: 3 levels), and the extent of disconnection from main channel (categorical: 5 levels).

Results

Water quality dynamics in the BDB were linked to rainfall events, tidal connectivity and seasonal temperature variations. In 2018 the BDB experienced three heavy rainfall events that led to some creeks (Worthington Creek, Scrubby Creek, Eurimbula Creek and Deepwater Creek) rising to several metres above than their normal levels, with freshwater conditions extending throughout most of the areas studied (See supplementary material). However, during dry periods freshwater flow ceased in upper estuarine areas of all systems except Baffle Creek, with pools becoming increasingly saline during tidal disconnection (Table 1) as evaporation increased salinity concentrations (Sheaves, 1996). For instance, Eurimbula Creek and Worthington Creek displayed very high salinities (about 45‰) in most pools during periods of low rainfall. In contrast, Baffle Creek, with year-round freshwater flows, maintained reduced salinities (~7‰) in upstream estuarine areas despite receiving tidal connection almost every day (Table 1).

Temperature in most pools ranged from 15 °C in winter, to 31 °C in summer (see supplementary material), although in some extreme situations (e.g. WM3), temperatures fell to 10 °C in winter months, or rose as high as 36 °C in summer (e.g. W1) (Table 1). These extremes were likely exacerbated by logger position and environmental setting. Both extremes were captured by loggers in shallow waters (< 10 cm), either receiving direct sunlight for most of the day (e.g. W1), or little to no sunlight due to high banks (e.g. WM3). Despite seasonal fluctuations, there were no instances of large day-to-day fluctuations. On the other hand, the extent of tidal connectivity was highly variable across the sampled pools, ranging from daily connections in more downstream areas and highly connected upper estuarine pools (e.g. Eurimbula Creek pools E0 and E1), to only being connected on a few days a year in some upstream pools (e.g. WM3) (Table 1, see supplementary material for details).

Compared to the relatively simple patterns of salinity and temperature, dissolved oxygen (DO) showed complex fluctuations over multiple temporal scales. On a daily basis there were three main patterns of DO fluctuation (Figure 3); a) ‘normoxic’ which is consistent high DO, characterized by DO fluctuating around 100% saturation, with only occasional small sags to around 50% saturation during the night and early in the morning (Figure 3); b) ‘fluctuating DO’, with DO ranging from saturated or hyper-saturated (> 120%) to very low saturation (<20%) following a diel pattern; and c) ‘hypoxic’, with DO commonly observed below 50% saturation regardless of the time of the day. These classifications reflect the level of threat they likely pose to aquatic life, with pattern (a) usually considered normoxic and therefore unlikely to stress estuarine organism, (b) likely to pose physiological stress to some organisms, and (c) likely to exclude most species from using the area during hypoxic conditions, unless they possess specific adaptations (Davis, 1975; Vaquer-Sunyer and Duarte, 2008; Riedel et al., 2012). Simply considering the daily fluctuations cannot fully encapsulate DO patterns and organismic responses because occasional low DO events may not be sufficient to prevent some species utilizing a system (Dubuc et al., 2017; Dubuc et al., 2019). Consequently, to fully understand the likely influence of DO within a system, it is necessary to understand long-term dynamics rather than simply focusing on extreme values. For instance, DO readings in pool WP1 (Figure 3a) showed a sudden dip following a slight increase in water depth. This brief DO decline, which returned to normoxic levels within a few days, was likely the result of a small rainfall event that caused a sudden increase in carbon load and triggered a localised, short term blackwater event (Meyer, 1990; Howitt et al., 2007). Similarly, pool WM2 (Figure 3b), showed a similar small freshwater event and coupled sudden DO decline. However, unlike pool WP1, pool WM2 did not recover and continued to show large within-day fluctuations in DO. (See Supplementary material for details).

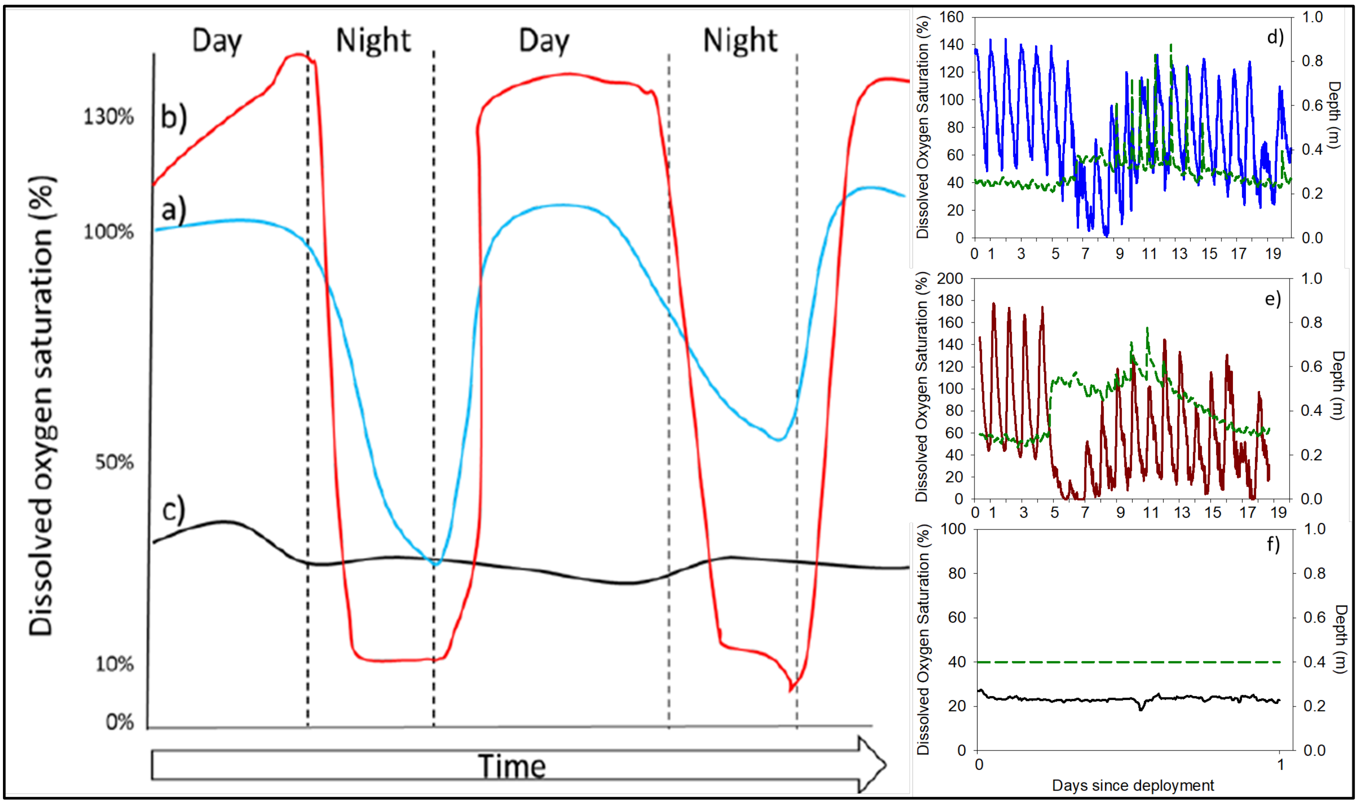

Figure 3: Conceptual diagram (on the left) of the 3 common diurnal dissolved oxygen fluctuation patterns observed in BDB upstream pools. Blue line depicts pattern (a) 'normoxic' high daytime oxygen levels with only occasional nighttime declines below 50%, Red line depicts (b) 'fluctuating' daytime oversaturation with regular declines to low levels at night, often lasting for several hours, Black line depicts (c) 'hypoxic' constant depressed dissolved oxygen levels (hypoxic). The panels on the right show actual DO reading collected during the study and reflect the conceptual diagram classification. The dashed green line is the water depth while the solid line is DO: d) Worthington Creek pool WP1, normoxic, high DO; e) Worthington Creek pool WM2, fluctuating DO; f) Deepwater Creek freshwater section above weir, hypoxic.

A total of 40 fish and 2 shrimp species were identified during this study, of which only 10 species were found across more than 5 sites (Table 1). Of these, one sparid (*Acanthopagrus australis*) two lutjanids (*Lutjanus argentimaculatus* and *Lutjanus russellii*) and a mugilid (*Mugil cephalus*) are of commercial and/or recreational value in Australia. All individuals of the two lutjanid species were identifiably juvenile, and many of the sparids also appeared to be juveniles. All identifiable mugilids were adults of *M. cephalus*, although small juvenile mugilids, too small for confident species identification, were present at some sites. The remaining fish species observed during the study were small species, such as ambassids, gobiids and eleotrids, commonly found in estuarine or freshwater environments (Sheaves et al., 2007b) (see supplementary material for full species list).

Table 1: Summary descriptions of the study locations and specific sites showing the overall physical characteristics and the most common species that occur throughout the BDB. The data summarize the minimum predicted tide level at which inundation is detectable, tidal connection per year (with classification in brackets, VH= very high connection, V= High Connection, L= low connection, VL= Very Low connection), salinity level during periods of low rainfall, temperature (min and max) experienced during the study (temperature in brackets indicate no summer data were collected), the DO classification pattern the pools experienced (value in brackets are expected trends where no logged data were available), and the maximum numbers of individuals seen in a video at one time (MaxN) for each site for species encountered at more than 5 sites. (Blue shading indicates fisheries species, dashes (-) indicate no videos were recorded for that site, NA means that no logger was placed at that site).

									Maximum number of individuals seen in videos for each site									
Location	Site	Predicted tidal height to allow noticible connection	Connection days per year	Salinity during dry season	Max dept	Temperature	DO pettern	Nursery	*Acanthopagrus australis*	*Lutjanus argentimaculatus*	*Lutjanus russellii*	*Hypseleotris compressa*	*Ambassis spp*	*Mugil cephalus*	*Gerres filamentosus*	*Pseudomugil signifer*	*Gerres oyena*	*Microcanthus strigatus*
Baffle Ck	Baffle Mouth (estuary)	Every tide (inc. neaps)	365 (VH)	40‰	>2 m	-	a		10	0	1	0	9	0	2	0	3	4
	Bottle Ck (estuary)	Every tide (inc. neaps)	365 (VH)	40‰	>2 m	-	a		12	0	2	0	28	0	0	0	1	1
	Essedean Bridge (upstream)	Every tide (inc. neaps)	365 (VH)	7‰	>2 m	15-(26)	(a)	✓	5	0	0	2	10	4	7	5	2	0
	Mollenhagen (freshwater)	none detected	0 (VL)	0‰	<1 m	-	c		0	0	0	30	0	0	0	6	0	0
Deepwater Ck	upper estuary	Every tide (inc. neaps)	365 (VH)	40‰	>2 m	22-29	a	✓	14	2	1	40	20	1	2	0	1	0
	upper estuary beow weir	Every tide (inc. neaps)	365 (VH)	35 ‰	>2 m	22-29	a	✓	4	0	0	60	50	1	1	6	0	0
Eurimbula Ck	E0 - upper estuary rock pool	Every tide (inc. neaps)	365 (VH)	40 ‰	>2 m	15-30	a	✓	12	6	1	70	65	2	2	0	0	0
	E1 - upper estuary rock pool	Every tide (inc. neaps)	365 (VH)	40 ‰	>2 m	-	a	✓	15	2	0	100	12	1	0	8	0	0
	E2 - upstream rockbar 1	2.8 m	120 (H)	40 ‰	>2 m	17-30	a	✓	1	2	0	43	0	0	0	0	0	0
	E3 - upstream rockbar 2	2.8 m	120 (H)	40 ‰	>2 m	17-30	b	✓	3	2	0	11	0	3	0	0	0	0
	E4 - upstream rockbar 3	3 m	60 (L)	35‰	>2 m	-	(b)		0	0	0	40	0	0	0	0	0	0
	E5 - upper tidal margin	NA	NA	15 ‰	<50 cm	-	c		0	0	0	25	0	0	0	0	0	0
	E6 - freshwater	none detected	0 (VL)	0‰	<1 m	15-27	c		0	0	0	4	0	0	0	0	0	0
	E7 - freshwater	none detected	0 (VL)	0‰	>2 m	13-(18)	c		0	0	0	40	0	0	0	0	0	0
	E8 - freshwater	none detected	0 (VL)	0‰	>2 m	-	c		0	0	0	6	0	0	0	0	0	0
Scrubby Ck	SC1 - Upstream below culver	2.7 m	192 (H)	35‰	>1 m	15-31	(a)	✓	11	0	0	12	6	4	0	0	0	0
	SC2 - Upstream above culver	2.9 m	60 (L)	29‰	>1 m	16-31	(b)	✓	6	1	0	30	6	1	2	5	0	0
	SC3	NA	50 (L)	10‰	<1 m	-	(b)		1	0	0	15	8	0	0	45	0	0
	SC4 - upper tidal margin	3.1 m	48 (L)	5‰	<1m	12-31	c		0	0	0	50	3	0	0	7	0	0
	SC5 - freshwater	none detected	0 (VL)	0‰	<50 cm	-	c		-	-	-	-	-	-	-	-	-	-
Worthington Ck	Estuary	Always	365 (VH)	35 ‰	>2 m	-	a	✓	7	1	7	0	25	5	0	0	2	5
	W1 - upper estuary	Every tide (inc. neaps)	365 (VH)	45 ‰	>2 m	15-36	a	✓	6	1	1	0	2	0	0	0	0	1
	W2 - upper estuary	Every tide (inc. neaps)	365 (VH)	45 ‰	>2 m	15-(25)	a	✓	11	1	3	0	20	6	2	0	0	2
	W3 - upstream	> 2.6 m	130 (H)	50 ‰	> 1 m	-	a		-	-	-	-	-	-	-	-	-	-
	W4 - upstream	> 2.6 m	130 (H)	50 ‰	> 1 m	-	a	✓	10	4	9	5	0	7	0	0	0	0
	W5 - upstream	NA	NA	35 ‰	> 1 m	-	(a)		-	-	-	-	-	-	-	-	-	-
	W6 - freshwater	none detected	0 (VL)	0 ‰	<50 cm	-	c		0	0	0	10	0	0	0	0	0	0
	WP1 - upstream	2.8 m	130 (H)	45 ‰	> 1 m	17-35	a	✓	2	4	1	0	30	4	0	0	0	0
	WP2 - upper tidal margin	3.2 m	36 (L)	15 ‰	> 1 m	16-34	b		0	0	0	22	29	0	0	0	0	0
	WP3 - freshwater	none detected	0 (VL)	0 ‰	>2 m	-	c		0	0	0	6	0	0	0	0	0	0
	WM1 - upstream	3 m	60 (L)	45 ‰	< 1 m	-	a		-	-	-	-	-	-	-	-	-	-
	WM2 - upstream	3 m	60 (L)	45 ‰	< 1 m	14-37	b		0	0	0	40	0	0	0	0	0	0
	WM3 - upper tidal margin	3.5 m	5 (L)	35 ‰	< 1 m	10-(19)	c		0	0	0	8	0	0	0	0	0	0

At the whole-of-estuary scale there was little variability in nekton communities among systems in the BDB. Within estuary systems, most of the variability was attributable to the extent of tidal connectivity, with the most connected areas (e.g. downstream estuary, upstream pools regularly connected by the tide) having a distinctly different communities from areas with poorer tidal connection (e.g. upstream reaches and freshwater areas) (Figure 4). When the vectors of the species most correlated with the two-dimensional space are superimposed on the ordination, this pattern becomes more evident, with freshwater species (e.g. *Melanotaenia nigrans,* palemonid shrimps) displaying a negative correlation with more estuarine species (e.g. *Gerres* spp., *Herklotsichthys castelnaui*). The four species of fisheries value (*A. australis*, *L. argentimaculatus*, *L. rusellii* and *M. cephalus*) were mostly found in areas experiencing high frequencies of tidal connections.

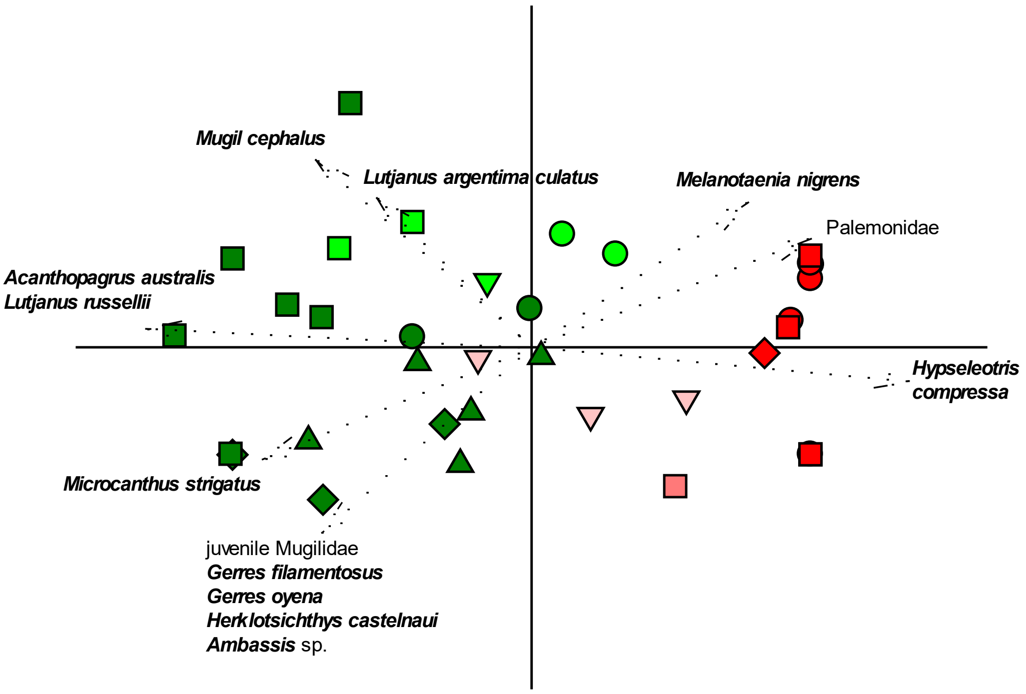

Figure 4: *nMDS ordination of the species composition in the Baffle Drain Basin. Location: (Squares = Worthington Creek; Circles = Eurimbula Creek; Upward triangle = Deepwater Creek; Downward Triangle = Scrubby Creek; Diamond = Baffle Creek). Tidal connectivity increases from right to left across the ordination, indicated by symbol colours (Red = very low connection <5 times a year; Pink = low connection < 60 times a year; Light Green = high connection < 130 times a year; Dark Green = very high connection> 130 times a year). Superimposed vectors represent species that correlated > 40% with the 2-dimensional ordination space.*

The mCART provides more details on the factors affecting the nekton community in the study systems. The most important factor was the level of connectivity, with areas and pools connected for more than 125 days in a year displaying higher occurrences of most species than areas connected less often (Figure 5). Upstream areas that received less frequent tidal connection were characterized by a single species, the empire gudgeon (*Hypseleotris compressa*). After accounting for the extent of connectivity, the next most influential factor in determining relative occurrence of most species was the amount of structure. Areas of low structural complexity (bare sand, mud or rocky pavement) or only small-scale structure (e.g. sticks and grass), had lower species occurrence than areas with greater structural complexity (e.g. woody debris). This effect was nuanced for different species; the level of structural complexity had little influence on the occurrence of *A. australis*, while species such as *L. argentimaculatus* were substantially influenced by the presence of structural complexity. Other variables (sampling event, size of the pool, pool identity, substrate type, extent of disconnection from main channel) were not influential in the mCART model.

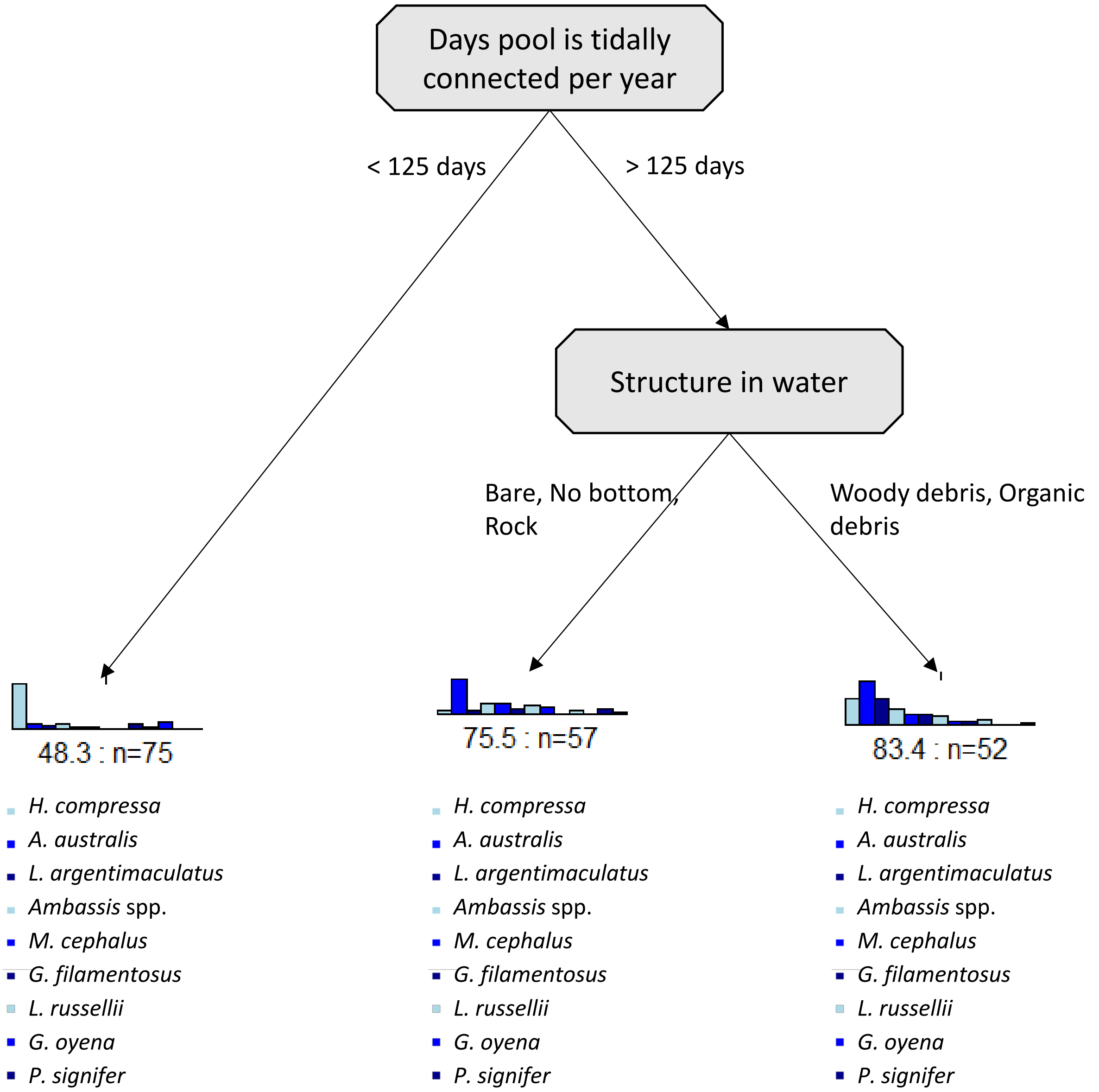

Figure 5: Multivariate regression tree for the community composition at Baffle Creek constructed using various environmental characteristics of the pools (sampling event, size of pool, connectivity in days per year, pool name, substrate type, structure in the water, and the extent of disconnection from main channel). Bars represent the relative proportional occurrence of species in the different terminal nodes.

The pools used most extensively by juveniles of *L. argentimaculatus*, *L. russellii* and *A. australis*, shared the same key long-term characteristics, with all three species having highest

PoEs in medium to large pools that became hypersaline during long period of low rainfall (Table 2). All three species preferred well-connected pools that received connections at least during the largest monthly spring tides. *L. russellii* was more constrained by the level of connectivity than the other two species. Similarly, it had higher PoE in areas with high salinity and more reliably high DO than the other two species. In fact, *L. argentimaculatus* and *A. australis* appear to be found in areas with greater DO fluctuations than *L. russellii*.

Table 2: Summary of the long-term characteristics of the pools/systems with high (green rows) and low (red rows) presence of juveniles L. argentimaculatus, L. russellii, and A. australis based on the CART results carried out using pool identity as explanatory variable.

Species	**Juvenile rresence**	**Pool size**	**Reach**	**Tidal connection days a year**	**When is pool disconnected from rest of system**	**Dry season salinity (ppt)**	**DO pattern**
L.argentimaculatus	**High**	Large/Medium	Upstream/Medium	> 60	At every low tide/During low spring tide	29-50	a/b
	Low	Small	Mouth/Permanent Freshwater	< 60	Always connected/During neap high tide/Never tidally connected	0-30	c
L. russellii	**High**	Large/Medium	Mouth/Upstream	> 130	Always connected/At every low tide/During low spring tide	35-45	a
	Low	Small	Medium/Permanent Freshwater	< 130	During neap high tide/Never tidally connected	0-35	b/c
A.australis	**High**	Large/Medium	Mouth/Upstream/ Medium	> 60	Always connected/At every low tide/During low spring tide	7-50	a/b
	Low	Small	Permanent Freshwater	< 60	During neap high tide/Never tidally connected	0-7	c

For all species the primary split in the uCART assessing in-pool structures was on 'structural complexity' (see supplementary material for details), however, the pattern of response to structure varied among the species (Figure 6). *L. argentimaculatus* was almost exclusively observed in videos where woody debris (e.g. logs, fallen trees, twigs) were clearly observable in the background. The other two species were also proportionally more likely to be detected near woody debris, however they were also observed in high proportion in areas with no clear structure, although this does not mean that structure was not in the vicinity (e.g. behind the video camera).

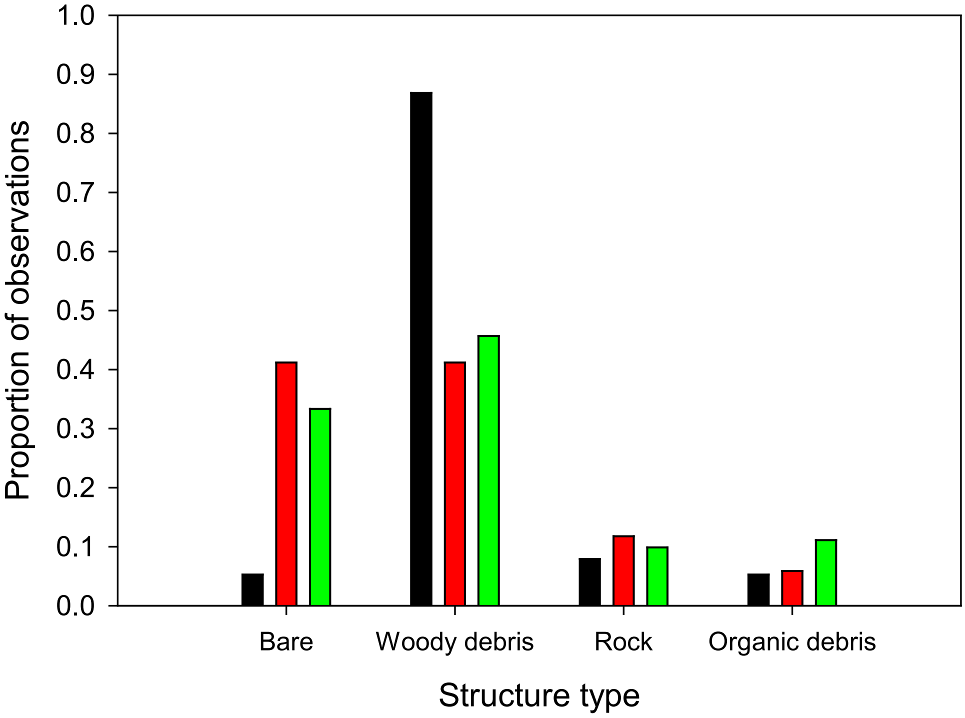

Figure 6: Proportion of species observed over the different Structure types, based on the first node of the uCARTs constructed to assess the within pool variability in juvenile observations for L. argentimaculatus (Black bars), L. russellii (Red bars), and A. australis (Green bars).

Discussion

Upstream estuarine pools provided the highest nursery value for juveniles of fisheries species in the BDB. The features of the environment that appear to serve as nurseries were not structural per se, e.g. mangroves, but rather a level of relative isolation facilitated by the interaction of geomorphology, tides and physical conditions in the intertidal zone. The juveniles of the three focal species utilized similar, well connected upper estuarine areas, which appear to function as important nursery grounds. Tidal connectivity was the most important factor regulating the nursery function of these areas, along with dissolved oxygen and salinity patterns, and within-pool habitat structure. Identifying the specific factors that provide nursery value for species is complex, because of the multitude of influences likely to determine the occurrence of an organism. Even if two areas appear similar in many ways, a single factor can render one area uninhabitable and prevent occupation, thus negating the value of other favourable conditions. During this study we evaluated many parameters (temperature, level of human impacts, system size, freshwater seasonality, substrate type, dissolved oxygen, tidal connectivity, river morphology, submerged structural complexity, salinity, bank elevation, tidal gradient), however only a few had substantial influence on each of the species, and thus acted to constrain species occupancy throughout the estuary systems studied.

Upper estuarine tidal pools may be providing a nursery refuge for fish due to reduced predation pressure. This could be the result of upper estuaries areas having large water quality fluctuatiions as well as reduced connectivity patterns, which could exclude some taxa (potential predators) during period of tidal disconnection. Indeed, tidally connected upstream pools had a reduced fauna overall when compared to downstream areas, and only a small overlap with some freshwater taxa when salinity was not elevated. Taxa that use upstream areas were typically juveniles of species commonly observed in marine and brackish areas of the system (e.g. snappers and bream). This reduced species diversity upstream seems to indicate that fewer taxa are capable of utilizing these highly dynamic areas, which can remain isolated over long periods at low tide and over neap tides, and therefore can experience large water quality fluctuations. For an upstream pool to provide habitat for fish during low tide, it needs to retain a sufficient volume of water during disconnection to prevent physical conditions from degrading to a point that causes severe stress or death (Waltham and Sheaves, 2017). This can act either at the species level, or change based on the life stage of the individual. As a result, only species adapted to cope with such dynamics would be able to utilize these areas. For instance, the highly influential factor of DO is known to limit taxa occupancy in marine systems (Rabalais et al., 2002; King et al., 2012). Therefore, pools that experience large DO fluctuations are likely to be avoided by fish with low tolerance to poor DO. On the other hand, taxa such as *L. argentimaculatus,* and *A. australis* were often found in areas with substantial daily DO fluctuations, which means that they are likely able to tolerate large shifts in DO, as long as hypoxic conditions do not last for extended periods (e.g. days). In particular, *L. argentimaculatus* is likely to be adapted to live in systems that experience large DO fluctuations as their association with mangrove estuaries, which often experience poor oxygen conditions, is likely to expose them to DO extremes on a daily basis (Mattone and Sheaves, 2017; Dubuc et al., 2019).

The presence of *L. argentimaculatus* in upstream hypersaline pools in the BDB indicates the species can cope with a wide range of water quality conditions, in contrast with previous reports that indicated the species prefer freshwater areas as nurseries (Russell and McDougall, 2005). However, previous reports were restricted by their sampling methodology (electrofishing) which is only effective in freshwater. Tolerance to a wide range of water quality conditions compared with their predators could provide juveniles acess to areas with reduced predation pressure, which could provide one explanation for the presence of high numbers of juveniles in upstream areas at low tide.

Different suites of constraints determined the extent to which each species utilised the various sites (Figure 7). While tidal connectivity was the most important factor contributing to the occupation of upper estuarine tidal pools, levels of necessary connectivity varied between species, and covaried with other factors. *L. argentimaculatus* and *A. australis* commonly occurred in areas that are tidally connected at least 60 days a year, and 30 days for *L. russellii.* This difference in preference between the two snappers could be the result of *L. russellii* preferring areas with brackish to hypersaline conditions and avoiding area with reduced salinity (Sheaves, 1998). In-pool factors were also important in determining occurrence. In particular, subtidal structure was an important determinant of site occupancy, with *L. argentimaculatus* in particular showing a strong association with complex structure - often found in close association with submerged timber, rocks and other form of subtidal complexity, a common trait for lutjanids (Sheaves, 1995; Thrush et al., 2002; Piko and Szedlmayer, 2007; Baker et al., 2019). Thus, for *L. argentimaculatus* the extent of structural complexity appears to be a key factor determining nursery occupation in upstream BDB pools. The same trend was not as strong for *A. australis,* which occurred both in areas with and without complex structure, suggesting that *A. australis* does not cue on structure to the same extent as *L. argentimaculatus*, hence structure appears to be less of a constraint on utilization. However, this lack of strong association with habitat complexity in the immediate vicinity does not mean that *A. australis* does not benefit from the presence of complex structure within the system.

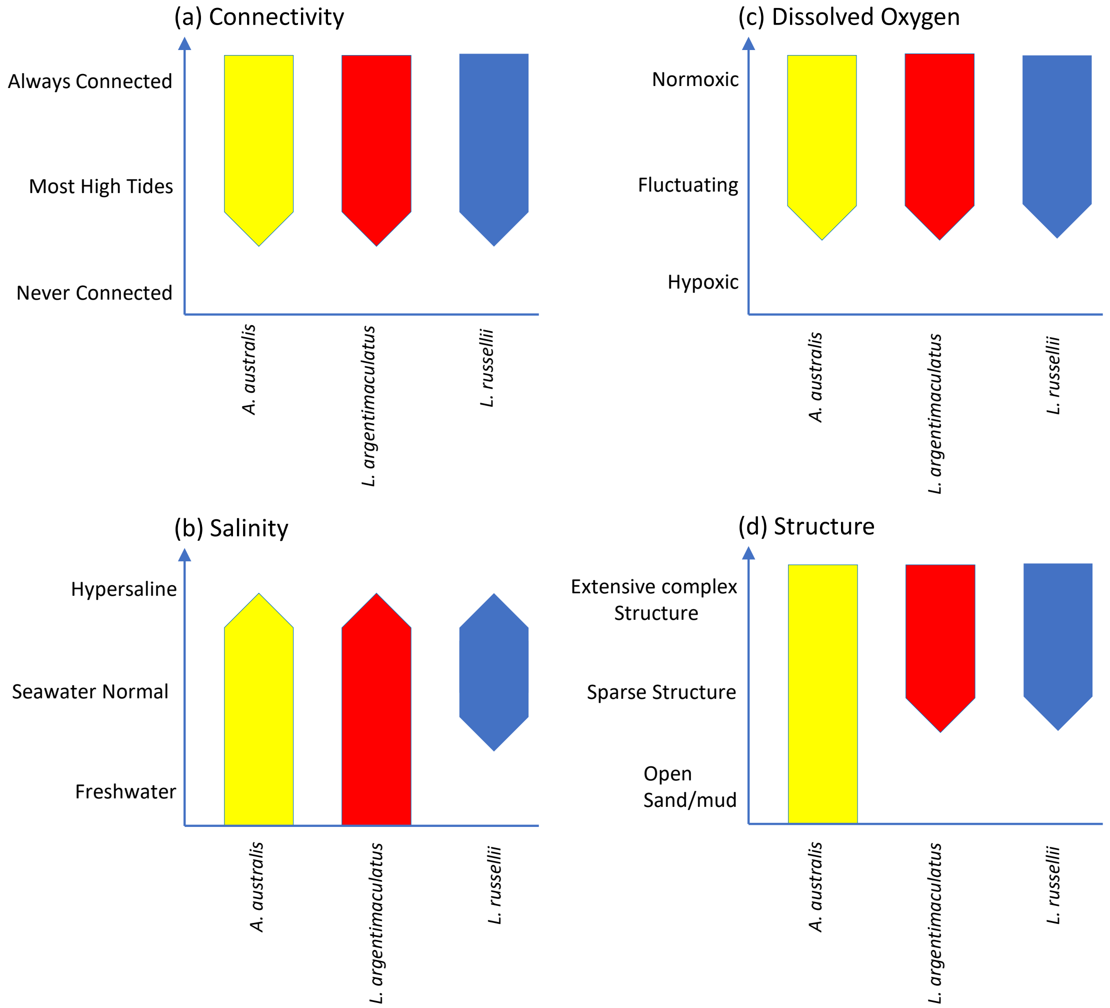

Figure 7 : Conceptual diagram of the major constraints for A. australis (Yellow), L. argentimaculatus (Red), and L. russellii (Blue) juveniles, based on the pool characteristics found in the BDB. The arrow shape bar represents the upper/lower limits of the species for that characteristic.

The constraints acting on the juveniles of these species, and how these constraints relate to characteristics of different estuary systems, can be depicted in a conceptual map that illustrates the areas and physical attributes that provide the highest potential for the provision of valuable nurseries for these species (Figure 8).

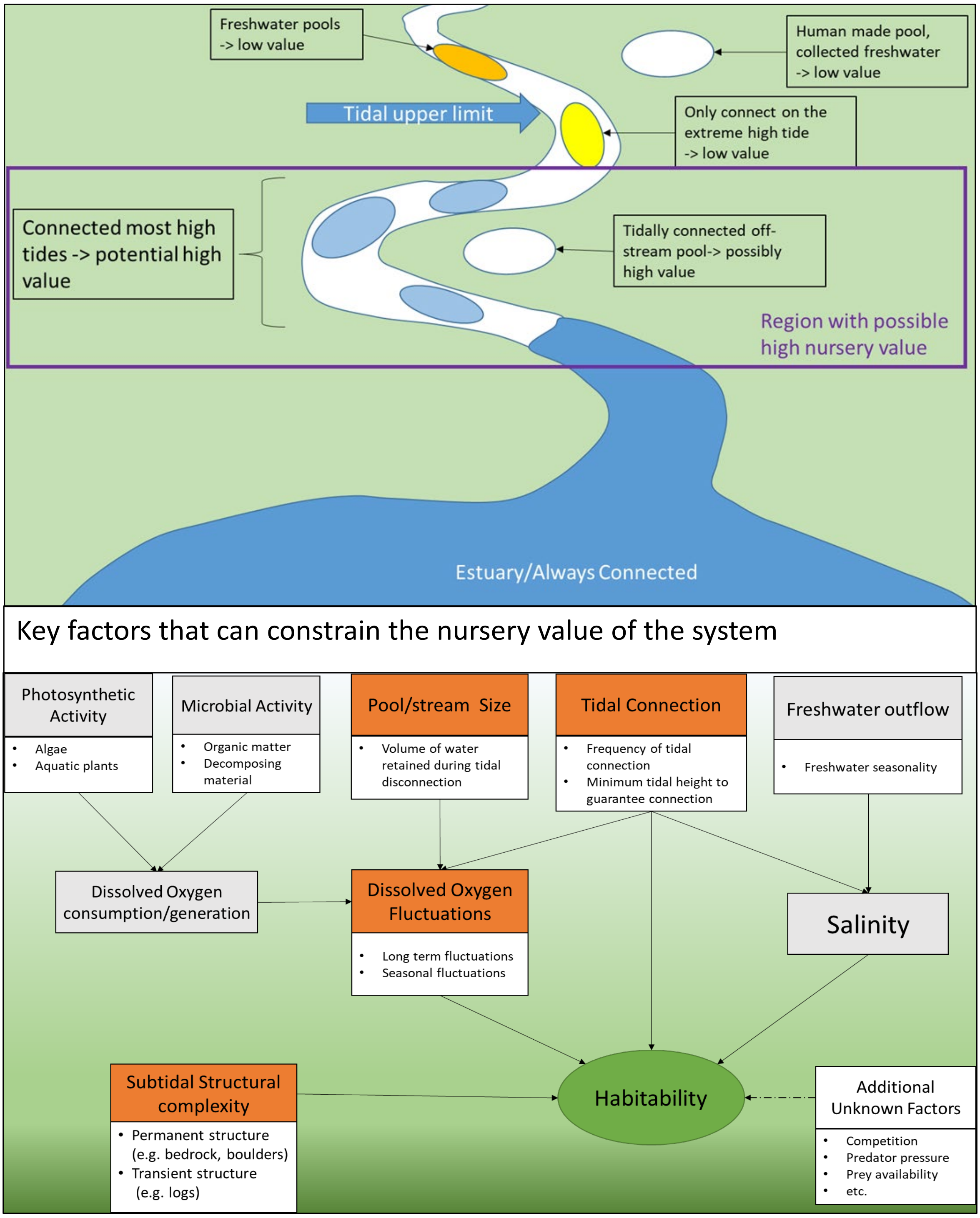

Figure 8: Conceptual diagram indicating the region with the highest potential to have nursery ground value and factors that can constraint (red boxes indicate key nodes that assist determining the habitability of the area) the utilization of these pools/region by juveniles of L. argentimaculatus, L. russellii and A. australis (these factors are key nodes utilized for the construction of the Bayesian belief net).

Theoretical understanding of nursery ground function is underpinned by a straightforward trade-off between the levels of growth and mortality that juvenile fish experience among different habitats habitats (Werner and Gilliam, 1984). If appropriate food, refuge and physical conditions are more easily obtained in alternative habitats, then the use of nurseries makes ecological sense. However, how these values are derived and supported in a particular location is often both complex (Sheaves et al., 2015; Litvin et al., 2018) and context specific (Bradley et al., 2020). The constraint set established here is specific to the region in which it was created and tested, and to the environmental settings that characterise it (e.g. annual rainfall, tidal range, geomorphology, seasonality).

The particular context of our study region directly shaped the set of constraints for juvenile fisheries species. Much global literature on the nursery value of estuaries points to the shallowness of estuaries as providing areas of refuge from predation (Nixon, 1980; Ruiz et al., 1993; Whitfield, 2020). However, predation in shallow waters is complex (Baker and Sheaves, 2021) and in an area where water depth may change by 4m in a tidal cycle, the way in which shallowness confers refuge will be intimately linked to tidal dynamics. The key factor defining the location of nursery grounds within each system, degree of tidal disconnection, will likely be irrelevant in predicting the location of nursery grounds in highly connected microtidal contexts (e.g. Nagelkerken et al., 2000) or in estuaries with continuous freshwater flow, such as many European systems. Other factors are likely to be important constraints under different contexts. For example, the temperatures experienced were probably not extreme enough to influence the distribution of juveniles at the scale of our study, however temperature can be a key constraint or under different circumstances, such as in temperate estuaries (e.g. Able 1999).

A number of factors that could constrain the occurrence of juvenile fisheries species were not quantified in the present study. Turbidity, which did not vary greatly in our study, can both support or hinder predation in depending on the particular situations (Minello et al. 1987, Lunt and Smee 2019). Additionally, a range of biological and ecological processes can influence nursery ground function and availability beyond the geomorphological and physical aspects that could be assessed during this study. For instance, competition among species (Hixon and Jones, 2005; Link and Auster, 2013)**,** prey availability (Davis et al. 2014b, Le Pape and Bonhommeau, 2015), and proximity to adult habitats and larval supply (Pineda et al., 2010), can all result in the absence of juveniles even though an area appears to be suitable. As a result, the constraint set defined in this study should not be seen as static, but rather as providing a starting set that can be tested and improved in other areas. Over time this procedure could be employed to develop a general constraint set for these and other species, as well as an understanding of how the limiting set needs to be nuanced in particular situations.

The species observed in this study can be found along much of the tropical/subtropical east coast of Australia, and across the Indo-Pacific in some cases. These large geographic ranges are likely to provide a variety of different combinations of environmental characteristics. For instance, while the BDB is characterized by meso-tides (up to 4 m) with seasonal rainfall, the two snappers encountered there can also be found in Papua New Guinea under microtidal regimes (<1 m), with much greater annual rainfall and with a different suite of co-occurring species. As a result, some of the constraints observed in the study are likely to be more or less influential under other contexts (Bradley et al., 2020), and new constraints may apply in different areas. For example, the use of upstream saline pools by *L. argentimaculatus* juveniles in the BDB is in contrast with work from short, fast flowing, wet-tropics streams that indicated an affinity for freshwater nursery areas (Russell and McDougall, 2005).

In this study, we move beyond traditional structural definitions of nursery habitat by employing the concept of ecological constraint mapping (Sheaves et al., 2021). The lack of knowledge regarding the identification of nursery grounds for specific species is a significant impediment to managing species, particularly species of commercial and recreational importance. This is complicated further by species-specific and context-specific differences in nursery requirements. A reliance on definitions of nursery requirements which lack global transferability (Bradley et al., 2020) has left a serious knowledge deficit. Filling this gap, by understanding the context-specific set of constraints for juvenile fish, is vital if an understanding of nursery ground value is to be incorporated into active management, restoration optimisation and monitoring strategies.

Acknowledgment

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