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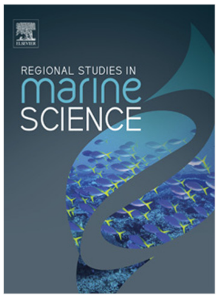

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Catchment-derived stressors, recruitment, and fisheries productivity in an exploited penaeid shrimp

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Running Title: Catchment stressors, recruitment and fishery productivity

Abstract

Many factors can affect growth, survival, reproduction, and fisheries productivity of estuarine species, including structural and physico-chemical habitats, and freshwater inflow to estuaries. Land-based activities can lead to poor catchment condition, and catchment-derived stressors can adversely impact estuarine systems. Using the Eastern School Prawn (*Metapenaeus macleayi*) in a south-eastern Australian estuary (Camden Haven Estuary) as a case study, we examine juvenile recruitment and fisheries productivity alongside a comprehensive suite of catchment-derived stressors, and interpret patterns in the context of existing studies of lethal and sub-lethal impacts of these stressors on penaeid prawns. Logged dissolved oxygen data indicated a moderate frequency of hypoxia throughout the system, with occasional periods of anoxia. Dissolved aluminium concentrations remained above the relevant marine water quality guideline for the majority of the study period, and concentrations tended to correlate with estuarine inflow. Hypoxia led to depressed prawn abundance, and both hypoxia and high estuary inflow led to decreased somatic condition in prawns. Long-term commercial catch negatively correlated with estuary inflow, which was the opposite of the expected pattern for the species. These patterns highlight the potential cumulative impacts of a complex array of catchment-derived stressors on an important exploited penaeid species. Similar patterns probably occur for prawn species across other floodplain estuaries across south-eastern Australia, and suggest a hitherto unquantified economic impact of degraded catchments through losses in fisheries productivity.

KEYWORDS: Penaeidae; *Metapenaeus macleayi*, acid sulfate soils; seagrass; pH; aluminium

1 Introduction

Estuaries are dynamic ecosystems, representing the interface between terrestrial and marine environments (Attrill and Rundle 2002). These systems support multiple ecological and economic functions, with one of the most significant being a nursery habitat for transitory or resident aquatic species (Elliott et al. 2007). Estuarine ecosystems are supported by productivity derived from aquatic micro- and macrophyte producers, which proliferate in shallow and sheltered habitats within these systems (Raoult et al. 2018). Many aquatic macrophytes also create structural habitats and refuges for fauna, and the combination of habitat function (structural and physico-chemical) and primary productivity supports both refuge and growth for the early life history stages of many species.

A diverse range of exploited fish and crustacean species are supported by estuaries during juvenile and adult stages of their lifecycle (e.g. Boesch and Turner 1984; Potter et al. 2016). Thus, the provisioning of fisheries productivity is a major ecosystem service derived from estuarine ecosystems (Barbier et al. 2011; Creighton et al. 2015). A substantial level of fisheries harvest often occurs within estuaries themselves, or the adjacent coastal ecosystems to which they are linked (Pease 1999). It follows that natural variability in estuarine systems can have a large impact on fisheries productivity, influencing reproductive and recruitment cycles, juvenile growth, survival, distribution and density, or stimulating certain adult behaviours (such as aggregation) which are exploited for fisheries harvest. However, as estuaries are inextricably linked to the catchments that they drain, much of this variability is derived from natural and anthropogenic processes in adjacent catchments (Loneragan and Bunn 1999; Caddy 2000; Gillanders and Kingsford 2002).

Penaeid prawns (=shrimp) are an important group of exploited crustaceans distributed in estuarine and coastal habitats around the world (Dall et al. 1990). These fecund, fast-growing and productive crustaceans also represent important prey for a range of higher trophic level species, and support extensive fisheries (e.g. Turner 1977; Blaber et al. 1990; Haywood et al. 1998; Taylor et al. 2018a). Estuarine and coastal inshore ecosystems are obligate habitats for many species (Dall et al. 1990), and can also represent areas where fishing effort and harvest is concentrated (Vance et al. 1998; Loneragan et al. 2005; Loneragan et al. 2013; Taylor et al. 2017a). Thus, this group of exploited species is particularly susceptible to the variability that occurs within estuaries, and potential stressors derived from adjacent catchments (Loneragan and Bunn 1999).

Many factors can affect growth, survival, reproduction, and fisheries productivity of prawns within estuaries. Saltmarsh, mangrove and seagrass habitats have all been clearly linked with prawn productivity (e.g. Loneragan et al. 2005, Manson et al. 2005; Sheaves et al. 2007; Loneragan et al. 2013; Taylor et al. 2017b). In certain species (e.g. the Eastern School Prawn, *Metapenaeus macleayi* and Banana Prawn, *Penaeus merguiensis*), freshwater inflow into the estuary can enhance recruitment, growth and fisheries harvest (see Ruello 1973; Vance et al. 1985) whereas these conditions can adversely affect other co-occurring penaeid species (Tyler et al. 2017). Land-based activities can also moderate the potentially positive effects of freshwater inflow, particularly where catchment clearing has occurred or overall catchment condition is poor. This can lead to poor water quality in estuaries such as hypoxia (e.g. Diaz 2001; Tweedley et al. 2016), acidification (e.g. Sammut et al. 1996; Wilson et al. 1999), heavy metal contamination (e.g. Wilson and Hyne 1997), sedimentation (e.g. Newcombe and Jensen 1996) and nutrient loading (e.g. Hagy et al. 2004). These factors can adversely affect both the aquatic vegetation in estuarine ecosystems as well as prawns and the fisheries they support. In addition, these factors may act interactively, and be amplified in microtidal (tidal range < 2 m) estuarine systems (Warwick et al. 2018). Consequently, quantifying relationships between catchment-derived stressors and estuarine and coastal fisheries is essential for both identifying productivity bottlenecks and designing management measures to address them.

Using the Eastern School Prawn (*M. macleayi*, hereafter referred to as School Prawn) as a case study, the overall aim of this research was to examine juvenile (generally sizes smaller than size-at-maturity occur in NSW estuaries, Racek 1959) recruitment and fisheries productivity alongside a comprehensive suite of catchment derived stressors (described below) in a south-eastern Australian estuary (Camden Haven Estuary, Fig. 1). Specifically, we sought to: 1) establish whether long-term changes in habitat may have affected fisheries productivity; 2) quantify prawn abundance in the estuary as a proxy for juvenile recruitment, and assess the relationship between variability and changes in water quality; 3) evaluate patterns of change in fisheries catch, and its relationship with estuary inflow; and, 4) interpret variability in prawn densities and environment in the context of existing knowledge from laboratory studies of lethal and sub-lethal effects of dominant stressors on penaeid prawns. School Prawn resides in estuaries for most of its life, but moves to inshore coastal areas to spawn, with maturation and spawning migration enhanced by estuary inflow (Racek 1959). This species supports the largest coastal penaeid fishery (by catch volume) in south-eastern Australia, and is harvested in most commercially fished estuaries within its range, as well as inshore coastal areas (Taylor et al. 2016) after large rainfall events (Glaister 1978). The species also supports recreational harvest in this region (Reid and Montgomery 2005). Recent work has demonstrated some relationships between water quality variables (temperature, dissolved oxygen, flow, and nutrients) and School Prawn harvest from an urbanised estuarine system (Pinto and Maheshwari 2012), and generally supported the patterns identified in earlier work that demonstrated a positive relationship between flow and School Prawn landings (Ruello 1973; Glaister 1978).

2 Methods

2.1 Study system, productivity bottlenecks, and catchment stressors

Camden Haven Estuary is an wave-dominated barrier estuary on the mid-north coast of New South Wales (Roy et al. 2001). The estuary has a trained, permanently open entrance, covers a waterway area of 32 km^2 and has a catchment area of 589 km^2 (Fig. 1). Catchment land use is primarily state forest and national park, but the catchment includes pockets of agricultural activity (mainly grazing pasture) particularly along the main tributaries (Ryder et al. 2012). The lower estuary also includes a residential settlement (~17,000 people) concentrated around Camden Haven Inlet. The estuary supports a wild harvest fishery dominated by crustaceans (School Prawn, Mud Crab *Scylla serrata*, Blue Swimmer Crab *Portunus armatus*) and Sea Mullet *Mugil cephalus*, and also has extensive aquaculture lease areas where Sydney Rock Oyster (*Saccostrea glomerata*) are cultured. Two large, shallow (< 1 m depth) lakes form prominent features of the estuary, comprising much of the available waterway area (Fig. 1). Queens Lake in the north is fed by Herons Creek, and is connected to the main channel of the estuary (Camden Haven Inlet) by Stingray Creek. Watson-Taylor Lake lies on the main tributary (Camden Haven River), but is also fed by Stewarts River from the south-west. These tributaries are typically much deeper than the shallow lake systems.

Anecdotal information from commercial fishers in the Camden Haven Estuary suggest that productivity bottlenecks periodically occur for commercially fished species in this system, especially with School Prawn but also with Mud Crab and Blue Swimmer Crab. This recently culminated in 2006/2007, when fishers noticed that School Prawn were smaller than usual, and that School Prawn were present in significantly smaller numbers the following year. This was followed by a sustained period of depressed annual landings from 2006-2013 (~5 tonnes per annum) relative to the landings from 1998-2005 (~17 tonnes per annum). Similar anecdotes have been reported for School Prawn during this period from other estuaries in south-eastern Australia that support School Prawn fisheries (e.g. Clarence River, New South Wales).

Previous monitoring work conducted in the Camden Haven Estuary and associated tributaries indicated that several catchment-derived stressors may impact estuarine water quality (Ryder et al. 2012) and macrophyte habitat (Creighton 1982), and could have concomitant impacts on School Prawn. These included low levels of dissolved oxygen, high levels of aluminium, freshwater inflow, and sedimentation. Low dissolved oxygen is thought to occur due to the build-up and decomposition of terrestrially-derived organic matter in the deeper bathymetry of the tributaries to Watson-Taylor and Queens Lake, which suffer from poor tidal exchange, but can also occur as a by-product of acid sulfate soils (see Sammut et al. 1996). Aluminium is a by-product of acid sulfate soils present in the catchment (Ryder et al. 2012), and can have deleterious effects on aquatic biota (e.g. Sammut et al. 1995; Hyne and Wilson 1997; Corfield 2000). Brackish water is also thought to provide essential juvenile habitat for School Prawn (Ruello 1973; Taylor et al. 2017a), but freshwater discharge into the estuary usually takes place over a short time period, so brackish conditions quickly dissipate (Creighton 1982). Finally, sedimentation in the lake systems may lead to increased turbidity and contribute to changes in macrophyte distribution and species composition (Creighton 1982), which may affect School Prawn abundance and distribution.

2.2 Sample collection and sorting

Sampling was conducted monthly from spring 2015 to autumn 2018. A full survey of abundance was conducted across all 18 sites in the estuary, including the three tributary rivers, approximately every two months (which sampled 18 sites), and a subset of four sites in Watson-Taylor Lake and Queens Lake were surveyed every other month when the full survey was not conducted (Fig. 1). These data were collected as a proxy for recruitment levels, to quantify the distribution of juvenile School Prawn across the estuary, and to provide data to model the potential impact of estuarine water quality on prawn abundance (and recruitment). During the months when the full abundance survey was conducted, comparative data on prawn abundance were also collected from four sites in an adjacent estuary (Wallis Lake) of similar geomorphology and habitat, for qualitative comparison of sample numbers.

Prawns were sampled using a benthic sled net with a 0.75 x 0.45 m mouth, a 4-m long 26-mm diamond mesh body and a 1 m 6-mm octagonal mesh cod-end (see Hart et al. 2018). Sampling commenced after dawn (School Prawn are diurnally active), and each tow was of ~5 min duration, covering a distance of ~100 m and an area of ~75 m^2. A GPS waypoint was marked at the start and finish of each tow to calculate the exact tow-length. Depth and spot measurements of benthic water quality (salinity, pH, dissolved oxygen [mg L^{-1}] and temperature [°C]) were recorded at each site during each survey, measured using a Horiba U-52 multi-parameter water quality meter. The concentrations of dissolved aluminium were compared with the marine water quality guideline of 0.024 mg L^{-1} (based on no-observed-effect concentrations from 11 algae, fish and invertebrate species, Golding et al. 2015). During the full abundance surveys, four tows were normally conducted at each site at each time. Upon landing, fish and cephalopods were sorted from the sample and returned to the water, prawns were placed into labelled snap-lock bags, and stored on ice for < 2 h before being frozen.

Samples were thawed and sorted in the laboratory. Prawns were identified to species and counted, and a random sub-sample of up to 50 prawns was measured (carapace length [CL, mm] and weight [g]). The tow length (m) was calculated using a Euclidean formula, and this variable was used with the gear dimensions and a gear efficiency estimate (0.48 [M.D. Taylor, unpublished data], determined using the depletion approach described in Loneragan et al. 1995) to standardise abundance estimates to prawns-per-hundred-square-metres (ind. 100 m^{-2}).

2.3 Logging of water quality parameters, dissolved aluminium measurement and mapping estuarine macrophytes

Four logger stations were established within the Camden Haven Estuary, with one at the mouth of Herons Creek, two on the delta of the Camden Haven River, and one at the mouth of Stewarts River (Fig. 1). Hobo U26-001 Dissolved Oxygen (DO) loggers (Onset Corporation, Bourne, MA) were deployed at each station from November 2015 until January 2018, which logged dissolved oxygen and temperature at 15 minute intervals. Loggers were equipped with a U26-GUARD-2 antifouling protective cap, and DO sensor caps (U26-RDOB-1) were replaced every ~ 5-6 months. Odyssey Conductivity and Temperature loggers (Dataflow Systems, Christchurch, New Zealand) were added to one logger station at the mouth of Herons Creek and one at the Camden Haven River mouth to record conductivity and temperature at 15 minute intervals. Daily average flow data were obtained for gauging stations 207009 (Camden Haven River) and 207008 (Stewarts River) from the New South

Wales Government Water Data Portal (https://realtimedata.waternsw.com.au/water.stm, data were only available from 2007 onwards).

During full abundance surveys, water samples were collected at each site, placed on ice, and shipped directly to the Environmental Analysis Laboratory (EAL) at Southern Cross University for analysis of aluminium using Inductively Coupled Plasma Mass Spectrometry (ICPMS). Existing spatial imagery held in the NSW Department of Primary Industries Fisheries Spatial Database (https://www.dpi.nsw.gov.au/about-us/science-and-research/spatial-data-portal) were used to quantify the cover of major macrophyte habitats in the estuary, and changes in macrophyte cover over time.

2.4 Data exploration and analyses

Initially, spatial patterns in the abundance of School Prawn in the two lake systems was visualised by conducting Global Polynomial Interpolation in ArcGIS v 10.3 (ESRI). The relative condition of prawns in each of the two lake systems was assessed by calculating the standardised residuals from the relationship between log(Carapace Length) and log(Weight), which provided a size-independent measure of the somatic condition of an individual (Moltschaniwskyj and Semmens 2000). To evaluate the potential impact of dissolved oxygen levels on relative condition, data were grouped for whether dissolved oxygen (logger measurements) dropped below 3 mg L^{-1} during the month (classified as “critical”, or < 3 mg L^{-1}) prior to capture and compared with other samples (classified as “normal”, or ≥ 3 mg L^{-1}) for Watson-Taylor Lake and Queens Lake using a two-factor ANOVA. Relative condition following the top 25% of all estuary inflow events (classified as “high flows) was compared with condition following all other flows (classified as “normal flows”) using *t*-tests, for estuary inflow from both Stewarts River and Camden Haven River, separately. For the main nursery area, the effect of key water quality parameters on School Prawn abundance was analysed using a Generalised Additive Mixed Model (GAMM, Gaussian family with identity link) in R (R Core Team 2016). To evaluate the relationship between freshwater inflow to the estuary and fisheries catch, monthly commercial set pocket net landings (see Macbeth et al. 2005 for description) for September to March were obtained for the years from 2009 until 2017 from the NSW Department of Primary Industries Commercial Fisheries Catch Statistics Database, and regressed against estuary inflow data from Camden Haven River as the independent variable (unlagged, $Catch_t \sim Flow_t$; and slightly lagged, $Catch_t \sim Flow_{t-1}$), using simple linear regression.

3 Results

3.1 Water quality and habitat

Logger data provided an almost continuous time-series of dissolved oxygen and temperature (Fig. 2). Broad-scale variation in temperature followed seasonal cycles but with some short-term variability. Temperatures ranged from 12 – 30°C, and were typically ~25°C from November until March. The dissolved oxygen data series indicated a moderate frequency of hypoxia events (< 4 mg L^{-1}) at all logger stations, and occasional brief and extended periods of severe hypoxia or anoxia (designated as Critical, see above, Fig. 2). This was most common in Stewarts River, but also occurred in Herons Creek, and these events were up to two weeks in duration. Conductivity varied throughout the study period, although logger failure meant there were substantial gaps in the time series (Fig. 3). The conductivity in Herons Creek was much more variable than that in Camden Haven River with frequent rapid fluctuations between 10 and almost 60 ms cm^{-1} (equivalent to a salinity of ~5 and ~40 respectively, Fig. 3), while Camden Haven River experienced a maximum conductivity of ~50 ms cm^{-1} (equivalent to a salinity of ~35) and tended to take longer to increase following freshwater events (Fig. 3). Periods of hypoxia or anoxia did not appear to consistently coincide with periods of low conductivity. Periodic spot measurements of water quality variables during sampling generally reflected the logger data (at the closest station – data not shown). Spot measurements revealed that pH fell as low as 5, but generally remained relatively stable during the study (8.1 ± 0.7; mean ± SD).

Dissolved aluminium concentrations were also very variable across the study period (Fig. 3). There was a notable peak in aluminium in mid-March 2017 (up to 6.8 mg L^{-1}, Fig. 3), which coincided with a peak in flow at the same time (Fig. 3). At all locations, aluminium concentrations remained above the marine water quality guideline of 0.024 mg L^{-1} (Golding et al. 2015) for the majority of the study period. Generally, trends in aluminium concentration tended to follow trends in estuarine inflow, being greatest during times of greatest flow (Fig. 3).

The abundance and distribution of vegetated habitat changed markedly from 2004 until 2015 (Fig. 4, Table 1). Total seagrass cover was greatest in 2004 (960 ha), and then steadily declined in 2009 (784 ha) and again in 2015 (602 ha), representing a decline in cover from 30% to 18.8% of the total waterway area during this 12 year period. The assemblage composition of seagrass also changed markedly, with mixed *Zostera* and *Halophila* beds becoming dominated by *Zostera* (Table 1). Given the increase in *Zostera* in 2015, it is likely that the majority of the lost seagrass during the 12 years was *Halophila* (Table 1). *Ruppia* was only recorded in 2009, with 73 ha of cover (plus cover in mixed *Zostera/Halophila/Ruppia* beds, Table 1). There was only minor variation in the abundance of mangrove and saltmarsh habitats over this time period, although saltmarsh habitat decreased by approximately 10%. When the spatial coverage was examined, *Zostera* and

Zostera/*Halophila* beds were almost completely lost from Watson-Taylor Lake between 2004 and 2015 (Fig. 4). While a gradual retreat of the main seagrass bed was also evident in Queens Lake, there was also a shift from mixed *Zostera*/*Halophila*, and *Ruppia* vegetation (2009 only) to almost complete dominance by *Zostera* in 2015 (Fig. 4)

3.2 Abundance, condition and commercial catch of School Prawn

The abundance and distribution of School Prawn differed spatially and temporally across the estuary (Table 2, Fig. 5). The mean abundance in each of the eight major regions increased in November or January, and decreased after autumn (i.e. after May), with the trend being evident across all sites in Camden Haven Estuary, and in the reference location Wallis Lake (Table 2). During the months when prawns were in relatively high abundance, catch rates were much higher in Watson-Taylor Lake, Camden Haven River and Stewarts Creek, than in other locations. This was particularly evident between November 2016 and May 2017, when exceptional recruitment was recorded in these regions (with a maximum recorded abundance of 3,260 ind. 100 m^{-2}, Table 2). The abundance of prawns in most regions was greater than in Herons Creek, where very few prawns were caught throughout the study (Table 2). Samples from Wallis Lake indicated similar temporal variation to Camden Haven Estuary, and abundances similar to those found in Queens Lake (Table 2).

Overall, School Prawn were far more abundant in Watson-Taylor Lake than Queens Lake (Fig. 5), with the greatest abundance in the western half of the lake. In 2018, there was a peak in School Prawn abundance in the south-western part of Queens Lake, adjacent to Herons Creek. Of the tributary systems, the greatest abundances were detected in Stewarts River (Table 2, Fig. 5). These data indicate that the western half of Watson-Taylor Lake is the most significant nursery for juvenile School Prawn in the Camden Haven Estuary, and the subsequent analyses of prawn abundance focus on data from this region.

Length-frequency distributions in Watson-Taylor Lake were highly variable throughout the study period, but confirmed seasonal progression through the nursery following the strongest recruitment in early summer (Fig. 6). There was also evidence of additional recruitment in January and March each year, with several modes evident in the carapace length distributions (Fig. 6). Analysis of the relative condition in School Prawn indicated that there was a decrease in condition following critical low dissolved oxygen events ($F_{1,5896}$ = 10.92, P < 0.001, Fig. 7), but there were no differences between lakes, and the interaction between these two factors was not significant. In addition, the relative condition of School Prawn in Watson-Taylor Lake decreased following high estuary inflow events (the top 25% of all estuary inflow events) for both Camden Haven River flow (t_{4826} = -2.26, P = 0.0032, Fig. 7) and Stewarts River flow (t_{1296} = -3.05, P = 0.002, Fig. 7).

Generalised additive mixed models (GAMMs), excluding the exceptional recruitment that occurred in January 2017 (Table 2), indicated there were relationships between $\log_{10}$-transformed School Prawn abundance and both dissolved oxygen and salinity. There was a non-linear relationship between dissolved oxygen and abundance (spline equivalent degrees of freedom = 3.8, F = 7.57, P << 0.001, Fig. 8), whereby abundance was greatly reduced at dissolved oxygen concentrations less than ~4.5 mg L^{-1}. While the fitted spline closely reflected patterns in the data, it should be interpreted with caution due to variance heterogeneity. Abundance formed a negative linear relationship with salinity (t_{225} = -6.01, P << 0.001, Fig. 8), and indicated that abundance decreased by an order of magnitude over the salinity range from 2 (predicted value ~250 ind. 100 m^{-2}) to 35 (predicted value ~20 ind.

100 m^{-2}, Fig. 8). The cluster of samples at salinities < 5 (Fig. 8) were collected following minor estuary inflow events and so likely represented an aggregating effect of prawns pushed down the tributaries to Watson-Taylor Lake, the main nursery area. The effect of salinity was not significant when these data were excluded from the analysis (t_{186} = 0.69, P = 0.491, Fig. 8).

Long-term commercial catch data formed significant relationships with several metrics describing estuarine inflow (Fig. 9). Direct relationships between log-transformed flow and monthly catch were evaluated using unlagged ($Catch_t \sim Flow_t$), and slightly lagged ($Catch_t \sim Flow_{t-1}$) monthly average flow data. A significant negative relationship was detected for the relationship between catch and flow at the same time (unlagged, $F_{1,94}$ = 10.99, P = 0.001, Fig. 9) and catch and flow of the previous month (slightly lagged, $F_{1,93}$ = 18.63, P << 0.001, Fig. 9). Taken together, these relationships indicate that generally School Prawn catches are lower during wetter years.

4 Discussion

This data set represents the most comprehensive study of juvenile Eastern School Prawn yet reported. Abundance in Queens Lake and Watson-Taylor Lake was usually equivalent to, or greater than, abundance measured in the nearby reference estuary (Wallis Lake). Temporal patterns in the data were consistent with the previous studies on School Prawn, which indicates that the major pulse of recruitment occurs in spring and early summer (Nov - Jan, e.g. Racek 1959), but there was evidence for multiple cohorts recruiting until March. Prawn abundance was substantially lower over winter, suggesting both a recruitment hiatus over this period and that most individuals had emigrated from the estuary by the end of autumn. Also, there appeared to significant asymmetry in recruitment to putative juvenile nursery areas across the estuary, with consistent disproportionately high abundance in Watson-Taylor Lake and its tributaries (Stewarts River and Camden Haven River). This is likely a function of two things. Firstly, Watson-Taylor Lake and its tributaries to the east have greater tidal connectivity than Stingray Creek and Queens Lake, which is important for supply of ocean-spawned post-larvae. Secondly, Camden Haven River is a larger tributary than Herons Creek, and appears to have more sustained periods of brackish salinity. This may lead to a stronger recruitment signal from this part of the estuary (Ruello 1973), and also provide more sustained brackish water areas for juveniles. These impacts, however, may periodically be tempered by the impact of catchment-derived stressors, such as lower dissolved oxygen, elevated concentrations of dissolved aluminium, and possibly lower pH, as discussed below.

4.1 Habitat-derived productivity bottlenecks

The substantial loss of seagrass in both Watson-Taylor Lake and Queens Lake is likely to partially contribute to a productivity bottleneck in the system, however factors that contributed to the loss are unclear. In Watson-Taylor Lake, *Zostera* sp. was the main species of seagrass lost. While *Zostera* tends to be seasonally variable (McKenzie 1994), the three time points mapped point to an overall downward trajectory in abundance (and observations made during field trips confirmed there was minimal *Zostera* sp. present in eastern Watson-Taylor Lake for the majority of the study period). In Queens Lake, much of the lost seagrass was *Halophila* sp. and *Ruppia* sp. *Halophila ovalis* is known to be particularly sensitive to light deprivation when compared to larger seagrass species, with complete plant death occurring following 30 days of light deprivation (Longstaff et al. 1999). Similarly, *Ruppia maritima* requires a comparatively high level of surface irradiance for survival (Erftemeijer and Robin Lewis 2006), but a high degree of abiotic-driven interannual variation is observed in this species (Garth Harrison 1982). This suggests that sedimentation and increased turbidity in the system could impact these species (identified several decades ago by Creighton 1982). Ryder et al. (2012) found the highest turbidity levels in the lower estuary (in 2011) occurred in Watson-Taylor Lake, and peak suspended sediment in Camden Haven River of 12.8 t d^{-1}. Over the temporal window examined here, the main changes that could have increased sedimentation include the construction of a large highway that traversed all the major tributaries to the estuary, and rapidly increasing urban development around the estuary (Hastings Council 2002). However, there is little direct evidence to link these factors with water quality and seagrass extent in the estuary.

Seagrass has been shown to provide important habitat for juvenile tiger prawn species *P. esculentus* and *P. semisulcatus* (Obrien 1994; Haywood et al. 1995; Loneragan et al. 1997; Loneragan et al. 2013), and can be an important source of organic carbon for penaeid shrimp in tropical estuaries (Loneragan et al. 1997). However, *Metapenaeus* spp. in general, are less dependent on seagrass than tiger prawns (e.g. Staples et al. 1985; Taylor et al. 2017a). Saltmarsh is a major source of organic carbon for School Prawn in seagrass limited systems (Raoult et al. 2018), and recent work examining these relationships in systems containing both seagrass and saltmarsh indicates that seagrass (*Zostera* sp.) can be the dominant source where saltmarsh is less abundant (Hewitt 2018). In both these studies, fine benthic organic matter was of minor importance as a carbon source for School Prawn.

Given the low abundance of saltmarsh in Camden Haven Estuary, seagrasses could represent an important primary producer supporting School Prawn productivity in this system. Some evidence of this can be seen in the fatty acid composition of School Prawn captured in Camden Haven Estuary (Taylor et al. 2018b), where fatty acids characteristic of marine primary productivity were abundant under non-flood conditions. Despite losses of seagrass habitat in Queens Lake, seagrass remains abundant in this part of the estuary but this area appears to be of lesser importance for juvenile School Prawn. The near complete loss of seagrass from Watson-Taylor Lake is concerning, and since this area represents the main nursery for juvenile School Prawn in the estuary, this could constrain productivity of the species.

4.2 Catchment-derived impacts on juvenile School Prawn

Logger data provided strong evidence of hitherto unknown anoxic and hypoxic events in the Camden Haven Estuary lasting for up to two weeks in different parts of the system. As described earlier, anoxic and hypoxic water in Stewarts River is hypothesised to originate due to stagnant bodies of high salinity water that rest in the deeper bathymetry of the tributary rivers (> 2 m, relative to the depth of ~ 0.4 m where the tributaries enter Watson-Taylor Lake), but can also arise through chemical processes associated with acid sulfate soils (Sammut et al. 1996). Tidal magnitude is greatly attenuated at the tributary mouths (Creighton 1982), and thus detritus and allochthonous organic matter can accumulate in these bodies of high salinity water on the tributary bed with microbial decomposition removing oxygen (stratification, hypoxia, and presence of this leaf litter have been confirmed; M.D. Taylor, pers. obs.). There was no consistent relationship between these events and declines in salinity (indicative of freshwater flow), and the force mobilising this low oxygen water is currently unclear. The international literature suggests relatively poor links between hypoxia and broad-scale declines in fisheries productivity (see review by Breitburg et al. 2009), however consideration of the specific mechanisms at play suggest that such a relationship is possible, particularly for School Prawn.

Recent work investigating the lethal effects of hypoxia on School Prawn has revealed that the species is moderately resilient during acute exposure to hypoxic water (C. McLuckie, unpubl. data), with prawns surviving well at concentrations > 4 mg L^{-1}, but mortality rapidly increasing at concentrations < 3 mg L^{-1}. In Herons Creek, the main tributary flowing into Queens Lake, a single window of hypoxia or anoxia was recorded during each summer, but there was a consistent lack of prawns in this tributary (potentially due to a connectivity effect as suggested above). Thus, hypoxia in Herons Creek would probably have limited impact on prawn productivity, but these events could affect prawn productivity in the western area of Queens Lake. The lower relative condition of School Prawn observed in Queens Lake School Prawn following critical low dissolved oxygen events (< 3 mg L^{-1}) in Herons Creek provides some evidence of this.

Camden Haven River and Stewarts River directly feed into the main School Prawn nursery in the western Watson-Taylor Lake. Critical hypoxic or anoxic events were less common in Camden Haven River (the largest tributary in the estuary), but Stewarts River experienced regular and occasionally protracted hypoxic events. There were fewer critical events during the 2016/17 season, which coincided with the greatest abundances of School Prawn (although there was a gap in data collection in early 2017). Coupled with the modelled relationship demonstrating decreasing mean abundance under hypoxic conditions, and the impact of critical dissolved oxygen events on prawn condition, these data suggest that anoxic/hypoxic water flowing from Stewarts River into western Watson-Taylor Lake (the main nursery area for School Prawn) is likely to adversely affect juvenile School Prawn.

Aluminium concentrations measured in the estuary consistently exceeded the water quality guideline of 0.024 mg L^{-1} proposed in Golding et al. (2015). Russell (2017) conducted comprehensive testing of lethal and sub-lethal effects of aluminium in School Prawn. While exposure to aluminium did not result in direct mortality at normal marine pH levels (pH ~8), acute exposure lead to structural degradation of the gill surfaces, and these sub-lethal impacts were exacerbated at lower pH. Consequently, with average aluminium concentrations of 0.16 mg L^{-1} and a maximum value of 6.8 mg L^{-1}, it is unlikely that aluminium concentrations led directly to mortality of School Prawn in Camden Haven Estuary. However, chronic exposure to aluminium at these levels means that degradation of the gill surfaces may have occurred, which could further exacerbate the effect of hypoxia and lead to mortality. Aluminium is a known indicator of acid sulfate soils in the catchment (Ryder et al. 2012, also see Fig. 1), and the correlation between aluminium and estuary inflow (Fig. 3) suggests that run-off from the catchment adjacent to Watson-Taylor Lake carries the by-products of acid sulfate soil oxidation (aluminium and acidic water) into the main School Prawn nursery area. The decreased condition of School Prawn in Watson-Taylor Lake following estuary inflow indicates a potential impact of these catchment derived stressors.

4.3 Implications for prawn productivity

Links between catchment-derived stressors such as acid sulfate soils and estuarine species have been proposed previously (Sammut et al. 1995), but there has been little attention given to the potential impact on exploited prawn stocks. Russell et al. (2011) indicated that remediation of acid sulfate soil-affected tidal wetlands in a north-eastern Australia led to increased Banana Prawn (*Penaeus merguiensis*) abundance, which suggests some impact of acid sulfate soil on this species. Other than this, there are few examples that have investigated the potential impact of acid sulfate soil on prawn populations. In pond aquaculture systems, the LC_{50} (i.e. the concentration that causes mortality in 50% of the population) was pH ~4 for the Giant Freshwater Prawn *Macrobrachium rosenbergii*, but EC_{50} (half maximal effective concentration for reduced growth) was as high as pH 6.25 (Chen and Chen 2003). Allan and Maguire (1992) suggested that the minimum acceptable pH for Black Tiger Prawn *Penaeus monodon* was ~6, and Russell (2017) showed reductions in School Prawn survival from ~100% at pH 8, to 70% after acute exposure to pH 5 at a salinity of 32. Furthermore, Kroon (2005) showed that School Prawn actively avoided acidic water in laboratory tests, although it is unclear whether this behaviour is possible under natural conditions. The impact of reduced pH on relative prawn condition, prawn survival and behaviour suggest that acidic water moving into the estuary following rainfall may be driving the negative relationship between estuary inflow and School Prawn harvest in the Camden Haven Estuary (Fig. 9).

Multiple studies have demonstrated positive correlations between School Prawn productivity and freshwater discharge into estuaries (Ruello 1973; Glaister 1978; Loneragan and Bunn 1999; Ives et al. 2009; Gillson et al. 2012), and prolonged dry weather normally adversely affects School Prawn and results in a smaller population and harvest (Ruello 1973). As noted earlier, estuary inflow is generally important for juvenile School Prawn, but it is also important in the maturation, emigration and aggregation of sub-adults and adults (Ruello 1973; Glaister 1978). Our data illustrate that despite some aggregative effect increasing abundance in the main nursery area, estuary inflow directly decreased prawn condition and the overall catchment runoff appeared to adversely impact School Prawn catch. Thus, it appears that catchment-derived stressors may impact spawning (through effects on adult prawns), recruitment processes, as well as juveniles in the nursery, leading to an overall reduction in productivity of the fishery when moderate to high rainfall levels occur in the catchment.

4.4 Potential management interventions, and conclusion

This study highlights the potential cumulative impacts of a complex array of habitat changes (physico-chemical and vegetated) and catchment-derived stressors, particularly low dissolved oxygen, runoff from acid sulfate soil affected land, and elevated aluminium on an important exploited penaeid species. The densities of School Prawn in some parts of the system were reasonably high, particularly in Watson-Taylor Lake, indicating that prawns were recruiting to the system during the study period. The large reduction of seagrass from the main nursery area (Watson-Taylor Lake) has potentially contributed to decreased productivity of prawns, while anoxia and hypoxia in the nursery reduces survival and somatic condition, and stressors carried in catchment runoff may also affect the gill structure, survival, behaviour and catchability of sub-adults and adults. The abiotic measurements collected here are supported by the most recent assessment of estuarine condition in this system (Ryder et al. 2012), which identified the lower Camden Haven River as the site of poorest water quality in the system. These factors likely contributed to the observed changes in fishery productivity within Camden Haven Estuary. Furthermore, anecdotal reports from fishers have indicated similar patterns occurring for School Prawn in other floodplain estuaries in south-eastern Australia (M.D. Taylor, pers. comm.) and hypoxia remains an issue for penaeid fisheries in other parts of the world (e.g. Smith et al. 2014). The scale of the impact of catchment stressors and their impacts on aquatic fauna is thus likely to extend too many other estuaries along the south-east coast of Australia.

The data presented here suggest that acid sulfate soils are a potential driver of biotic problems in the estuary, however additional data need to be collected to support specific recommendations regarding targeted remediation strategies. While the aluminium spikes in estuary water following flow events and the negative relationship between flow and School

Prawn catch provide a “smoking gun” which implicates acid sulfate soils as a potential source for the catchment-derived stressors, no suitable time series of pH data are available to confirm this, either from the current study or previous studies (and comments in Snowy Mountains Engineering Corporation 1998; e.g. Ryder et al. 2012). If acid sulfate soils are a significant source of stressors to the biota of the estuary, the extensive acid sulfate soils across the western catchment suggests that more fine-scale information is required to identify the areas that contribute most to the issue and then prioritise those locations for remediation. Such high quality information could support targeted, cost-effective on ground works which would likely result in a positive impact on the fishery. Longer-term and spatially stratified monitoring of turbidity is essential to identify and remediate the sources of sedimentation in the catchment that are having the greatest impact on estuarine flora and fauna. Potential remediation strategies could include concerted efforts to re-establish benthic shellfish reefs in both lakes (noting that most oyster aquaculture in the system occurs seaward of the lakes), as well as re-establishing wetlands adjacent to Stewarts River. In addition, increasing tidal flow to the tributaries would improve flushing, and potentially reduce hypoxia/anoxia.

Our findings have implications far broader than School Prawn, with a broad spectrum of species in eastern Australia, such as Barramundi *Lates calcarifer*, Banana prawn *Penaeus merguiensis*, and Mud Crab *Scylla serrata*, whose abundances are positively linked with estuary inflow (e.g. Vance et al. 1998; Loneragan and Bunn 1999; Gillanders and Kingsford 2002; Staunton-Smith et al. 2004; Robins et al. 2005; Meynecke et al. 2006; Gillson et al. 2009; Meynecke et al. 2010; Taylor et al. 2014). Further characterisation of relationships between catchment–derived stressors and fisheries productivity for additional species will clarify the scope of these issues. Ultimately, such research can also support the estimation of the economic costs of poor catchment and estuary health through reductions in fisheries harvest, and thus provide an economic impetus for remediation (such as those strategies outlined above).

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Tables

Table 1 Temporal change in the spatial extent of macrophyte cover over time in Camden Haven Estuary.

Macrophyte	2004 (ha)	2009 (ha)	2015 (ha)
Zostera sp.	134	71	575 (264)*
Zostera/*Halophila* spp. complex	826	513	25
Zostera/*Ruppia* spp. complex		11	
Zostera/*Halophila*/*Ruppia* spp. complex		103	
Halophila sp.		13	2
Ruppia sp.		73	
Total seagrass	960	784	602
Mangrove	141	146	150
Saltmarsh	77	75	70

* Bracketed value indicates area of fragmented *Zostera* sp. meadows

Table 2 Average School Prawn densities (ind. 100 m^{-2}, standard error in brackets) from quantitative sampling throughout the study period.

Estuary and Location	2015	2016						2017						2018	
	Nov	Jan	Mar	May	Jul	Sep	Nov	Jan	Mar	May	Jul	Sep	Nov	Jan	Mar
Camden Haven															
Queens Lake	77	73	[illegible]	35	36	14	28	52	228	6	13	17	11	187	34
	(12)	(38)	(8)	[illegible]	(9)	(10)	(10)	(26)	(66)	(2)	(7)	(11)	(5)	(64)	(7)
Herons Creek	9	0	6	0	5	1	1	1	0	3	0	0	2	4	2
	(6)	(0)	(4)	(0)	(2)	(1)	(0)	(1)	(0)	(2)	(0)	(0)	(1)	(2)	(2)
Stingray Creek	108	35	[illegible]	[illegible]	0	0	5	68	94	23	0	0	4	88	35
	(41)	(25)	(2)	(4)	(0)	(0)	(4)	(18)	(37)	(8)	(0)	(0)	(2)	(40)	(14)
Watson-Taylor Lake	148	[illegible]	[illegible]	35	0	57	29	1508	472	180	156	46	36	390	37
	(47)	[illegible]	(7)	(14)	(0)	(22)	(16)	(441)	(139)	(32)	(34)	(18)	(13)	(94)	(9)
Camden Haven River	316	162	12	3	0	2	4	40	335	78	9	6	20	15	7
	(87)	(52)	(9)	(2)	(0)	(1)	(1)	(18)	(76)	(29)	(6)	(4)	(10)	(10)	(5)
Stewarts River	31	284	[illegible]	29	0	2	9	998	281	122	20	20	155	19	49
	(29)	(67)	(21)	(8)	(0)	(1)	(2)	(386)	(77)	(25)	(13)	(9)	(119)	(9)	(19)
Camden Haven Inlet	0	4	1	0	0	2	0	19	70	6	35	10	0	10	1
	(0)	(4)	(1)	(0)	(0)	(2)	(0)	(15)	(24)	(6)	(11)	(7)	(0)	(5)	(0)
Wallis Lake	10	88	2	5	0	3	17	36	184	12	6	0	10	23	3
	(3)	(29)	(1)	(4)	(0)	(1)	(9)	(9)	(38)	(3)	(2)	(0)	(4)	(10)	(1)

Figure captions

Figure 1 Map of Camden Haven Estuary showing the two main lakes (Queens Lake and Watson-Taylor Lake), site names, and the main tributaries into each of these lake systems. Trawl samples are indicated as grey circles, and the position of the four logger stations is indicated. Acid sulfate soil probability is indicated as red (high probability), orange (medium probability) and green polygons (no known occurrence). The location of the study estuary on the eastern Australian seaboard is indicated in the upper left panel.

Figure 2 Dissolved oxygen (solid line) and temperature (dotted line) information collected on four fixed position logger stations over the course of the study (indicated in Fig. 1). The horizontal dashed line indicates the critical dissolved oxygen threshold used in the analysis. Some gaps in the data series appear due to logger loss or logger failure.

Figure 3 Conductivity data (upper panel) from Camden Haven River (black line) and Herons Creek (light blue line), average aluminium concentrations (middle panel) measured throughout the study period at various locations across the Camden Haven Estuary, and estuary inflow measured in Camden Haven River and Stewarts River (lower panel). Location names correspond to those indicated in Fig. 1. The horizontal dashed line indicates the calibration limit for the conductivity logger in the upper panel, and the trigger value for aluminium reported in Golding et al. (2015) in the middle panel. Some gaps in the data series appear due to logger loss or logger failure.

Figure 4 Map showing the change in the extent of seagrass extent over time in Watson-Taylor Lake (top panels) and Queens Lake (lower panels). Time points include 2004 (left panels), 2009 (centre panels) and 2015 (right panels), and actual areas are presented in Table 1. Macrophyte habitats are coloured as per the figure legend.

Figure 5 Interpolated surface showing the spatial distribution of relative abundance of School Prawn in Watson-Taylor Lake (top panels) and Queens Lake (lower panels). Time points include 2016 (left panels), 2017 (centre panels) and 2018 (right panels), and reflect samples collected in January of each year (when recruitment was generally greatest). The colour bar (legend) indicates the relative abundance within a year, but colours are not comparable among years (i.e. red in 2018 implies a different relative abundance to red in 2017).

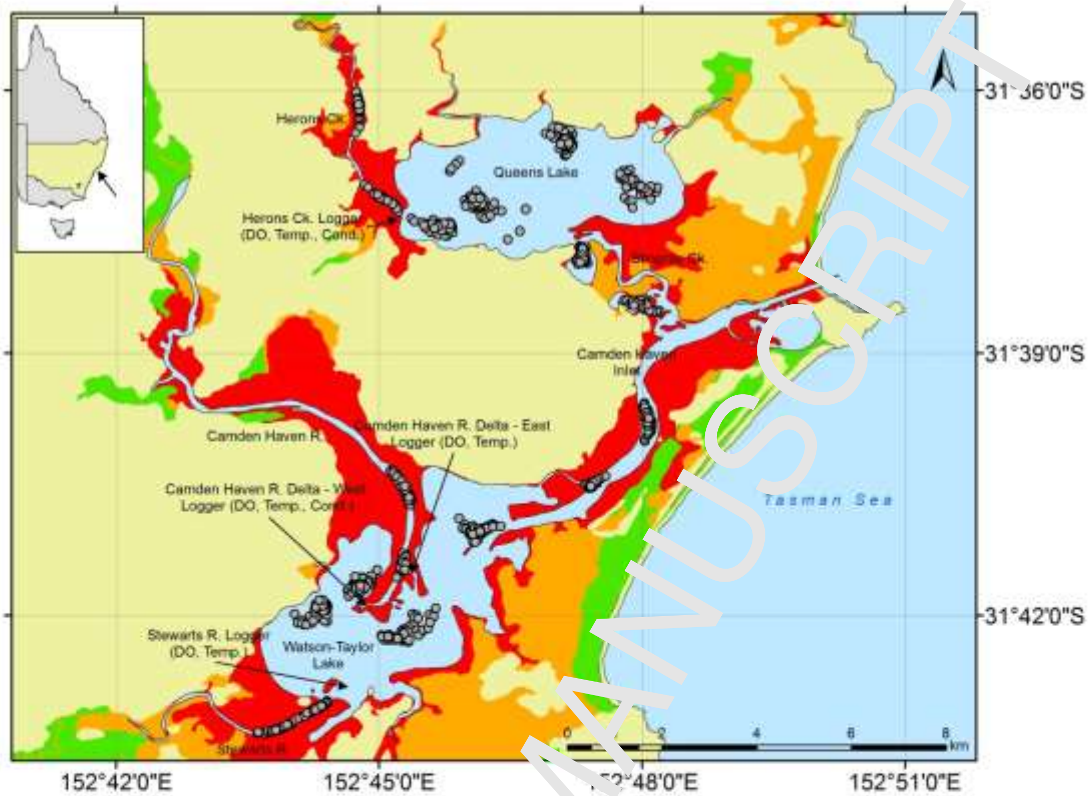
Figure 6 Unweighted length-frequency distributions for School Prawn captured in Watson-Taylor Lake (WTL) during the 2015/16 season (left column, November 2015 – April 2016), the 2016/17 season (middle column, November 2016 – April 2017), and the 2017/18 season (right column, November 2017 – March 2018). For each plot title, the month and year is coded as YYYYMM (e.g. November 2015 is 201511).

Figure 7 Standardised residuals (mean ± SE) of the length-weight relationship as a measure of relative condition in School Prawn captured from Watson-Taylor Lake and Queens Lake under normal conditions, and following critical dissolved oxygen (DO) events (<3 mg L^{-1}) as detected by loggers (upper panels). Also shown (lower panels) is the relative condition of School Prawn captured in Watson-Taylor Lake following high flows (the top 25% of all estuary inflow events) and under normal estuary inflow conditions (all other flows). Different letters indicate statistically significant differences.

Figure 8 GAMM smoothing curves indicating the partial effects of dissolved oxygen (upper panel), and salinity (lower panel) on the abundance of School Prawn in Watson-Taylor Lake. Red dashed lines indicate 95 % confidence intervals, and the black dashed line on the lower panel indicates the refitted linear relationship following removal of low salinity data.

Figure 9 Relationships between monthly School Prawn catch (across summer and autumn) and estuarine inflow (top panel), and estuarine inflow lagged by one month (lower panel) in Watson-Taylor Lake. Note that actual data points cannot be shown to protect the privacy of individual fishing businesses.

Figure 1



Herons Ck.
Queens Lake
Herons Ck. Logger
(DO, Temp., Cond.)
Camden Haven
Inlet
Camden Haven R.
Camden Haven R. Delta - East
Logger (DO, Temp.)
Camden Haven R. Delta - West
Logger (DO, Temp., Cond.)
Tasman Sea
Stewarts R. Logger
(DO, Temp.)
Watson-Taylor
Lake
Stewarts R.
0
2
4
6
8
km
31°39'0"S
31°42'0"S
152°42'0"E
152°45'0"E
152°51'0"E

Figure 2

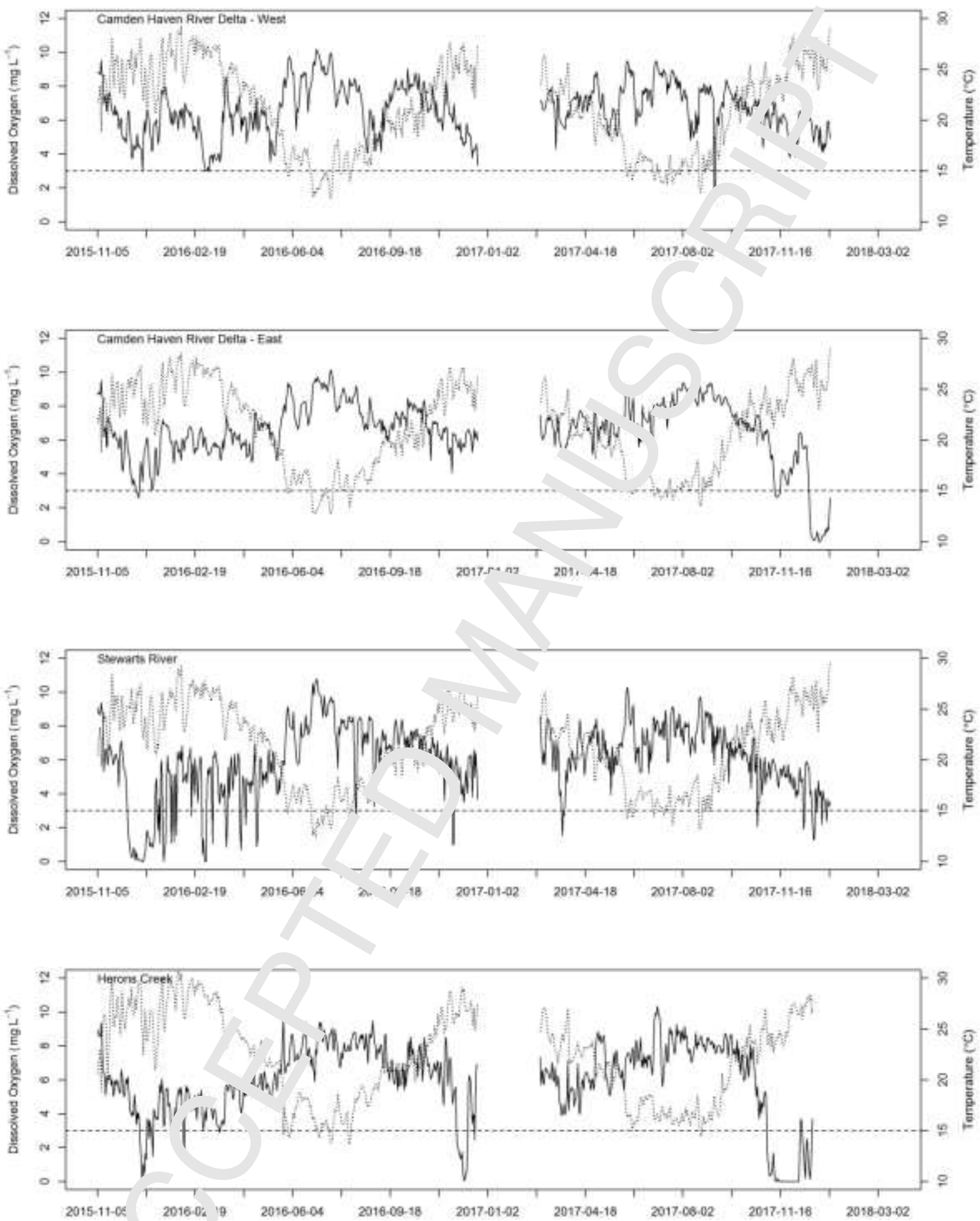

Camden Haven River Delta - West
Camden Haven River Delta - East
Stewarts River
Herons Creek
Dissolved Oxygen (mg L⁻¹)
Temperature (°C)
2015-11-05
2016-02-19
2016-06-04
2016-09-18
2017-01-02
2017-04-18
2017-08-02
2017-11-16
2018-03-02

Figure 3

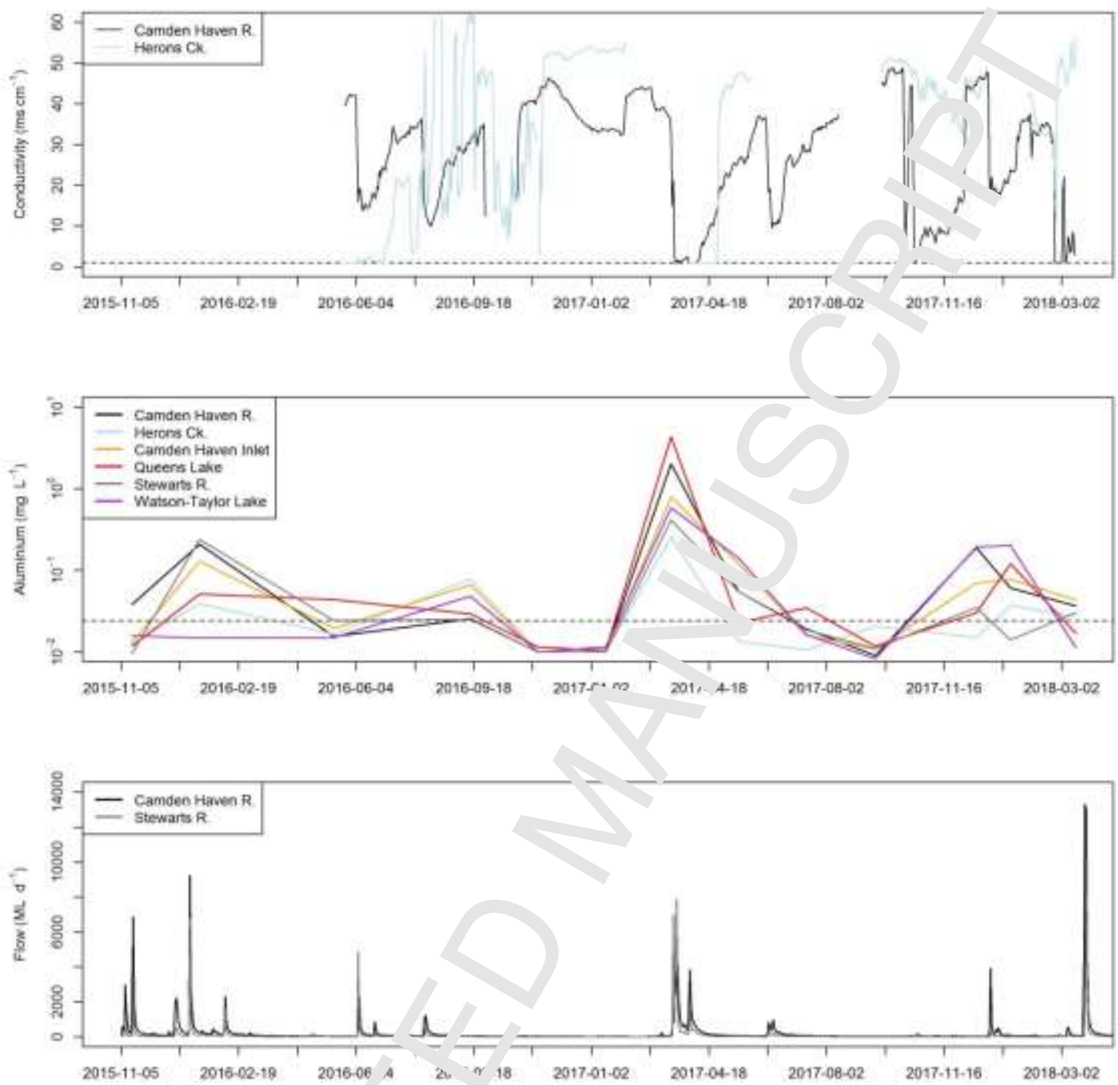
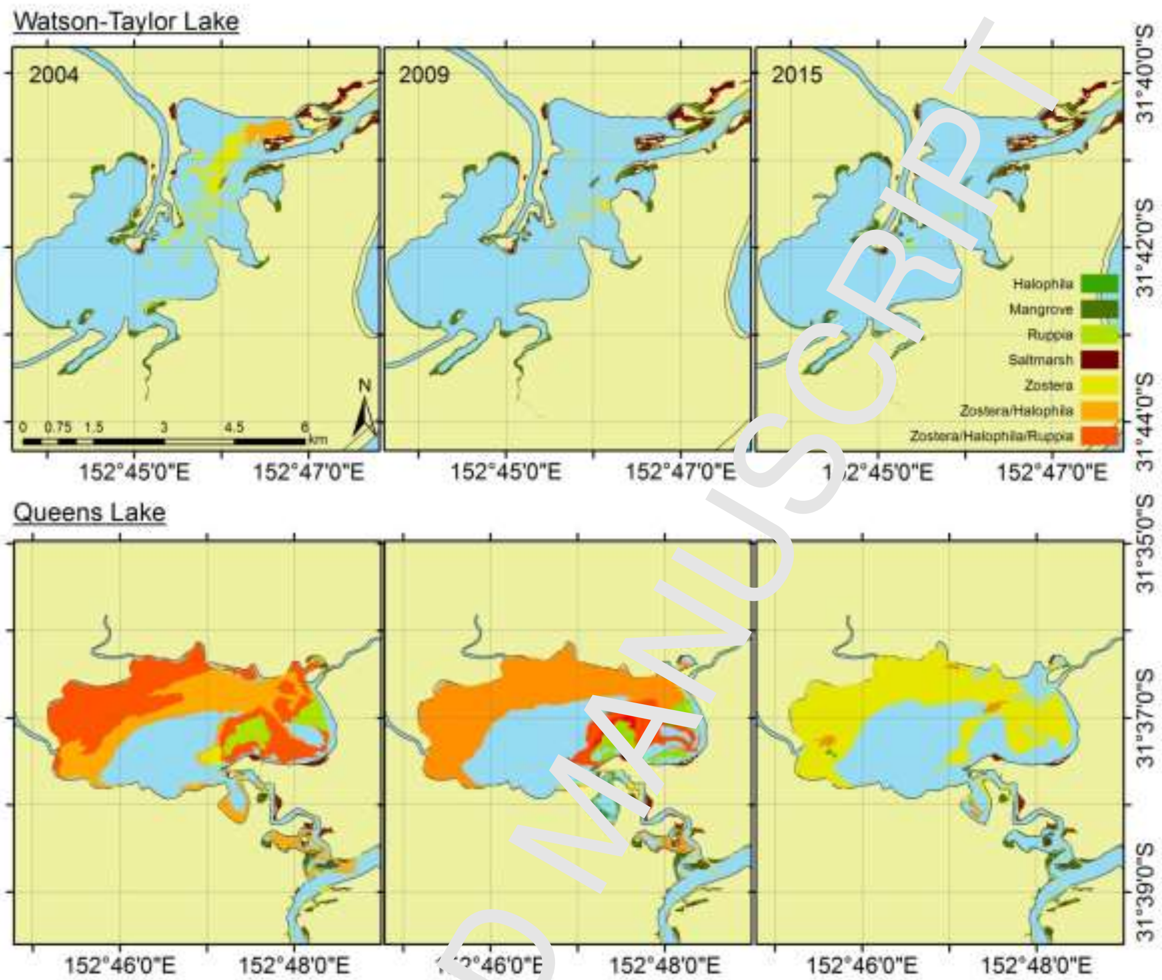

Camden Haven R.
Herons Ck.
Conductivity (ms cm⁻¹)
2015-11-05
2016-02-19
2016-06-04
2016-09-18
2017-01-02
2017-04-18
2017-08-02
2017-11-16
2018-03-02
Camden Haven R.
Herons Ck.
Camden Haven Inlet
Queens Lake
Stewarts R.
Watson-Taylor Lake
Aluminium (mg L⁻¹)
Camden Haven R.
Stewarts R.
Flow (ML d⁻¹)

Figure 4


Watson-Taylor Lake
2004
2009
2015
Halophila
Mangrove
Ruppia
Saltmarsh
Zostera
Zostera/Halophila
Zostera/Halophila/Ruppia
N
0 0.75 1.5 3 4.5 6 km
152°45'0"E
152°47'0"E
31°40'0"S
31°42'0"S
31°44'0"S
Queens Lake
152°46'0"E
152°48'0"E
31°35'0"S
31°37'0"S
31°39'0"S

883 Figure 5

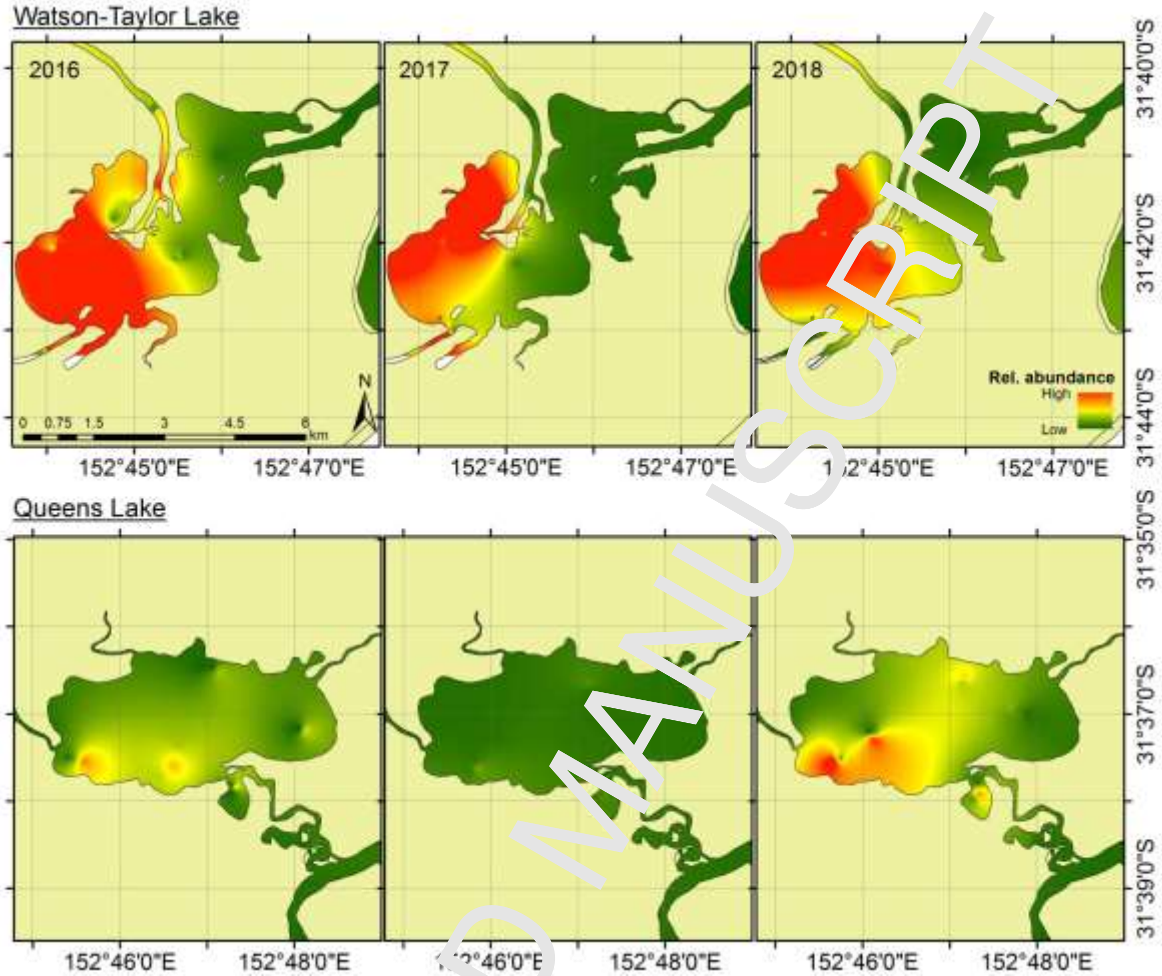
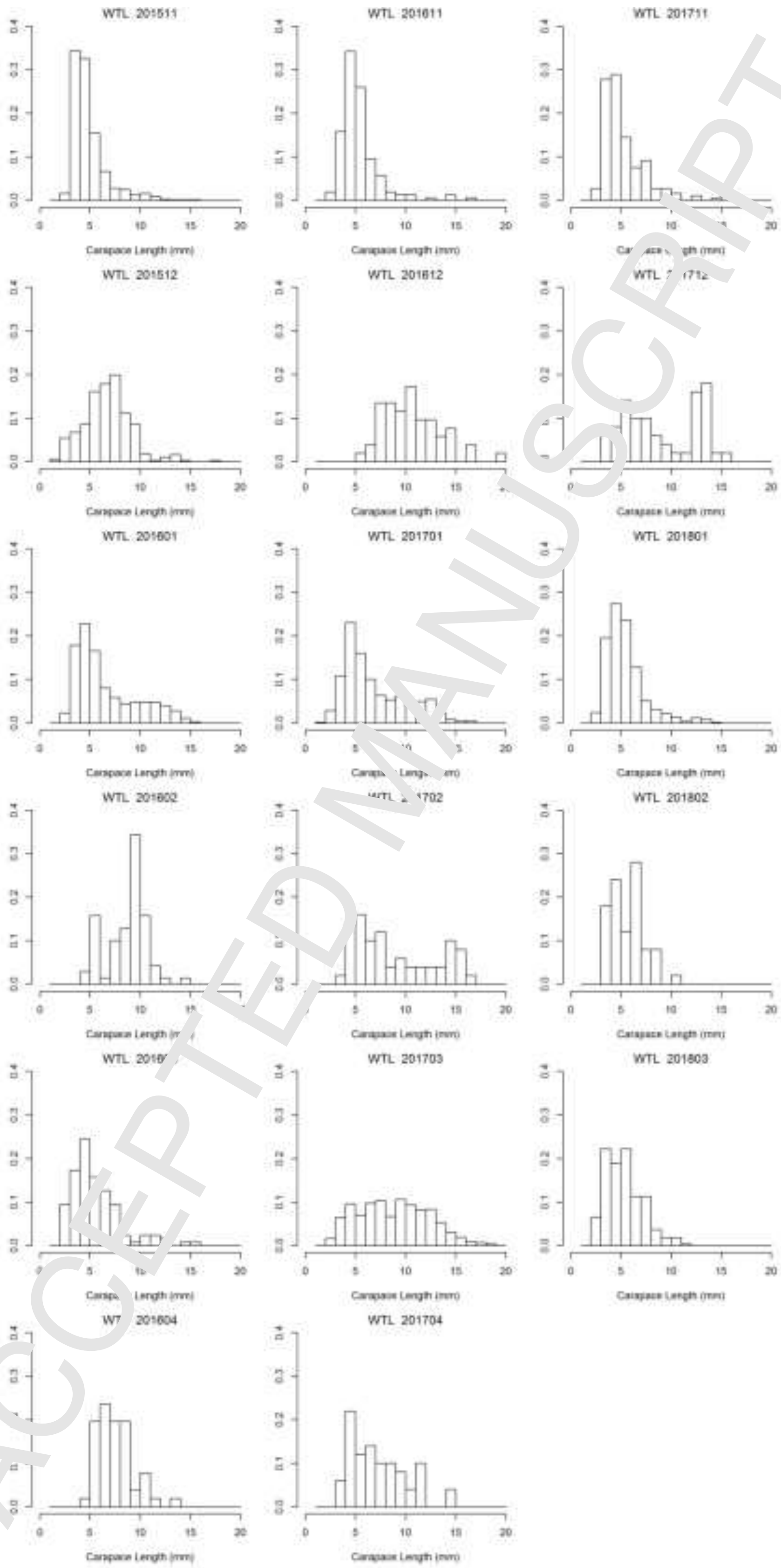
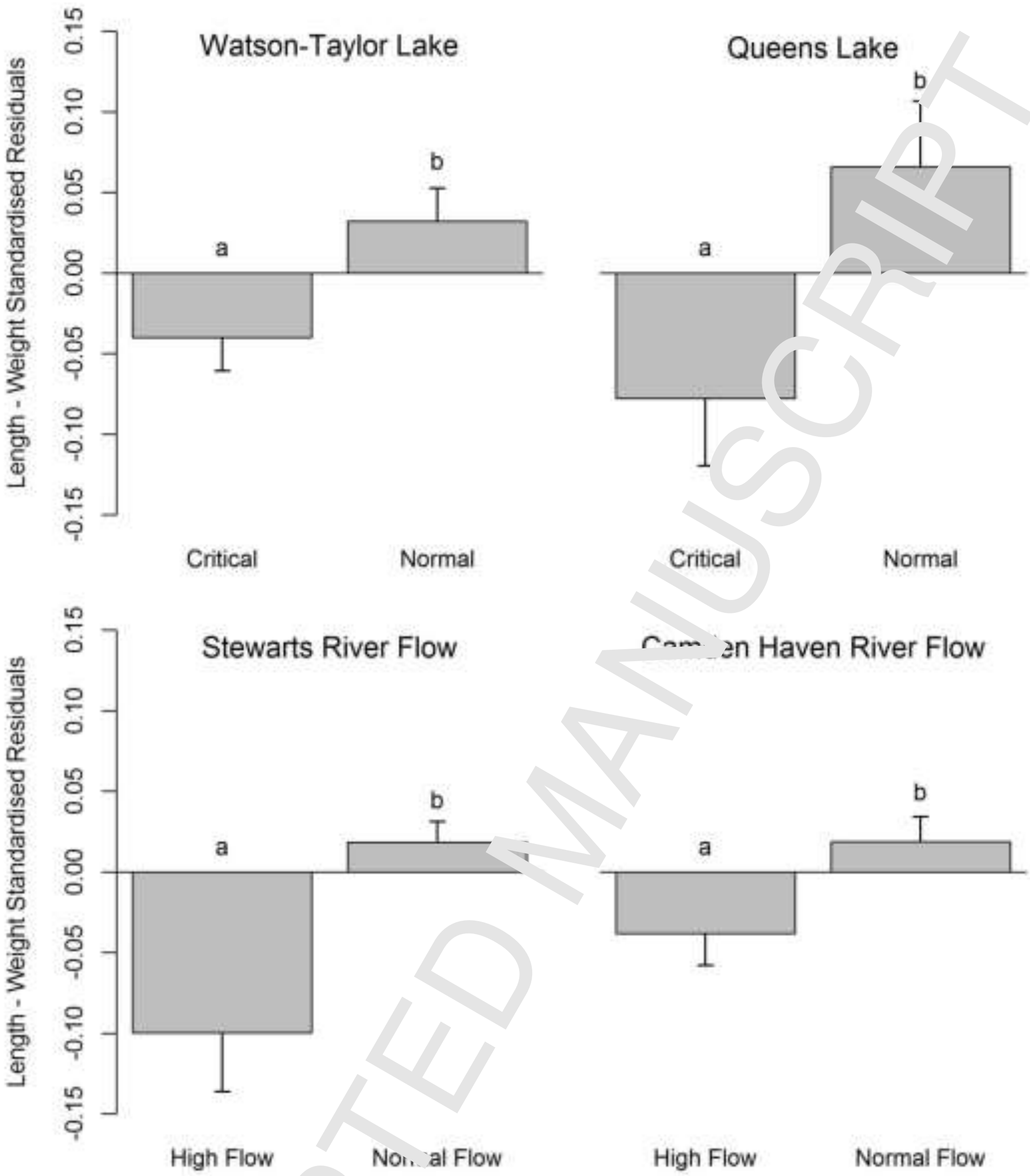
884 

Figure 6

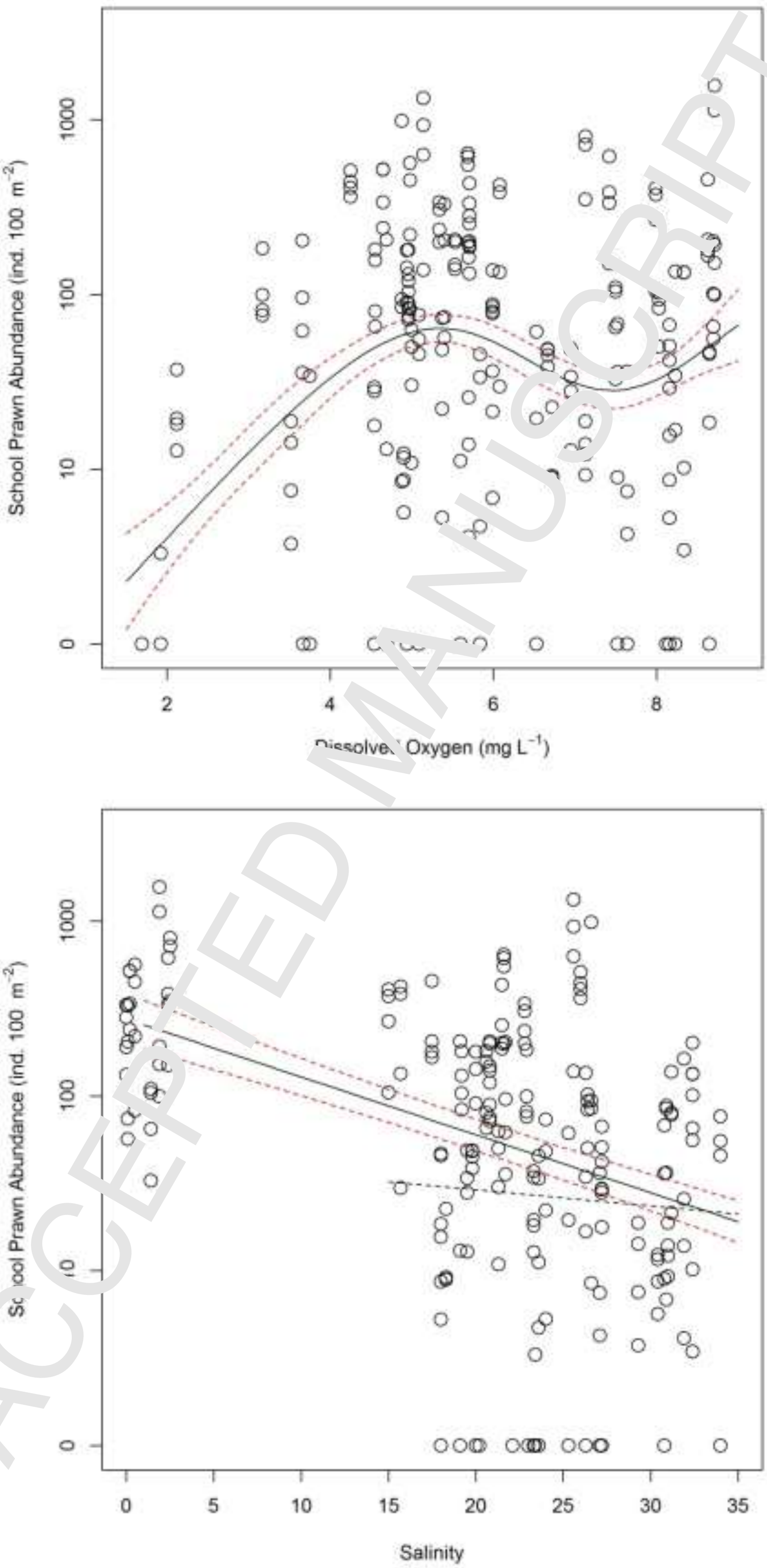

WTL 201511
WTL 201611
WTL 201711
WTL 201512
WTL 201612
WTL 201601
WTL 201701
WTL 201801
WTL 201602
WTL 201802
WTL 201703
WTL 201803
WTL 201704
Carapace Length (mm)

888 Figure 7

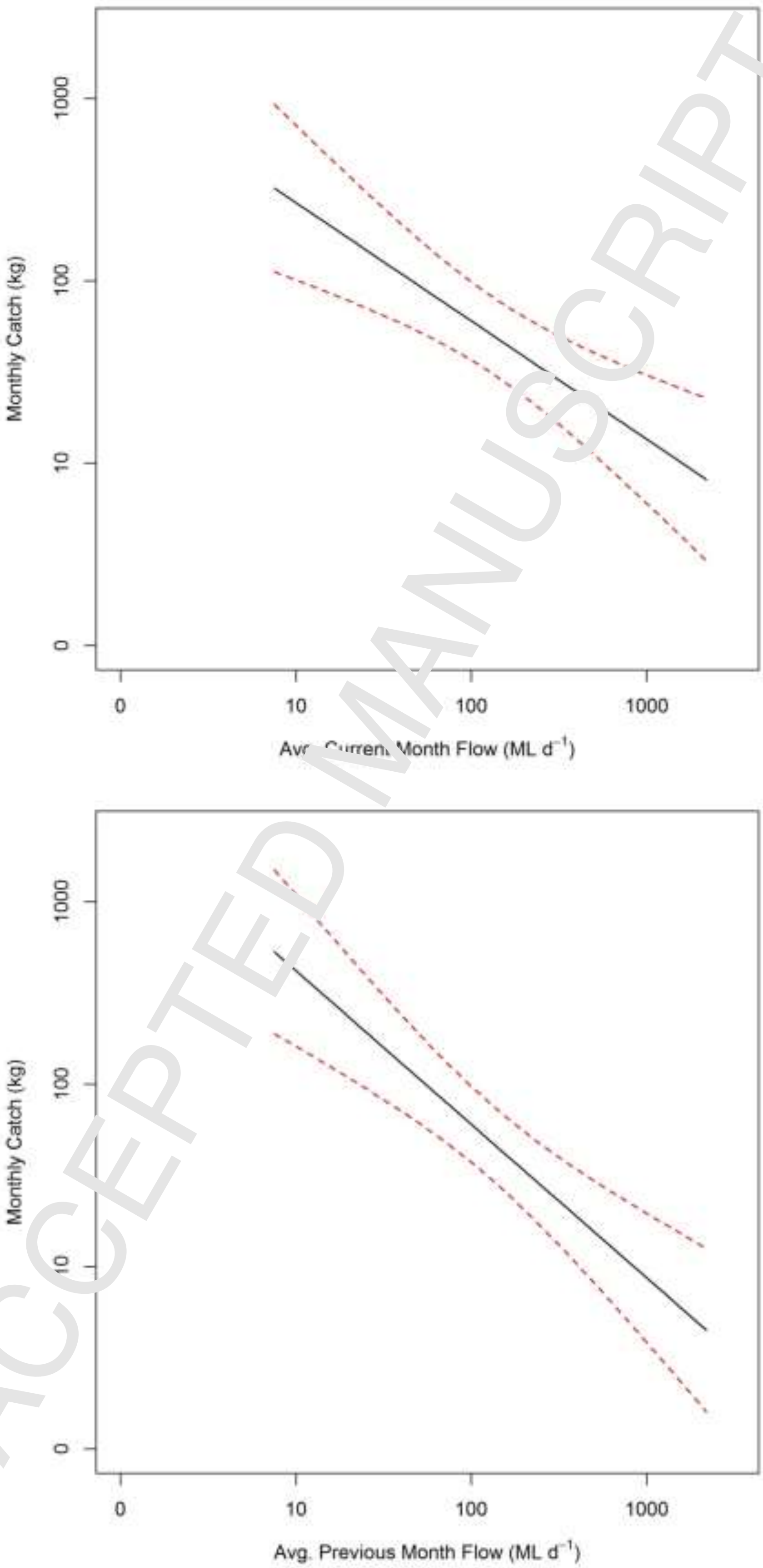


889

Figure 8


School Prawn Abundance (ind. 100 m^{-2})
0
10
100
1000
2
4
6
8
Dissolved Oxygen (mg L^{-1})
School Prawn Abundance (ind. 100 m^{-2})
0
10
100
1000
0
5
10
15
20
25
30
35
Salinity

892 Figure 9



893