The effects of environmental filtering on *Kuhlia rupestris* distribution in the Daintree rainforest region of the Australian Wet Tropics

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Abstract

The effects of flow velocity on biodiversity in freshwater streams are well documented and reveal a role as a potential environmental filter. For the jungle perch, *Kuhlia rupestris* (Kuhliidae), one of the most abundant fish in the Australian Wet Tropics Bioregion, understanding distribution is integral to anticipating the impacts that any change to the environment may have on the species' diversity. Due to the linear relation between body size and top speed we expect to see high flow rates restricting the habitat of smaller *K. rupestris.* Through underwater visual censuses and flow rate measurements in two coastal streams it was found that smaller fish comprise a lower proportion of the population in pools preceded by higher flow velocity. Similarly, smaller *K. rupestris* are restricted from the high flow microhabitats farther from the streambed. Changes to these aquatic environments may affect the distribution of *K. rupestris* and the resulting impact they have on the surrounding biome.

Key Words: macrohabitat, microhabitat, niche segregation, flow velocity, flow management, Kuhliidae*,* swim speed, habitat partitioning

Introduction

Concerns regarding the effect of water flow rates on aquatic organisms and resulting biodiversity have been increasing for several decades; water flow is deemed a crucial aspect of freshwater habitats and their riparian zones (Bunn and Arthington 2002; Iwasaki *et al.* 2012; Jowett and Duncan 1990; Kennard *et al.* 2007; Poff and Zimmerman 2010; Vorosmarty *et al.* 2010). Flow has a major effect on both plant and animal behaviour and life histories by defining river geomorphology, sediment transport, habitat availability, and transport of carbon (Humphries *et al.* 2008). In tropical streams, the high base flow rate, and predictability of changes in flow, is considered to be one of the most integral means of maintaining their biodiversity due partially to the effects of environmental filtering (Donaldson *et al.* 2013; Grossman and Ratajczak 1998; Humphries *et al.* 2008; Januchowski-Hartley *et al.* 2011; Kennard *et al.* 2010; Thuesen *et al.* 2011). Environmental filtering is defined broadly as the effects of environmental conditions responsible for the selection of species, or members of species, capable of persisting in a particular location (Cadotte and Tucker 2017). Variations in those environmental factors would therefore alter the distribution of species. Climate change and human disturbance pose a threat to the flow rates of streams in the Australian Wet Tropics, and any change will likely have dramatic effects on the biodiversity of the rainforest and

some of the endemic or ancient species that live there. Through damming, human presence and increased or decreased rainfall, the annual flow rates of these crucial coastal streams could be irreversibly altered (Morrongiello *et al.* 2011; Poff and Zimmerman 2010; Vorosmarty *et al.* 2010).

A well-documented, positive correlation exists between the size of any given fish and its maximum speed (Fulton 2007; McGarvey and Ward 2008; Starrs *et al.* 2011). Fulton (2007) shows this linear relationship in 73 different species of coral reef fishes, and the intraspecific relationship is even more evident (Starrs *et al.* 2011). This allows us to anticipate that an increase in size will result in a greater ability to traverse faster flows and to occupy microhabitats of greater velocity. Therefore, smaller fish of any species are expected to be excluded from faster flow areas where larger fish of that species persist (Facey and Grossman 1992; Grossman and Ratajczak 1998; Henry and Grossman 2008; Langerhans 2008). Several studies have been carried out on the effect of flow velocity on members of the benthic Gobiidae family in the fast-flowing tropical streams of the Indo-Pacific (Donaldson *et al.* 2013; Blob *et al.* 2006; Ebner *et al.* 2011) as well as a number of experiments into vertical water column distribution across a variety of taxa (Gerstner 1998; Jeppesen *et al.* 1997; Werner *et al.* 1977). In this study, we compare the intraspecific habitat partitioning of a free-swimming species of fish directly with the velocity at both the stream and microhabitat level, as we would expect to observe environmental filtering on both levels. Evidence of such filtering may provide insight into the effects of a changing climate on the riparian zones of the Australian Wet Tropics.

The subject of our study, *Kuhlia rupestris* (Kuhliidae) (Lacépéde 1802), is one of the most abundant species of fish in the Australian Wet Tropics (Allen *et al.* 2002). Commonly referred to as the jungle perch, it has gained a reputation in Australia as a 'legendary angling species' and, as the largest of the Kuhliidae family, is considered excellent to eat (Merrick and Schmida 1984). Occurring throughout the Indo-Pacific from Hawaii to Eastern Africa they are omnivorous and feed on small fish, insects, crustaceans and some fruits (Allen *et al.* 2002). *K. rupestris* is diadromous, spawning in marine environments and migrating upstream as adults (Feutry *et al.* 2012; Lewis and Hogan 1987). Little else is known about this enigmatic fish and there is a distinct lack of previous literature regarding them. Due to their abundance and eating habits, they are likely to have numerous interactions in the coastal, tropical streams they inhabit. For this reason, any information regarding their behaviour or occurrence may be valuable. On the coast of the Australian Wet Tropics their migration pattern relies on an ability to move upstream through fast-flowing, mountainside riffles characteristic of the tropical Indo-Pacific (Keith 2003; Thuesen *et al.* 2011). We aimed to determine the size distribution of *K. rupestris* in pools above riffles of different flow intensities and the distribution of different body sizes vertically within the water column of each pool to evaluate whether environmental filtering is affecting their distribution.

We hypothesised that there will be a lower proportion of small *K. rupestris* in pools preceded by higher flow rates due to environmental filtering and that those smaller members of the population will be restricted to low flow microhabitats nearer to the streambed. If no environmental filter existed, we expected to see the population distributed proportionally throughout the creeks and the water column.

Methods

Study sites

Observation took place in two freshwater streams in Far North Queensland; Emmagen Creek and Oliver Creek (marked with 'X' in Figure 1). Emmagen Creek has a freshwater length of 5.8 km and an estuary of 650 m, draining a 12.3 km² catchment from Mt Halcyon (872 m). Oliver Creek is 4.75 km long, has a 1.8 km estuary and a catchment of 5.9 km² from the top of Mt Hemmant (1,065 m) (Donaldson *et al.* 2013). Chosen for their characteristics representative of tropical Indo-Pacific streams; both creeks have small estuaries, rainforest riparian zones, steep slopes and relatively high flow throughout the year (Donaldson *et al.* 2013; Finlayson and McMahon 1988). The pools studied were those nearest to the coast: in ascending order, 1 to 3 at Emmagen Creek and 4 and 5 at Oliver Creek.
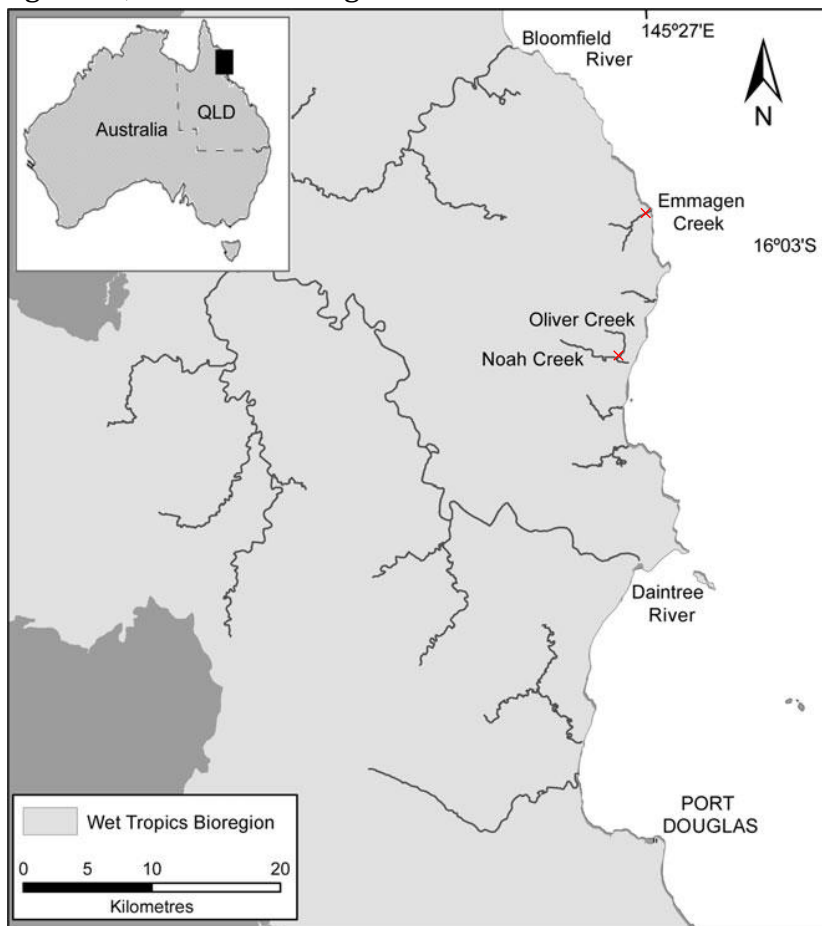
Figure 1: Map depicting Emmagen and Oliver creeks on the coast of the Wet Tropics Bioregion of Far North Queensland. Source: Donaldson *et al.* (2013).

Survey of individual size and population census

Prior to any estimates of total length or depth, an average error was determined for each individual observer. Surveyors estimated the length of a rock underwater before it was measured. This was repeated 6 times at each pool. The resulting discrepancies were used in analysis to determine and adjust for the relative bias of each observer.

A survey to determine both the population of *K. rupestris* and their relative size was achieved by underwater visual censuses in the manner of Donaldson *et al.* (2013).

Two to three snorkellers move simultaneously upstream in a slight zigzag pattern. *K. rupestris* is a very diver positive species and may school around a human observer once they have passed; for this reason, care was taken not to overlap with the other observer(s) and to move forward at the same rate. The total length of each *K. rupestris* (individual) was estimated to the nearest centimetre and recorded.

In order to compare the presence of different sizes of *K. rupestris*, we divided the population into three size categories: ≤5 cm, 6–15 cm and ≥16 cm. The total number of fish per size category was determined for each pool surveyed.

Measurements of flow velocity

Concurrently to the population survey, the flow rate (m/s) of downstream riffles for each pool was measured using an open impeller (model FLO-BTA; Vernier Corporation, Beaverton, OR, USA). A minimum of 10 measurements, each of 15 seconds, were taken for each riffle at a level 5 cm above the stream bed and averaged to determine the ambient flow velocity. These measurements were taken during the dry season (July 2017) and locations chosen based on appearance of variable flow rate to obtain an average indicative of the riffle for this season.

Flow velocity and survey of microhabitat

In the two days following the initial population survey, a second underwater visual census was undertaken in each pool to collect microhabitat data for *K. rupestris.* In addition to the estimated total length observed we also recorded the distance of that individual from the stream bed (to the nearest 5 cm) and placed a numbered bolt marker in the location that individual was first seen. Immediately afterwards, the flow rate and water depth (cm) were measured in that location and recorded alongside the corresponding bolt number. The depth of the water was measured using the scale on the flow meter. Approximately 20 individuals were measured in each pool, and locations spread throughout. For simplicity, the water column was divided into equal thirds and labelled 'Low', 'Medium' and 'High' as determined by the total depth of the pool in each individual location.

Observer bias and statistical analysis

Adjustment for observer bias was done by calculating the average percentage difference (APD) between estimated total length (TL_E) and actual total length (TL_A) measurements from the calibration process and multiplying subsequent TL_E measurements by the inverse: *(1 – APD) x TL_E = TL_A*. This was done for each observer, and all subsequent analysis is based solely on those adjusted measurements.

Chi-square tests were conducted on both macrohabitat and microhabitat data to determine if the size frequency distribution differed from the null hypothesis that all fish were distributed in proportion to the observed total size frequency. The population of each creek was kept separate for the macrohabitat test as the two populations do not interact. A significant value would indicate that there are one or more external factors influencing the distribution, of which we suggest environmental filtering plays a role.

Results

Survey of individual size and population census

A distinctly smaller proportion of the population in pools with faster riffle flow rates was found to be made up of *K. rupestris* ≤5 cm in length (Figure 2). An exception occurs in Oliver 5, the second pool upstream in Oliver Creek. A preceding riffle flow rate of 1.02 m/s was the second slowest flow rate of those measured, but Oliver 5 contained the highest proportion of small category fish (44%, Figure 2). In addition, it is located above Oliver 4, which is preceded by a riffle flow rate of 1.05 m/s. This does not adhere to expectations of flow rate increasing with distance from the coast. The proportion of large fish present was relatively consistent across all pools (with the exception of Emmagen 1). There was more variation in the proportion of *K. rupestris* in the small and intermediate categories (Figure 2).
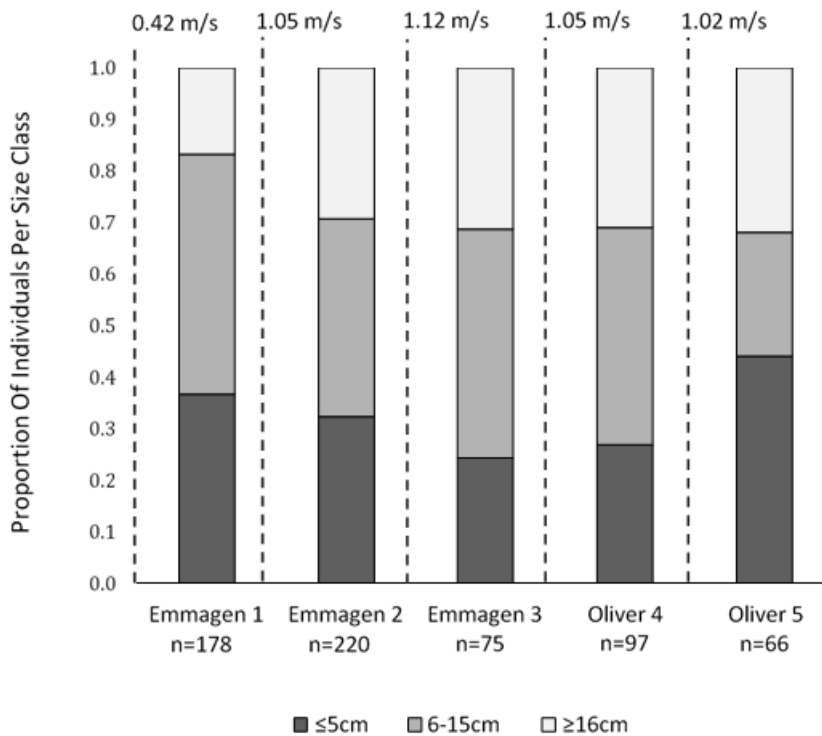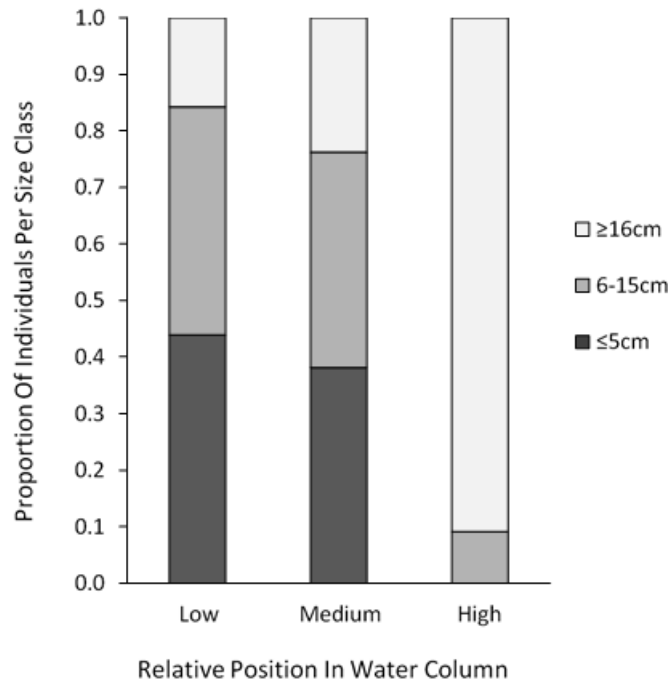

Figure 2: Distribution of *K. rupestris* by size class in five freshwater pools (Emmagen and Oliver creeks). Includes population of each pool (n = x), and flow rate of preceding riffle (m/s). Fish ≤5 cm make up a greater proportion of the population in pools preceded by lower flow rates while fish ≥16 cm remain relatively consistent. The intermediate category is more variable.

Flow velocity and survey of microhabitat

Small sized *K. rupestris* were absent from the top third of the water column and favoured low positions over the middle (Figure 3). The high region was heavily dominated by the largest fishes observed; those ≥16 cm were also not commonly found in the lower levels while intermediate fishes were relatively consistent in the lower two-thirds of the water column, occasionally being found in higher positions (Figure 3).

Figure 3: Distribution of *K. rupestris* by size class across three levels of the water column. The smallest fish are excluded from the top third, the largest fish only a small proportion of the population found in the lower two-thirds. Data collated from all five studies.

Chi-square tests on both macrohabitat and microhabitat data returned statistically significant results (Tables 1 and 2). There is a statistical relationship between the size frequency distribution and pool location as well as level in the water column.

Table 1: Chi-square test for each size category in both Emmagen and Oliver creeks respectively. Observed size frequency distribution compared to expected for total population in each creek (n = 946, n = 326). All results are statistically significant.

| | **Macrohabitat** | | | | | |
| | Emmagen Creek | | | Oliver Creek | | |
Size category	small	medium	large	small	medium	large
***p*-value**	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001

Table 2: Chi-square test for each size category in all three levels of the water column: low, medium, high. Observed size frequency distribution compared to expected for entire sample (n = 178). All results are statistically significant.

| | **Microhabitat** | |
Size category	small	medium	large
***p*-value**	< 0.001	< 0.001	< 0.001

Discussion

The manner in which flow rates affect the distribution of organisms is integral to our understanding of aquatic ecosystems and biodiversity as well as that of surrounding terrestrial biomes. The proportion of small *K. rupestris* farther upstream is smaller than that in pools downstream. This is likely impacted by the increasing flow velocity in riffles that corresponds with the increase in elevation (Finlayson and McMahon 1988; Kennard *et al.* 2010; Poff *et al.* 1997). There are several potential explanations for the inconsistency seen in Oliver 5 (Figure 2); for example, the relatively low flow rate of the preceding riffles and the small sample size of the population at this site (n = 66). It is unfortunate that a larger sample size was not available at this location and we were unable to survey the third pool in Oliver Creek. Understanding this allows us to anticipate and prepare for the effects of a potential change in flow rate.

Likewise, we saw an exclusion of small *K. rupestris* from microhabitats higher in the water column. This self-partitioning appears to be influenced by body size and the inherent ability of faster fish to withstand higher flow rates, a pattern noted in various global studies (Facey and Grossman 1992; Grossman and Ratajczak 1998; Henry and Grossman 2008; Jackson *et al.* 2001). It is important to note that only the lowest portion of the water column in these streams provides any opportunity for flow-refuging and may contribute significantly to the proportion of smaller fishes found there (Gerstner 1998; Gerstner and Webb 1998; Johansen *et al.* 2007).

We must also acknowledge the possibility of double-counting fish while surveying and human error in the estimation of size. While the surveying methods employed and adjustment for bias were designed to minimise this it was impossible to avoid completely.

Niche segregation

The range of body size among juvenile to adult *K. rupestris* allows the population to expand into a variety of flow rates and reduces the habitat-induced restrictions of population size. We suggest that fish large enough to be capable of passing through very high velocity riffles continue moving upstream in search of more abundant food, thereby creating more space for smaller fishes to inhabit pools closer to the coast.

A similar behaviour occurs in the vertical partitioning of microhabitats within each individual pool. Several other studies have shown a tendency for larger fish to move upwards in the water column despite significantly faster flows and the associated energetic cost (Facey and Grossman 1992; Henry and Grossman 2008; Jackson *et al.* 2001). This is presumably to avoid competition for food near the stream bed from both smaller *K. rupestris* and other species.

Climate change and conservation

While it has long been widely accepted that climate change will result in a gradual warming of the Australian Wet Tropics, the change to rainfall, and extreme weather events, is less predictable (Hughes 2003; Eliot *et al.* 1999; Morrongiello *et al.* 2011; Williams *et al.* 2003). A 5 to 10 per cent change in rainfall is expected by 2030 with greater seasonality and intense rainfall events. This will increase the seasonality of flow rates and likely result in longer low-flow periods. In addition, the cyclones that

buffet the rainforest will be more intense, and we can expect a 0.32 m rise in sea level (Morrongiello *et al.* 2011).

For narrow, coastal streams like Emmagen and Oliver creeks, this increase in tidal penetration will have a significant effect on both flow rates and water temperatures. Therefore, while we are uncertain of the precise change to flow velocities, we can expect a change in the distribution of *K. rupestris* that will likely directly impact the biodiversity of these coastal, rainforest streams. Considering the overall impact of climate change and human intervention on the Australian Wet Tropics, this will only serve as another front on which to fight the extinction of numerous species (Dudgeon *et al.* 2006). *K. rupestris* may very well cease to inhabit these streams in the face of increasing temperatures or flows: the risk here is not to *K. rupestris* themselves but to the many endemic species they interact with that are not capable of relocating. Our challenge is to keep this crucial fish in the environment to support the biodiversity of the region. Further research on the adaptability of *K. rupestris* is required to determine how well they will fare with the upcoming climatic challenges.

Future research directions

There is a great deal to know about the *K. rupestris* including more regarding their life history cycle, behavioural ecology, adaptability and the effects of environmental filtering. For more comprehensive information on the effect of flow rates on the distribution we would like to see more time spent in the Australian Wet Tropics and across the Indo-Pacific region throughout the year and within a wider range of study sites. As this experiment was conducted in July 2017 measurements are from base-flow water levels and do not reflect the intense velocity that these streams are capable of reaching in the wet season (Donaldson *et al.* 2013). As noted regarding the results of Oliver 5, a larger sample size and a survey of the third pool will increase the certainty with which this conclusion can be drawn. This seasonal study may also reveal something of the jungle perch's elusive spawning habits.

Conclusions

Environmental filtering in the form of flow velocity is potentially influencing the proportion of small *K. rupestris* further upstream, and we suggest that the preceding riffle speed of each pool has a direct impact on size distribution. Smaller *K. rupestris* are typically found lower in the water column and appear to be restricted to microhabitats with lower flow rates. This is an insight into the distribution of this common species and changes to their environment could have dramatic effects on their interactions with their surroundings, potentially affecting the biodiversity of the Australian Wet Tropics. Other factors, both biotic and abiotic, remain unexplored. More research is required to form a complete understanding of *K. rupestris* and its effects on the Australian Wet Tropics, including flow rates as an environmental filter.

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