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SPECIAL ISSUE: CONCEPTS AND CONTROVERSIES IN TIDAL MARSH ECOLOGY REVISITED

The Mouths of Estuaries Are Key Transition Zones that Concentrate the Ecological Effects of Predators

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Abstract

Whether and how landscape context and habitat traits combine to shape animal assemblages and the rate and distribution of ecological functions remains unresolved in many aquatic settings. Saltmarshes are one such ecosystem in which these considerations are frequently acknowledged as important, but quantitative studies of these effects are rare, especially for ecological functions. In this study, the influence of landscape configuration and habitat traits on the composition of fish assemblages and rates of predation were quantified around 30 saltmarshes in three estuaries (i.e., 10 per estuary) in eastern Australia. Fish assemblages were surveyed using unbaited underwater video cameras, and predation was quantified using videoed "Squidpop" predation assays at 10 sites at each saltmarsh. The structure of fish assemblages was best explained by the estuary in which saltmarsh was located, the proximity of sites to estuary mouth, and the area of nearby saltmarsh and mangroves. Predation was dominated (90% of total predation events) by yellowfin bream *Acanthopagrus australis* (Sparidae), and so rates of predation correlated positively with yellowfin bream abundance. Predation peaked in the lower reaches of estuaries at saltmarshes with lower vegetation cover. These findings suggest that the mouths of estuaries might function as key transition zones that concentrate prey, the products of trophic relay, and the ecological effects of predators near the estuarine-sea interface.

Keywords Assemblage · Fish · Landscape · Predation · Saltmarsh · Trophic relay

Introduction

The condition and structure of ecosystems is tightly linked to the diversity, abundance and behavior of species, and the ecological functions they perform (Manning et al. 2018; Henderson et al. 2019b). Understanding how different environmental variables drive variation in assemblages, the abundance and distribution of species that perform important functions, and the condition of ecosystems is recognized as an important consideration for natural resource management in marine (Hale et al. 2019), freshwater (Bakker et al. 2016), and terrestrial (Prather and Belovsky 2019) ecosystems. Changes to the diversity and functioning of ecosystems can also affect the delivery of key ecosystem services, such as fisheries catches (Manning et al. 2018; Gilby et al. 2020). The distribution of species that are either economically valuable, of significance for conservation, or are linked to the delivery of important ecological functions are therefore often used as surrogates in natural resource management (Lindenmayer et al. 2015; Hunter et al. 2016; Henderson et al. 2019b). Incorporating knowledge of how human impacts and management decisions might modify animal assemblages, and the rates and distribution of key ecological functions are therefore vital in maximizing the ecological and economic outcomes of management interventions (Pierson and Eggleston 2014; Soler et al. 2015).

Approximately one-third of the global human population lives within 100 km of the coastline (Halpern et al. 2008). Impacts from human activities such as transformation of natural ecosystems to urban (e.g., coastal squeeze of the terrestrial-marine interface) (Truong et al. 2017) and agricultural (e.g., runoff of nutrients, pollutants, and sediment)

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landscapes (George et al. 2001), and overharvesting of marine species (Clark and Tittensor 2010), combine to degrade the condition of coastal seascapes globally (Halpern et al. 2019). These impacts homogenize seascapes, change animal assemblages, modify the rates and distributions of key ecological functions (Wehkamp and Fischer 2013; Henderson et al. 2019a), and can reduce the provision of ecosystem services (Alberti 2010; Gilby et al. 2020). For example, up to 50% of saltmarshes have been lost in some regions as a result of anthropogenic impacts like storm water input, agricultural grazing, and land reclamation (Boon et al. 2015; Accad et al. 2016; McOwen et al. 2017). Saltmarshes provide an array of important ecosystem services, so changes to the extent and complexity of saltmarshes can affect the capacity for estuaries to support key seafood species and sequester carbon and nutrients (Alberti 2010; Gilby et al. 2018b; Saintilan et al. 2018). The desire to conserve and restore saltmarshes in coastal seascapes is therefore increasing globally (Waltham et al. this issue), but it is difficult to optimize the functional effects of restoration and conservation because data on the distribution of ecological functions and ecosystem services is lacking (Bremner 2008; Frid et al. 2008; Decker et al. 2017; Gilby et al. 2018a).

Saltmarshes contribute to the productivity of coastal seascapes by providing food and habitat for a diversity of species, including many of commercial and recreational significance (Raoult et al. 2018; Prahalad et al. 2019; Gilby et al. 2020). Different species rely upon saltmarshes at different stages of their lifecycle and use them in different ways. For example, saltmarshes provide habitats for some estuarine resident species throughout their lifecycle (Prahalad et al. 2019), as well as spawning and nursery habitats for a variety of species who migrate ontogenetically between estuaries and offshore ecosystems (Thomas and Connolly 2001; Ziegler et al. this issue). Consequently, saltmarsh loss has been linked to poorer catches of seafood species in some regions (Saintilan et al. 2018; Prahalad et al. 2019). Fish may enter saltmarshes at high tide to access prey such as terrestrial insects, adult and larval crustaceans, and small fish (Hollingsworth and Connolly 2006; McPhee et al. 2015). Saltmarshes can also contribute more broadly to estuarine food webs because food and organic material produced within the marsh can move to surrounding ecosystems through either the active movement of species or the passive movement of materials with waves, wind, and tides (McPhee et al. 2015; Wegscheidl et al. 2015; Whitfield 2017; Jinks et al. 2020). Therefore, areas surrounding saltmarshes might be considered hotspots for the consumption of these food materials in coastal seascapes (Whitfield 2017).

Predation is an important ecological function that maintains assemblage structure in ecosystems through top-down pressure on lower trophic levels (Terborgh and Estes 2013; Duncan et al. 2019). Predation regulates the abundance of prey species within ecosystems, and affects the rates of ecological functions performed by species at lower trophic levels (Heath et al. 2014; Hughes et al. 2014). Predation also transfers energy and nutrients to higher levels of food webs. Understanding the rates and distribution of predation around saltmarshes, especially the mesopredation of small invertebrates by fish, is important in establishing the value of saltmarsh-derived energy and nutrients (e.g., crabs, crab larvae, and fish) for fish (Taylor et al. 2018). Saltmarsh-derived energy often supplements estuarine fish species, either through the direct consumption of energy from saltmarsh (i.e., herbivory or detritivory), or indirectly via the consumption of prey that were nourished by carbon and nutrients that originated in saltmarshes (McPhee 2017). This trophic relay from saltmarshes is often fueled by invertebrates that secure nutrients from the marshes, and that later become prey for mobile predators that move into marshes with the tide to feed on invertebrates (McPhee et al. 2015). This movement distributes saltmarsh-derived nutrients and energy to alternate habitats throughout estuaries and offshore (Kneib 1997; McPhee et al. 2015; Raoult et al. 2018). Quantifying predation around saltmarshes can, therefore, deliver information about the degree to which saltmarshes provide carbon, nutrients, and energy to surrounding marine ecosystems (Hollingsworth and Connolly 2006), and their value for coastal fish and fisheries (Taylor et al. 2018; zu Ermgassen et al. this issue). Determining the attributes of saltmarshes and surrounding seascapes that maximize rates of predation near the marsh edge might, therefore, be used to optimize the design of restoration projects or the placement of marine reserves (Duncan et al. 2019).

The value of saltmarshes for trophic relay might be modified by several attributes of the saltmarsh and surrounding ecosystems (Ziegler et al. this issue). For example, the size of the marsh (França et al. 2012), plant assemblage composition and density (Valiñas et al. 2012), and proximity of saltmarshes to nearby human impacts (Lowe and Peterson 2015) can significantly affect the abundance of invertebrates in and around saltmarshes, and could therefore modify the assemblage structure of fish and rates of predation in the surrounding estuary. Furthermore, the size, shape, and position of both saltmarshes and alternate complimentary fish habitats (e.g., reefs, seagrass meadows, mangrove forests), their seascape context, can alter the number and type of fish present at different sites (Irlandi and Crawford 1997; Micheli and Peterson 1999; Meynecke et al. 2008; Olds et al. 2016). Consequently, the condition (Kovalenko et al. 2012) and landscape context (Olds et al. 2016) of saltmarshes and other ecosystems combine to structure the abundance and diversity of species, the rates, and distributions of key ecological functions, and therefore the movement of energy and nutrients across seascapes (McPhee et al. 2015; Pittman 2018). In this study, we tested for combined effects of habitat traits (e.g., saltmarsh size, plant structure, and assemblage) and seascape context (e.g., the area of and distance to nearby ecosystems) on the assemblage structure of fishes and the rate and

distribution of predation around saltmarshes in three subtropical estuaries in southern Queensland, Australia. We hypothesized that the edges of saltmarshes with greater connectivity to alternate complementary marine habitats (e.g., mangroves, seagrasses), greater abundance of invertebrates (e.g., crabs), and greater diversity and complexity (i.e., cover) of plant species would harbor a more abundant and diverse fish assemblage, and support enhanced rates of predation, compared to more isolated and degraded saltmarshes.

Methods

Study System

We sampled fish assemblages and measured predation at the edge of 30 saltmarshes in three subtropical estuaries (10 marshes per estuary) during the austral winter on the Sunshine Coast, Queensland, Australia (Fig. 1). Surveys were conducted over the winter period to ensure the greatest level of water visibility throughout each estuary (Gilby et al. 2018b). We chose estuaries that differ markedly in the level of urbanization, and the dominant form of land-use in each catchment. Therefore, the saltmarshes surveyed encompass a range of sizes and ecological structures (e.g., plant composition, vegetation cover), and levels of urbanization, with the Mooloolah estuary being the most heavily modified, the Noosa estuary being most natural, and the Maroochy estuary having an intermediate level of urbanization (Brook et al. 2018).

Saltmarsh Surveys

The area of each saltmarsh site was quantified by creating a polygon layer in QGIS (Version: 3.0.1-Girona, 2019) over a NearMap raster layer, which was ground truthed in the field using a handheld GPS. In each saltmarsh, we used randomly placed 10 m^2 quadrats to count plant species richness and measure vegetation height. The number of replicate vegetation

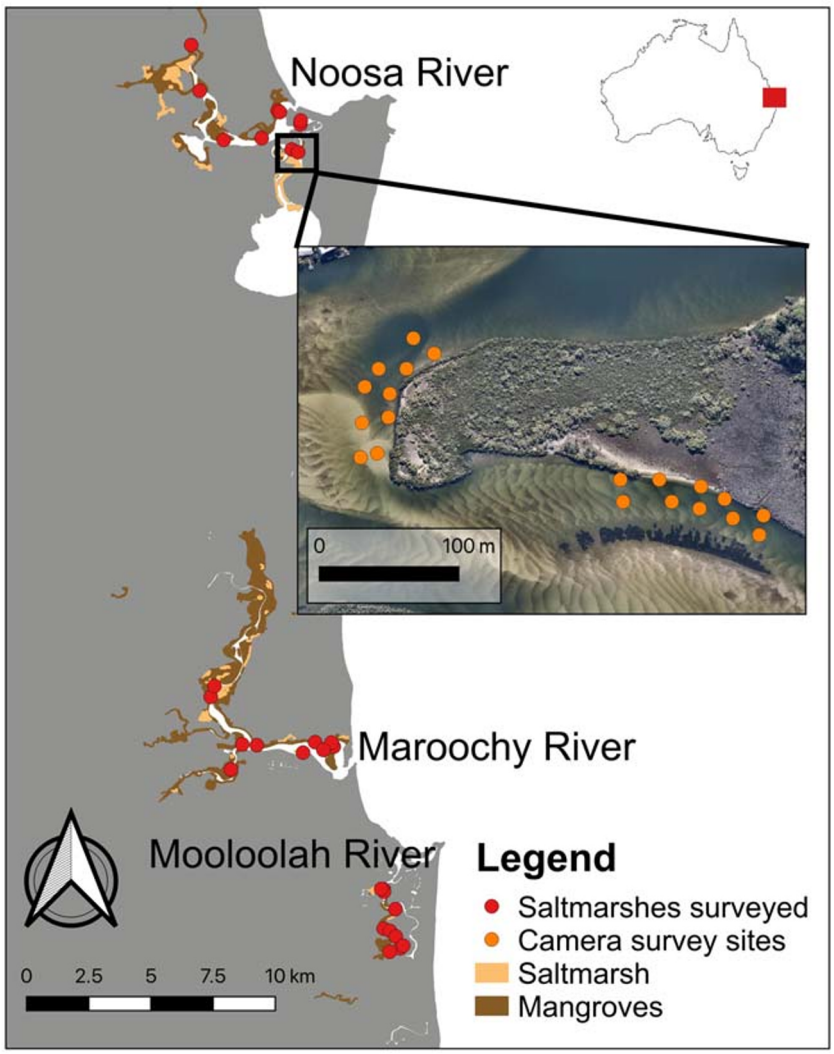

Fig. 1 Map of study estuaries, sites, and the key environmental variables included in statistical models. The inset shows the layout of camera survey positions for two (out of 10) saltmarsh sites in the Noosa River. Points in the inset are therefore nested within points in the broader map

quadrats per site was adjusted for marsh size as follows: (i) < 40 m^2: a single quadrat; (ii) > 40 m^2 but < 80 m^2: $n = 2$; (iii) > 80 m^2: $n = 3$ (Bradley et al. 2017; Gilby et al. 2018b). We measured vegetation cover (%), height (m) and composition in each quadrat, and counted the number of crab burrows (an index for the abundance of adult crabs; Schlacher et al. 2016) in four 1-m^2 quadrats that were nested at random within the larger 10-m^2 quadrats (Table 1).

Fish Sampling

Fish assemblages were sampled at the edge of each saltmarsh using remote underwater video stations (RUVS). RUVS were made of a circular 5-kg weight plate, with a high definition GoPro HERO7 camera (4 k × 60 fps) affixed to record the fish that swim into the field of view for 30 min. To mitigate any potential misrepresentation of either benthic or midwater-pelagic fish communities, a wide-angle camera setting was used and the field of view incorporated equal parts of the benthos and surrounding water column. Ten RUVS were deployed simultaneously adjacent to the saltmarsh in a gridded pattern (5 × 2 cameras). Lines of five cameras were deployed parallel to the estuarine bank, at distances of 3 and 25 m from the saltmarsh edge; all deployments were separated by 25 m (Fig. 1). This resulted in a total of 300 RUVS deployments for the study ($n = 10$ RUVS × 10 sites per estuary × 3 estuaries). The relative abundance of all fish species was quantified from videos using *MaxN*; the maximum number of any one species in a singular frame within each RUVS video. We sampled fish within 2 h either side of the diurnal high tide to have suitable water clarity to accurately identify and count species within camera frame and accounting for fishes moving within and between saltmarshes throughout this part of the tidal cycle (Connolly 2005; McPhee 2017).

Predation Assays

We quantified relative rates of predation at the edge of each saltmarsh using squidpops. Squidpops are 1-cm^2 pieces of dried squid mantle tethered with a 15-cm piece of fishing line to a 20-cm long bamboo stake. Squidpop arrays were made of the above-described RUVS unit, with a piece of PVC conduit that affixes the squidpop stake at a distance of 50 cm from the camera. Videoing squidpop deployments allows for both the identity of the predator, and the time to predation to be quantified. Squidpops are considered consumed when all squid tissue has been removed from the fishing line. Squidpop arrays were deployed for 1 h immediately after the RUVS survey, resulting in a total of 300 squidpop deployments for the study ($n = 100$ deployment per estuary × 3 estuaries). Squidpops were deployed immediately after the RUVS to avoid any potential biases associated with the species assemblages recorded in the RUVS as a result of the squid bait. Squidpops were used solely to quantify predation, and RUVS were used solely to quantify fish assemblages. We then quantified the level of predation pressure which had occurred

Table 1 List of environmental variables included in analyses, their definition, and data source

Variable	Definition
Landscape context	
Distance to mangroves	The distance (in m) from each site to the nearest mangrove forest. Data source: Queensland Government (2019).
Mangrove area	The area (in m^2) of mangrove forest within a 500 m buffer of each camera deployment. Data source: Queensland Government (2019).
Seagrass area	The area (in m^2) of seagrass meadow within a 500 m buffer of each camera deployment. Data source: (Gilby et al. 2018b)
Saltmarsh area	The area (in m^2) of saltmarsh immediately abutting a sampling site.
Distance to permanent urbanized structure	The distance (in m) from each site to the nearest permanent urbanized structure (e.g. pontoon, armored wall, boat ramp). Data source: Queensland Government (2019).
Distance to estuary mouth	The distance (in m) from the site to the estuarine opening to the sea and correlates with salinity and turbidity in these estuaries. Data source: Queensland Government (2019).
Habitat attributes	
Plant species richness	The number of plant species at each site (in a 10m^2 survey area).
Vegetation cover	The average vegetation cover (in %) of four 1m^2 quadrats within 10m^2 survey area at each site.
Average vegetation height	The average height (in m) of vegetation within a 10m^2 quadrat at each site.
Invertebrate burrows	The average number of crab burrows in four 1m^2 quadrats within 10m^2 survey area at each site.

at each of the squidpop deployments, by indexing the time to which had elapsed prior to the initiation of a predation event as a scale from 0 (not consumed after 60 min) to 1 (consumed at time 0, immediately upon deployment). Squidpops were chosen as the focal assay (over, for example, other scavenging assays or live tethering) for this study for two reasons. Firstly, the movement of the small squid piece mimics the motions of a small prey species (either invertebrate of small fish) in the water column. Therefore, this method addresses our questions regarding the movement of small prey in and around saltmarsh and consumption by mesopredators. Secondly, squidpops are an internationally recognized method to index predation rates ethically (i.e., without having to tether live baits like small fish or invertebrates) in coastal ecosystems (Duffy et al. 2015; Duncan et al. 2019).

Statistical Analysis

We quantified the effects of nine environmental variables on fish assemblage structure and predation rates at the edge of saltmarshes (Table 1). These variables were chosen based on previous studies which indicate their likely importance in modifying the abundance and composition of fish species within coastal ecosystems both locally (Brook et al. 2018; Gilby et al. 2018b; Olds et al. 2018), and more broadly (Pittman 2018; Whitfield 2017). Environmental variables could be broadly grouped into two categories. Firstly, the seascape context of each saltmarsh was quantified using both proximity-based measurements (i.e., distance from estuarine mouth, mangrove forest, and/or urban structure to focal saltmarsh sites in meters), and the areas (in m^2) of saltmarsh, mangrove forest, and seagrass meadows. Secondly, we quantified the effects of the above-described attributes of each saltmarsh (see 'Saltmarsh surveys'). We also included the variable 'estuary' in our analyses (three levels; Noosa, Maroochy and Mooloolah estuaries).

We identified correlations between our environmental variables and the structure of fish assemblage at each site using a ManyGLM from the package *mvabund* (Wang et al. 2012) in R (R Core Team 2020). We identified the best fit model using reverse stepwise simplification on Aikaike's Information Criterion (AIC). The ManyGLM also identified fish species that best correlated with variables in the best fit model. We visualized these results using a nonmetric multidimensional scaling ordination (nMDS) with Pearson vector overlays.

Results

Fish Assemblages

We observed 1362 individual fish from 39 species and 26 families on RUVS. Yellowfin bream *Acanthopagrus australis* (Sparidae) were the most abundant (27% of individuals), followed by sea mullet *Mugil cephalus* (Mugilidae; 16%) and common hardyhead *Atherinomorus vaigiensis* (Atherinidae; 14%). Assemblage composition differed amongst estuaries ($X^2 = 257$, $P < 0.001$), and was influenced by the area of adjacent saltmarsh ($X^2 = 126$, $P < 0.001$), the area of mangroves located within 500 m of each deployment site ($X^2 = 88$, $P < 0.001$), and the distance of saltmarsh to the estuary mouth ($X^2 = 109$, $P = 0.002$) (Fig. 2). Variation in fish assemblage composition was best explained by the abundance of yellowfin bream (as identified from the ManyGLM); more yellowfin bream occurred where saltmarshes and mangrove forests were smaller, and at saltmarshes nearer to the mouth of estuaries (Fig. 2). All other variables were removed during the reverse stepwise model simplification, and therefore do not affect assemblage composition in this study.

Predation

Yellowfin bream dominated predation, accounting for 90% of predation events across all deployments. This equated to 100% of predation events in both the Mooloolah and Noosa Rivers, and 83% in the Maroochy River. The other predation events in Maroochy River were by black rabbitfish *Siganus fuscescens* (Siganidae; 13%) and diamond fish *Monodactylus argenteus* (Monodactylidae; 4%). Both the likelihood of predation events and predation pressure, which was indexed as the time elapsed before the start of a predation event, were positively correlated with the abundance of yellowfin bream (Fig. 3). Predation events were more likely at the edge of saltmarshes which had lower vegetation cover, and were more rapid and intense at the mouths of estuaries (Fig. 3). All other variables were removed during the reverse stepwise model simplification, and therefore do not affect predation in this study.

Discussion

Natural resource management often seeks to enhance or reestablish animal populations and promote the ecological functions that animals perform in ecosystems. Identifying whether and how different environmental variables affect the abundance and diversity of assemblages, and the rate and distribution of key ecological functions that support those assemblages is therefore key in optimizing management decisions (Mazzotta et al. 2019; Gilby et al. 2020). In this study, we show that variation in the composition of fish assemblages abutting saltmarshes is associated with changes in the seascape context of saltmarsh, but not the habitat attributes of the saltmarsh itself. The abundance of yellowfin bream, a functionally important species (Olds et al. 2018) that is recreationally and commercially harvested in the region

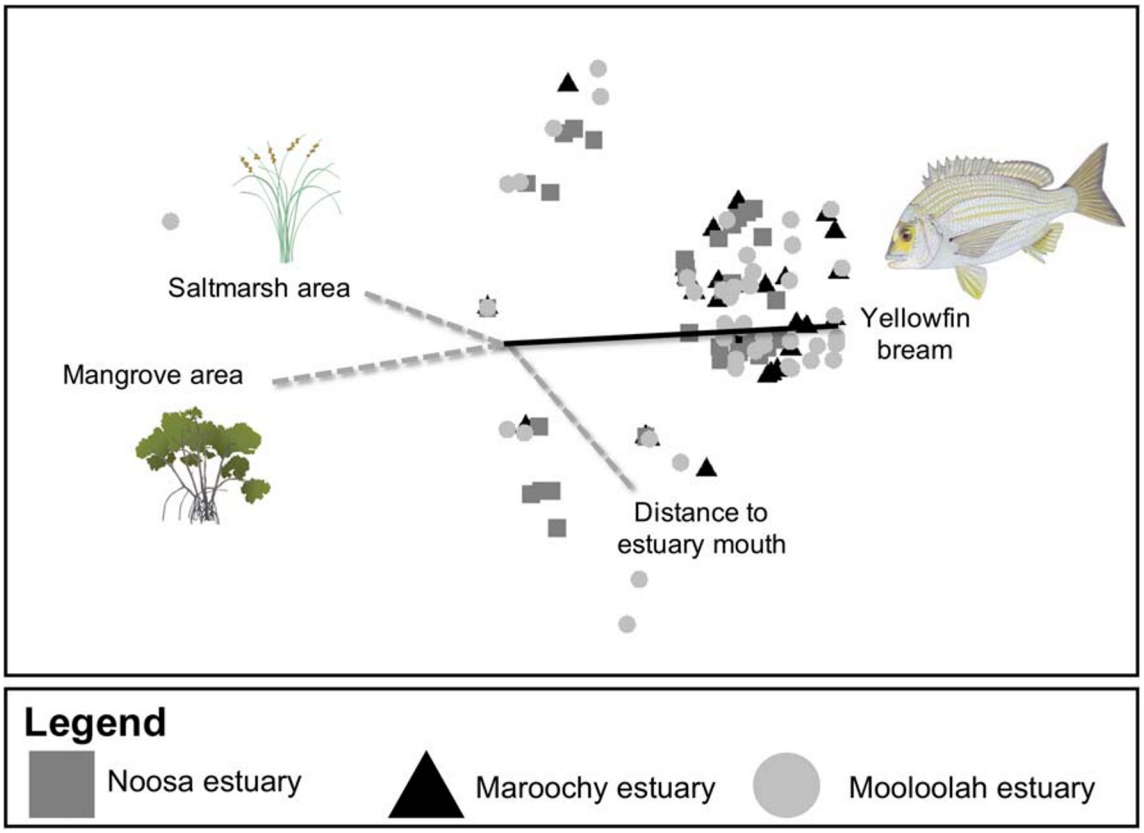

Fig. 2 Multidimensional scaling ordination of fish assemblages at the edge of saltmarshes in three estuaries in eastern Australia. Variables plotted with symbols (estuary) and Pearson vector overlays (dashed grey lines) are those included in the best fit ManyGLM analysis. Pearson vector overlays of fish species (solid black lines) show species that best correlated with overall patterns in the best fit Many GLM. Fish symbols from eFishAlbum and plant symbols from the IAN Network

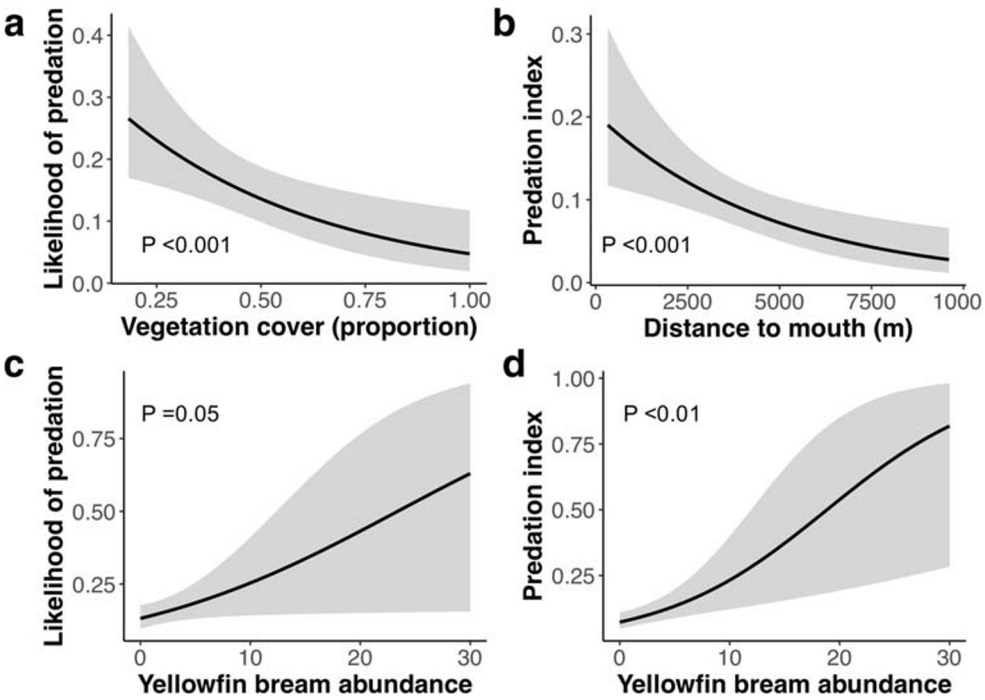

Fig. 3 Outputs of generalized linear models (GLMs) for relationships between probablility of predation (0 = not consumed and 1 = consumed) (**a** and **c**) and predation index (time for a predation event to initiate; 0 for 0 min and 1 for 60 min) (**b** and **d**) with variables from the best fit models (**a** and **b**) and yellowfin bream abundance and (**c** and **d**)

(Webley et al. 2015), was highest adjacent to smaller saltmarshes that were nearer to estuary mouths, and at sites that were further from both large saltmarshes and mangrove forests. Given the importance of seascape context in shaping these fish assemblages, these results partially support our first hypothesis. However, the trajectory of these relationships was surprising because we hypothesized that larger saltmarshes and greater mangrove area would have a higher abundance of key species such as yellowfin bream. This result potentially reflects a predator avoidance behavior exhibited by yellowfin bream; this species may be using smaller habitat patches in an effort to avoid being predated upon by larger piscivorous fishes that often concentrate around larger, more structurally complex habitat patches (Campanella et al. 2019). Conversely, however, there is also evidence to suggest that such larger predators also congregate around estuary mouths in these estuaries (Gilby et al. 2018b).

Rates of predation followed the abundance of yellowfin bream and were higher near the mouths of estuaries, with consumption also occurring more quickly at sites close to smaller saltmarshes. The trajectories of these patterns were also counter to our hypotheses. These findings for both fish assemblages and predation rates suggest that the ecological effects of predators might be concentrated in transition zones in the lower reaches of estuaries, possibly reflecting both the distribution of prey and the effects of trophic relay (Kneib 1997; Bouillon and Connolly 2009). Trophic relay occurs when food items are transported (both actively and passively) from saltmarshes and concentrate in deeper channels that occur downstream from marshes, resulting in a greater abundance of consumers in these areas and elevated rates of predation (Saintilan and Mazumder 2017). Alternatively, stability in water temperature and salinity may encourage predatory species to remain at locations nearer the mouth of the estuary for longer periods than sites further upstream (Greenwood 2007). Similarly, higher water clarity at the mouths of estuaries in the study region may allow for squidpops to be consumed more readily by visual predators like yellowfin bream. Indeed, proximity to estuary mouth correlates with both salinity and turbidity levels in this region (Gilby et al. 2018b). Larger and more complex habitat patches closer to mangroves may provide a higher diversity and abundance of potential food resources for fish (Whitfield 2017), resulting in reduced resource competition between conspecifics and likelihood of squidpop consumption at these sites (Meakin and Qin 2020). Consequently, restoration and conservation actions for saltmarsh should aim to represent saltmarshes of various sizes and attributes in multiple positions of the seascape (Waltham et al. this issue).

Habitat type, condition, and connectivity with other habitat patches are well documented as important in shaping fish assemblages across seascapes (Olds et al. 2016; Gilby et al. 2018b); especially in estuaries (Whitfield 2017; Gilby et al. 2018b). Whilst habitat area and connectivity did modify fish assemblages around saltmarsh habitats in this study, the trajectory of these relationships did not follow widely reported patterns of greater fish abundance and diversity with higher connectivity (Olds et al. 2016). Many of these existing studies were, however, conducted on larger reefs and seagrass meadows in open embayments, meaning that their comparability to the results found in these narrower estuaries are debatable (Irlandi and Crawford 1997). In this study, the abundance of yellowfin bream was highest near smaller saltmarshes that are nearer to estuarine mouths, and at sites with a lower extent of mangroves. There are several potential mechanisms for these findings. First, we posit that because areas composed of more, but smaller habitat patches are more spatially heterogenous, such greater seascape heterogeneity translates into greater fish habitat for key species like yellowfin bream (van Lier et al. 2018). There is increasing evidence from studies on structured habitats in estuaries both within this region (Duncan et al. 2019; Gilby et al. 2019), and beyond (Rutledge et al. 2018) that small, but structurally complex habitat patches that are interspersed among larger unvegetated areas promote fish that aggregate around and at them. In the systems studied here, smaller saltmarshes at the mouths of the estuaries, where intertidal flats can be extensive (Gilby et al. 2017) may play this role. Smaller, fragmented saltmarsh patches in this region are known to behave very differently from larger marshes in another aspect of food web ecology, namely the movement and contribution of saltmarsh carbon to crab diets (Guest and Connolly 2006). Also, previous studies in estuaries have highlighted the importance of connectivity with the open sea for fish assemblages in mangrove forests (Connolly and Hindell 2006; Gilby et al. 2018b). Consequently, estuarine mouths may support a greater diversity of species due to an increase in connectivity between diverse ecosystems (Meynecke et al. 2008; Olds et al. 2016). Estuarine mouths, including in this study region, are often heavily urbanized. This heavy urbanization at the mouths of estuaries may provide additional novel habitat structure for generalists, such as yellowfin bream (Brook et al. 2018; Henderson et al. 2019a), and promote the effects of these species on ecological functions (Olds et al. 2018; Henderson et al. 2019a).

We chose to survey during winter to maximize water column visibility and aid in more accurate species identifications and relative population counts. Additionally, the confounding effects of highly variable summer rainfall on estuarine salinity levels can potentially redistribute and modify fish presence in subtropical estuaries. Some species might, however, move seasonally through these estuaries to spawn or disperse, and these potential seasonal effects warrant further investigation.

Understanding the environmental variables that most modify rates of predation around saltmarshes can help establish the value of saltmarsh-derived energy for the broader estuary

(Taylor et al. 2018). Saltmarshes contain a large diversity and biomass of macrofauna which in turn supports the dietary requirements of many species across several trophic levels (Saintilan and Mazumder 2017; Reis et al. 2019). For example, during winter, the season in which this study was conducted, many macrofaunal species (e.g., saltmarsh grapsid crab *Helograpsus haswellianus*) release zoeae into estuaries during ebb tides (Saintilan and Mazumder 2017), and these are fed upon by fish (McPhee et al. 2015; McPhee 2017). During flood tides, small fishes (e.g., perchlets, Ambassidae) move onto inundated saltmarshes to feed, and then return to subtidal estuarine habitats with the outgoing tide (Hollingsworth and Connolly 2006). These macrofauna and smaller fish species are important food sources for numerous economically important species, including yellowfin bream (McPhee 2017). We suggest that the relationship between predation rates and vegetation cover might reflect the level of protection that saltmarshes afford to prey species from predation. Habitats with lower vegetation cover may allow predatory species to more easily detect and access prey sources (e.g., crustaceans and small fishes), thereby provide a reduced level of protection prey species (Crowder and Cooper 1982). Additionally, reduced vegetation cover likely increases the likelihood of food items being passively washed off lower complexity, and sparser, saltmarshes (Kovalenko et al. 2012; Reis et al. 2019).

Yellowfin bream occur in high abundance in urbanized estuaries in the region (Olds et al. 2018), and are a generalist and highly mobile consumer that feeds on a variety of benthic plants and animals (Pollock 1982; Froese and Pauly 2019). As a consequence, it may be that this mobile generalist had a greater likelihood of encountering and consuming squidpops. There is no evidence to suggest that squidpops are more palatable to yellowfin bream than any other similar species; this broad palatability is indeed one of the appeals of the squidpop method (Duffy et al. 2015). These results do, however, support the results of previous studies in highlighting the importance of yellowfin bream in the spatial patterning of ecological functioning and nutrient and energy distribution in this region (Olds et al. 2018; Henderson et al. 2020).

Saltmarshes contribute significantly to the amount of organic material (e.g., zoeae and detritus) in estuaries (McPhee et al. 2015; Wegscheidl et al. 2015), and these organic materials are vital for the productivity of fisheries (Taylor et al. 2018; Prahalad et al. 2019; Jinks et al. 2020). The greater abundance of the most dominant predatory species in this study, the yellowfin bream, and faster rates of predation observed at sites abutting saltmarshes nearer to estuary mouth is potentially a result of the effects of trophic relay in estuaries. Trophic relay is an important ecological process that redistributes organic material through predator-prey interactions from vegetated habitats such as saltmarshes in the upper reaches of estuaries, to habitats in the lower reaches of estuaries, and to open ocean ecosystems (McPhee et al. 2015; Xenopoulos et al. 2017). Fish that consume these resources might therefore tend to align their distributions (Sheaves et al. 2014; Nagelkerken et al. 2015) by, for example, concentrating around the lower parts of estuaries to maximize their likelihood of encountering food (Grenouillet et al. 2002), reducing resource competition amongst individuals, and resulting in quicker predation times (Bonin et al. 2015). Studies have also suggested that the features of estuarine mouths, such as depth and structural complexity, may alter the ability for fishes to evade predation from larger piscivorous species (Becker et al. 2016). Consequently, prey from saltmarshes may be accumulating in the lower sections of estuaries as a result of hydrological processes forcing nutrients and energy from the estuarine ecosystem to the estuary mouth and open ocean (Becker et al. 2016; Xenopoulos et al. 2017). Combined, these effects might tend to centralize the abundance of key consumers in the lower reaches of estuaries, resulting in hotspots of intense predation in transition zones at the mouth of estuaries.

Saltmarshes are important habitats in coastal seascapes because they sequester carbon, provide protection from wind, waves, and tides, and provide food and habitat for a variety of functionally and economically important fish species (Wegscheidl et al. 2015; Taylor et al. 2018; Prahalad et al. 2019; zu Ermgassen et al. this issue). The impetus to conserve and restore these ecosystems is, therefore, increasing globally. Saltmarsh complexity and connectivity jointly shape fish assemblages, and the rate and distribution of key ecological functions, and these effects may proliferate across estuaries. This process of trophic relay modifies the rate and distribution of ecological functioning and perhaps food webs in estuarine seascapes (Mazumder et al. 2006; McPhee et al. 2015). Given the established importance of saltmarsh as habitat and food sources for a variety of species (Hollingsworth and Connolly 2006; Saintilan 2009; McPhee 2017), maintaining extensive saltmarshes within estuaries is critical, particularly where other habitats have been removed. Consequently, restoring and conserving saltmarshes of various sizes and attributes in multiple positions of the seascape is a spatial conservation goal that may be beneficial for coastal ecosystems.

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