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The intertidal mudflats of Barr Al Hikman, Sultanate of Oman, as  
feeding, reproduction and nursery grounds for brachyuran crabs

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**ABSTRACT**

Brachyuran crabs are an important ecological and economical, yet often unstudied aspect of intertidal mudflats of the Arabian Peninsula. Here we provide baseline density estimates of crabs at the relatively pristine intertidal mudflats of Barr Al Hikman (Sultanate of Oman) and provide information on their life cycle and habitat preference. Across the winters of 2012–2015 crabs were sampled on a grid covering the entire intertidal depth gradient. 29 species were found and average densities varied between 12 and 54 crabs/m<sup>2</sup>. Deposit-feeding and herbivorous crabs were the most abundant species across all winters. Size frequency data and the presence of ovigerous females show that most crabs species reproduce in the intertidal area. *P. segnis*, the most important crab for local fisheries, was found to use the intertidal area as a nursery ground. We analysed the relationship between the two most abundant crab species, *Macrophthalmus sulcatus* and *Thalamita poissonii* and the environmental variables: seagrass density, tidal elevation, median grain size and sediment depth using Random Forest models. The predictive capacity of the models and the relative importance of the environmental predictors varied between years, but crab densities in general were positively associated with seagrass density, presumably because seagrass offers feeding habitat.

## INTRODUCTION

Intertidal mudflats are highly productive ecosystems with many ecological and socio-economical values (Levin et al. 2001). For instance, these soft-sedimented areas provide essential foraging, nursery and reproduction habitat for a large variety of species such as shorebirds, and (commercially important) shellfish, shrimps, crabs and fishes (Levin et al 2001; van de Kam et al. 2004; Dissanayake et al. 2018). However, intertidal mudflats are rapidly deteriorating on a global scale due to anthropogenic pressures (Murray, et al. 2018). Intertidal mudflats adjacent to the Arabian Peninsula are among worlds' most threatened intertidal habitats with major threats including habitat destruction, overfishing, eutrophication, climate change and pollution (Sheppard et al. 2010, Burt, 2014). Improving awareness of the value, importance and ecology of Arabian mudflats is timely for ecosystem understanding and conservation (Sale et al. 2011; Burt, 2014).

Brachyuran crabs are a diverse and abundant faunistic group of the Arabian mudflats (Simões et al. 2001; Naderloo, et al. 2013). They are central to the ecosystem functioning of these mudflats, for instance, because deposit-feeding and scavenging crabs are important for nutrient recycling (by decomposing organic material) (Qureshi & Saher, 2012; Safaie, 2016), because burrow-hiding crabs increase the water and air content in the sediment (by their burrowing activities) (Qureshi & Saher, 2012; Safaie, 2016) and because some predatory crabs exert exceptionally strong top-down selection pressure on molluscs in this part of the world (Vermeij et al. 1977), with potential important food-web consequences (Bom et al. 2018). Furthermore, crabs are a vital food source to many 1000s of shorebirds wintering en breeding at the Arabian shores, including some species that are highly specialized crab predators (Bom et al. 2018; Gommer et al 2018). Moreover, some of the crab species utilizing the intertidal area provide a major source of income for local fisheries (Mehanna et al. 2013). A description of the crab community and their relationships with the intertidal environment is

therefore fundamental to ecosystem understanding. Here, we study the diversity, abundance, life-cycle and habitat preference of the largely unstudied crab community on the relatively pristine intertidal mudflats of Barr Al Hikman in the Sultanate of Oman (Fig 1a).

Barr al Hikman is a peninsula of approximately 900 km<sup>2</sup>, surrounded with about 190 km<sup>2</sup> of intertidal mudflats (Fig. 1b). The intertidal zone is a gentle sloping area, characterized by a patchwork of bare sediment areas and seagrass beds, intersected by a network of gullies and small scattered fossil and polychaete reefs of the annelid *Pomatoleios kraussii* (Baird, 1864) (Fouda & Al-Muharrami, 1995; Bom et al. 2018). Based on the environmental heterogeneity we expected crabs to be distributed heterogeneously across the intertidal zone. Specifically, we expected associations with seagrass beds (Edgar, 1990; Kunsook et al. 2014), exposure time (Henmi, 1992; Flores et al. 2005; Jensen et al. 2005), sediment grain size (Henmi, 1992) and sediment depth. These variables are associated with food, shelter and physical conditions imposing limitations on burrowing activity of crabs. Furthermore, we expected that some crabs, after larval settlement, spend their whole lives in the intertidal zone and locally reproduce, while others may use it as a nursery ground (Potter et al. 1983).

Here, we first describe species composition of crabs and their life cycles in the Barr-Al-Hikman intertidal ecosystem using the data collected on a spatial grid of 6×8 km across four subsequent winters (2012–2015). To investigate whether crabs reproduce in the area or use it as a nursery ground, we assessed crab-size distributions and checked for ovigerous females. Next, to better understand the spatial distribution of the two most abundant crabs *Macrophthalmus sulcatus* (Milne Edwards, 1852) and *Thalamita poissonii* (Audouin, 1826), we analysed the relationships between crab densities and seagrass density, median grain size (mgs), tidal elevation as a measure of exposure time and sediment depth using Random Forests (RF) models. Reflecting on our results, we discuss the ecological and economical importance of crabs in Barr Al Hikman.

84

85 **2. METHODS**86 **2.1 Study area and crab sampling**

87 Our study area was situated on the east coast of the Barr al Hikman peninsula south of  
88 Shannah, in an area of about 6×8 km (Lat 20.6714° – 20.7772°N, Lon 58.6366° – 58.7122°E,  
89 Fig. 1). The study area consists almost exclusively of intertidal mudflats, with a few reef  
90 structures just below or above the surface.

91 We sampled crabs on a grid with an inter-sampling distance of 200 m, with 20%  
92 additional random stations on the gridlines (Fig. 1c) to enable improvement of the short-range  
93 accuracy of spatial interpolation (Bijleveld et al. 2012). Samples were taken in the period  
94 2012–2015. The sampling periods were: 7 November – 15 December 2012, 5 – 20 December  
95 2013, 7 November – 15 December 2014 and 6 – 18 November 2015. The sampling periods  
96 coincides with the cold season (Mettraux et al. 2011), well after the yearly Somali coastal  
97 upwelling that brings cool, turbid and eutrophic water to the area (between June and October).  
98 (Jupp et al. 1996).

99 In 2012, a large grid with 440 stations (including random stations) was sampled. In the  
100 three successive years, a smaller part of the large grid (hereafter, small grid) was sampled  
101 (Fig. 1c). The number of stations sampled on the small grid were 80, 73, 75 and 72 in 2012,  
102 2013, 2014 and 2015, respectively. Sampling took place during low tide. At each station, four  
103 sediment samples were taken within a square meter with a 15 cm diameter corer to a depth of  
104 20 cm (total volume of a sample was 3534 cm<sup>3</sup>). The samples were sieved separately over a  
105 mesh size of 1 mm and crabs were collected. We also noted all crabs that were outside the  
106 samples to obtain a list of crabs that is as comprehensive as possible.

The collected crabs were stored in a 4% formalin solution and shipped to the NIOZ Royal Netherlands Institute for Sea Research where each crab was identified, measured and inspected for eggs. Crabs were identified using keys assembled by Naderloo (2017). Carapace width and length were measured to the nearest 0.1 mm with a callipers. Biomass in gram ash-free dry mass (AFDM) was obtained by drying the crabs (at 55°C for a minimum of 72 hours), weighing (to the nearest 0.1 mg), incineration (at 560°C for 5 hours) and weighing again (Compton et al. 2013).

## 2.2 Crab densities, diversity and life cycles

The numerical and biomass densities of the eight most abundant crabs were calculated for each sampling year. For the year 2012, densities were calculated both for the large and small grids. We used the average of the four samples per station to compute the winter average and standard deviations. In most years, most species were absent at more than half of the sampled stations, which made the data zero inflated.

As a measure of species diversity, we calculated the mean Shannon-Wiener index and Pielou-evenness index for the numerical crab densities averaged (i) per station, (ii) per sampling campaign and (iii) for all stations together. Shannon's index  $H$  (Pielou 1966, 1977) was calculated using the formula:

$$H = - \sum_{i=1}^S p_i \log_b p_i$$

where  $p$  is the proportional abundance of species  $i$  and  $b$  is the base of the logarithm.

Shannon's index is high either when there are a high number of unique species or when species share similar abundances within the community. Pielou evenness  $J$  was calculated as

$$J = \frac{H}{\ln S}$$

Where  $S$  is the total number of species.  $J$  ranges between 0 and 1; a lower number indicates the presence of dominant species. We included the species that we encountered within the grid but outside the grid samples in the diversity analysis and set their density at 0.

To study the lifecycles of the eight most abundant crabs we evaluated size range (carapace width) and show the percentage of ovigerous females. Using ANOVAs we checked if there was a difference between ovigerous females and non-ovigerous individuals. While sampling in the area we observed large numbers of blue swimming crabs *Portunus segnis* (Forskål, 1775) moving in and out the area with the tidal flow. To investigate the size and reproductive biology of *P. segnis*, we caught crabs in the water column using a scoop net and measured and sexed them and checked for eggs. In 2012, 2013, 2014 and 2015 the respective numbers of *P. segnis* scooped were 326, 0, 38, 255.

## 2.3 Species distribution modelling

We modelled the numerical densities of the two most abundant crab species (*Macrophthalmus sulcatus* and *Thalamita poissonii*) as functions of four environmental variables: seagrass densities, tidal elevation, sediment grain size and sediment depth. Below we describe how environmental variable were sampled.

### 2.3.1 Seagrass densities

Seagrass in the study area consisted of *Halodule uninervis* (Forsskål) and *Halophila ovalis* (R. Brown). Aboveground seagrass density of both species was visually assessed at each grid station following the classification of Braun-Blanquet (Braun-Blanquet, 1932) (Fig. 2a). This scale separates seagrass density into seven classes based on the following coverage: (1) 0%, (2) 0–5%, (3) 5–12.5%, (4) 12.5–25%, (5) 25–50%, (6) 50–75% and (7) 75–100%.



### 2.3.2 *Tidal elevation*

The elevation of the intertidal area was derived from an intertidal elevation model (Supplementary Material 1) on the basis of the waterline method (Zhao et al. 2008). In this approach, waterlines are extracted from satellite imagery using the infra-red band. It is assumed that the waterline of each image represents a line of equal elevation. We used seven Landsat satellite images captured at different times through the tidal cycle. Predicted water level was obtained from a gauge at Ras Hilf port (~ 25 km from our study site). Tidal elevations of locations between the waterlines were computed by means of linear interpolation (Fig. 2b).

### 2.3.3 *Sediment grain size*

The upper 5 cm of the sediment was collected with a PVC tube of 19 mm diameter in November-December 2011 at 240 stations on the sampling grid. Samples were frozen and shipped to NIOZ. Grain size distributions were measured by means of a particle size analyser which uses laser diffraction and Polarization Intensity Differential Scattering technology (Coulter LS 13 320, optical module 'grey', grain sizes from 0.04 to 2000  $\mu\text{m}$  in 126 size classes). All sediments were analysed according to the 'biological approach', i.e. organic matter and calcium carbonate were not removed from the samples. Further details concerning sediment analysis are in Compton et al. (2013). Only the sediment samples from the random stations ( $n = 39$ ) were analysed. The median grain size (mgs, in  $\mu\text{m}$ ) was used for further analysis. This variable was interpolated across the study area with universal kriging. Mgs was positively correlated with the shortest squared distance to the coast ( $d_c$ ). To improve interpolation accuracy, we added  $d_c^2$  as a covariate for modelling the variogram (Supplementary Material 2). To meet the normality assumptions, we used the log transformed value of mgs. In R (R Development Core Team, 2013), using the package *gstat* (Pebesma,

2004), we checked if the assumptions of residual patterns and normally distributed residuals were met. For visualization purposes we back-transformed the interpolated values of mgs (Fig. 2c).

#### **2.3.4 Sediment depth**

At some of the grid stations an impenetrable layer was reached within the 20 cm of the corer used to sample the crabs. For these stations, the maximum sediment depth was recorded to the nearest cm (Fig. 2d).

#### **2.3.5 Statistical modelling**

For species distribution modelling we used Random Forest (RF) algorithm. RF models are useful for explorative studies such as ours, because of their ability to model non-linear relationships and complex interactions among predictor variables (Breiman, 2001; Cutler et al. 2007). RF which fits many classification trees to a data set, and then combines the predictions from all the trees (Cutler et al. 2007). For each tree about one third of the data is left out which are used for validation (the out-of-bag [OOB] sample) and combined in an overall OOB error estimate. RF makes no distributional assumptions (Cutler et al. 2007).

RF models were fitted using log-transformed numerical crab densities as response variables. Log-transformed values were used to reduce the relative importance of high densities. The value of 1 was added to all numerical densities to avoid taking the log of zero. Separate models were fitted for each species and each year. For 2012, models were fitted on the data collected on the large and small grid separately. The area to which mgs could be interpolated did not completely cover the sampled area and therefore the number of stations that were included in the RF modelling equaled 228 for the large grid and 54 for the small grid. Seagrass cover class was converted into a continuous variable by assuming that the

percentage of coverage of a cover-class is the midpoint of the range of that cover-class, i.e. we assumed that cover-classes 1-7 resembles seagrass abundance of 0%, 2.5%, 8.75%, 18.75%, 37.5%, 62.5%, 87.5% respectively. Seagrass densities fluctuated considerably between years, with average midpoint densities ( $\pm$ SE) of  $7.6 \pm 0.59\%$  (large grid 2012),  $8.1 \pm 1.3\%$  (2012),  $15.8 \pm 2.7\%$  (2013),  $6.7 \pm 1.0\%$  (2014),  $36.6 \pm 4.1\%$  (2015). The other environmental variables were assumed to remain the same (tidal elevation and mgs) or varied little (sediment depth).

We applied the RF algorithm within the R environment (R Development Core Team, 2013) using the package *randomForest* (Liaw & Wiener, 2002), using default settings. The performance of the RF model was examined as the percent variance explained: pseudo  $R^2 = 1 - \text{MSE}_{\text{OOB}} / \text{observed variance}$ , where  $\text{MSE}_{\text{OOB}}$  is the mean square error between observations and OOB predictions (Wei et al. 2010). Predictor importance was determined as the difference in model performance in terms of contribution to prediction accuracy with or without a randomly permuting predictor variable (Breiman, 2001). We analysed the nature of the relationships between crab densities and predictor variables by means of partial dependence plots. Partial dependence plots show the marginal effect of a response variable after accounting for the average effects of the other variables on the response (Friedman, 2001). Partial dependence plots were fitted in R using the *pdp* package (Greenwell, 2017).

Random forest can deal with collinear variables as RF “spreads” the variable importance across all the variables, thereby guarding against the elimination of ecologically important variables (Cutler et al 2007). Yet it is still good to check for collinearity as this may affect model interpretation. In our study, the correlation coefficient  $r$  was below 0.4 for all the environmental variables studied in any year. Hence, none of the variables showed collinearity.

### 3. RESULTS

#### 3.1 Crab community of Barr Al Hikman

In the grid samples, we identified 12 crab species (Table 1). Outside the grid samples, we identified another 17 species (Table 1). The species belonged to 13 families. With six species, members of the Macrophtalmidae family were the most common, followed by the Ocypodidae family (five species) and the Portunidae family (four species). We identified 12 species to be deposit-feeding crabs, eight species as scavengers/predatory crabs and two species as herbivorous (Table 1). All deposit-feeding crabs were burrowing crabs, the others were epifaunal/burying species.

The mean Shannon-Wiener Index of diversity  $H$ , calculated over the average numerical crab densities per station, was 0.19 and Pielou's evenness  $J$  was 0.38. Calculated over the average crab densities per sampling campaign (2012 (large and small grid), 2013, 2014 and 2015),  $H$  was 1.75, 1.79, 1.55, 1.32 and 0.85 and  $J$  was 0.62, 0.74, 0.53, 0.60, 0.47 respectively. Calculated over the average crab densities per for all years together,  $H$  was 1.37 and  $J$  was 0.50

### 3.2 Crab densities and life cycles

Across the winters of 2012–2015 the total numerical crab densities ranged from 12.1 to 53.9 crabs/m<sup>2</sup> and biomass densities ranged from 0.44 to 1.35 g AFDM/m<sup>2</sup> (Table 2, Fig. 3). *M. sulcatus* and *T. poissonii* were the most abundant species; together they contributed to at least 60% of numerical and biomass density during all winters (Table 1, Table 2, Fig. 2e & 2f & Fig. 3). In 2012, the estimated densities for all species on the large grid were similar to the densities estimated on the small grid (Table 2).

Carapace width of the crabs sampled on the grid and in the water column are given in Fig. 4. Ovigerous females were found in all of the eight most abundant species, except for *P. segnis* (Table 1, Fig. 4). For all species, ovigerous females were on average larger than non-ovigerous individuals. This difference was significant for *M. sulcatus* ( $F_1 = 68.4$ ,  $P < 0.001$ ),

*T. poissonii* ( $F_1 = 53.38$ ,  $P < 0.001$ ) and *S. crabricauda* ( $F_1 = 9.01$ ,  $P = 0.004$ ) and, presumably due to a low sample, not significant for Leucosiidae ( $F_1 = 0.89$ ,  $P = 0.349$ ), *M. sinuspersici* ( $F_1 = 1.659$ ,  $P = 0.206$ ), *M. laevis* ( $F_1 = 3.393$ ,  $P = 0.0884$ ) and *M. serenei* ( $F_1 = 3.685$ ,  $P = 0.0839$ ). None of *P. segnis* caught in the water column were ovigerous.

### 3.3 Species distribution modelling

Model performance of RF for *M. sulcatus* and *T. poissonii* varied considerably between years. The pseudo  $R^2$  for the 2012 data covering the large grid was 7% for *M. sulcatus* and 25% for *T. poissonii* (Table 3). For the ‘large grid models’ seagrass was the environmental variable which explained most of the variance of the crab densities (Table 4). The pseudo  $R^2$  by the RF models for the small grid ranged from -19 to 30% for *M. sulcatus* and from -9% to 10% for *T. poissonii*. For the ‘small grid models’ no single environmental variable could be selected as the best explanatory environmental variable because  $MSE_{OOB}$  differed substantially between years (Table 4). The partial dependence plots showed some generalities in the relationships between crab densities and predictor variables (Fig. 5). Particularly across all years, crab densities were positively associated with seagrass densities and sediment depth and negatively associated with tidal elevation and median grain size.

## 4. DISCUSSION

Our study shows that the intertidal mudflats of Barr Al Hikman provide feeding, reproduction and nursery habitat to at least 29 species of brachyuran crabs, of which one species, *P. segnis*, is particularly important for local commercially fisheries. We have provided baseline density values for the most abundant species and also identified some interactions with environmental variables, noticeable seagrass. We discuss our main results and highlight some implications for conservation.

#### 4.1 Crabs of Barr Al Hikman

All 29 recorded species were previously observed in the Arabian region (Simões et al. 2001; Naderloo et al. 2013; Naderloo, 2017) and nine of them had previously been reported from Oman (Clayton, 1996; Clayton & Al-Kindi, 1998; Khorov 2012). The number of recorded crab species at Barr Al Hikman is at the same order of magnitude as in nearby areas such as intertidal mudflats in United Arab Emirates (13 species) Iran (about 34 species on soft-sedimented habitat) , Kuwait (19 species), Yemen (about 25 species in soft-sedimented sediments), India (14 species) and Mozambique (12 species) (Cooper, 1997; Simões et al. 2001; de Boer & Prins, 2002; Al-Yamani et al, 2012; Naderloo et al. 2013; Shukla et al, 2013). Note that we sampled only the intertidal mudflats and not the intertidal reefs and mangroves, which usually have a more diverse crab community than intertidal mudflats (Naderloo et al. 2013; Simões et al. 2001).

The crab community at Barr Al Hikman shows similarities with crab communities at other tropical intertidal mudflats. For instance, deposit-feeding crabs and herbivorous crabs were found to dominate many other (sub)tropical intertidal mudflats (Naderloo, 2017; Naderloo et al. 2013; Simões et al. 2001), contrary to crab communities at temperate zones which are usually dominated by carnivorous species (Beukema, 1989). Furthermore, the baseline numerical densities provided of 10-50 crabs per m<sup>2</sup> is within the range measured at other tropical mudflats (Swennen et al, 1982; Clayton & Al-Kindi, 1998; Karlsson, 2009; Otani et al. 2010). Likewise, 5-fold inter-annual fluctuations in crab densities are regularly reported at temperate (Beukema, 1989; Beukema, 1991) and tropical (Clayton & Al-Kindi, 1998) intertidal mudflats. Also, the calculated diversity indexes are within the same order of magnitude as other tropical systems (e.g. de Boer & Prins, 2002; Bertini & Fransozo, 2004).

## 4.2 Life cycle

In seven of the eight most abundant crab species, we found ovigerous females which shows that these species reproduce in Barr Al Hikman (Fig. 4). We also found small individuals in all the abundant species, presumably the first post-larval size, suggesting that these species are entirely intertidal in their non-larval life.

The blue swimming crab *P. segnis* was the only species in which no ovigerous females were found, despite that over 600 crabs were checked. According to local fisherman (Giraldes et al. 2016), and similar to other species of swimming crabs (Hill et al. 1982; Potter et al. 1983; Seitz et al. 2005), this species is thought to reproduce in deep water and small juveniles use shallow (intertidal) areas as nursery grounds. Our data substantiate this idea: The size-range of the inspected individuals in our study (21-93 mm) is almost exclusively outside the size-range of (ovigerous) *P. segnis* reported from sublittoral waters. For instance, the minimum carapace width of ovigerous *P. segnis* caught in the sublittoral waters of the Sea of Oman was 92 mm (Safaie 2013), and the size range of *P. segnis* in the waters adjacent to Barr Al Hikman was 57–206 mm (data for winter and spring) (Mehanna et al 2013).

## 4.3 Species distribution modelling

The performance of random forest models explaining the spatial distribution of *M. sulcatus* and *T. poissonii* varied considerably between years, with pseudo  $R^2$  ranging from 0 to 30%. The models were relatively good at predicting crab distribution in years with intermediate crab densities and particularly bad in explaining the variation in crab densities in the year with low (2014) densities of crabs. The latter may not be surprising given that there was hardly any variation in the response variable in 2014. The explanatory capacity of the models may seem low, but it is not uncommon that species distribution models for invertebrates at intertidal

mudflats explain little of the total variance; for instance, in a large study by Compton et al. (2013), environmental variables explained between 4–9% of the deviance across three years.

Despite low model performance, some of the spatial variation in crab densities could still be explained by the environmental variables. Particularly, seagrass densities could explain some variance in some years. Partial dependence plots showed that, *within years*, there was a positive association between seagrass densities and crab densities. We explain this positive association from a food resource perspective; isotope data collected in 2014 showed that (detritus of) seagrass is the main food resource for both *T. poissonii* and *M. sulcatus* (Al Zakwani et al. unpublished data). Also gut contents of *T. poissonii* collected at Barr Al Hikman in December 2012 showed the presence of seagrass roots ( $n = 12$ , unpublished data). The positive association may also be caused by the safe-habitat function that seagrass meadows provide (Kunsook et al. 2014). At the same time, the seagrass may profit from the presence of detritus-eating crabs which reduce the high levels of detrimental organic material (Koch, 2001; Folmer et al. 2012) and also from soil aeration promoted by burrowing crabs (Smith et al, 1991).

The other environmental variable could also explain some of the variance in some years. Partial dependence plots showed that crab densities were negatively associated with median grain size and elevation and positively associated with sediment depth across most years. The positive association with sediment depth, especially for *M. sulcatus*, likely reflects the inability of these burrow-hiding crabs to construct burrows in sediments with limited depth. Lower crab densities closer to the shore presumably reflects the inability of crabs to tolerate large fluctuations in temperature and oxygen and could also be related to desiccation (Flores et al. 2005; Jensen et al. 2005). Finally, median grain size was in some years a relatively good predictor of crab densities, yet, because the association varied between years,



the association remains unexplained. Clearly, experiments are needed to further investigate the interaction between crabs and the studied environmental variables.

#### **Temporal variation in crab densities**

We found large variation in crab densities in time, suggesting that the population dynamics of crab species are to a large extent determined by environmental factors changing over time rather than space (van der Meer, 1999). This is also indicated by the partial dependence plots that showed that across all four years of study the slopes between crab densities and environmental variables were in general similar, but the heights of the response curves differed (van der Meer, 1999). We speculate that seagrass could be such environmental factor that determining crab densities *between* years, as there seems to be a positive relation between seagrass densities crab densities *between* years (Fig. 6b). This, again, could mean that seagrass has an important connection with crabs, for instance because it is a food source or provide shelter. Yet we cannot exclude that also other time-related variables such as weather conditions may affect crab survival (Beukema, 1991; Seitz et al. 2005). Weather conditions such as drought can also affect seagrass conditions and thus indirectly affect crab densities (de Fouw et al 2018).

#### **4.4 Economical values and conservation**

The nursery function of Barr Al Hikman for *P. segnis* highlights the direct economic value of intertidal mudflats for Oman as *P. segnis* provides a major income for local fisheries (Mehanna et al. 2013; MAFW, 2014; Giraldes et al. 2016). With densities up to 0.7 crabs m<sup>-2</sup> and an intertidal area encompassing 190 km<sup>2</sup>, the entire annual production in Barr Al Hikman is in the order of hundreds of millions of *P. segnis*. This probably is a conservative estimate because we sampled during one period in winter whereas spawning continues throughout the

winter (Safaie et al. 2013; Safaie et al. 2015). We do not know how many crabs reach the harvestable size of 100 mm, yet the estimated production number shows the enormous potential that intertidal areas can have for *P. segnis*.

We conclude that our results show that crabs and seagrass habitat should be considered in effective conservation planning of the Barr-Al-Hikman ecosystem. This is important for the conservation of biodiversity, for the crabs themselves, but also, for instance, for the many 100.000s of birds that feed on them (de Fouw et al. 2017; Bom et al 2018). It is also important for the sustainability of *P. segnis* fisheries. Conservation planning is an issue of priority since *P. segnis* is currently overexploited in the region (Safaie et al. 2013; Giraldes et al. 2016) and mudflats systems in the region, including the mudflats of Barr Al Hikman, are threatened by rapidly increasing human pressure (Burt, 2014, Times of Oman 2020).

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Data availability: original data will be made available at the NIOZ online archiving system

404 **Tables & Figures**

405 Table 1. List of brachyuran crab families and species observed on the intertidal mudflats of  
 406 Barr Al Hikman (Sultanate of Oman), with reference to feeding modes (from literature, see  
 407 captions) and, if collected on the grid, the average winter densities (number per m<sup>2</sup>) over the  
 408 period 2012–2015 (based on samples of the small grid, see method) and % of ovigerous  
 409 females. Taxonomic names are in accordance with those listed in the World Register of  
 410 Marine Species (WoRMS, <http://www.marinespecies.org/>, accessed: 29 July 2020).

Family	Species	Feeding type	Average winter density (# m <sup>-2</sup> ± SD)	Ovigerous females (%)
Dotillidae	<i>Dotillidae</i> sp.	deposit <sup>1</sup>	-	-
	<i>Scopimera crabicauda</i> (Alcock 1900)	deposit <sup>1</sup>	0.71 (±1.05)	56
Dromiidae	<i>Tumidodromia dormia</i> (Linnaeus, 1763)	predator <sup>1</sup>	-	-
Grapsidae	<i>Metopograpsus messor</i> (Forskål, 1775)	unknown	-	-
	<i>Grapsus albolineatus</i> (Forskål, 1775)	herbivore <sup>2</sup>	-	-
Leucosiidae	<i>Leucosiidae</i> sp.	unknown	1.94 (±1.44)	5
	<i>Nursia</i> sp.	unknown	-	-
Inachidae	<i>Camposcia</i> sp.	unknown	-	-
Matutidae	<i>Matuta victor</i>	scav/pred <sup>1</sup>	-	-
Macrophthalmidae	<i>Chaenostoma sinuspersici</i> (Naderloo & Türkay, 2011)	deposit <sup>1</sup>	0.54 (±0.51)	100
	<i>Macrophthalmus depressus</i> (Rüppell, 1830)	deposit <sup>1</sup>	0.20 (±0.39)	0
	<i>Macrophthalmus grandidieri</i> (Milne-Edwards, 1867)	deposit <sup>1</sup>	0.18 (±0.25)	0
	<i>Macrophthalmus laevis</i> (Milne-Edwards, 1867)	deposit <sup>1</sup>	0.27 (±0.42)	67
	<i>Macrophthalmus serenei</i> (Takeda & Komai, 1991)	deposit <sup>1</sup>	0.14 (±0.09)	20
	<i>Macrophthalmus sulcatus</i> (Milne-Edwards, 1867)	deposit <sup>1</sup>	12.22 (±7.19)	54
Ocypodidae	<i>Ocypode saratan</i> (Forskål, 1775)	scav/pred <sup>1</sup>	-	-
	<i>Ocypode rotundata</i> (Miers, 1882)	scav/pred <sup>1</sup>	-	-
	<i>Ocypode platytarsis</i> (Milne-Edwards, 1852)	scav/pred <sup>1</sup>	-	-
	<i>Uca annulipes</i> (Milne-Edwards, 1837)	deposit <sup>3</sup>	-	-
	<i>Uca</i> sp.	deposit <sup>1</sup>	0.14 (±0.29)	0
Pilumnidae	<i>Pilumnus</i> sp.	unknown	0.04 (±0.09)	0
Pinnotheridae	<i>Pinnotheres</i> sp.	deposit <sup>1</sup>	-	-
	<i>Xenopthalmus</i> sp.	deposit <sup>1</sup>	-	-
Portunidae	<i>Portunus segnis</i>	scav/pred <sup>5</sup>	0.27 (±0.30)	0
	<i>Thalamita crenata</i> (Rüppell, 1830)	predatory <sup>4</sup>	-	-
	<i>Scylla serrata</i> (Forskål, 1775)	predatory <sup>1</sup>	-	-
	<i>Thalamita poissonii</i>	herbivore <sup>1</sup>	10.97 (±14.40)	31
Varunidae	<i>Asthenognathus</i> sp.	unknown	-	-
Xanthidae	<i>Xanthidae</i> sp.	unknown	-	-

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411 <sup>1</sup>own observation, <sup>2</sup>Naderloo et al. (2013), <sup>3</sup>de Boer and Prins (2002), <sup>4</sup>Cannicci et al. (1996),  
412 <sup>5</sup>Safaie (2016)

413 Table 2. The average ( $\pm$  SD) numerical and biomass density of the eight most abundant crab species across four years based on the samples  
 414 collected on the grid (large and small) and in the water column. Species are ranked according to their abundance, with most abundant species on  
 415 top. AFDM refers to ash-free dry mass.

		2012 large grid	2012	2013	2014	2015
numerical density (#/m <sup>2</sup> )	<i>Macrophthalmus sulcatus</i>	3.47 ( $\pm$ 8.71)	4.9 ( $\pm$ 11.38)	17.26 ( $\pm$ 20.68)	7.28 ( $\pm$ 11.12)	19.44 ( $\pm$ 23.82)
	<i>Thalamita poissonii</i>	7.29 ( $\pm$ 15.41)	6.65 ( $\pm$ 13.36)	4.03 ( $\pm$ 9.76)	0.93 ( $\pm$ 4.20)	32.28 ( $\pm$ 41.21)
	Leucosiidae	1.18 ( $\pm$ 4.43)	0.7 ( $\pm$ 3.07)	3.84 ( $\pm$ 8.50)	2.24 ( $\pm$ 6.92)	0.97 ( $\pm$ 4.29)
	<i>Scopimera crabriacauda</i>	1.11 ( $\pm$ 7.51)	2.27 ( $\pm$ 10.55)	0.19 ( $\pm$ 1.64)	0.37 ( $\pm$ 3.23)	0
	<i>Macrophthalmus sinuspersici</i>	1.11 ( $\pm$ 4.13)	1.23 ( $\pm$ 4.56)	0.38 ( $\pm$ 2.30)	0.19 ( $\pm$ 2.76)	0
	<i>Macrophthalmus laevis</i>	0.45 ( $\pm$ 3.38)	0.88 ( $\pm$ 5.61)	0	0.19 ( $\pm$ 1.62)	0
	<i>Portunus segnis</i>	0.41 ( $\pm$ 2.55)	0.7 ( $\pm$ 3.79)	0.19 ( $\pm$ 1.64)	0	0.19 ( $\pm$ 1.65)
	<i>Macrophthalmus serenei</i>	0.32 ( $\pm$ 2.29)	0.18 ( $\pm$ 1.57)	0	0.19 ( $\pm$ 1.62)	0.19 ( $\pm$ 1.65)
biomass density (g AFDM/m <sup>2</sup> )	<i>Macrophthalmus sulcatus</i>	0.27 ( $\pm$ 0.75)	0.28 ( $\pm$ 0.70)	0.89 ( $\pm$ 1.22)	0.32 ( $\pm$ 0.54)	0.53 ( $\pm$ 0.77)
	<i>Thalamita poissonii</i>	0.39 ( $\pm$ 1.23)	0.18 ( $\pm$ 0.50)	0.09 ( $\pm$ 0.41)	0.02 ( $\pm$ 0.16)	0.64 ( $\pm$ 1.10)
	Leucosiidae	0.03 ( $\pm$ 0.16)	0.01 ( $\pm$ 0.04)	0.12 ( $\pm$ 0.29)	0.09 ( $\pm$ 0.33)	0.02 ( $\pm$ 0.08)
	<i>Scopimera crabriacauda</i>	0.01 ( $\pm$ 0.10)	0.03 ( $\pm$ 0.14)	0 ( $\pm$ 0.03)	0 ( $\pm$ 0.01)	0
	<i>Macrophthalmus sinuspersici</i>	0.03 ( $\pm$ 0.13)	0.02 ( $\pm$ 0.07)	0 ( $\pm$ 0.03)	0 ( $\pm$ 0.01)	0
	<i>Macrophthalmus laevis</i>	0.05 ( $\pm$ 0.36)	0.07 ( $\pm$ 0.45)	0	0 ( $\pm$ 0.01)	0
	<i>Portunus segnis</i>	0.08 ( $\pm$ 0.65)	0.07 ( $\pm$ 0.39)	0.01 ( $\pm$ 0.08)	0	0.11 ( $\pm$ 0.95)
	<i>Macrophthalmus serenei</i>	0.02 ( $\pm$ 0.14)	0.02 ( $\pm$ 0.15)	0	0 ( $\pm$ 0.02)	0.04 ( $\pm$ 0.31)

417 Table 3. Percentage of variance explained in the spatial distribution of two species of crabs by  
 418 the Random Forest models for the different years and sample grids. Negative values imply  
 419 models that do not predict better than an average value.

	2012				
	large grid	2012	2013	2014	2015
<i>Macrophthalmus sulcatus</i>	7.08	29.53	29.58	-18.67	-7.20
<i>Thalamita poissonii</i>	25.01	7.20	4.62	-8.94	10.04

420

421

422 Table 4. Mean predictor importance ( $MSE_{OOB}$ ) on numerical crab abundance for species for  
 423 different years and sample grids. Values indicates the contribution to Random Forest  
 424 prediction accuracy for that variable. Negative values imply models that do not predict better  
 425 than a mean value.

	<i>Macrophthalmus sulcatus</i>					<i>Thalamita poissonii</i>				
	2012 large grid	2012	2013	2014	2015	2012 large grid	2012	2013	2014	2015
Seagrass	14.22	14.43	16.33	-1.07	-1.67	19.48	6.59	2.66	1.06	0.52
Median grain size	0.51	7.5	7.06	-0.58	0.33	10.79	10.25	12.69	6	6.94
Intertidal elevation	6.69	9.38	8.64	4.31	5.13	17.17	6.88	6.16	2.94	6.77
Sediment depth	9.13	15.38	16.06	-0.07	7.87	7.46	3.14	-0.32	-1.5	11.65

426

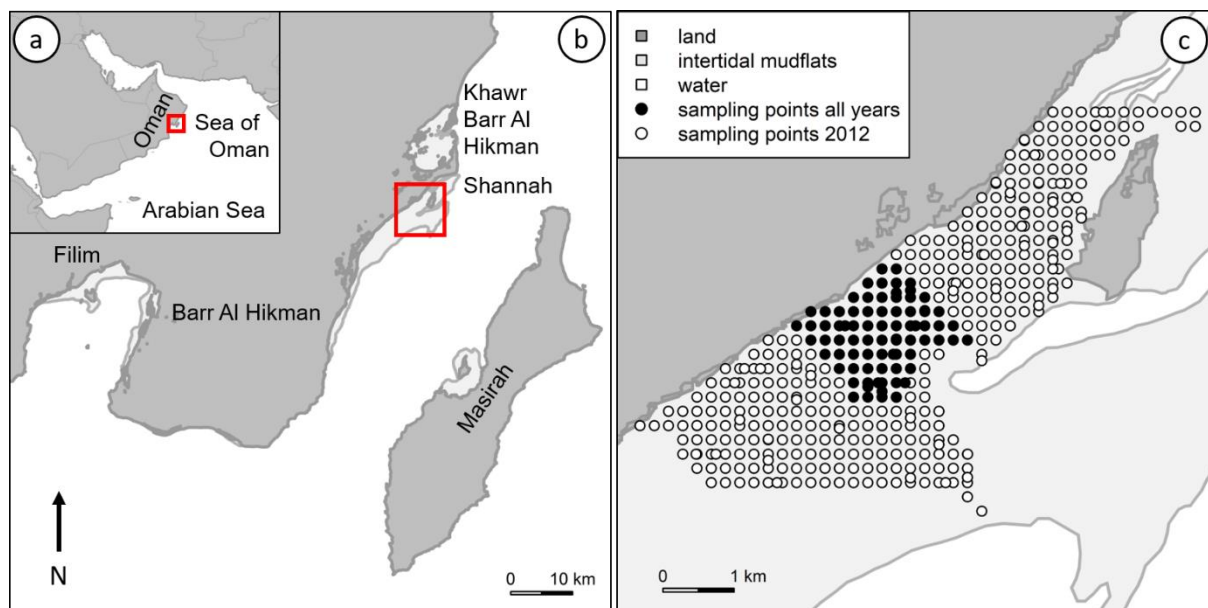


Fig.1 (a) The Sultanate of Oman with Barr Al Hikman Peninsula in the red square. (b) Barr Al Hikman, with the study area in the red square. (c) The study area with the grid sampling points. Black points refer to the small grid of 80 points sampled in 2012-2015. White points refer to the large grid which was sampled in 2012



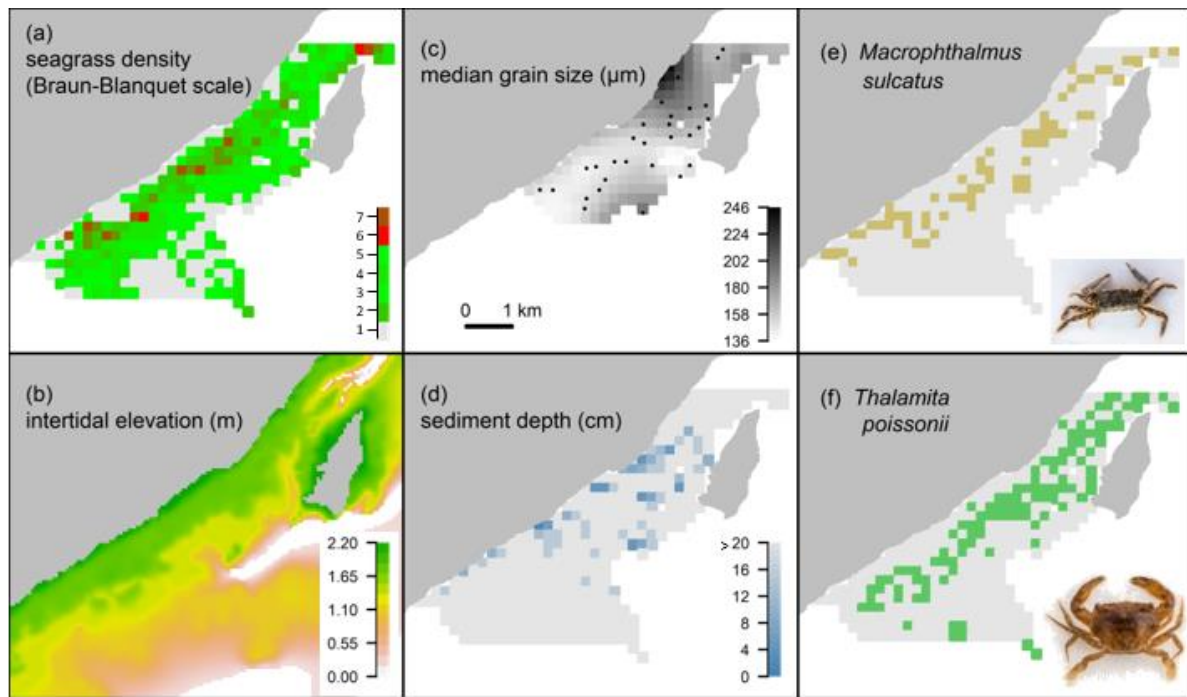


Fig 2 Study area in Barr Al Hikman with environmental variable used for species distribution modelling: (a) Seagrass cover class (Braun-Blanquet scale) in November 2012 (b) intertidal elevation based on satellite data collected between 2010 and 2012, (c) interpolated median grain size, with black points showing sampling sites, and (d) sediment depth based on samples taken in November 2012. Spatial distribution (presence/absence) of (e) *Macrophthalmus sulcatus* and (f) *Thalamita poissonii*, the two most abundant crabs in the area, in November 2012. Coloured blocks in (e) and (f) denote presence and grey blocks absence

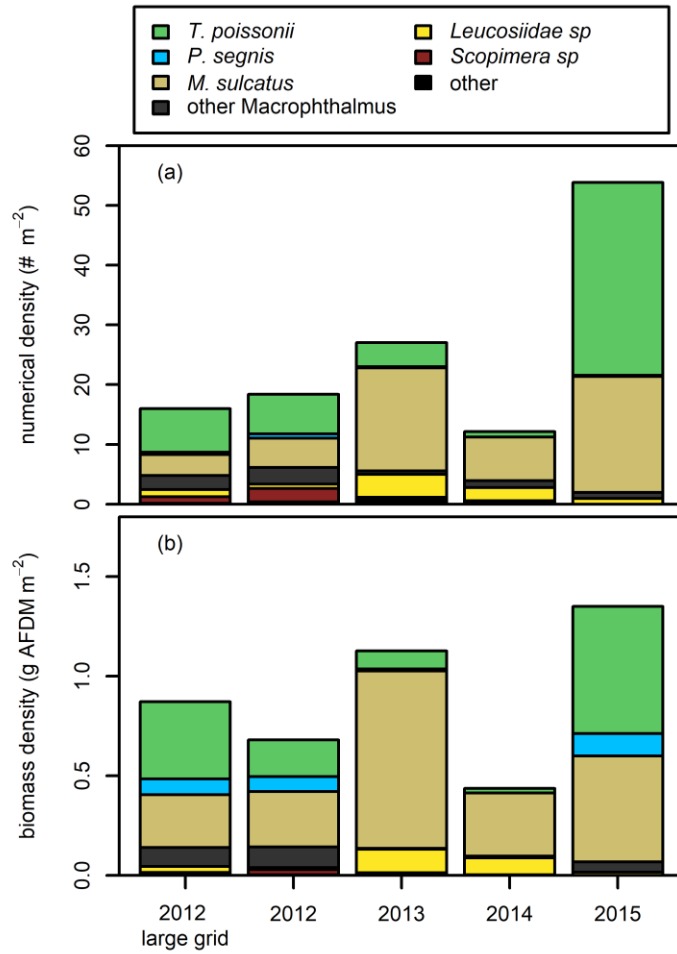


Fig. 3 Average numerical densities (a) in number per m<sup>2</sup> and biomass densities (b) in g ash-free dry mass (AFDM) per m<sup>2</sup> of *M. sulcatus*, *T. poissonii*, *Leucosiidae sp*, *P. segnis*, all other *Macrophthalmus* and all other crabs during five subsequent winters. Variation (SD) of the means are given in Table 2

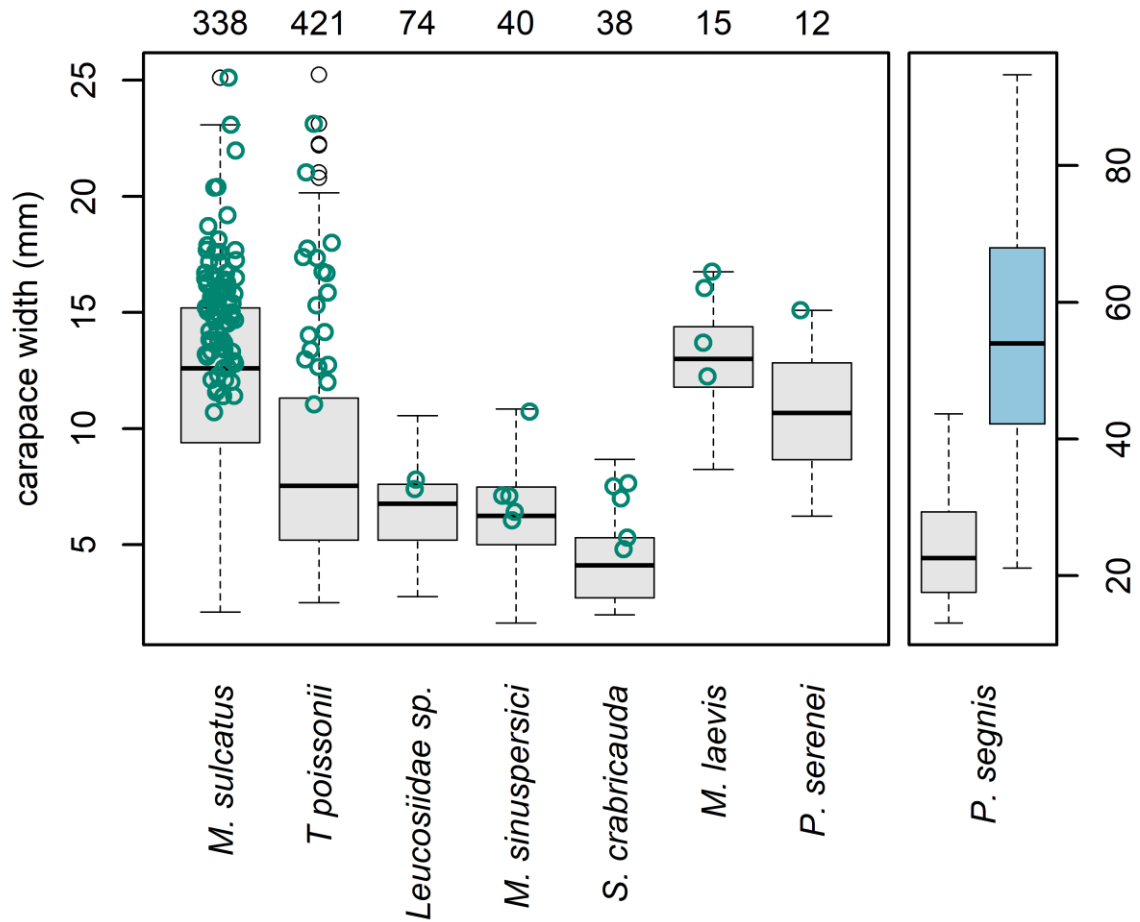


Fig 4 Boxplots showing carapace width for the eight most abundant crab species across four winters. Thick horizontal lines show medians, top and bottom lines of the box show the 25<sup>th</sup> and 75<sup>th</sup> percentiles respectively, whiskers show maximum and minimum values or 1.5 times the interquartile range (whichever is the smaller). For *P. segnis* grey box show crabs sampled on the grid and the blue box shows crabs collected in the intertidal water column. The green points represent the individual ovigerous female crabs (note the absence of these in *P. segnis*). Numbers on top show sample size

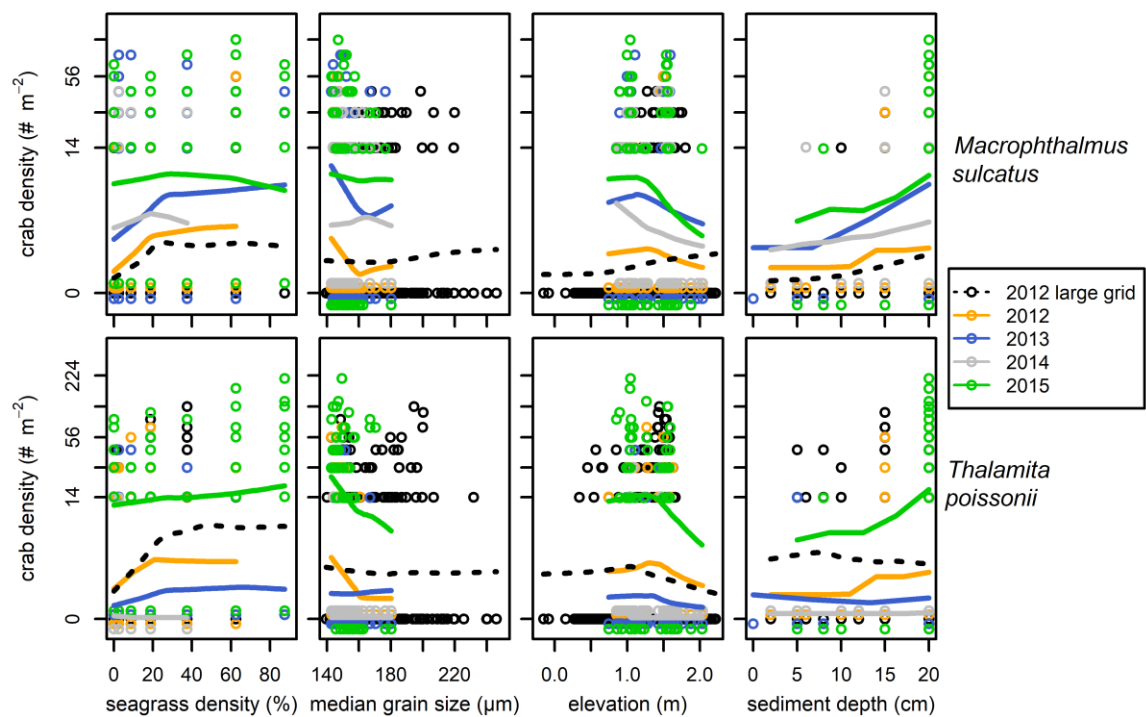
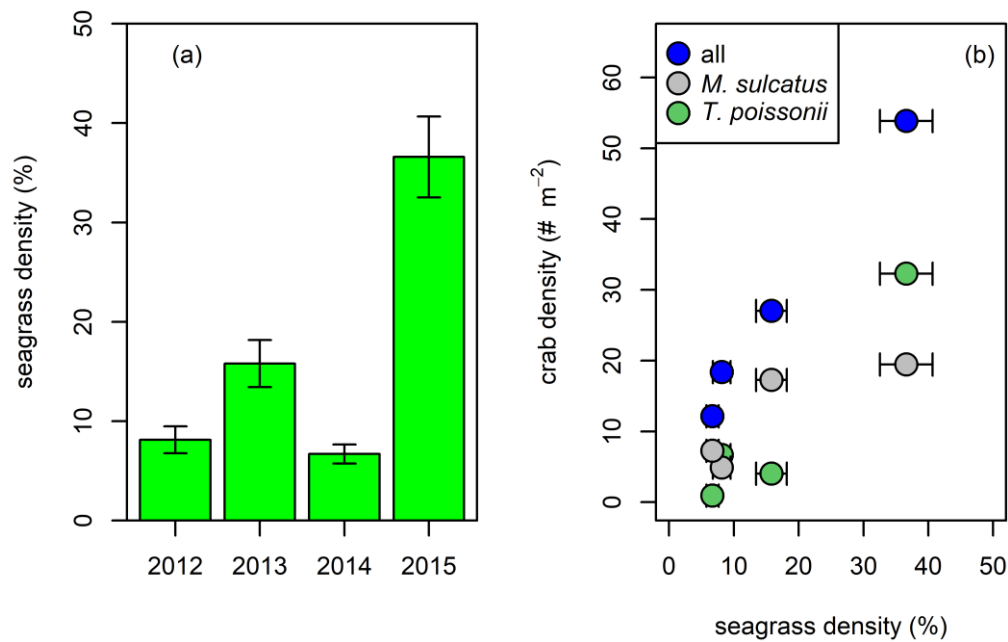


Fig. 5 Partial dependence plots for the modelled relationships between crab densities and the predictor variables. Lines indicate modelled relationships and points represent the data. Note the log scale on the y-axis

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462

463 Fig 6 (a) Average % seagrass density between years and (b) annual average % seagrass  
 464 density plotted against average numerical density. Error bars represent standard errors. In  
 465 these figures, seagrass was converted into a continuous variable by assuming that the  
 466 percentage of coverage of a class scored according to the Braun-Blanquet method is the  
 467 midpoint of the range of that cover-class (see methods)

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