



# Urbanisation and Fishing Alter the Body Size and Functional Traits of a Key Fisheries Species

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## Abstract

Human pressures on ecosystems from landscape transformation and harvesting can result in changes to body size and functional traits of affected species. However, these effects remain very poorly understood in many settings. Here we examine whether and how fishing and the attributes of coastal seascapes can operate in concert to change the body size and functional traits of the giant mud crab, *Scylla serrata*; a prized fisheries species. We captured 65 legal sized (> 15 cm carapace width) male giant mud crabs from 13 estuaries in southeast Queensland, Australia. These estuaries span a wide range of fishing and catchment landscape transformation intensity. We made a total of 9000 external morphometric measurements in the study. There was a distinct effect of estuarine landscape context on body size, with the largest individuals captured from systems with bigger inlets and lower extent of intertidal flats. Variation in functional traits was most often associated with variation in fishing pressure and human population size in the catchment. Crabs from areas with less commercial fishing pressure and lower human populations in the catchment had the largest chelipeds. We also found effects of urbanisation (negative correlations), intertidal flats (inconsistent effects) and mangrove extent (positive correlations) on the size of some functional traits. Our results show that human pressures can have sublethal effects on animals in estuaries that alter body size and functional traits. These phenotypic responses might have consequences for the fitness and ecological roles of targeted species, and the yields of fisheries catches.

**Keywords** Landscape · Mangroves · Morphology · Giant mud crab · *Scylla* · Queensland

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## Introduction

Human impacts on ecosystems are widespread and growing in frequency and intensity (Søndergaard and Jeppesen 2007; Bishop et al. 2017; Halpern et al. 2019). These impacts modify both habitats and the animals that inhabit them in many ways and at multiple spatial scales (Worm et al. 2006; Hooper et al. 2012). For example, human impacts to ecosystems can reduce the rate and modify the distribution of key ecological functions (Hector and Bagchi 2007; Olds et al. 2018). They can also change the assemblage composition of plants and animals (McCauley et al. 2015; Gilby et al. 2018b), potentially altering the provision of ecosystem services (Cardinale et al. 2012; Haddad et al. 2015). Some anthropogenic impacts have particularly strong consequences for specific components of ecosystems; this can result in disproportionate changes in population structure (Pillans et al. 2005), body condition and organismal health of these species (Acevedo-Whitehouse and Duffus 2009). These impacts can propagate to changes in the morphology and functional traits of individuals, as species adapt either genetically or phenotypically to environmental

variation (Villéger et al. 2010; Mouillot et al. 2013; Gagic et al. 2015). Determining how anthropogenic pressures impact on the body size, morphology and functional traits of species that have economic, social or functional significance is, therefore, a priority for both conservation and fisheries management.

The joint effects of fishing, habitat loss and degradation and runoff from modified catchments widely affect the health of marine ecosystems and species (Halpern et al. 2008; Barbier et al. 2011; Teichert et al. 2016). For example, fishing significantly modifies coastal faunal assemblages, and has either direct (through destructive fishing methods) (Lambert et al. 2014; Clark et al. 2015) or indirect and cascading effects (Mumby et al. 2006; Gilby and Stevens 2014) on the structure and condition of marine habitats and faunal assemblages. Whilst there are well-established challenges in quantifying the catch and effort of both commercial and recreational fishing sectors (McCluskey and Lewison 2008; Lancaster et al. 2017), the consequences of fishing are perhaps some of the most widely studied and best understood anthropogenic impacts on coastal systems (Pauly et al. 2005; McCauley et al. 2010). However, the effects of fishing do not occur independently of broader landscape transformations and other anthropogenic impacts that reduce the condition of ecosystems. For example, fishing impacts may operate in concert with impacts from habitat loss and water quality (Halpern et al. 2008). The consequences of joint effects from fishing and landscape transformation have been documented in coastal seascapes (e.g. Micheli et al. 2013; Gilby et al. 2016), but the potential implications of these impacts for variation in body size, morphology and functional traits are rarely measured.

Estuaries are highly valuable sites for human settlement, resource use and recreation (Barbier et al. 2011), resulting in substantial coastal development and coastal fishing pressure and associated change in the condition of estuarine ecosystems (Cloern et al. 2016). Further, the effects of run-off from degraded catchments are concentrated in the lower reaches of estuaries before being discharged into the ocean (Hopkinson and Vallino 1995). Consequently, the joint effects of a suite of anthropogenic impacts that threaten coastal ecosystems can be prominently manifested in estuaries. However, estuaries are also pivotal ecosystems for many commercially, recreationally and economically important species that use them either periodically (i.e. for spawning or as nurseries) or more permanently (i.e. estuarine resident species) (Elliott et al. 2007; Whitfield 2017). It is for this reason that estuaries are widely regarded as a priority for research that seeks to both understand the ecosystem-wide effects of human activities, and design effective management and restoration interventions to mitigate these threats (Barbier et al. 2011; Gilby et al. 2016; Elliott et al. 2017; Gilby et al. 2018a).

Giant mud crabs (*Scylla serrata*) are an ecologically and economically important portunid in muddy, mangrove-

dominated estuaries of the Indo-West-Pacific (Alberts-Hubatsch et al. 2016). The species is highly prized by consumers because of its large body size (to > 23 cm carapace width) and chelipeds containing ample consumable flesh and is therefore targeted heavily by both commercial and recreational fishers (Fratini et al. 2010; Dumas et al. 2012; Alberts-Hubatsch et al. 2016). In some regions, giant mud crab catch is both size- and sex-biased. For example, in Queensland, Australia, only male crabs with carapace widths greater than 15 cm may be kept by fishers. This catch bias can result in significant changes in size and sex ratios in wild populations (Pillans et al. 2005). Removing the competitive-dominant, territorial and aggressive larger males from a population through fishing might reduce competition between conspecifics for space and mates. In systems where the abundance of male giant mud crabs is higher, they may need to spend a greater proportion of their time competing with other males, and/or a greater amount of energy growing larger body size and chelipeds to outcompete conspecifics (Beattie et al. 2012). Similarly, sub-dominant males in systems with large males (i.e. due to less fishing) may have larger claws to defend themselves against larger conspecifics. Simultaneously, however, the abundance, size and functional traits of giant mud crabs might also be shaped by the condition of the surrounding ecosystem, especially the availability of high quality foods and habitats (especially their preferred muddy mangrove habitats) (Fratini et al. 2010; Unhalu et al. 2015; Alberts-Hubatsch et al. 2016). Male giant mud crabs are an ideal species to test the effects of anthropogenic pressures on body size and shape in coastal species for three reasons: (1) they are specifically targeted in some fisheries; (2) they are highly competitive, a trait that may make them more susceptible to habitat loss because of behavioural displacement; and (3) they have small home ranges as adults (usually < 1 km) (Hyland et al. 1984; Bonine et al. 2008), making it plausible that any changes in size and/or functional traits reflect the conditions of an estuary. Whilst the effects of anthropogenic pressures (including fishing, habitat loss and catchment runoff) on giant mud crab population structure and abundance are relatively well understood (e.g. Pillans et al. 2005; Bonine et al. 2008; Webley et al. 2009; Fratini et al. 2010; Meynecke et al. 2012), any impacts from fishing and landscape transformation that may jointly alter crab functional traits remain untested.

Here we assess whether and how anthropogenic pressures on estuaries can combine to modify the body size and functional traits of giant mud crabs in southeast Queensland, Australia. Southeast Queensland is an ideal study region for this test as the region has multiple estuaries that span a broad gradient of environmental conditions, catchment land use change (particularly urbanisation), and fishing effort (Gibbes et al. 2014; Gilby et al. 2018b). There is also a significant commercial and recreational demand for giant mud crabs (Webley et al. 2015); a continual growth in human population

size in the region (Australian Bureau of Statistics 2017); and changes to the condition, area and distribution of key marine ecosystems (especially seagrasses and mangroves) (Manson et al. 2003; Saunders et al. 2013). We hypothesised that male giant mud crabs captured from areas where fishing pressure was lower would be larger and have larger chelipeds. This is because higher densities of male giant mud crabs might cause greater competition amongst males, thereby driving an increase in the size of chelipeds to increase individuals' competitiveness. Similarly, we hypothesised that there would be additive effects of the extent of marine ecosystems on body size and functional traits of male giant mud crabs by providing access to food and territory (i.e. crabs from estuaries with extensive mangroves might be larger) and by mediating the competitiveness of male giant mud crabs with each other (by providing define territories and refuges).

## Methods

### Study Region and Giant Mud Crab Collections

We collected 65 giant mud crabs from 13 estuaries in south-east Queensland, Australia (Fig. 1). Estuaries were chosen to represent a gradient in coastal modifications, ranging from relatively 'natural' systems with abundant mangroves to highly urbanised ones (Gilby et al. 2018b)(Table S1). In each estuary, crabs were collected from the lower reaches, operationally defined to extend from the mouth to long-term (> 10 year) salinity values averaging > 28 ppt (EHMP 2019). We sampled the lower reaches for three key reasons: (1) to keep the sampling extent consistent between estuaries that differed in size, (2) because these reaches are the central locations for crab fishing pressure in the region and (3) because the effects of the loss of marine habitats and degraded catchments is centralised in the lower reaches of estuaries. We collected two to nine males of legal size (> 15 cm carapace width) from each estuary between September 2018 and February 2019. Fishers are only permitted to keep male giant mud crabs greater than 15 cm carapace width in Queensland. Crabs were sampled with traps (four per estuary) baited with sea mullet. Trapped crabs were euthanised in an ice slurry within a few minutes of retrieval and frozen (−20 °C) within 2 h upon return to the laboratory.

### Functional Trait Measurements

We weighed each giant mud crab to the nearest 1/10 of a gram using laboratory scales. We quantified functional traits from standardised still images analysed with the geomorph package in R (Adams et al. 2018). Images of crabs were captured in 'planar bird eye perspective' by mounting a digital camera (Nikon W300 in macro mode; 24–120 mm equivalent lens)

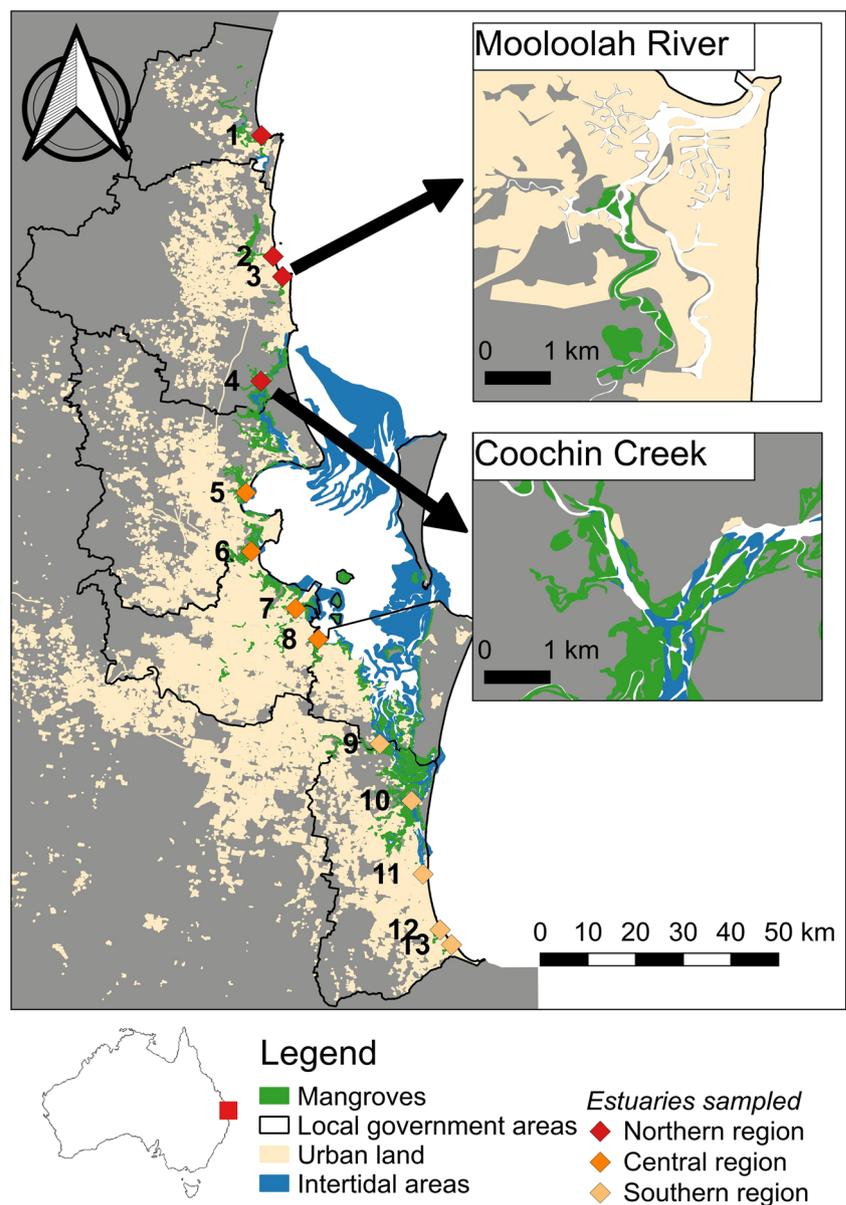
on a tripod. We took images of the ventral and dorsal surface (including all walking legs) and the inside of the left and right chelipeds. From the four images taken for each individual, we measured 145 morphometrics in four categories (Fig. S1): (1) the dorsal carapace ('top'; henceforth labelled 'T'), (2) the ventral carapace ('underside'; labelled 'U'); (3) the chelipeds (labelled 'C'); and (4) the walking legs (labelled 'L'). Morphometric values for walking legs and chelipeds were averaged between right and left body sides, thus yielding a total of 90 morphometrics per individual to be included in the numerical analyses. To account for variation in overall body size, we standardised all morphometrics by carapace width (i.e.  $x' = x/\text{carapace width}$ ), with carapace width (defined as the maximum width of the upper surface of the carapace) also being calculated in geomorph.

## Statistical Analyses

We gauged the association between body size and functional traits with environmental variables that fall, broadly, into three groups (Table 1): (1) at the estuarine scale we modelled the influence of estuarine inlet size and the area and extent of mangroves and intertidal flats; (2) to account for smaller-scale environmental effects (for individuals with small home ranges) we modelled the influence of variation in mangrove, tidal flats and urban land within 1 km of capture sites; and (3) to index broad pressures from fishing and development, we used data on commercial crab catches and human population size in three subregions of our study region (Table 1, Table S1, Fig. S2). These were based on the available commercial fishing data grids provided by the Queensland State Government (Queensland Department of Agriculture and Fisheries 2019), that divided our sampling reach into a northern, central and southern region, and population census by the Australian Bureau of Statistics (Fig. 1, Table 1, Table S1). The variables intertidal flats corrected correlated strongly (> 0.7 Pearson's *R*) with intertidal flats total, estuary mouth width, urban area and mangroves area, and mangroves total and urban catchment correlated strongly (> 0.7 Pearson's *R*) with urban area and mangroves corrected, so these variables were not included in subsequent analyses. The remaining variables did not covary.

We used generalised additive models (GAMs) in the mgcv package of R (Wood 2017) to test for correlations between environmental variables and giant mud crab carapace width, weight and standardised weight (weight divided by carapace width). To minimise overfitting, we ran GAMs with all possible combinations of three environmental variables or fewer (Barton 2018), and restricted GAM fits to three polynomial lines or fewer ( $k = 3$ ). Best fit GAMs were identified using AIC values. We calculated relative variable importance by summing the weighted AIC values for each model containing the variable

**Fig. 1** Map of study region and estuaries sampled in southeast Queensland, Australia. Inserts illustrate estuaries with intensive human modifications of the floodplain and catchment (Mooloolah River, top) and more natural settings with substantial areas of mangrove forest remaining (Coochin Creek, bottom). Estuary numbers correspond to estuary details in Table S1



of interest, with values nearer to 1 indicating greater importance of the variable in explaining overall patterns.

We used a distance-based linear model (distLM) in PrimerE to identify the suite of variables that best correlated with all functional traits (Anderson et al. 2008). The distLM model was calculated on normalised functional traits, using a stepwise approach and Akaike information criterion (AIC). The best-fit distLM model was visualised using distance-based redundancy analysis (dbRDA). We identified the functional traits most driving these relationships (i.e. ‘important’ functional traits) by overlaying Pearson’s vectors over the ordination space with correlations greater than 0.5. Pearson’s vector overlays illustrate the strength and trajectory of variable relationships across the ordination surface. Here, the direction of the vector indicates the direction in which the variables are

the largest, and the length of the vector indicates the strength of that correlation. We used GAMs to further examine patterns between variables from the best-fit distLM model, and important functional traits. GAMs followed the same procedures as outlined above.

## Results

### Body Size

Body size was consistently associated with variation in width of the estuarine inlet and the extent of intertidal flats (Fig. 2). Whilst some patterns were non-linear, typically the heaviest individuals and those with the largest carapace widths were

**Table 1** List of environmental metrics included in statistical models their definitions and justifications

Variable	Definition	Justification/hypothesis	Source/reference
<b>1. Estuary-scale</b>			
Estuary mouth width	Width of the estuary mouth at high tide in metres	Larger estuaries with greater connectivity to the ocean may provide greater access for larval giant mud crabs, better conditions for the growth of giant mud crabs via access to food, especially juvenile early life history stages.	(Becker et al. 2016; Gilby et al. 2017a; NearMap 2018)
Urban catchment	The percentage of each catchment classified as urban land	Greater urban areas within catchments result in greater runoff of pollutants and modified water flow regime that might reduce the size of animals that inhabit estuaries.	(Kennish 2002; Queensland Government 2015a; Gilby et al. 2017a)
Mangroves total	Total area of mangrove forests in the catchment (m <sup>2</sup> )	Estuaries with greater total extent of mangroves might contain more giant mud crabs and therefore greater competition between individuals and provide better access to food and shelter thereby allowing crabs to grow larger.	(Queensland Government 2015b; Queensland Government 2018)
Mangroves corrected	Area of mangroves in the catchment divided by the distance from the estuary mouth to the most upstream mangroves (giving areas of mangroves per metre of estuary, m/m <sup>2</sup> ).	Larger estuaries can often have a greater extent of mangroves, so this metric corrects for the size of estuaries. Estuaries with a longer reach abutted by mangrove forests that cover a larger area are expected to provide better overall habitat for giant mud crabs. It is plausible that better habitat quality is reflected in body size and/or shape.	(Queensland Government 2015b)
Intertidal flats total	Area of intertidal sand/mud flats in the catchment (m <sup>2</sup> )	Estuaries with greater total extent of intertidal flats might be of lower quality for giant mud crabs because they prefer mangrove habitats closer to deep channels. This might modify functional traits by selecting for individuals that have a good capacity for movement over long distances.	(Hyland et al. 1984; Queensland Government 2015b; Alberts-Hubatsch et al. 2016; Queensland Government 2018)
Intertidal flats corrected	The proportion of the aerial extent of the estuary that is intertidal sand/mud flats (as a proportion)	Larger estuaries can often have a greater extent of intertidal flats, so this metric corrects for the size of estuaries. Here, estuaries with more intertidal flats, over longer parts of the estuary would be lower-quality crab habitat, and this will modify body size and the functional traits of the walking legs.	(Hyland et al. 1984; Queensland Government 2015b)
<b>2. Site-scale</b>			
Mangrove area	The area of mangroves within 1 km of the capture site	Giant mud crabs (especially males, who do not undertake spawning migrations) larger than 100 mm CW do not normally move more than 1 km in enclosed, mangrove-lined creeks.	(Queensland Government 2015b; Alberts-Hubatsch et al. 2016)
Urban area	The area of urban development within 1 km of the capture site	Giant mud crabs (especially males, who do not undertake spawning migrations) larger than 100 mm CW do not normally move more than 1 km in enclosed, mangrove-lined creeks.	(Queensland Government 2015a; Alberts-Hubatsch et al. 2016)
Intertidal flats area	The area of intertidal flats within 1 km of the capture site	Giant mud crabs (especially males, who do not undertake spawning migrations) larger than 100 mm CW do not normally move more than 1 km in small, mangrove-lined creeks.	(Queensland Government 2015b; Alberts-Hubatsch et al. 2016)
<b>3. Fishing pressure</b>			
Commercial fishing pressure	A categorical variable with three levels (low, moderate and high) reflecting the commercial catch of giant mud crabs in subregions within our study region over the previous 10 years.	The Queensland Government reports on commercial fishing effort and catch in 30-min grids-lower resolution is not available due to fisher's privacy and associated rights. Estuaries were categorised according to their position within these grids in north, central, and south zones. There are clear differences	(Queensland Department of Agriculture and Fisheries 2019)

**Table 1** (continued)

Variable	Definition	Justification/hypothesis	Source/reference
Human population	A categorical variable with three levels (low, moderate and high) reflecting the number of people living in subregions of our study region.	in commercial fishing catch of giant mud crabs between the grids that overlay our region (see Fig. S2A). The number of people that reside within an area is a good indicator of various pressures on natural ecosystems, including, but not limited to, potential recreational fishing pressure in local waterways and landscape transformation in the catchment. Recreational fishing data is notoriously difficult to gather, and recreational catch data are not available for the study region. There are, however, clear differences in human population size of the local government areas that fit in the grids that overlay our region (per commercial fishing effort), that can be easily categorised into this metric (see Fig. S2B).	(Australian Bureau of Statistics 2016)

captured in estuaries with wider inlets and smaller extent of intertidal flats (Fig. 2). Urban area was included in the best-fit model for carapace width (Fig. 2a), but neither urban area nor mangrove area individually were significant predictors of giant mud crab body size. Estuary mouth width and the total extent of intertidal flats were, however, not significant for corrected weight (Fig. 2c).

### Functional Traits

The gross morphology of giant mud crabs correlated best with commercial fishing pressure, human population size, urban area and extent of mangroves and intertidal flats in the estuary (Fig. 3). Twelve morphometrics correlated ( $R > 0.5$ ) with the ordination space (Fig. 3b, c). We found distinct clusters of giant mud crabs from areas of high, intermediate and low commercial fishing pressure in ordination space (Fig. 3a). dbRDA vectors suggest that crabs from regions with lower commercial catches and fewer people in the broader catchment tend to have larger morphometrics, especially of the carapace and walking legs. Crabs from estuaries where populations are high, but commercial catches are of intermediate intensity are morphometrically distinct, tending to have larger chelipeds. Finally, crabs from estuaries with the highest commercial catches and highest human populations in the catchment tended to have smaller and narrower chelipeds.

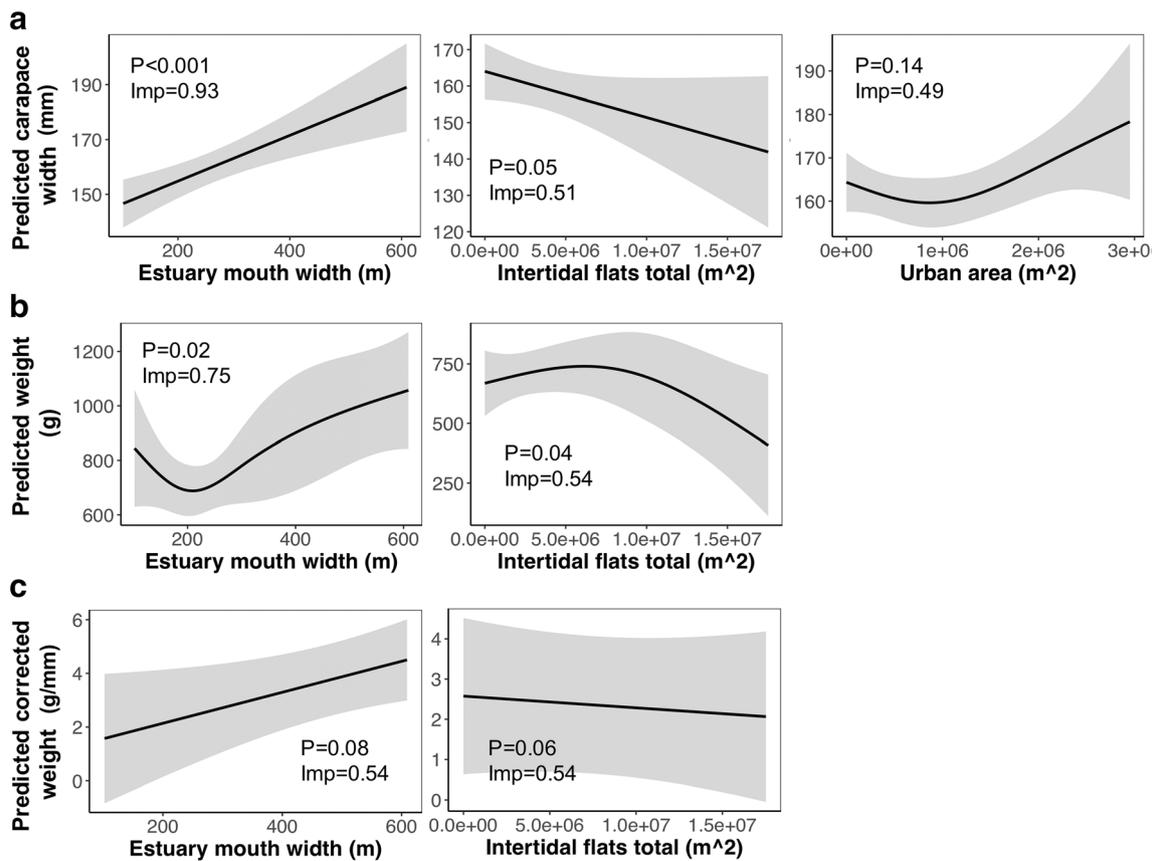
Each of the environmental variables from the best-fit distLM correlated significantly with at least one of the important morphometrics (Fig. 4). However, the shape of associations was variable. Main cross carapace morphometrics (morphometrics T13 and T16, i.e. the 13th and 16th morphometrics of the top of the carapace) (Fig. 3a) were the largest in areas with moderate human populations (Figs. 3, 5a, S3). Morphometric T13 was also higher in areas with greater

intertidal flat extent (Fig. S3). No environmental predictor correlated significantly with the underside of the body (Fig. 3). The length of the end segment of the second walking leg (L10) was shorter in areas with greater area of urban development nearby (Fig. 3).

Whilst there were inconsistent effects of environmental variables on morphometrics of the carapace and walking legs, cheliped morphometrics were consistently the lowest in areas with high commercial fishing pressure and were always highest in areas of low human populations (Fig. 5b, S4). Here, commercial fishing pressure correlated significantly with all of the important cheliped morphometrics, and human population correlated significantly with five of seven (Fig. 4). We also identified consistent correlations between urban areas on cheliped morphometrics. Urban area was associated with some cheliped morphometrics: individuals captured from sites with low urban land use nearby had the largest C6 and C15 morphometrics (Fig. 5b, S4). Morphometric C30 was the largest in areas with moderate commercial fishing pressure and greater corrected mangrove extent (Fig. 5b, S4).

### Discussion

The cumulative influence of human impacts can reduce the body size and change the functional traits of some species within modified ecosystems (Acevedo-Whitehouse and Duffus 2009; Villéger et al. 2010; Mouillot et al. 2013; Gagic et al. 2015). Some behavioural or ecological traits of species may make them more vulnerable to particular human impacts. For example, sex- and size-biased fishing practices and landscape transformations may combine to affect the condition and functional traits of highly valued and often highly competitive and territorial species (Beattie et al. 2012; Unhalu



**Fig. 2** Generalised additive model output plots showing variables included in the best fit models for **a** carapace width, **b** body weight and **c** standardised body weight (weight/carapace width).  $P$  values are those from the best fit model and importance values (Imp.) scale from 0 being

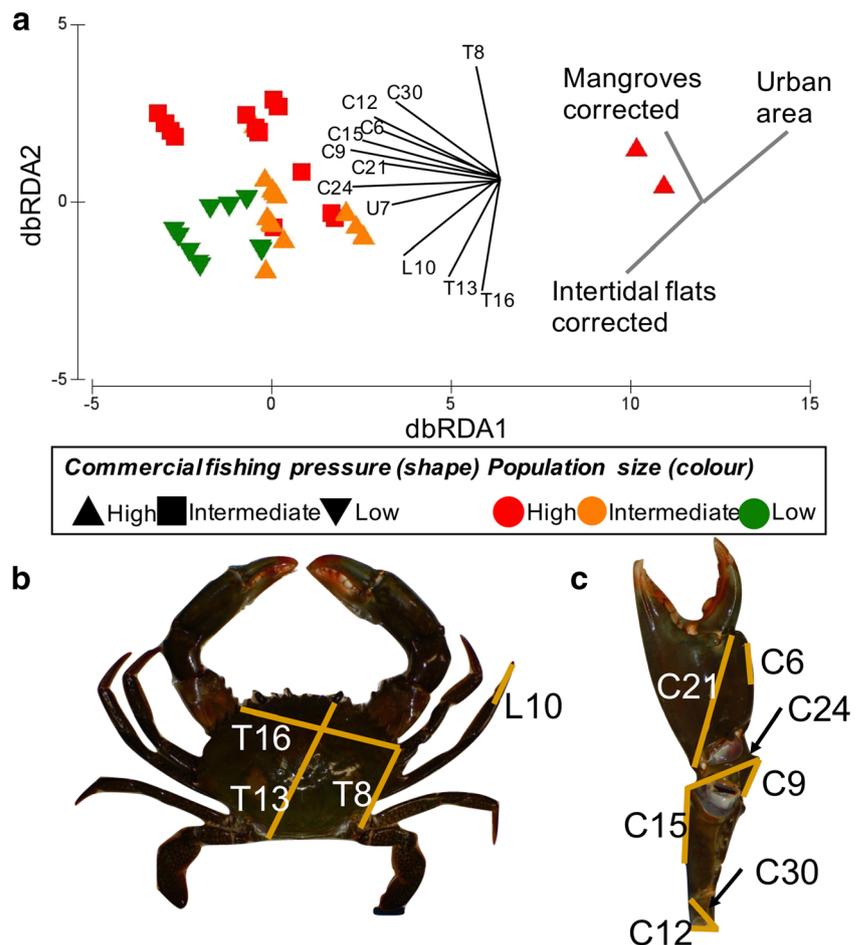
not important to 1 being very important in explaining overall patterns. All error measurements are 95% confidence intervals. Note that axis scales differ between panels

et al. 2015; Alberts-Hubatsch et al. 2016). This can affect the health of wild populations and the value of catches. In this study, we found significant correlations between the extent of marine ecosystems (intertidal sand flats and mangroves), urbanisation and fishing pressure on the body size and/or functional traits of giant mud crabs in southeast Queensland. Giant mud crab carapace size and weight was the greatest in estuaries with larger estuary mouths and lower extents of intertidal flats, thereby indicating that both natural attributes of estuaries and the ways in which humans modify estuaries (i.e. by modifying the mouths of estuaries and dredging intertidal flats) can potentially affect the body size of giant mud crabs. Correlations between cheliped size and fishing pressure and increases in urban footprint around coastal ecosystems are of concern to consumers because the flesh from the chelipeds is some of the most prized for consumption. Further reductions in the size of individual crabs (as measured by weight or carapace width), especially if linked with reductions in the relative size of chelipeds may reduce the value of catches in the future. Given the social and economic importance of giant mud crabs throughout their range (Alberts-Hubatsch et al. 2016), understanding how these sub-lethal effects of

anthropogenic impacts proliferate both through their population size and structure, as well as their body size and functional traits, is vital in optimising management responses.

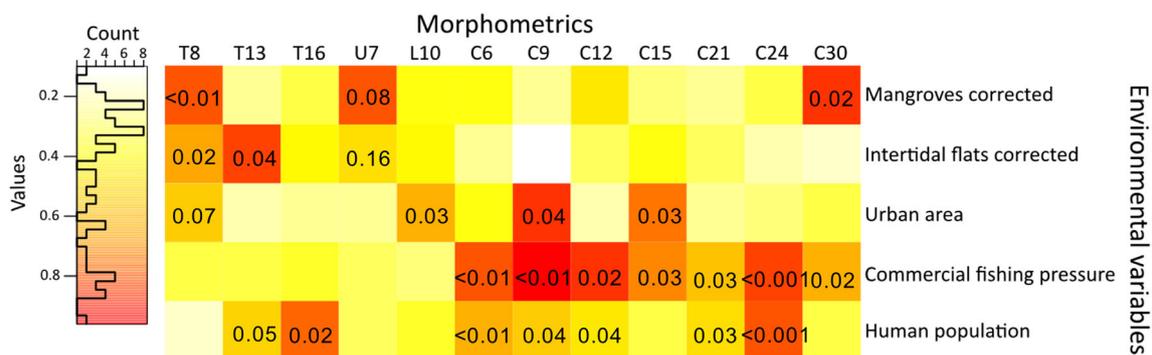
We found that legal-sized male giant mud crabs were larger and heavier in estuaries with wider estuary mouths and lower extent of intertidal flats in southeast Queensland. Estuaries with larger estuary mouths have greater oceanic water flow in the lower reaches, greater connectivity with the open ocean and therefore lower residence time of low saline water during runoff events in the stretches of the estuaries we sampled (Meyer and Posey 2009; Becker et al. 2016; Gilby et al. 2017b). This potentially results in greater temporal periods and broader extent of high salinity water to allow giant mud crabs to grow larger, especially during early developmental phases (Nurdiani and Zeng 2007; Alberts-Hubatsch et al. 2016). This greater water flow may also reduce the residence time of poor water quality runoff in these larger estuaries. Large male giant mud crabs prefer to inhabit subtidal areas of narrow, mangrove-lined estuaries and are often captured at the mouths of small inlets that drain tidally within these estuaries (Alberts-Hubatsch et al. 2016). These sorts of seascape compositions are less common in estuaries with extensive

**Fig. 3** Distance-based redundancy analysis (dbRDA) of relationships between environmental variables and the morphometrics of giant mud crabs from the best-fit distance-based linear model (distLM) (a), and visualisations of the morphometrics that correlated best with the ordination for legs and carapace measurements (b) and chelipeds (c)



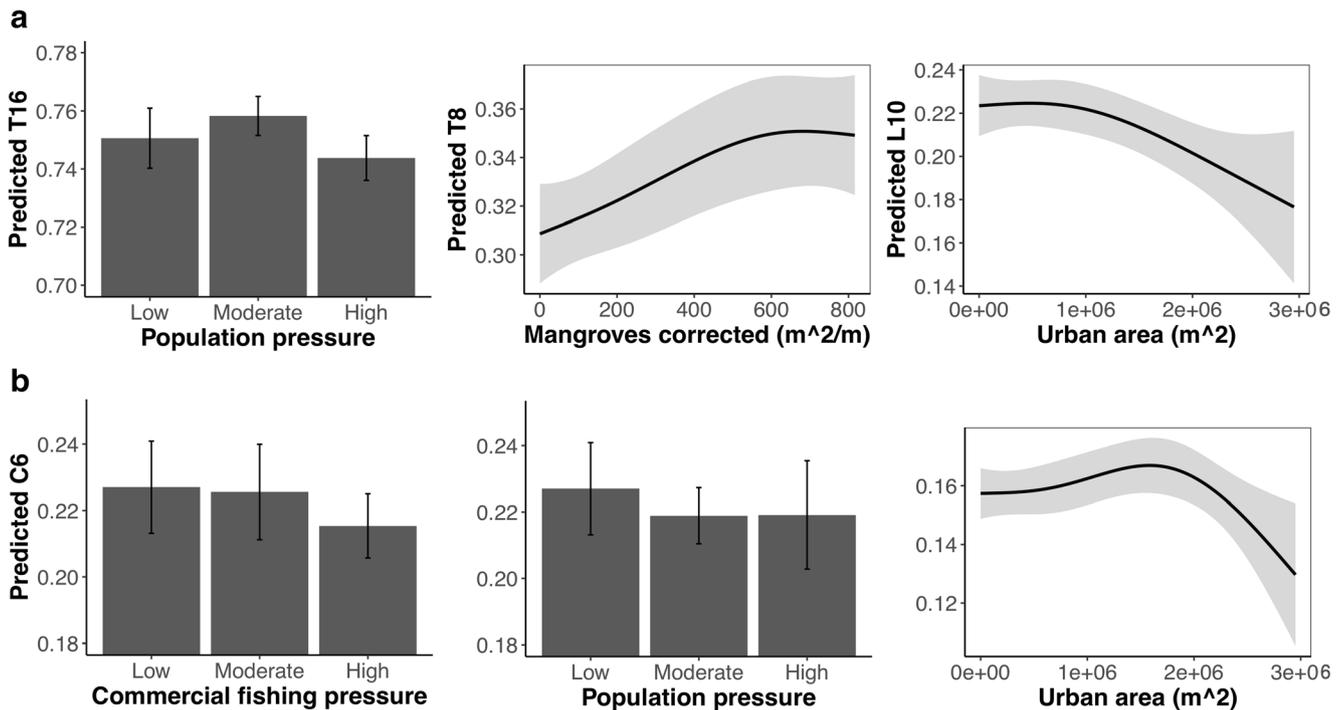
intertidal flats. Giant mud crabs also make routine movements for foraging, and the extent of these movements depend on the composition of the seascape in which the giant mud crab lives (Alberts-Hubatsch et al. 2016). For example, giant mud crabs that occur in open embayments with extensive intertidal flats exhibit significantly larger home ranges than the crabs studied in narrow estuaries such as those in this study (1 km in

estuaries versus 3.7 km in open embayments; for further details, see Hyland et al. 1984). This increased energy expenditure and movement of individuals across extensive intertidal flats could potentially affect the amount of energy used for growth and weight gain. Adult giant mud crabs are top benthic predators consuming a variety of macroinvertebrates and carrion (Prasad and Neelakantan 1988; Alberts-Hubatsch et al.



**Fig. 4** Heat map of importance values for environmental variable in the generalised additive models (GAMs) for each morphometric that correlated strongly with results from multivariate analyses (see Fig. 3). Importance values range from 0 (being the least important variables, white) through to 1 (being the most important variables, dark red).

Values within boxes indicate *P* values of variables included in the best-fit model. Legend on the left provides a histogram of the distribution of values across the range. *T*, top of carapace; *U*, underside of carapace; *L*, legs; *C*, chelipeds



**Fig. 5** Example generalised additive model output plots showing usual trends for morphometrics from the carapace and legs (**a**), and the chelipeds (for morphometric C6 only) (**b**). All error measurements are

95% confidence intervals. See Figures S3 and S4 for the remaining plots from the best fit models for all other morphometrics. Note that axis scales differ between panels.

2016). Extensive areas of low-complexity intertidal flats may not provide the same abundance and diversity of these food items as more channelised estuaries with more direct access between mangroves and adjacent deeper waters. Large estuaries with less extensive intertidal flats may also have higher flow rates from river outputs, meaning that giant mud crabs in these estuaries may receive greater feeding opportunities from catchments, in turn resulting in a lower requirement for moving to find food and meet their dietary needs. Animals that move less might also be less likely to encounter a competitor. Combined, these results indicate the importance of accounting for the broader landscape context of estuaries when considering the influence of human impacts on the body size of coastal species.

We found consistent effects of commercial fishing pressure and human population size in the surrounding catchment on the functional traits of giant mud crab, especially their chelipeds. These effects were consistent between both multivariate and univariate analyses of our functional trait data. Here, greater human populations and commercial fishing pressure correlated with smaller cheliped morphometrics. There are several potential mechanisms underlying this correlation. Male giant mud crabs are highly territorial and compete for territory and mates with other males within their range (Beattie et al. 2012). Males with larger chelipeds have an edge in these competitive interactions (Yoshino et al. 2011). In

systems where many male giant mud crabs are removed due to fishing, the necessity to have large claws to outcompete conspecifics is significantly reduced. Conversely, there might be a genetic underpinning of this change if there is biased removal of male crabs with disproportionately large chelipeds. This genetic change might, however, be considered unlikely because of (1) homogenisation of giant mud crab larvae over large spatial scales due to offshore spawning by females (Alberts-Hubatsch et al. 2016), and (2) the unlikelihood of fishers biasedly remove individuals with larger chelipeds as fishers would keep legal-sized crabs even if they had proportionately smaller chelipeds. Therefore, the changes observed in this study are likely to be within the phenotypic spectra of the males following settlement and related to competition and competitiveness amongst the males within this sex-biased fishery.

Whilst the metrics of fishing pressure included in this study are coarse, categorical metrics, the included variables reflect the best possible data available in the region to quantify these effects. For commercial fishing, data is not available at a finer spatial scale due to privacy issues surrounding the identification of individual fishers. Our human population size variable is used in this analysis as a proxy for both broader impacts within the catchment, and likely local recreational fishing pressure. Collecting accurate recreational fishing pressure information is a consistent challenge for coastal ecologists

(McCluskey and Lewison 2008; Steffe et al. 2008; van Poorten et al. 2015), and the finest information available publicly in this region covers most of the estuaries sampled in a single data point (Webley et al. 2015). Including this metric that uses population size as a proxy for likely effort is likely fair given the abundance of people across the entire region that undertake recreational fishing activities (Webley et al. 2015). Nevertheless, this is the first attempt, to our knowledge, of quantifying the potential effects of these two key pressures on crab fisheries (Dumas et al. 2012; Alberts-Hubatsch et al. 2016) with key metrics of the functional traits and body size of the catch.

We found very few consistent effects of our environmental variables on the functional traits of the walking legs or the carapace. Whilst we did find a correlation between urban area and the extremities of the second walking legs, it is difficult to establish causality between this variable and changes in the morphometric without further evidence of changes in other similarly positioned segments. In this sense, there is no obvious mechanism underlying change in the size of this particular leg segment, and so the patterns found here are likely a coincidental correlation. In this study, increases in our metrics of the carapace do not necessarily mean larger body size as they are scaled with carapace width. Consequently, our results indicate changes in the proportions of the carapace relative to carapace width and therefore changes in the depth and breadth of certain areas of the carapace with different environmental conditions. These inconsistencies between the carapace and walking legs potentially infer that variability in these morphometrics is due to specific adaptations to movement or burrowing in estuaries with different habitat types and distributions and/or sediment profiles. We did, however, find a correlation between human population size and morphometrics T13 and T16: two major, cross carapace morphometrics. These patterns are likely similar to those found between fishing pressure and the morphometrics of the chelipeds and related to reduced competitiveness of males with conspecifics in areas of higher fishing pressure. Further studies are required to more thoroughly disentangle the causative effects of the patterns found here, and to better appreciate whether these morphological changes are beneficial or disadvantageous for the giant mud crab. Irrespective of these potential effects, the lack of consistent patterns across our carapace and walking leg morphometrics and the relatively low number of variables that correlated with environmental variables may mean that the variables we used are not those causing variation in these morphometrics, or that there is genuinely little predictable variation in these metrics.

Giant mud crabs are a commercially, recreationally and socially important species throughout their range. Impacts to their populations will therefore have diverse ramifications for people. With increasing demand for giant mud crab flesh and increasing fishing pressure and coastal

development across their range (all concomitant with increasing human population), quantifying the effects of human impacts, the spatial scale, and influence of those impacts and optimising management around these impacts to ensure maximum abundance and condition of their populations will become increasingly important (Ewel 2008; Dumas et al. 2012; Alberts-Hubatsch et al. 2016). In this study, we identified a combination of natural and human-associated variables that modify the body size and functional traits of giant mud crabs in southeast Queensland. Intensive fishing pressure and reduced marine habitat extent are well-understood pressures on the population size and structure of giant mud crabs (Pillans et al. 2005; Fratini et al. 2010; Unhalu et al. 2015). The results of this study show that these stressors can now be more strongly implicated in modifications to giant mud crab body size and functional traits. Giant mud crabs are significant ecological engineers in the systems they inhabit due to their large body size and extensive burrowing actions. Changes in the functional traits of this species may eventually affect this capacity. Our results support the assertions of other studies regarding the importance of properly managing fishing effort of these larger, site-attached portunids in coastal ecosystems (Dumas et al. 2012). The results of this study add to this by highlighting the potential influence of pressures on crab populations and their environments on the value of catches, and not just the volume of catches. Ecological restoration and marine reserves that are implemented with the goal of conserving and enhancing giant mud crab stocks must more closely consider the landscape context of the actions. Quantifying the effects of human impacts and management interventions on coastal animal populations must also account for the potential effects of competitive interactions on variations in functional traits.

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