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Altering river flow impacts estuarine species and catches: lessons from giant mud crabs

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Anthropogenic alterations to river flow could have repercussions for flow-dependent species downstream but few studies account for these dynamic relationships or quantify impacts of altered river flow. *Scylla serrata*—a widely distributed portunid crab—was used as an example of a flow-dependent species to model impacts of altered flow on species abundance and catch. Crab population dynamics were modelled across a large semi-enclosed tropical sea in northern Australia. Environmental drivers, primarily river flow, but also temperature and the Southern Oscillation Index were linked to crab dynamics to explain variability in historical catches. Catch and abundance could then be predicted under altered flow scenarios. River flow significantly improved the ability to explain historical catches for some regions but not all, and the strength of this relationship varied across catchments. Altered flows had negligible effects for perennial rivers but for ephemeral and temporally variable rivers, predicted decreases in abundance and catch ranged from 36 to 46% on average. Our modelling approach showcases a way to dynamically and rigorously quantify impacts of altered river flow on a key species with potential to help inform natural resource management, including policy decisions on the timing, quantity, and method of water removed from rivers.

Keywords: crustacean, environmental driver, estuarine, fishery, freshwater flow, Gulf of Carpentaria, northern Australia, Portunidae, river development, water allocation.

Introduction

Seasonal and interannual variation in river flow can be critical for maintaining ecosystem function in downstream estuarine and coastal environments (Sklar and Browder, 1998; Gillanders and Kingsford, 2002; Rozas *et al*., 2013). Variation in river flow has shaped the life history strategies of many species (see review by Lytle and Poff, 2004). Moreover, river flow variability is known to also have strong impacts on fisheries production in associated downstream habitats (Gillson, 2011; Broadley *et al*., 2022).

Whereas the importance of river flow (and other environmental drivers) on downstream ecosystems is well known and the impacts of altered river flow regimes are becoming increasingly understood (Rolls and Bond, 2017; Schmutz and Moog, 2018; Belmar *et al*., 2019; Ezcurra *et al*., 2019), few studies quantify the spatial and temporal impacts on flow-dependent species. Indeed, challenges remain on understanding how variable flows impact resource abundance (Gillson, 2011) and there is a need to move beyond just documenting the presence or direction of flow-ecology relationships (Rosenfeld, 2017). Most studies either identify or describe these relationships (Warfe *et al*., 2011) or quantify them using static statistical analyses (Armstrong and Nislow, 2012; Meynecke *et al*., 2012; Alford and Walker, 2013; Broadley *et al*., 2020; Stewart *et al*., 2020). Here, we use the Portunid *Scylla serrata* (giant mud crab) as a case study of a flow-dependent species widely distributed across the Indo-Pacific and dynamically integrate flow and other environmental variables into a population model to help explain variabil-

ity in downstream abundance and catch under differing flow regimes.

In tropical northern Australia, riverine and coastal ecosystems along the remote Gulf of Carpentaria (GoC; Figure 1a) are relatively unimpacted by human development (King *et al*., 2015). Here, natural variability in river flow is extreme, with both high interannual and seasonal variability (Puckridge *et al*., 1998; Petheram *et al*., 2008). Much of the estuarine ecosystems in this region have been shaped by seasonal river flow and biota have evolved life history strategies to take advantage of these conditions (Warfe *et al*., 2011). Nonetheless, the GoC is a large heterogenous ecosystem spanning ∼300000 km^2 of shallow sea and 2000 km of coastline. It is influenced by different oceanographic, topographical, and catchment features such that relationships between environmental drivers and the ecology aren't homogenous.

The large portunid *S. serrata* is one of four species of *Scylla* that is widely distributed across Indo-Pacific estuarine habitats. It is fast-growing with a longevity of 3–4 years (Knuckey, 1999) and makes important contributions to commercial, recreational, and indigenous fisheries (Le Vay, 2001; Mirera, 2011; Robins *et al*., 2020). River flow is an important driver in the abundance (and catches) of mud crabs (Le Vay *et al*., 2001; Meynecke *et al*., 2012; Robins *et al*., 2020) and annual catches have been positively correlated with lagged summer river flow/rainfall [or the Southern Oscillation Index (SOI) as a proxy] in northern and eastern Australia, with peaks in catches coinciding with La Nina cycles (Meynecke *et al*., 2012). Moreover, Robins *et al*. (2020) found that in the Gulf
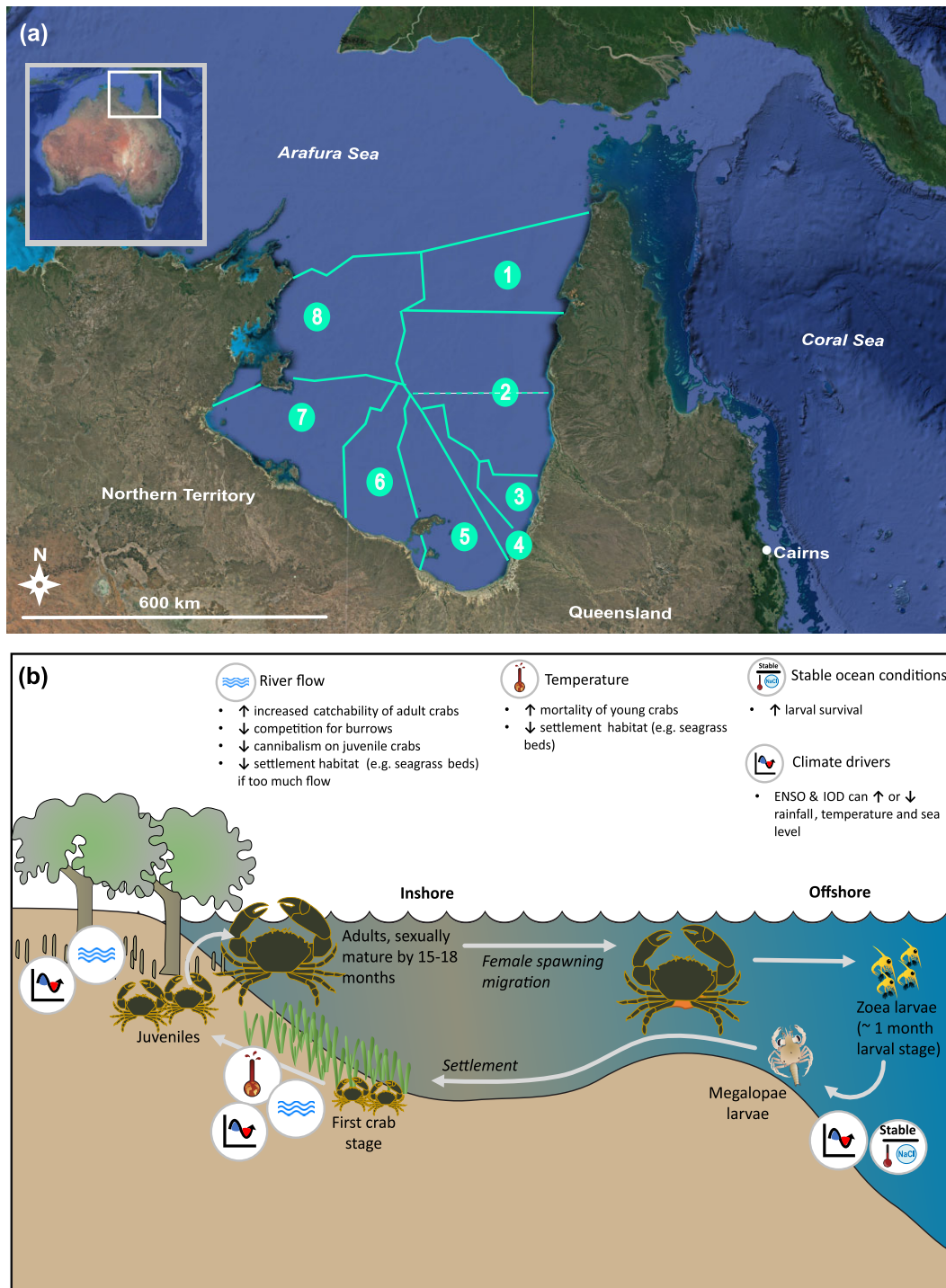
Figure 1. (a) Gulf of Carpentaria in northern Australia with the eight model regions overlaid. Region 2 was subdivided (dashed line; see Methods text). Each model region is influenced by a major river catchment as follows: Region 1—Embley River; Region 2—Mitchell River; Region 3—Gilbert River; Region 4—Norman River; Region 5—Flinders River; Region 6—Mornington; Region 7—Roper River; Region 8—Walker River/North Groote; (b) Schematic showing an overview of giant mud crab *Scylla serrata* life cycle and habitat use, as well as important physical drivers that influence mud crab abundance. Map in (a) is a Google Earth map (Data SIO, NOAA, U. S. Navy, NGA, GEBCO Image Landsat/Copernicus) and IAN symbols in (b) were sourced from the Integration and Application Network (ian.umces.edu/media-library/).

of Carpentaria, a mean sea level anomaly and a cumulative heat index had negative effects on catch rates. However, relationships with environmental drivers varied across the GoC, both in terms of significance of the driver and combinations of drivers used to explain catch variability (Robins *et al.*, 2020).

In contrast, reduced catches in the northern GoC have been anecdotally linked to high migration rates of mud crabs out of local fishing areas and recruitment failure, as a consequence of extended periods of freshwater run-off in the year of catch and also in the 2 years prior (Helmke *et al.*, 1998).

Whereas there are a suite of environmental variables that may drive spatial and temporal dynamics of marine and coastal ecosystems in the GoC, river flow is a prominent driver, not only for mud crabs, but also other species, e.g. common banana prawns (Vance *et al.*, 1985; Robins *et al.*, 2007) and barramundi (Staunton-Smith *et al.*, 2004; Robins *et al.*, 2005; Robins *et al.*, 2006). Over the last decade, there has been increasing interest in developing water resources in this region (Pusey 2011), including an assessment of its potential to support agriculture development (Petheram *et al.*, 2008; Petheram *et al.*, 2013). Hence, water extraction from rivers or water impoundment on rivers (e.g. dams) [hereafter termed water resource development (WRD)], for agricultural or other industry use, may have consequences for fisheries in the region.

Numerous studies have considered the impacts of WRD on associated downstream ecosystems in the GoC, but many of these have been qualitative (Warfe *et al.*, 2011; Bayliss *et al.*, 2014; Duggan *et al.*, 2019; Burford *et al.*, 2020; Burford and Faggotter, 2021; Stewart-Koster *et al.*, 2021; Venarsky *et al.*, 2022), or have used static statistical approaches in quantifying impacts (Leigh and Sheldon, 2008; Broadley *et al.*, 2020; Leahy and Robins, 2021; O'Mara *et al.*, 2021; Stewart-Koster *et al.*, 2021). Hence, although flow-ecology relationships have been identified in the GoC (Robins *et al.*, 2005; Meynecke *et al.*, 2012), few are integrated into models to dynamically quantify impacts of altered river flow. Here, we show how river flow (and also SOI and temperature) can be explicitly included in a mud crab population model to help explain historical catches. We then use this model to quantify impacts on catch and abundance under various WRD scenarios for three river catchments, which are the focus of current WRD in the GoC. Our dynamic approach to account for these drivers thus advances understanding of the way in which river flow and other drivers influence a widely distributed portunid crab. Moreover, our crab model feeds into a larger integrated ecological model that dynamically accounts for these relationships, using this approach to assess the impacts of WRD on key species, fisheries, and habitats (Plagányi *et al.* 2023). Importantly, a more rigorous quantification of WRD impacts to abundance and catch of a flow-dependent species has potential to help inform natural resource management, including policy decisions by water managers on the timing, quantity, and method of water removed from rivers.

Methods

Study area

The Gulf of Carpentaria (GoC) is a large, shallow sea in the remote northern tropical Australia. The western half of the GoC falls within the Northern Territory while the eastern half falls within the state of Queensland (Figure 1a). Management arrangements for the mud crab fishery differ between states—for example, the minimum legal size differs between the two jurisdictions and in Queensland, only male mud crabs may be caught, whereas in the Northern Territory, both male and female mud crabs may be caught (Knuckey 1999). In our study, the GoC was subdivided into eight spatial model regions (Figure 1a) based on discussions with stakeholders and the needs of a broader MICE ecosystem model (Plagányi *et al.* 2023), for which the mud crab model was one component. The main criteria behind the spatial divisions

Table 1. Summary of the four main WRD scenarios tested for the Mitchell River (M), Flinders River (F), and Gilbert River (G) relative to Base (baseline flows including any existing water development).

WRD scenario	Rivers affected	Type of WRD
Base	None	None
WRD1	Mitchell	M: Water allocation (2000 GL/year, low threshold for pumping, low pump rate).
	Flinders	F: Water allocation (400 GL/year)
	Gilbert	G: 2 Dams (yield 498 GL/year)
WRD2	Mitchell	M: Water allocation (1000 GL/year, high threshold for pumping, high pump rate)
	Flinders	F: Water allocation (160 GL/year)
	Gilbert	G: 1 Dam (yield 172 GL/year)
WRD3	Mitchell	M: Water allocation (1000 GL/year, low threshold for pumping, high pump rate)
WRD4	Flinders	F: Water allocation (160 GL/year)
	Gilbert	G: 1 Dams (yield 172 GL/year)

GL = gigalitres.

included (i) a focus on the main rivers most likely to be affected by water resource development (Mitchell, Gilbert, and Flinders rivers); (ii) the major river catchments and biogeographical regions; (iii) major fishing areas and stock regions for key resources (barramundi, common banana prawns, tiger prawns, and mud crab); and (iv) jurisdictional management arrangements. Model regions 1–6 fall within Queensland whereas regions 7–8 are within the Northern Territory boundaries. The mud crab model was fitted to catch data for each region.

Model structure

For each of the eight model regions, male and female mud crabs are modelled separately using an age-structured population model with a monthly time step and three age classes: 1, 2, and 3+ years [Table 2 Equations (1) to (3)]. We assumed no connectivity between model regions given adult mud crabs are unlikely to move between catchments (Gopurenko and Hughes, 2002; Robins *et al.*, 2020). The number of crabs in each month depends on the number of crabs in the month before subject to natural mortality, those that are caught by the fishery and those that are added through recruitment. Recruitment is defined as 1-year-old crabs (50% male and 50% female) entering the population. The number of recruits depends on the female spawning biomass and is modelled using a Beverton–Holt stock–recruitment relationship [Table 2 Equations (6–7)]. We assume that these recruits are spawned 14 months prior and that spawning takes place each month, with the main spawning event in September and October (Knuckey, 1999). Recruitment is also assumed to be influenced by flow through a recruitment-flow multiplier [estimated in the model; see Table 2 Equations (6), (10), and section below]. In some regions, depending on topography, recruitment was also assumed to be influenced by other environmental drivers, e.g. SOI [estimated in the model, see Table 2 Equations (6), (12), and section below], which can be a proxy for a suite of climate influences including flow/rainfall, mean sea level (i.e. connectivity between offshore environments and estuaries), as well

Table 2. Model equations used to capture mud crab population dynamics and links to environment. For a description of the variables and further details see Supplementary Material Tables S2 and S3.

Description	Equation	Eq No.
Recruits (age 1)	$N_{r,y+1,1,1}^{sex} = R_{r,y,1}$ for $a = 1$; $m = 1$ $N_{r,y,m+1,1}^{sex} = N_{r,y,m,1}^{sex} e^{-M_{r,y,m,1}} - C_{r,y,m,1}^{obs,sex} + R_{r,y-1,m+1}$ for $a = 1$; $m = 1$ to 11 r= region; y= year; m= month and a= age	1
Age 2 crabs	$N_{r,y+1,1,a+1}^{sex} = N_{r,y,m,a}^{sex} e^{-M_{r,y,m,a}} - C_{r,y,m,a}^{obs,sex}$ for $m = 12$ $N_{r,y,m+1,a}^{sex} = N_{r,y,m,a}^{sex} e^{-M_{r,y,m,a}} - C_{r,y,m,a}^{obs,sex}$ for $2 \leq a < z$; $m = 1$ to 11	2
Age 3+ crabs (the plus group)	$N_{r,y+1,1,z}^{sex} = (N_{r,y,12,z}^{sex} e^{-M_{r,y,m,z}} - C_{r,y,12,z}^{obs,sex}) + (N_{r,y,12,z-1}^{sex} e^{-M_{r,y,m,z-1}} - C_{r,y,12,z-1}^{obs,sex})$ for $a = z$; $m = 12$	3
Mortality rate	$M_{r,y,m,a} = M_{base}$ except for a temperature dependent form when $r = 7$ and $temp_{r,y,m} > temp^{opt}$, then $M_{r,y,m,a} = M_{base} \cdot M_{r,y,m}^{temp}$ (see Eq 13)	4
Spawning biomass	$B_{r,y,m}^{spn} = \sum_{a=1}^{z} f_{m,a} \cdot w_{m,a}^{sex} \cdot N_{r,y,m,a}^{female}$	5
Recruitment	$R_{r,y,m+1} = 0.5 \frac{\alpha_r B_{r,y-1,m-1}^{spn}}{\beta_r + B_{r,y-1,m-1}^{spn}} (\sigma_{r,y-1,m+1}^{flow} + \sigma_{y-1,m+1}^{SOI})$ for $1 < m < 12$ $R_{r,y+1,m} = 0.5 \frac{\alpha_r B_{r,y-1,m+10}^{spn}}{\beta_r + B_{r,y-1,m+10}^{spn}} (\sigma_{r,y,m}^{flow} + \sigma_{y,m}^{SOI})$ for $m = 1$ $R_{r,y+1,2} = 0.5 \frac{\alpha_r B_{r,y-1,m}^{spn}}{\beta_r + B_{r,y-1,m}^{spn}} (\sigma_{r,y,2}^{flow} + \sigma_{y,2}^{SOI})$ for $m = 12$ with $\sigma_{y,m}^{SOI} = 0$ for $r = 1, 2, 7, 8$	6
Stock-recruitment parameters	$\beta_r = \frac{(1-h)\sum_m B_{r,1970,m}^{spn}}{5h-1}$ $\alpha_r = \frac{\beta_r + \sum_m B_{r,1970,m}^{spn}}{SPR_r^{virg}}$ where $SPR_r^{virg} = \sum_m B_{r,1970,m}^{spn}$	7
Von Bertalanffy growth equation	$\ell_{r,y,m,a} = \ell_\infty (1 - e^{\kappa_a/12(a-t_0)})$	8
Mass-at-age	$w_{m,a}^{sex} = a(\ell_{m,a})^b$	9
Flow multiplier	$\sigma_{r,y,m}^{flow} = thres(flm_{r,y,m} - thresM)^2 + c_\sigma$	10
Flow catchability multiplier	$q_{r,y,m}^{flow} = 1/1 + c_q e^{-(flm_{r,y,m}-thresM)/thres^q}$	11
SOI multiplier	If $r = 3$-6: $\sigma_{y,m}^{SOI} = \eta \cdot \tau^{SOI}$ (else $\sigma_{y,m}^{SOI} = 0$) where $\eta = -1$ if $SOI < -7$ or $\eta = 1$ if $SOI > 7$ and τ^{SOI} is a recruitment $-$ related SOI parameter that is estimated in the model.	12
Air temperature multiplier	$M_{r,y,m}^{temp} = \tau^{temp}(temp_{r,y,m} - temp^{opt}) + c^{temp}$ where τ^{temp} is a temperature $-$ related mortality parameter that is estimated in the model, $temp_{r,y,m}$ is the monthly air temperature, $temp^{opt}$ is the long $-$ term mean air temperature for Nov $-$ Dec and c^{temp} is a fixed scaling parameter.	13
Commercially exploitable biomass	$B_{r,y,m}^{\exp,sex} = \sum_{a=1}^{z} S_{r,y,m,a}^{sex} A_{r,m}^{sex} w_{m,a}^{sex} N_{r,y,m,a}^{sex} e^{-M_{r,y,m,a}}$	14
Fished proportion	$F_{r,y,m}^{sex} = C_{r,y,m}^{pred,sex} / B_{r,y,m}^{\exp,sex}$	15
Catch-at-age numbers	$C_{r,y,m,a}^{sex} = S_{r,y,m,a}^{sex} A_{r,m}^{sex} F_{r,y,m}^{sex} N_{r,y,m,a}^{sex} e^{-M_{r,y,m,a}}$	16
Predicted catch	$C_{r,y,m}^{pred,sex} = q_r q_{r,y,m}^{flow} E_{r,y,m} B_{r,y,m}^{\exp,sex}$ *where,* $C_{r,y,m}^{pred,sex} = C_{r,y,m}^{pred,male}$ for $r = 1 - 6$ (only males caught) $C_{r,y,m}^{pred,sex} = C_{r,y,m}^{pred,male} + C_{r,y,m}^{pred,female}$ for $r = 7 - 8$ (both males and females caught)	17
Contribution to the negative log-likelihood	$-\ln L_r = \sum_y [\sum_m \ln \sigma_r + (\varepsilon_{r,y,m})^2/2(\sigma_r)^2]$ where $\varepsilon_{r,y,m} = \ln(C_{r,y,m}^{obs,sex}) - \ln(C_{r,y,m}^{pred,sex})$ and $\varepsilon_{r,y,m}$ from $N(0, (\sigma_r)^2)$ $-\ln L = \sum_r -\ln L_r$ for $r = 1 - 6$; $y = 1989 - 2019$; for $r = 7 - 8$; $y = 1983$ to 2018 $m = 1 - 12$ except when $r = 6$; $m = 1, 4 - 10$ and when $C_{r,y,m}^{obs,sex} > 0$, $C_{r,y,m}^{pred,sex} > 0$	18
Standard deviation of the residuals	$\hat{\sigma}_r = \sqrt{\frac{1}{n_r}\sum_y \sum_m (\ln C_{r,y,m}^{obs,sex} - \ln C_{r,y,m}^{pred,sex})^2}$ assumed to be independent of y and m, and set in the fitting procedure by its maximum likelihood value	19

as monsoonal patterns of wind and currents (Suppiah, [1992]). The number of crabs caught per region is sex-disaggregated based on sex ratios of catches from Knuckey ([1999]). The predicted catch (mass) of crabs can be computed based on a catchability coefficient (including a catchability coefficient based on flow—estimated in the model), monthly effort, and the biomass of crabs available to be caught by the fishery, termed the commercially exploitable biomass [Table 2 Equation (14)]. The exploitable biomass is determined by the availability of crabs each month and the selectivity of the fishery [Table 2 Equation (14); Supplementary Table S2].

Modelling environmental relationships

River flow

River flow is hypothesized to increase survival and growth of younger crabs given that adults are assumed to move downstream with moderate flood flows, thereby decreasing cannibalism on younger crabs and reducing competition for burrows (Loneragan and Bunn, [1999]), and increasing their catchability as they leave their burrows in search of more saline waters (Meynecke *et al.*, [2011]). Moreover, brackish conditions are optimal for the growth of crablets (Ruscoe *et al.*, [2004]). At high flood flow levels, the survival of younger crabs may be reduced (Ruscoe *et al.*, [2004]; Meynecke *et al.*, [2012]). We therefore linked river flow to (i) boost or reduce recruitment (defined as number of crabs surviving and entering the 1-year-old age class) and (ii) increase catchability of adult crabs.

Flow was linked to mud crab recruitment by calculating a flow residual, which either boosted or reduced recruitment [Table 2 Equation (6)] based on a dome-shaped parabolic relationship [Table 2 Equation (10)].

Thus, recruitment increased with flow up until a flow threshold (optimal flow), after which it decreased. There is little information to inform the optimum flow for mud crabs in each region. We considered that optimal flows would likely be above the regional long-term mean but not in the upper quantiles as extreme flood years are thought to negatively impact mud crabs (Meynecke *et al.*, [2012]) (Gary Ward, Karumba, pers. comm.). Based on time series flow-catch plots for each region, we set the optimum flow anomaly (dome-shape relationship) at 2.0–2.5 depending on the region (Table 4) and used this as our basis for our base-case flow-recruitment relationship. We then estimated the strength [i.e. slope, as defined by the *thres* parameter in Table 2 Equation (10)] of this relationship in the model for the relevant catchments.

Flow was also linked to mud crab catchability through an additional catchability term that was modelled using a logistic relationship [Table 2 Equation (11)].

Southern oscillation index

The SOI has been shown to be positively correlated with mud crab catches (Meynecke *et al.*, [2012]). The SOI is a proxy for rainfall, but also for mean sea level, the latter being negatively associated with mud crab catches in the south-eastern GoC (Robins *et al.*, [2020]). Hence, SOI was also linked to mud crab recruitment in the south-eastern GoC (regions 3–6) by calculating a SOI recruitment multiplier (through estimating recruitment-related SOI parameters), which either boosted (if SOI >7, i.e. La Nina years) or reduced (if SOI < −7, i.e. El Nino years) recruitment [Table 2 Equation (12)].

Table 3. Summary of the model ensemble and additional sensitivity test.

Model version	Description
Model 1	The base model with a fixed natural mortality of $M = 0.1$. Model start year (1970) spawning biomass was estimated and flow was linked to mud crab population dynamics via a parabolic flow relationship [see Table 2 Equation (10)]. Stock–recruitment steepness parameter of $h = 0.6$ in the Beverton–Holt stock–recruitment relationship
Model 2	The same as in Model 1 except the optimal flow parameter was reduced by 20%
Model 3	As in Model 1 except we adjusted M by increasing it by 20%, still within the range estimated by Knuckey ([1999])
Model 4	As in Model 1 except the estimated starting biomass was doubled
Model 5	As in Model 1 except we used a more conservative stock–recruitment steepness parameter $h = 0.4$, in which recruitment declines sooner in response to a reduction in spawning stock
Additional sensitivity (not part of ensemble)	As in Model 1 but instead of a parabolic flow relationship we trialled a logistic-type relationship, in which mud crab recruitment could be boosted by river flow up until a certain point (an optimal flow) after which, it plateaued (i.e. no additional increase in river flow impacted mud crab recruitment)

Further details are given in Supplementary Material S3.

Air temperature

Mud crabs are susceptible to periods of heating during the summer months when temperatures are high and the diurnal tides are low during the day, particularly in the southern GoC (catchments aligned with our model region 7). In this region, there are large, shallow coastal mud flats and air temperature is considered a reasonable proxy for water temperature in the shallow estuaries (Robins *et al.*, [2020]). Hence, for region 7, we used air temperature as one of the physical drivers for mud crab population dynamics. We included an additional mortality term that when air temperature exceeded the long-term summer mean in any given month, then the base monthly mortality was scaled up [Table 2 Equation (13)] otherwise at all other times (and for all other regions), mortality was set to the base monthly mortality of 0.1 [Table 2 Equation (4); Knuckey, [1999]].

Data

Mud crab catch and effort data

Queensland commercial catch data from the GoC (model regions 1–6) were provided by the Queensland Department of Agriculture and Fisheries and included monthly catch (kg) and effort (days fished per month) for the years 1989–2019. Northern Territory commercial catch data for the GoC (model regions 7–8) were provided by the Northern Territory Department of Primary Industry and Resources and included monthly catch (kg) and effort (number of pots per month) for the years 1983–2018. Further details are provided in Supplementary Material S1.

River flows

For the Mitchell and Roper rivers, end-of-system flow data (river flows) were produced using a calibrated Australian

Table 4. Parameter estimates (and associated standard deviations), as well as the likelihood contributions for each region and the overall likelihood for each of the five models in the ensemble. Fixed parameters are presented in italics and parameter descriptions are given in Table 2 and Table S2.

| Parameter	Model 1	Model 2	Model 3	Model 4	Model 5
Natural mortality base M_{base}	*0.10*	*0.10*	*0.12*	*0.10*	*0.10*
Stock recruitment steepness h	*0.6*	*0.6*	*0.6*	*0.6*	*0.4*
$\ln B^{spn}_{1,1970,1}$ region 1	1.5	2.2	1.6	2.2	1.76
	(0.05)	(0.05)	(0.05)	(–)	(0.05)
$\ln B^{spn}_{2,1970,1}$ region 2	1.4	2.1	1.5	2.1	1.64
	(0.04)	(0.04)	(0.04)	(–)	(0.04)
$\ln B^{spn}_{3,1970,1}$ region 3	3.3	2.9	3.3	4.0	3.51
	(0.09)	(0.05)	(0.09)	(–)	(0.08)
$\ln B^{spn}_{4,1970,1}$ region 4	3.3	2.4	3.3	4.0	3.66
	(0.16)	(0.07)	(0.16)	(–)	(0.16)
$\ln B^{spn}_{5,1970,1}$ region 5	2.7	2.2	2.7	3.4	2.89
	(0.09)	(0.06)	(0.10)	(–)	(0.09)
$\ln B^{spn}_{6,1970,1}$ region 6	2.0	1.5	2.0	2.7	2.27
	(0.15)	(0.13)	(0.15)	(–)	(0.15)
$\ln B^{spn}_{7,1970,1}$ region 7	4.2	4.4	4.3	4.9	4.34
	(0.10)	(0.08)	(0.09)	(–)	(0.06)
$\ln B^{spn}_{8,1970,1}$ region 8	3.6	3.9	3.7	4.3	3.78
	(0.07)	(0.08)	(0.07)	(–)	(0.05)
Catchability due to flow $thres^q$(reg 3-6)	2.36E+00	2.05E+00	2.84E+00	1.36E+00	2.35E+00
	(7.11E-01)	(5.86E-01)	(1.03E+00)	(2.43E-01)	(6.92E-01)
Recruitment parameter due to flow $thres$(reg 1-2)	-8.64E-02	7.00E-03	-8.64E-02	1.00E+00	-8.64E-02
	(1.78E-04)	(1.39E-02)	(1.72E-04)	(7.32E-05)	(1.37E-04)
$thres$(reg 3-6)	-7.45E-01	4.50E-02	-7.22E-01	-8.98E-01	-6.59E-01
	(2.44E-02)	(3.31E-02)	(2.61E-02)	(1.18E-02)	(1.97E-02)
thres(reg 7-8)	-1.33E-01	1.75E+00	-1.32E-01	-3.72E-01	-4.60E-08
	(4.73E-02)	(3.78E-01)	(4.55E-02)	(1.67E-02)	(1.46E-04)
Mortality parameter due to temperature τ^{temp}(reg 7)	3.46E+00	3.46E+00	2.96E+00	4.07E+00	3.12E+00
	(3.61E-01)	(3.46E-01)	(3.12E-01)	(3.21E-01)	(3.24E-01)
Recruitment parameter due to SOI τ^{SOI}(regs 3-6)	6.95E-01	9.92E-01	7.01E-01	1.51E-01	7.97E-01
	(1.10E-01)	(7.95E-02)	(1.10E-01)	(4.19E-02)	(1.08E-01)
Number of parameters	14	14	14	6	14
Likelihood contributions	Value (σ)	Value (σ)	Value (σ)	Value (σ)	Value (σ)
-lnL: Catch (reg 1)	92.8	107.2	88.5	103.2	88.6
	(0.8)	(0.9)	(0.8)	(0.8)	(0.8)
-lnL: Catch (reg 2)	66.9	62.2	63.3	71.1	62.0
	(0.8)	(0.7)	(0.7)	(0.8)	(0.7)
-lnL: Catch (reg 3)	43.1	55.8	40.4	60.6	18.1
	(0.7)	(0.7)	(0.7)	(0.7)	(0.6)
-lnL: Catch (reg 4)	93.8	128.1	91.3	116.1	76.4
	(0.8)	(0.9)	(0.8)	(0.9)	(0.8)
-lnL: Catch (reg 5)	94.5	124.8	89.5	93.9	96.0
	(0.8)	(0.9)	(0.8)	(0.8)	(0.8)
-lnL: Catch (reg 6)	46.1	48.0	46.4	46.4	44.9
	(1.1)	(1.1)	(1.1)	(1.1)	(1.1)
-lnL: Catch (reg 7)	-32.8	-36.2	-36.5	1.0	-12.9
	(0.6)	(0.6)	(0.6)	(0.6)	(0.6)
-lnL: Catch (reg 8)	58.1	54.7	58.2	91.0	61.4
	(0.8)	(0.8)	(0.8)	(0.9)	(0.8)
-lnL: overall	462.5	544.7	441.2	583.4	434.4
AIC	953.1	1117.4	910.4	1178.9	896.8
Other fixed parameters					
Catchability q_r (regs 1-6)	*5.00E-04*	*5.00E-04*	*5.00E-04*	*5.00E-04*	*5.00E-04*
Catchability q_r (regs 7-8)	*1.00E-06*	*1.00E-06*	*1.00E-06*	*1.00E-06*	*1.00E-06*
Optimum flow (standardised) $thresM$(regs 1-2)	*2.5*	*2.0*	*2.5*	*2.5*	*2.5*
$thresM$(regs 3-6)	*2.0*	*1.6*	*2.0*	*2.0*	*2.0*
$thresM$(regs 7-8)	*2.5*	*2.0*	*2.5*	*2.5*	*2.5*
Flow relationship scaler c_σ	*3.5*	*3.5*	*3.5*	*3.5*	*3.5*
Catchability-flow relationship scaler c_q	*0.5*	*0.5*	*0.5*	*0.5*	*0.5*
Long-term mean air temperature for Nov-Dec $temp^{opt}$	*34.5*	*34.5*	*34.5*	*34.5*	*34.5*
Temperature relationship scaler c^{temp}	*1.0*	*1.0*	*1.0*	*1.0*	*1.0*
El Niño constant η	*-1.0*	*-1.0*	*-1.0*	*-1.0*	*-1.0*
La Niña constant η	*1.0*	*1.0*	*1.0*	*1.0*	*1.0*
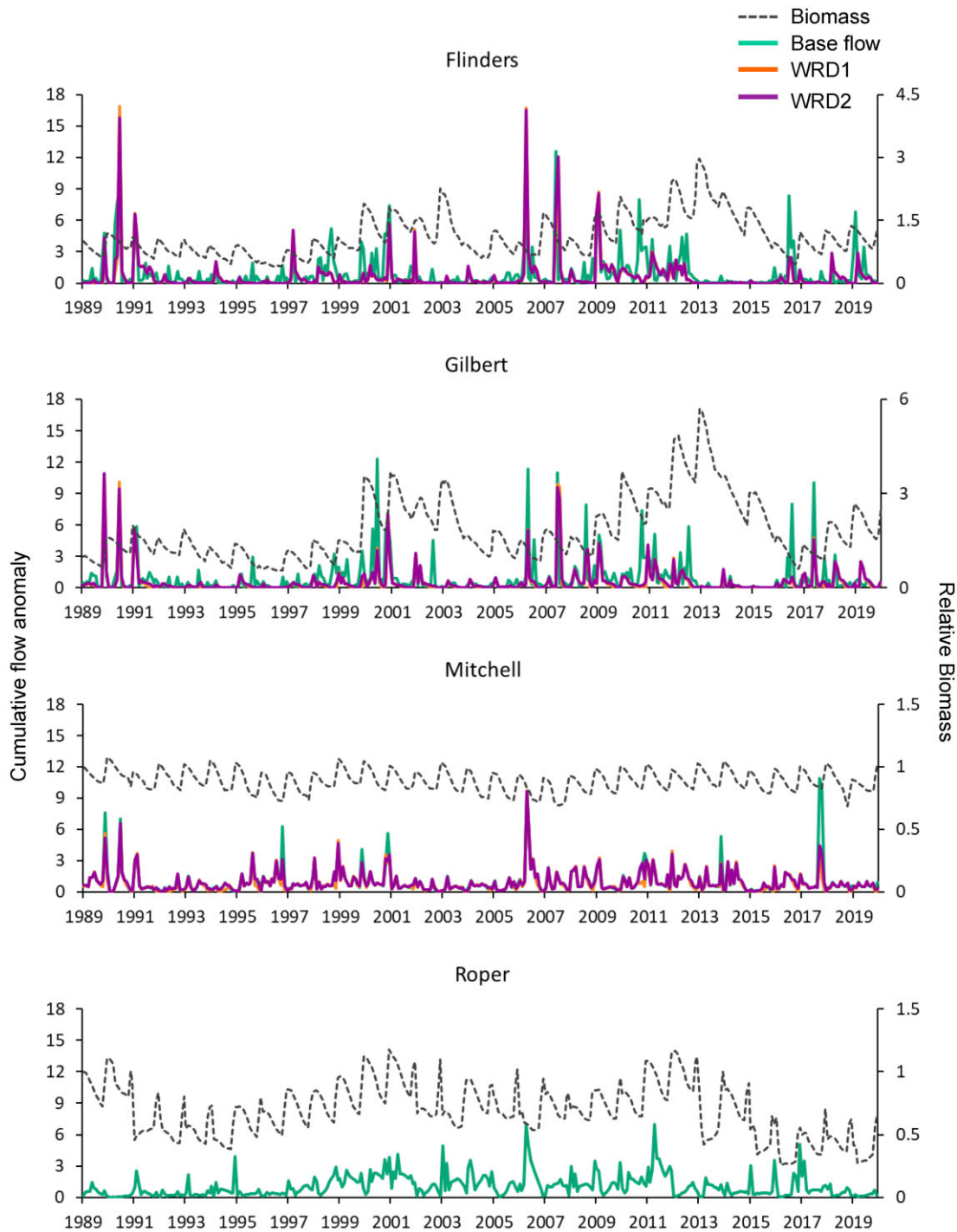
Figure 2. Example of monthly cumulative flow anomalies and model-predicted mud crab biomass (relative to biomass in January 1989) under baseline flows for the Flinders, Gilbert, Mitchell, and Roper rivers. Altered flows under WRD1 and WRD2 are also shown for the Flinders, Gilbert, and Mitchell rivers. No altered river flow scenarios were available for the Roper River.

Water Resources Assessment—River model (see Dutta *et al.*, 2017; Hughes *et al.*, 2017; Hughes *et al.*, 2018). For the Flinders and Gilbert rivers, end-of-system flows were produced using a river model predecessor—see Holz *et al.* (2013) and Lerat *et al.* (2013). In our study, all river models were updated to produce end-of-system flows to October 2019. Outputs were available as daily flow values (m³ s⁻¹), then summed to produce a cumulative monthly flow and a monthly flow anomaly (i.e. linear rescaling of monthly flow by dividing

monthly flow by the long-term mean monthly flow) for 1970–2019 (see Figure 2), which were input into the population model. Rivers were used to represent river flow in the eight model regions: Region 1: Embley River; Region 2: Mitchell River; Region 3: Gilbert River; Region 4: Norman River; Region 5: Flinders River; Region 6: Assume same as Flinders River in absence of flow data for Settlement Creek; Region 7: Roper River; Region 8: Assume same as Roper River in absence of flow data for Walker River.

Water resource development scenarios

Altered river flows under various water resource development (WRD) scenarios were available for three river catchments: the Mitchell, Gilbert, and Flinders rivers (see example in Figure 2). For the Mitchell River, a large array of hypothetical WRD scenarios were available using different volumes of water extracted, thresholds for pumping (i.e. minimum flow rate needed for pumped extraction to commence), and pump rates (number of days taken to extract water), while for the Flinders and Gilbert Rivers, only two scenarios were available. We ran WRD19 scenarios in total, which were a combination of hypothetical water developments across the three rivers (Supplementary Table S1). See Plagányi *et al.* (2022a) for further details on selection of these WRD scenarios tested.

Of the WRD19 scenarios run, we focused on four key scenarios. These ranged from high extraction scenarios that simultaneously explore impacts on all three key rivers (high extraction rates on Mitchell and Flinders and two dams on the Gilbert), but where volumes of water allocated are large such that annual reliability becomes problematic (WRD1), through to a moderate scenario on all three rivers (WRD2), a scenario (WRD3) with moderate extraction from the Mitchell and no WRDs on the Flinders and Gilbert, and finally a lower impact scenario (WRD4—no WRD on the Mitchell River and moderate extraction on Flinders combined with a single dam on the Gilbert River). Further details are provided in Supplementary Material S2 and summarized in Table 1.

Southern oscillation index

A monthly SOI was available from the Australian Bureau of Metrology (http://www.bom.gov.au/climate/enso/soi/).

Air temperature

Daily and monthly maximum air temperature data were available for various sites and time periods around the GoC (http://www.bom.gov.au/climate/data/). We linked air temperature to mud crab survival only for Model Region 7, which aligned with Robins *et al.* (2020). Centre Island temperature data were available from 1975 to 2021 and were used as a proxy for monthly maximum air temperature in this region. For the years 1970–1974, when no data were available, the monthly long-term mean was used instead.

Model fitting

The model was fitted to historical catch data for 1983–2018 (Northern Territory) and 1989–2019 (Queensland) instead of standardized catch-per-unit-effort data. This was to test if catch could be explained by effort and environmental drivers (primarily flow), to provide a basis for predicting catch under different flow scenarios. Model fitting was done by minimizing the negative log-likelihood in which the observed catch data were assumed to be log-normally distributed [Table 2 Equations (18–19)]. The model was implemented in the AD model builder (Fournier *et al.*, 2012) and for converged solutions (convergence criterion 0.00001), Hessian-based standard errors were computed for estimated model parameters. Fourteen parameters were estimated: eight model start-year spawner biomass parameters $B_{r,1970,1}^{spn}$ for 1 month in eight model regions; one flow-based catchability parameter $thres^q$; three flow-based recruitment parameters $thres$; one temperature-based mortality parameter τ^{temp}; and one SOI-based recruit-

ment parameter τ^{SOI}. Model output analysis and visualizations were done using R software (R Core Team 2021).

Model sensitivity testing

Given uncertainty in some of the key model parameters, we developed a model ensemble comparing five alternative model versions (and an additional sensitivity). A summary of these are provided in Table 3 and further details and reasoning are provided in Supplementary Material S3.

Cross-checking model predictions under reduced river flow

Model-predicted changes in mud crab abundance and catch under WRD scenarios are informed by fitting to historical data. Nonetheless, to build further confidence in our model results, we compared the model-estimated changes in catch under reduced WRD flows to changes in catch that would naturally occur between years under baseline flows, e.g. between a large-flow and low-flow year. To do this, first, we looked at changes in predicted historical catches across illustrative wet (large river flow), intermediate (intermediate river flow), and dry (little river flow) years for the baseline flow, and quantified reductions in catch between these years. For example, under baseline flow conditions, we assessed what had been the change in catch between a wet year and an intermediate year, and similarly between an intermediate year and a dry year. Second, we looked for years in which a WRD scenario (in this case, we used WRD1 as an example) reduced the baseline flow from, e.g. a wet year to an intermediate year, or an intermediate year to a dry year. We then quantified model-predicted reduction in catch (baseline vs. WRD1) for this particular year to see how comparable the change was with what could be expected from wet-to-intermediate or intermediate-to-dry under baseline conditions (i.e. cyclical fluctuations).

Results

Modelling historical mud crab catch using river flow and other environmental drivers

Fishing effort alone was able to explain mud crab catches for some but not all the regions in the GoC. For example, predicted catch matched the general trend in observed catch over the model period for regions 1, 2, and 8 but not for regions 3, 4, 5, and 7 (Figure 3). In regions 3, 4, 5, and 7 in particular, the model was not able to capture the sharp peaks in catches over the early 2000s and 2009–2013 periods (periods of high river flow, Figure 3). The addition of flow linked to recruitment significantly improved the model AIC from 1491.6 (no flow linked, only effort used to explain the catch) to 1129.4 (flow linked to recruitment) (Supplementary Table S4). For some regions, these large peaks in catches could only be captured by the addition of flow or flow and an additional environmental explanatory variable. The addition of flow linked to catchability for regions 3–6 significantly improved the model fit as determined by the AIC score (Supplementary Table S4). We also considered other drivers that were hypothesized to influence mud crab dynamics, such as SOI (regions 3–6) and temperature (region 7), which resulted in a significantly better model fit (Figure 3) with an AIC score of 953.1 (Supplementary Table S4) relative to when these drivers weren't included. Overall, our model captured the peaks and dips in catches relatively well. Fits
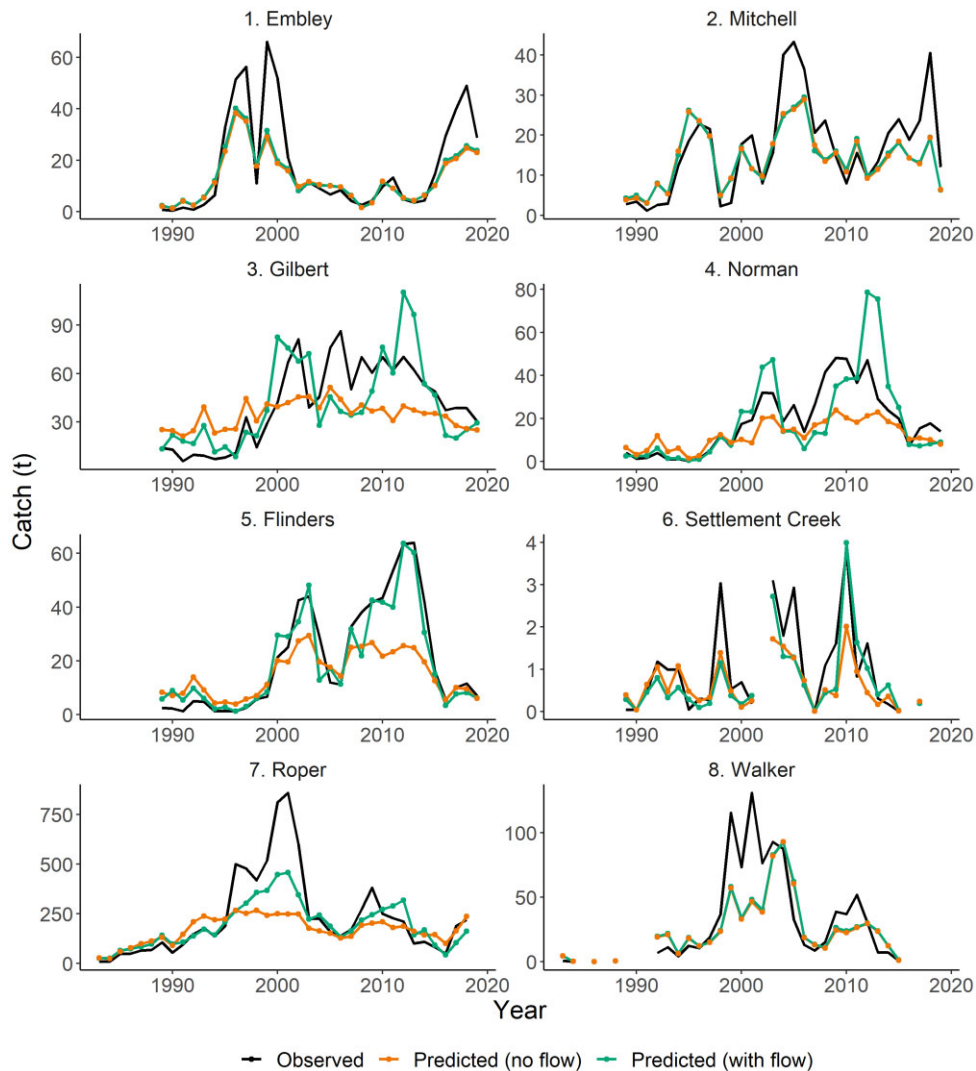
Figure 3. Comparison of the observed and model-predicted annual mud crab catch (tonnes) estimated with and without flow, using Model version 1, for each of the eight model regions. Predicted catches with no flow are those that are explained by effort alone, whereas predicted catches with flow are those driven by baseline flows, effort, and other environmental predictors, e.g. SOI for regions 3–6 (Gilbert, Norman, and Flinders rivers) and temperature for region 7 (Roper River). See Supplementary Material for observed vs. predicted catches under Model Versions 2–5.

might not appear good in a particular year, but the model may fit well in some months and poorly in other months (Supplementary Figures S1–S4, S6). For example, for region 7, the model fails to predict large catches in the 2000s, which is amplified on the annual scale. However, if one considers the monthly fits to the data, for some months in the 2000s, these peaks are captured better than in other months (Supplementary Figures S5–S6) and so the net overall effect is dampened.

The strength of the flow-recruitment relationship varied between regions, with a weak relationship estimated for the Embley-Mitchell rivers (regions 1–2), followed by the Roper River (regions 7–8). By contrast, a very strong flow relationship was estimated for the Gilbert, Norman, and Flinders (regions 3–6) rivers (Figure 4). For the eastern GoC, these flow relationships were estimated with high precision shown by the narrow 90% confidence intervals (Figure 4). There was less precision in the flow relationship for the Roper River relative to the other rivers.

Model sensitivity testing

The model version in which the optimal flow was reduced by 20% (Model 2) resulted in a worse overall fit for the model. Some regions had a substantially worse fit (regions 1, 3–5) while others showed little difference (regions 2, 6–8) (Table 4; Supplementary Figure S8). As an additional sensitivity test (not included in the ensemble), we also considered a logistic relationship (Supplementary Figure S7) in which crab recruitment increased with flow and was maximized under an optimal flow, and then remained at that level even under increased flows. When trialled, the model resulted in a significantly worse fit with an AIC score of 1389 vs. 953.1 with a parabolic relationship (Supplementary Figure S5).

Model 3 with a larger natural mortality (20% increase) performed better than the base case model as indicated by the AIC score (Table 4), although wasn't noticeable in the observed vs. predicted catch plots (Figure 2 vs. Supplementary Figure S9). Doubling the mud crab model starting biomass (Model 4) performed the worst of the sensitivities with the
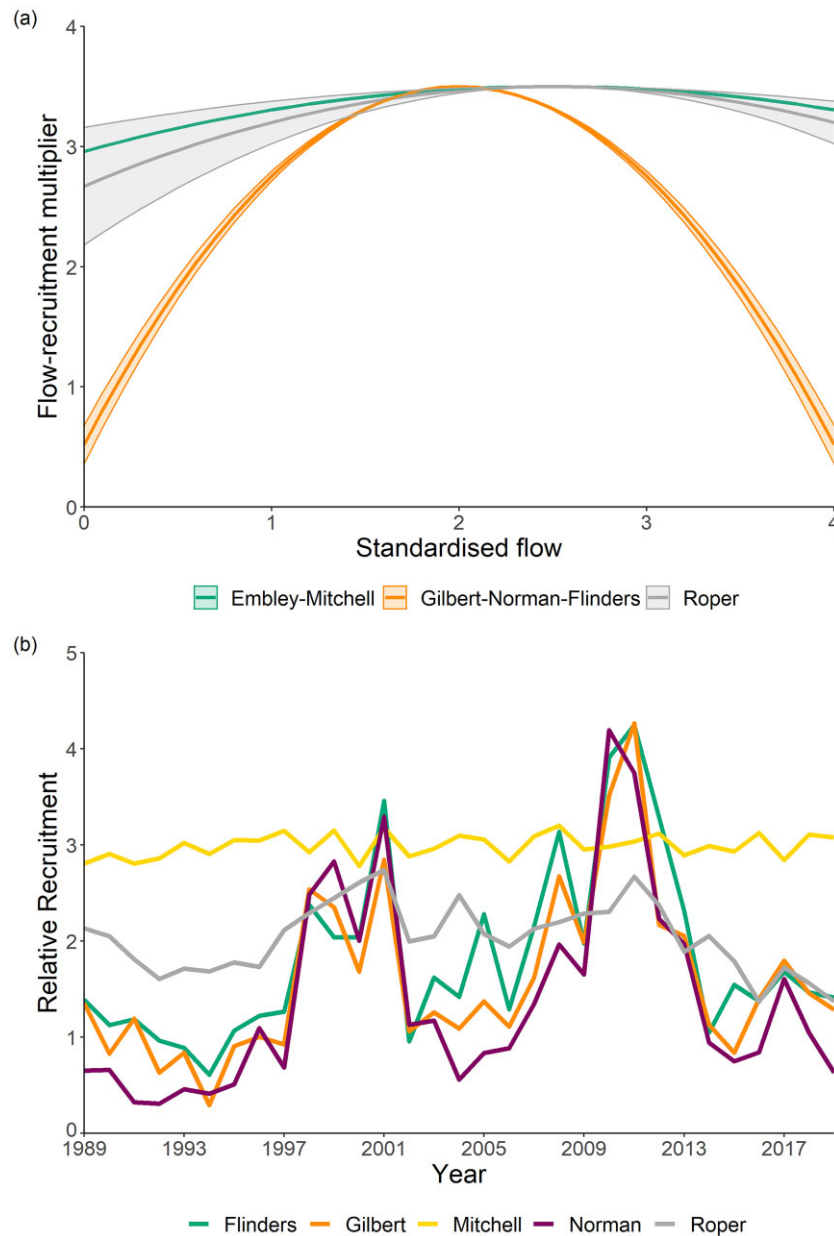
Figure 4. (a) Model-estimated parabolic functions used to describe the relationship between the standardized flow and mud crab recruitment for each of the catchment systems as shown, where the function yields a multiplier that describes recruitment relative to the base value. A total of 90% confidence intervals are shown by shaded areas, colour-coded for each region. (b) Time series of relative annual mud crab recruitment (averaged across models) between 1989 and 2019 for some of the modelled catchment regions. Recruitment is plotted relative to model start year.

largest AIC (1178.9; Table 4). However, an increased start-ing biomass did allow the model to better predict the peak catches in the 2000s for regions 7–8 but with the trade-off that it over-predicts catches for region 7 in 2011–2012 (Supplementary Figure S10) and thus the fit for this region was worse.

Model 5, which used a more conservative steepness param-eter h, performed the best with the smallest AIC score (896.8) and substantially improved model fits (likelihood scores) for regions 3–4, but little change or worse fits for regions 5–7 (Table 4; Supplementary Figure S1). However, improvements to the fits, both for model 5 and model 3, compared with model 1, were not noticeable in the observed vs. predicted catch plots (Figure 2 vs. Supplementary Figure S11). In each instance, these three models were broadly consistent with the

data and provided a similarly good representation of mud crab catch trends.

Predicted changes in mud crab catch and abundance under altered river flow

For the Flinders River, a high-allocation (WRD1) water de-velopment scenario resulted in an average catch reduction of 44% (range of 89% reduction to a threefold increase) and a moderate-allocation (WRD2 and WRD4) resulted in an aver-age catch reduction of 46% (range of 88% reduction to 95% increase), with the most extreme reduction being 83% when averaging across the five models (Table 5). Similarly, available biomass was, on average, predicted to halve under both mod-erate and high-impact water development scenarios (Table 5).

Table 5. Summary table showing minimum and mean catch, commercially exploitable biomass (Bcom), and spawning biomass (Bsp) for mud crabs predicted under four water resource development scenarios (WRD1–WRD4) relative to base line flows (BaseCase) for the Mitchell, Gilbert, and Flinders rivers, as well as the SE Gulf of Carpentaria (regions 2–6 combined).

WRD scenario	Region	Rel. catch (min)	Rel. catch (mean)	Rel. Bcom (min)	Rel. Bcom (mean)	Rel. Bsp (min)	Rel. Bsp (mean)
WRD1	Mitchell	0.94	1.00	0.95	1.00	0.96	1.00
WRD1	Gilbert	0.24	0.54	0.26	0.55	0.25	0.53
WRD1	Flinders	0.17	0.56	0.19	0.57	0.22	0.56
WRD1	SE Gulf	0.44	0.71	0.56	0.74	0.56	0.73
WRD2	Mitchell	0.99	1.02	0.99	1.02	1.00	1.02
WRD2	Gilbert	0.33	0.64	0.34	0.65	0.34	0.64
WRD2	Flinders	0.17	0.54	0.19	0.55	0.22	0.55
WRD2	SE Gulf	0.51	0.77	0.69	0.82	0.66	0.81
WRD3	Mitchell	0.95	1.00	0.96	1.00	0.97	1.00
WRD3	Gilbert	1.00	1.00	1.00	1.00	1.00	1.00
WRD3	Flinders	1.00	1.00	1.00	1.00	1.00	1.00
WRD3	SE Gulf	0.98	1.00	0.99	1.00	0.99	1.00
WRD4	Mitchell	1.00	1.00	1.00	1.00	1.00	1.00
WRD4	Gilbert	0.33	0.64	0.34	0.65	0.34	0.64
WRD4	Flinders	0.17	0.54	0.19	0.55	0.22	0.55
WRD4	SE Gulf	0.50	0.76	0.69	0.82	0.66	0.80

Results have been averaged across all five models.

There was temporal variability in catch reductions, with less impact on catches in years when catch was already low (presumably due to already lower flow in those years) and greater in years when catches were large (presumably due to higher flow in those years) (Figure 5, Supplementary Figure S12). Overall, there wasn't a noticeable difference between WRD1 and WRD2 (Figure 5, Table 5).

For the Gilbert River, a two-dam scenario (e.g. WRD1) had a more severe impact than a one-dam scenario (WRD2 and WRD4) (Figure 5). On average, catch was predicted to decline by 46% (range of 86% reduction to 17% increase) under WRD1 vs. 36% (range of 82% reduction to 16% increase) under WRD2 and WRD4. The largest reduction estimate was 76% under a two-dam scenario and 67% under a one-dam scenario when averaging across all five models (Table 5). Changes in predicted available biomass were similar (Table 5). The difference in predicted impacts between a one-dam and two-dam scenario was similar in some years, but greatest in years when catches were large. Although a one-dam scenario on the Gilbert River was predicted to have less impact than a Gilbert two-dam scenario and both Flinders River water extraction scenarios, it was nonetheless predicted to have substantial reductions in mud crab biomass and catch (Figure 5, Supplementary Figure S12, Table 5).

Water development scenarios for the Mitchell River had little to no impact on mud crab catch and biomass when averaged across the model period (Figure 5, Table 5) and this was consistent across all model versions as shown by the narrow confidence intervals in Figure 5 and across individual models in Figure S12. Nonetheless, at most, catch could drop by 23% or increase by 22%. Several WRD scenarios for the Mitchell River did allow for contrasts between scenarios (Supplementary Table S6). For example, WRD3 vs. WRD2; WRD8 vs. WRD9; and WRD18 vs. WRD19, which compare extraction of the same quantity of water at the same pump rate; but at different flow thresholds (i.e. level of flow needed before which pumping could occur). Modelling showed that the predicted effect on catch was negligible when pumping only occurred above river flows of 1800 ML d^{-1} (high threshold, see Supplementary Table S1 and results in Supplementary Table S6), thus allowing low-level flows to proceed down river. In contrast, a 2–5% decline in catch was predicted when pumping commenced at a lower threshold of river flow (200 ML d^{-1}, see Supplementary Table S1 and results in Supplementary Table S6).

Finally, for the south-eastern GoC region as a whole (Model regions 2–6), on average catches were reduced by ~23–29% when considering water development on all three river systems (WRDs 1, 2, and 4), with the greatest reduction being 49–56% (Table 5).

Cross-checking model predictions under reduced river flow

Baseline daily flow rates in the Gilbert region could average over a 1000 m^3 s^{-1} over November–February in a wet year (e.g. mean of 1059 m^3 s^{-1} for November–February 2010/2011) and reduced to ~44 m^3 s^{-1} for the same period in a dry year (e.g. 2014/2015 daily mean rate of 43.8 m^3 s^{-1} over November–February) (Figure 6a). Model-predicted catches under baseline flow following a wet year (1-year lag), for example, in 2010 (76t) or 2012 (110t) could be reduced by up to 67% for an intermediate year (e.g. 2006—36t) and by 41% when considering an intermediate to a dry year (e.g. 21t in 2016) (Figure 6a).

Under WRD1, river flow for the Gilbert River in 2010/2011 was reduced by more than half in most months over November–February, resulting in flows that corresponded more to an "intermediate" flow year. If we consider baseline vs. WRD1 catch for the corresponding year, this was reduced by 56% under WRD1. Similarly, baseline river flow in an intermediate year (e.g. 2018/2019) was reduced under WRD1 to a flow that could be expected in a dry year, and associated catch was predicted to decline by 34% (Figure 6b). Hence, when comparing mud crab catch from good, intermediate, and poor flow years, reductions under WRD1 were similar to what is observed due to annual variability in fishery catch (Figure 6b). Correspondingly for the Flinders region, catch reductions under WRD1 were similar to annual variability under baseline flows (see Supplementary Material S4 and Supplementary Figure S13).
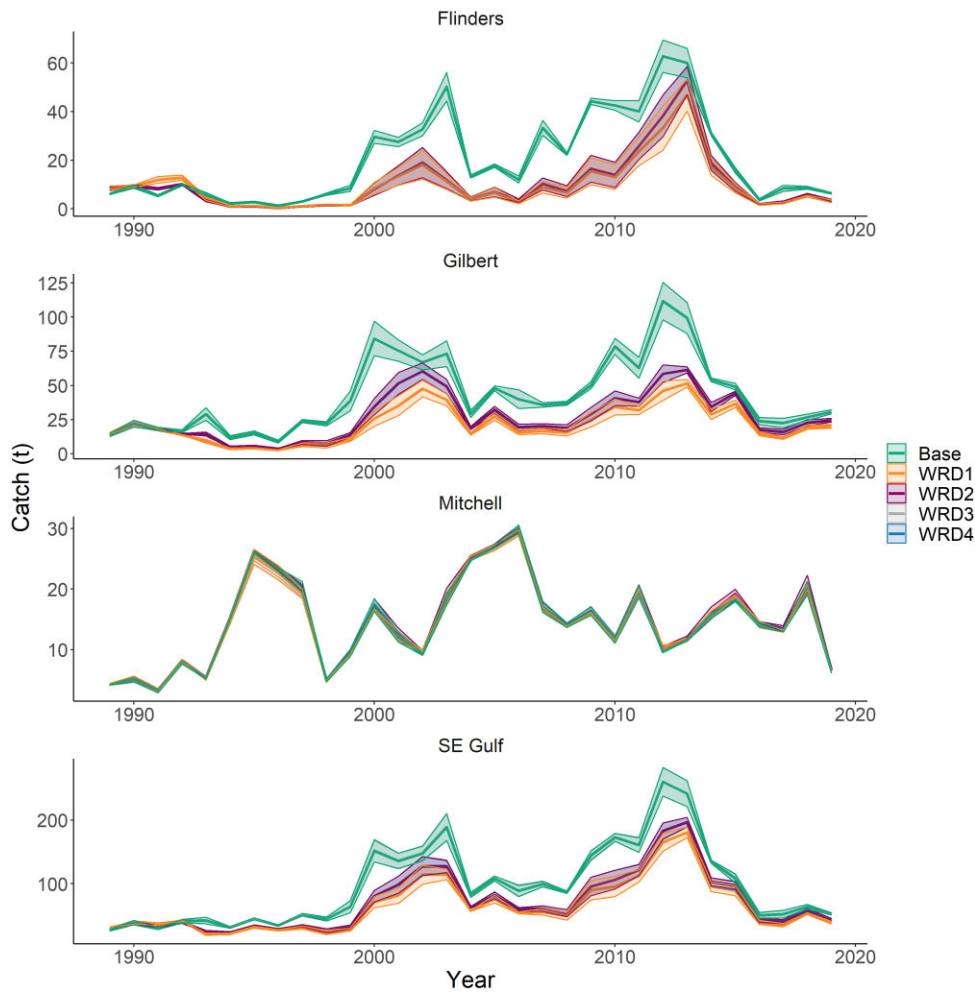
Figure 5. Model-predicted changes to mean total annual mud crab catch (t) (±90% *CI*, shaded area) under baseline (Base) flow conditions compared with four alternative WRDs, shown for the Flinders (region 5), Gilbert (region 3), and Mitchell (region 2) catchment systems, as well as the SE Gulf of Carpentaria (regions 2–6) as a whole. Results are averaged across all five model versions. Note for the Mitchell River, the Base, and all WRDs track under each other. For the other panels, the WRD3 trajectory tracks under Base and the WRD4 tracks under WRD2.

Discussion

River flow can influence species abundance in different ways. In freshwater ecosystems flow is a major determinant of physical habitat (e.g. runs, riffles, and pools), which in turn shapes the biota (Bunn and Arthington, 2002). In estuarine ecosystems, it is primarily habitat condition (e.g. salinity, nutrients, and temperature) that species respond to (Alber 2002). Progress has been made to distinguish between, and model, these fundamentally different mechanistic processes (Alber 2002; Palmer *et al.* 2011; Montagna *et al.* 2013). In the GoC, species abundance-flow relationships have been identified for mud crabs and the mechanisms behind these relationships are likely due to both availability of habitat (e.g. seagrass or mangrove fringe) and condition of habitat (e.g. temperature and salinity) (Hay *et al.* 2004; Ruscoe *et al.* 2004; Robins *et al.* 2020). Nonetheless, because we use a dynamic statistical approach fitted to data and not a mechanistic approach, we are able to estimate the net effect of environmental drivers, such as flow, on the population dynamics without needing to fully specify the underlying mechanisms. Hence, even if the mechanisms driving species abundance are not fully understood or described, or data to support them are limited, our study shows an example of how flow (and other environmen-

tal drivers) can still be dynamically incorporated into species population models to quantify impacts of altered river flow across space and time to inform policy development and management decisions relating to water harvesting from rivers.

Modelling dynamic species abundance-flow relationships

Modelling mud crab abundance-flow relationships has largely been confined to static statistical linear models to identify and quantify these relationships (Meynecke *et al.* 2012; Robins *et al.*, 2020). However, species' relationships with flow are not always linear, particularly when there are wide ranges in river flow (Rosenfeld, 2017) and both the literature (e.g. Helmke *et al.*, 1998; Meynecke *et al.*, 2012) and fishers' observations suggest mud crab abundance-flow relationships are non-linear. Through formal statistical fitting to monthly catch data, we were able to capture the dynamic, non-linear, and spatially variable relationships across catchments, thus advancing previous work on species-flow relationships.

Effort alone was sufficient to explain historical mud crab catches for catchments in the northern, eastern, and north-western regions of the GoC (regions 1, 2, and 8). Northerly regions had weak flow relationships, likely due to having
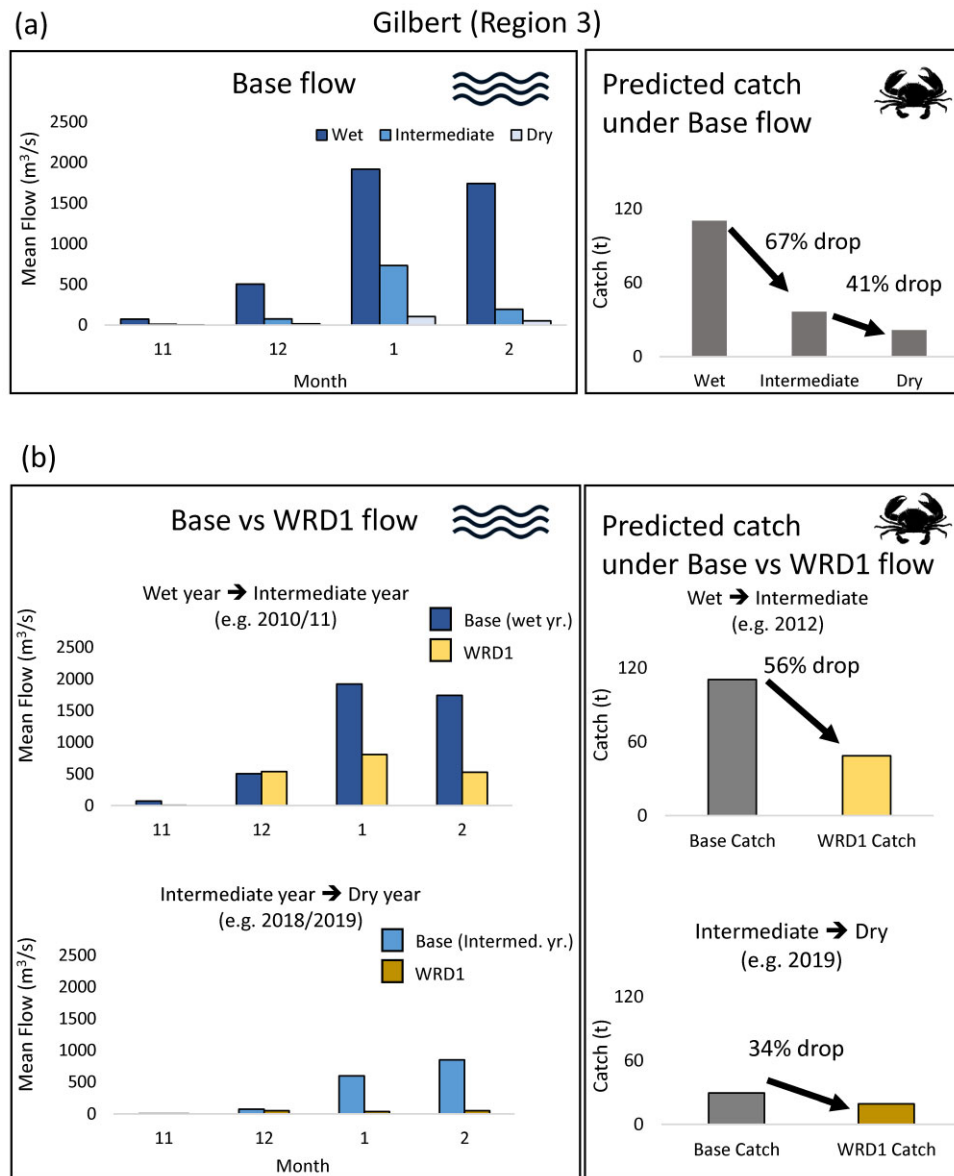
Figure 6. (a) Example of baseline mean daily flow rates ($m^3\ s^{-1}$) for November–February in a wet, intermediate, and dry year for the Gilbert catchment (region 3), with corresponding mud crab predicted catches (t) for these years showing percentage reduction when flow reduced—i.e. a 67% drop between a wet year and intermediate year; and a 41% drop between an intermediate year and a dry year. (b) Baseline flows can be significantly reduced under WRD1, changing flow from, e.g. a wet year to an intermediate year, or an intermediate year to a dry year. Corresponding catches were similarly reduced under WRD1.

a more moderate climate (more consistent rainfall and less temperature variability) than the southern and western GoC (Robins *et al.*, 2020). For catchments in the western and southern regions (regions 3, 4, 5, and 7), where climate variability is more extreme, the addition of river flow and other environmental drivers significantly helped explain historical catches. Flow-recruitment relationships were strong for regions in the south-east (regions 3, 4, and 5) but somewhat weaker for the west (region 7), reflecting the high variability in flow for catchments 3–5 and less so for the Roper River (Figure 2).

The shape of flow-ecology relationships is critical for determining the biological impacts of altered river flows (Rosenfeld, 2017). The stark contrast in impacts of WRD on mud crab catches in the Flinders and Gilbert Rivers, compared to

the Mitchell River may be attributable to the nature of the river systems (ephemeral vs. perennial) and the way the model captured the relationships in flow and recruitment, which was reflected in biomass and ultimately catches. For example, in the Flinders and Gilbert rivers, flow and the SOI were drivers for crab recruitment (1-year-olds entering the fishery) and flow was also a driver for catchability of adult crabs, with a strong relationship (steep slope) estimated for the link to recruitment, and this played out in large biomass and catch reductions when flow was reduced. The fitted flow relationship for the Mitchell River was weak (gentle slope), which we attribute to the perennial nature of the Mitchell River (and hence maintenance of an extensive brackish ecotone). Consequently, under WRD scenarios for this catchment, we found little change in catch or available biomass across all model versions. Spa-

tial variability across the GoC with regard to environmental drivers affecting crab catch was also detected by Robins *et al.*'s (2020) multi-variable analyses. Nonetheless, our results were dependent on various assumptions around the functional form of these species-flow relationships and although we accounted for some uncertainty in this through sensitivity testing and trialling different models, further refinement of these assumptions could be made with more mud crab data.

The effect of river flows on estuarine species is likely to be confounded by rapidly changing climates in these ecosystems (e.g. Scanes *et al.*, 2020). For mud crabs, other environmental variables can be difficult to disentangle from the impacts of river flow (Robins *et al.*, 2020). For example, in the western and southern GoC, the low relief of coastal flats and the unique tidal regimes (Church and Forbes, 1983) can exacerbate seasonal thermal regimes in these estuaries. This is in contrast to other regions in the Gulf, where seasonal thermal regimes of estuaries are mitigated by thermal stability of coastal waters. If some years have consistently high temperatures, low cloud cover resulting in high solar radiation over summer, a continual body of abnormally warm water may move upstream and increase mud crab mortality (Robins *et al.*, 2020). A combination of these conditions (extreme variability in rainfall with multiple hot and dry years) was most notable for the western and south-eastern GoC and less so for the eastern and northern GoC (Robins *et al.*, 2020). Sea level anomalies may also impact mud crab abundance and catch (Robins *et al.*, 2020), with anomalously low sea levels in 2015 being linked to an unprecedented and extensive mangrove dieback (Duke *et al.*, 2017). Indeed, elsewhere, changing climates (e.g. rising temperatures and ocean acidification) are expected to impact crab productivity (Swiney *et al.*, 2017; Szuwalski *et al.*, 2021).

Sensitivity settings and future considerations

Our mud crab model was designed to be able to feed into a larger MICE (Model of Intermediate Complexity for Ecosystem Assessment) (Plagányi *et al.* 2023) and thus, as per the philosophy of Collie *et al.* (2016) and Plagányi *et al.* (2022b), we tried to keep our model (and the MICE) as simple as possible, only adding complexity as needed and if there was a basis to do so (i.e. underlying hypotheses). We acknowledge that alternative, more mechanistic approaches could be used to model how flow (and other environmental drivers) can be dynamically incorporated into species population models. Such approaches specifically capture the influence of flow on ecosystem condition, which in turn impacts species abundance, and are a widely accepted framework in modelling estuarine ecosystems (Alber, 2002). The method we used to model the mud crab population, and indeed other components of the system in Plagányi *et al.* 2023, is not intended to capture the detailed mechanisms at play, nor is it intended to inform fisheries management of mud crabs (e.g. a stock assessment model). Instead, it is a case study of a broader approach taken by Plagányi *et al.* 2023 to assess the regional impacts of WRD on key species, fisheries, and habitats, all of which depend on river flow and some of which are connected between catchments. This broader approach is in line with global approaches to advance an ecosystem approach to fisheries (Smith *et al.*, 2007; Collie *et al.*, 2016). Moreover, because we use a dynamic statistical model fitted to data, we were able to estimate the impacts of flow

on species abundance without needing to fully capture the underlying mechanisms. Given the need to reliably estimate parameters in order to support decision-making, this approach was deemed more suitable as opposed to a mechanistic approach.

Some of the processes captured in the model are likely oversimplified and could be explored further. For example, M is likely to vary both temporally and across age and sex. To investigate, we included a model version with a larger M, which fell within the bounds of natural mortality reported by Knuckey (1999), and this improved the fit of the model. The base case model did not capture additional sources of mortality, e.g. larger mortality of juvenile crabs (through cannibalism from adult crabs; Mirera and Moksnes, 2013; Alberts-Hubatsch *et al.*, 2016), as well as increased mortality of female crabs that migrate offshore to spawn (Hill, 1994). We also restricted drivers of mud crab dynamics to those that best explained catch variability, namely river flow, SST or SOI. There are likely to be other drivers that influence variability in abundance, e.g. mean sea level, salinity, and also ecological links within the system, such as recruitment dependencies on habitat, e.g. seagrass and mangrove (Alberts-Hubatsch *et al.*, 2016).

Our base model used a stock–recruitment steepness parameter of $h = 0.6$ and we tested a more conservative value of $h = 0.4$, which provided the best model fit. We acknowledge that h can be quite high for some crustacean species, including crabs, but several crab species' stock assessments use low values for h, ranging from 0.24 to 0.8 (O'Neill *et al.*, 2010; Froehlich *et al.*, 2017; Lovett *et al.*, 2020) and similarly for other crustaceans ranging from 0.3 to 0.6 (Deng *et al.*, 2020; Plagányi *et al.*, 2021).

We assumed that mud crab recruitment occurred predominantly over a few key months (September–December) based on (Hill, 1994; Knuckey, 1999) and that this recruitment pattern was uniform across years. In reality, this could change slightly from year to year (e.g. earlier or later, or all in one month) and could be explored in future if more data become available, by estimating the proportion of recruitment each month instead of assuming a uniform spawning period.

Our spatial mud crab model doesn't account for connectivity between regions. Even though adult mud crabs are unlikely to move between catchments (Gopurenko and Hughes, 2002; Robins *et al.*, 2020), it is possible that there is some larval connectivity. A preliminary investigation into hydrodynamic and particle tracking of female mud crabs and larvae, found little connectivity between the western and eastern GoC, though there was some connectivity between regions within the southeastern GoC (Patterson, 2020). Most catchments were predominantly self-recruiting, except for catchments in region 3, which may receive over 40% of larvae from neighbouring regions. Hence, if mud crab abundance in region 3 is reduced by WRD, neighbouring regions (assuming they are not impacted by WRD and currently not limited by density dependence) may contribute to recruitment here. This hypothesis could be tested using our model.

Our study didn't explicitly include all rivers in the region and there are others that may have different dynamics. For example, region 7 was a large model region that was assumed to be influenced only by the Roper River despite other large rivers encompassed in the region. Here, the Roper flow-recruitment relationship was estimated with lower precision and the model struggled to predict very large catches. Before

further examining impacts of WRD for Region 7, future modelling work should consider subdividing the region as there may be slightly different flow dynamics at play across other catchments.

We have tried to account for uncertainties in our findings by cross-checking our results with historical natural variations in flow and catch, as well as by employing a model ensemble for the scenario testing. Nonetheless, more data and a refinement of the modelling approach and assumptions could help to reduce uncertainty further.

Water management implications

Although the WRD scenarios we tested are unlikely to be implemented in the short-to-medium-term, our spatially explicit, dynamic modelling approach could be used to help inform best-practice water management in the future.

The timing of flows in the GoC is critical for many species (Vance *et al.*, 1985; Staples and Vance, 1986; Robins *et al.*, 2005; Leahy and Robins, 2021). By using a monthly time step in our model, we account for the intra-annual variability in flow levels and species responses. Hence, the model could advise water managers on the timing and quantity of water removal that minimizes reductions in species abundance or fisheries production.

We found that both water extraction and water impoundment (dams) were equally impactful for mud crabs. We also tested the physical settings of water extraction to determine how the management of the same volume of water extraction would impact mud crab abundance and found less impact if pumping was only allowed to commence once a certain amount of flow had been allowed to pass through (i.e. using a high pump threshold rather than a low pump threshold to trigger pumping). Thus, our model has potential to provide water managers with recommendations on river flow extraction thresholds and pump rates that would minimize downstream impact on mud crabs (for other species and habitats, see Plagányi *et al.* 2023).

The spatial structure of our model identified differences in species-flow relationships across catchments, and how mud crabs in different catchments might respond to WRD, assisting managers to make decisions on regional placement of WRD. Moreover, the spatial, age-structured modelling approach simultaneously captured different management practices across two different jurisdictions and the impacts of environmental variables on these stocks. Hence, our model is informative to the fisheries management of mud crabs in the GoC and elsewhere, but has not been designed as a stock assessment model and further refinements would be required if it were to be used in fisheries management.

Finally, the impacts of flow alteration do not play out on a single species alone and a more holistic approach that accounts for other key components in the ecosystem is needed. As such, our mud crab model has been incorporated into a broader ecosystem model that can be used to inform management of WRD on downstream coastal ecosystems, particularly for key species, fisheries, and habitats that depend on seasonal flows (Plagányi *et al.* 2023).

In summary, our study adds to the limited number of previous studies (e.g. Szuwalski *et al.*, 2021; Punt *et al.*, 2022) that have successfully linked environmental variables to crab population dynamics using a rigorous quantitative population-based model, without needing to capture the underlying mechanisms. Moreover, our model advances understanding on how a species responds to river flow and other environmental drivers (whether it be directly or indirectly) at different spatial and temporal scales. We rigorously predicted impacts of altered river flow on species abundance and catch; hence in future, our model could be used to help inform management of water resource development. Our modelling approach also considered other drivers of mud crab variability and thus there is scope to assess impacts of climate change on mud crab abundance, including the impacts of WRD under climate change.

Supplementary data

Supplementary material is available at the *ICESJMS* online version of the manuscript.

Conflict of interest

Laura Blamey, Éva Plagányi, Rob Kenyon, Roy Deng, Justin Hughes and Shaun Kim work for the CSIRO who receives funding to carry out research. Julie Robins works for the Queensland Department of Agriculture and Fisheries. None of the authors have any financial interest in the fishery.

Author contributions

Conceptualization: EP, LB, and JR; Data analysis: LB, EP, RD, and RK; Modelling analysis: LB, EP, and RD; River model development: JH and SK; Visualizations: LB; Stakeholder engagement and workshop convening: EP and LB; Project administration, funding acquisition, and supervision: EP; Data curation: RD; Writing of first draft: LB, EP, and RK; Writing, reviewing, and editing of subsequent drafts: all authors.

Data availability

Commercial fishery catch data may be requested from the data custodian as follows: Queensland Department of Agriculture and Fisheries (info@daf.qld.gov.au) data request number (DR2976); Northern Territory Department of Industry, Tourism, and Trade (FisheriesLicensing.DPIR@nt.gov.au).

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