Estimating animal populations and body sizes from burrows: Marine ecologists have their heads buried in the sand

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ABSTRACT

1. Most ecological studies require knowledge of animal abundance, but it can be challenging and destructive of habitat to obtain accurate density estimates for cryptic species, such as crustaceans that tunnel deeply into the seafloor, beaches, or mudflats. Such fossorial species are, however, widely used in environmental impact assessments, requiring sampling techniques that are reliable, efficient, and environmentally benign for these species and environments.

2. Counting and measuring the entrances of burrows made by cryptic species is commonly employed to index population and body sizes of individuals. The fundamental premise is that burrow metrics consistently predict density and size. Here we review the evidence for this premise. We also review criteria for selecting among sampling methods: burrow counts, visual censuses, and physical collections.

3. A simple 1:1 correspondence between the number of holes and population size cannot be assumed. Occupancy rates, indexed by the slope of regression models, vary widely between species and among sites for the same species. Thus, 'average' or 'typical' occupancy rates should not be extrapolated from site- or species specific field validations and then be used as conversion factors in other situations.

4. Predictions of organism density made from burrow counts often have large uncertainty, being double to half of the predicted mean value. Whether such prediction uncertainty is 'acceptable' depends on investigators' judgements regarding the desired detectable effect sizes.

5. Regression models predicting body size from burrow entrance dimensions are more precise, but parameter estimates of most models are specific to species and subject to site-to-site variation within species.

6. These results emphasise the need to undertake thorough field validations of indirect census techniques that include tests of how sensitive predictive models are to changes in habitat conditions or human impacts. In addition, new technologies (e.g. drones, thermal-, acoustic- or chemical sensors) should be used to enhance visual census techniques of burrows and surface-active animals.

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1. Introduction

Though small as measured against the all, I have been so instinctively thorough about my crevice and burrow. Robert Frost (1874–1963), "A Drumlin Woodchuck."

Numbers of individuals are a fundamental, arguably *the* fundamental, metric in the fields of ecology, conservation biology, and environmental impact assessment. Obtaining accurate and precise abundance estimates can, however, be onerous in many situations, especially in habitats that are physically harsh or remote, and when sampling rare or cryptic species. To reliably assign a reliable detection probability to the species of interest and to collect density data consistently and effectively can often be challenging (Thompson, 2004). In addition, intensive sampling can negatively impact the species of interest, causing direct mortality or habitat destruction. Therefore, proxies that estimate abundance are often used and assumed to be reliable alternatives (Carlson et al., 2007, Turlure et al., 2010, Couturier et al., 2013).

Crypsis is a very widespread trait in several groups of large marine crustaceans that tunnel, often deeply, into the seabed and shores (Lucrezi and Schlacher, 2014). These crustaceans are central to several fundamentally important aspects of coastal ecology, including: the capacity of wetlands to process land-based nutrient inputs (Lee et al., 2014); the secondary productivity sustaining key fishery food webs in estuarine and coastal waters (Bouillon et al., 2008); and the high rates of carbon burial and long-term storage in coastal wetland sediments (McLeod et al., 2011). The most prominent fossorial crustaceans that construct burrows are thalassinid shrimp ("ghost shrimp", "mud lobsters", "yabbies") and various brachyuran crabs (e.g. "ghost crabs", "fiddler crabs", "sesarmid crabs").

Obtaining precise abundance values for fossorial species typically requires physical collection of animals through extraction of individuals from their burrows. This can be physically difficult when excavating large volumes of mud or sand, and is damaging to both organisms and their habitats. As an alternative, non-invasive techniques have been developed to count surface-active individuals or use burrows as proxies of abundance (Butler and Bird, 2007). These indirect methods of 'sampling' are widely used, especially in mangroves, mudflats, saltmarshes, and sandy beaches (e.g. Vermeiren and Sheaves, 2015).

Field sampling of burrow entrances is particularly common for estimating the abundance of crabs, often in the context of measuring the impacts of human activities or ecological changes attributed to climate change (Bean et al., 2012, Wood and Otley, 2013, Schlacher et al., 2014, Benchimol and Peres, 2015, Schoeman et al., 2015, Ureña-Aranda et al., 2015, Schlacher et al., 2016, Stelling-Wood et al., 2016). The technique is based on the fundamental premise that the number of burrow entrances visible on the sediment surface is consistently related to the density of fossorial individuals residing below (i.e. occupancy rates of burrows is either constant to index abundance or abundance can be predicted from occupancy models). The size (usually diameter) of burrow openings is also used to predict the size (i.e. carapace width or length) of individuals inhabiting burrows (Lucrezi et al., 2009a, Schlacher and Lucrezi, 2010b). As is the case with burrow numbers, this technique hinges on the premise that burrow dimensions are proportional to body size in a consistent manner.

Given the widespread application of burrow proxies to index population and body sizes of fossorial marine decapods, we review evidence on the performance of the technique. To this end, we ask two complementary questions: 1.) How accurate are predictions of density and body size that are made from counts and measurements of burrow openings?, and 2.) To what extent do occupancy rates of burrows vary between species and sites?

2. Methods

Our intent was to assess the accuracy of burrow proxies to estimate density and body size in fossorial marine species based on a representative sample of published studies. Because the method is particularly widely used in ghost crabs, our starting point was to search Scopus and the Web of Science using the two genus names for ghost crabs, "*Ocypode*" OR "*Hoploycypode*", as primary search terms; this yielded a combined list of 339 papers (Scopus: n = 220; Web of Science: n = 250). We then examined each paper whether it contained data on the relationship between burrow metrics and abundance or body sizes of ghost crabs; this reduced the initial list to nine papers. Many papers on ghost crabs that used burrow counts to estimate abundance (often in the context of environmental assessments; reviewed by Schlacher et al., 2016) cited a few studies done on other decapods to justify the 'burrow proxy method'. Such methods papers were included if they contained useable data for the meta-analysis. Furthermore, we searched each paper from the first list whether it contained other cross-references to published studies reporting on burrow-density or burrow-body size relationships in estuarine or marine crustaceans.

All studies reviewed here had to be peer-reviewed: reports from the 'grey literature' with no clear evidence of peer-review were excluded. Papers also needed to report numerical values on density, body size and burrow metrics per sample unit in sufficient detail to allow us to extract data to construct regression models. The final list used for the meta-analysis reported here comprised 24 studies. We also aimed to include a broadly representative selection of studies for larger marine crustaceans that reflected differences in burrow fidelity. Thus, our selection contains taxa that undertake surface movement away from the burrow for feeding (e.g. ghost crabs, mud crabs) as well as taxa that feed inside the burrows (e.g. callianassid shrimp).

We extracted data from tables or graphs in each paper that contained information on: (a) burrow counts and matched densities of individuals; or (b) burrow opening diameters and matched measurements of body size of individuals inhabiting burrows. Studies obtained crab densities (number of individuals) by excavating crabs from the sediments within sample units for which burrow counts had previously been made. All authors using burrow size as a proxy for body size measured the opening diameter of burrows and either the width or length of the carapace of crabs retrieved from burrows.

Analytically, we addressed the question of how accurately abundance or body size can be predicted from burrow measurements using the 95% prediction intervals from least square regression models (Zar, 1984, Quinn and Keough, 2002). The size of the prediction interval relative to the predicted value was used as a metric for uncertainty. This was calculated for 'small' (first quartile of observation), medium (median) and 'large' (upper quartile) individuals and densities in each regression model. Occupancy rate is mathematically defined as the slope of the regression line for densities predicted from hole counts.

3. Results

3.1. Burrow occupancy rates

We found a wide range in occupancy rates among studies and species (Table 1). Across all studies, the mean reported number of individuals per burrow was 0.67 (se = 0.11), ranging between 0.05 (Barnes et al., 2002) and 1.30 (Xiong et al., 2010). Seven of twelve studies did not test for, or report on, spatial variation in occupancy rates (Table 1). Of the five papers that examined spatial variation in occupancy rates, three reported no differences between sites (Xiong et al., 2010, Silva and Calado, 2013) or beach types (Pombo and Turra, 2013), whilst two studies reported differences in occupation rates for burrows located in different vegetation types (Xiong et al., 2010) or in different tidal zones within a mangrove forest (Warren, 1990). Published data on the temporal variation of occupancy rates are limited to McPhee and

Table 1

Reported occupancy rates (*OR*) for burrows of marine, decapod, fossorial crustaceans (*OR* = No. individuals/No. burrows; n is the number of sites/stations across which OR statistics were calculated).

Higher taxon	Species	Habitat	n	Mean	s	Min	Max	Spatial variation between sites?	Source
Brachyura, Portunidae	*Scylla serrata*	Mangroves	3	0.05	0.05	0.00	0.11	na (no test reported)	Barnes et al. (2002)
Axiidea, Callianassidae	*Trypaea australiensis*	Mudflat	1	0.11				na (no test reported)	McPhee and Skilleter (2002)
Brachyura, Ocypodidae	*Ocypode quadrata*	Sandy beach	2	0.19	0.06	0.15	0.23	Not significant (sites)	Silva and Calado (2013)
Brachyura, Ocypodidae	*Ocypode quadrata*	Sandy beach	9	0.51	0.19	0.20	0.71	No (morphodynamic beach state)	Pombo and Turra (2013)
Axiidea, Callianassidae	*Trypaea australiensis & Biffarius arenosus*	Mudflat	3	0.53	0.09	0.48	0.63	na (no test reported)	Butler and Bird (2007)
Brachyura, Ocypodidae	*Uca annulipes*	Tidal flat	1	0.79				na (no test reported)	Macia et al. (2001)
Brachyura, Heloeciidae	*Heloecius cordiformis*	Mangrove	2	0.83	0.12	0.74	0.91	Yes (varies with distance landward)	Warren (1990)
Brachyura, Heloeciidae	*Heloecius cordiformis*	Mangrove	1	0.85				na (no test reported)	MacFarlane (2010)
Brachyura, Dotillidae	*Ilyoplax deschampsi*	Tidal flat/saltmarsh	1	0.90				Yes (varies between vegetation types)	Xiong et al. (2010)
Brachyura, Dotillidae	*Dotilla fenestrata*	Sandflat	1	0.96				na (no test reported)	Flores et al. (2005)
Brachyura, Varunidae	*Helograpsus haswellianus*	Saltmarsh	2	1.05	0.00	1.05	1.05	na (no test reported)	Breitfuss (2003)
Brachyura, Sesarmidae	*Chiromantes dehaani*	Tidal flat/saltmarsh	3	1.30	0.29	1.00	1.58	Not significant	Xiong et al. (2010)

Skilleter (2002), who found that the relationship between the number of burrow openings and yabby density varied significantly through time.

3.2. Predicting abundance from burrow counts

Predictions of density made from burrow counts using regression models had widely divergent coefficients of determination and prediction intervals (Figs. 1 & 2; Tables 1 & 2). Burrow counts explained on average 66% (se = 8%) of variation in density, with R^2-values ranging from 17% (Xiong et al., 2010) to 97% (Breitfuss, 2003). At median observed densities, uncertainty of predictions was considerable: the width of the 95% prediction interval for new observations averaged ±88% (se = 16%) of the predicted values, meaning that new abundance values predicted from burrow counts could, on average, be roughly double or half the mean prediction (Table 2). The narrowest prediction interval (±24%) was in the model of Breitfuss (2003) for *Helograpsus haswellianus*, whilst the largest (±1538%) was reported for *Scylla serrata* (Barnes et al., 2002). Accuracy was considerably lower for predictions made at lower abundance values: at the lower quartile of observed abundance values, prediction uncertainty was ±186% (se = 53%) for new observations, ranging between ±37% (Breitfuss, 2003) and ±647% (McPhee and Skilleter, 2002). Conversely, at higher abundances (upper quartile of observations) predictions could be made more accurately, the average prediction uncertainty being ±58% of the mean (se = 9%, range = 18–122%). Most regression models relating burrow numbers to abundance did not depart significantly from linear relationships (Fig. 2). Runs tests indicate linear relationships in all but the model of Macia et al. (2001) for *Uca annulipes* (P = 0.003).

3.3. Predicting body size from burrow dimensions

Regression models of burrow opening diameter against body size (carapace width or length) had a mean coefficient of determination (R^2) of 0.81 (se = 0.05, min. = 0.43, max. = 0.98; Table 3). In ghost crabs, burrow entrance dimensions accounted on average for 81% (se = 0.06) of the variance in body size of individuals inhabiting burrows, ranging between 51% in *Ocypode cursor* on Cape Verde (Rodrigues, 2012) to 98% in Wolcott's (1978) study of *Ocypode quadrata* (Table 3).

Predictions of body size made from burrow opening diameter varied in precision among studies (Table 3; Fig. 2). Prediction uncertainty (95% prediction interval) of regression models at the median observed (measured) body size varied between ±9% (Wolcott, 1978) and ±65% (Yong et al., 2011). Predictions of body size for smaller individuals (i.e. lower quartile of observed body sizes) were significantly (t = 3.11, df 21, P = 0.005) less accurate (prediction error range: 13–98%, mean:

44%) than those for larger (upper quartile) individuals (error range: 8–43%, mean: 24%). There is no significant (t = 0.93, df 10, P = 0.37) difference in the mean prediction uncertainty for between ghost crabs (mean = 48%, se = 7%) and other brachyurans (mean = 37%, se = 6%); similarly, mean prediction uncertainty for larger (i.e. upper quartile) individuals is comparable (t = 0.29, df 8, P = 0.78) between ghost crabs (mean = ±25%, se = 4%) and the two other crab species analysed by us (mean = ±23%, se = 6%; Table 3).

Prediction uncertainty also differed within the same species measured at different locations. There are four published studies available for *Ocypode ceratophthalma* and three each for *O. quadrata* and *O. cursor* to assess intraspecific variation in burrow-body size relationships (Fig. 2). Prediction uncertainty at median observed body size ranged between ±9% and ±44% in *O. quadrata*, between ±16% and ±65% in *O. ceratophthalma*, and between ±22% and ±35% in *O. cursor* (Table 3). In *O. ceratophthalma*, regression slopes are similar between studies (ANCOVA, F = 1.22; df 3,123; P = 0.306), but the intercept is significantly (P < 0.05) larger in the study of Chan et al. (2006) as compared with other models of the same species (Lim et al., 2011, Yong et al., 2011, Lim and Yong, 2015). By contrast, slopes differ significantly between studies in *O. quadrata* (ANCOVA F = 5.85; df 2,242; P = 0.003) and in *O. cursor* (ANCOVA, F = 6.85; df 2,62; P = 0.002).

Most regression models relating burrow dimensions to body size did not depart significantly from linear relationships (Fig. 2). Runs tests did, however, indicate non-linear relationships in two data sets for *O. quadrata* (Alberto and Fontoura, 1999, Valero-Pacheco et al., 2007) and in one dataset for *Cardisoma gaunhumii* (Govender and Rodríguez-Fourquet, 2008).

Nine out of ten models for ghost crabs had slopes significantly different from unity, indicating that burrow - body size relationships are not isometric (i.e. body size scales allometrically with burrow sizes; Fig. 2). Of these nine allometric scaling relationships, all show that larger individuals inhabit disproportionally narrower burrows than smaller crabs (i.e. slopes are <1); this indicates that smaller crabs either excavate disproportionally wider burrows or opportunistically inhabit burrows excavated by larger crabs (i.e. the actual body size of crabs in burrows with large opening diameter is relatively smaller than those of crabs in smaller burrows; Fig. 2). A similar allometric scaling relationship where large burrows contained disproportionally smaller crabs was reported in *Cardisoma guanhumii* (Fig. 2n; Govender and Rodríguez-Fourquet, 2008) and *Heloecius cordiformis* (Fig. 2m; MacFarlane, 2010), whereas *Uca annulipes* showed the opposite pattern (Fig. 2k; Skov and Hartnoll, 2001).

4. Discussion

The observed variation in burrow occupancy is likely caused by varying degrees of burrow sharing, burrows being abandoned after surface
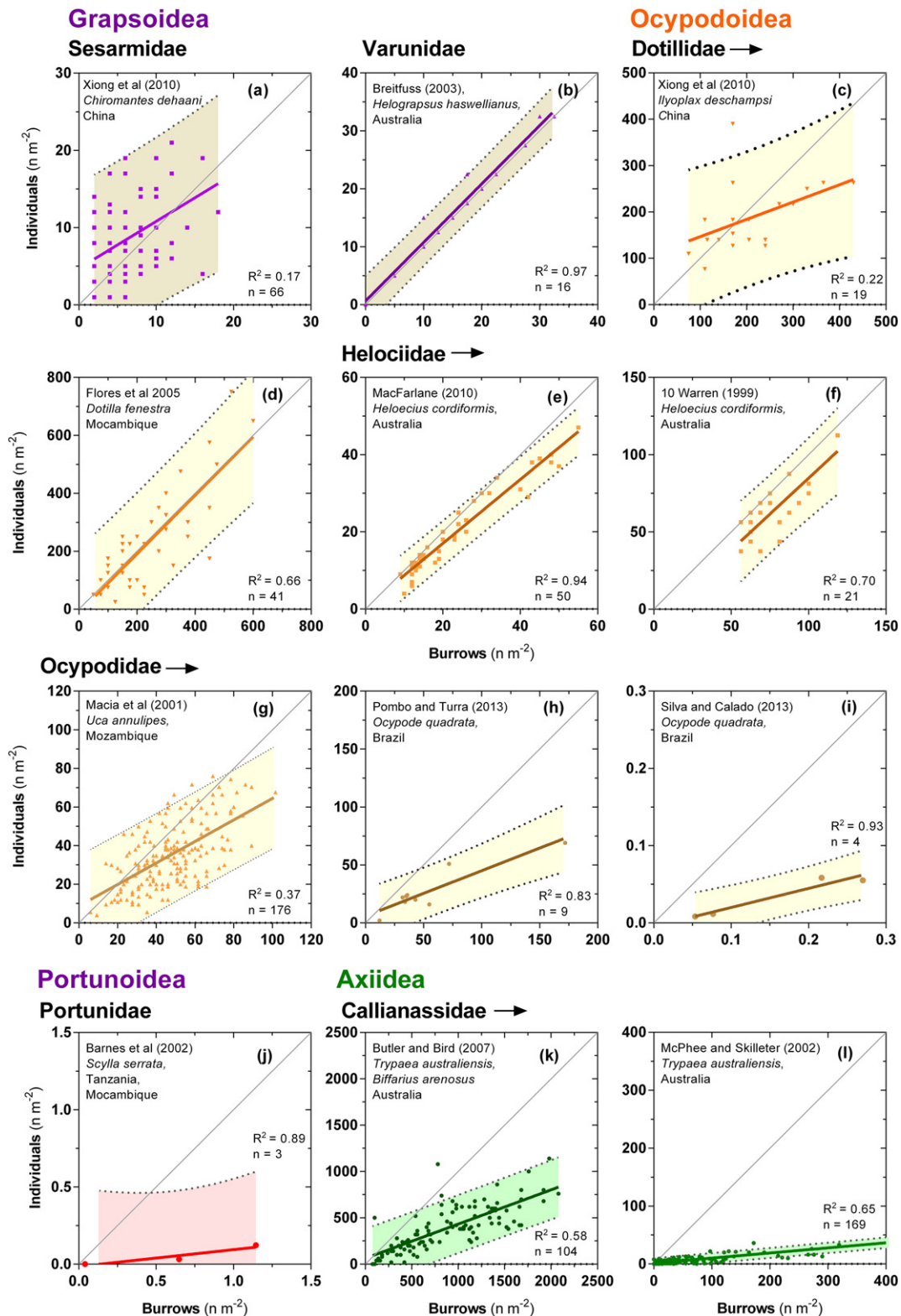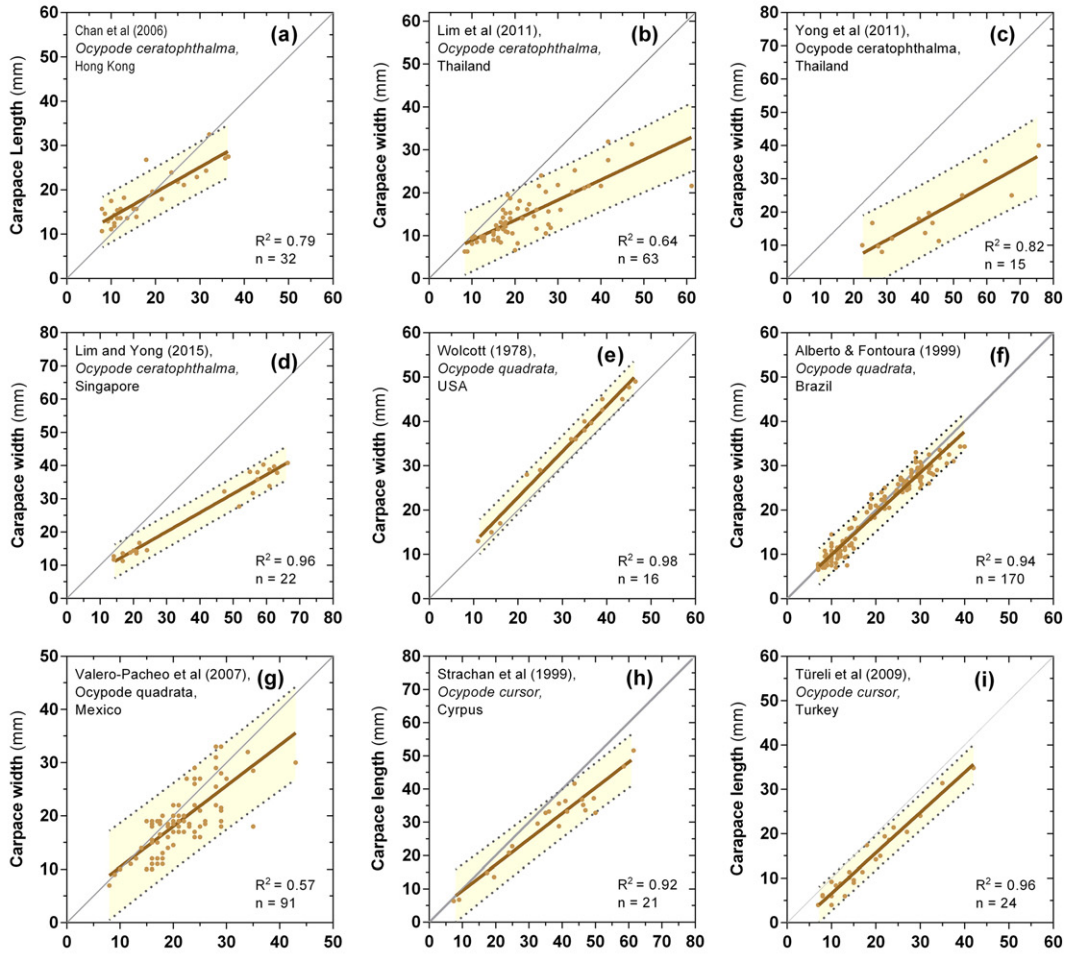
Fig. 1. Relationship between burrow opening counts and the density of individuals in marine, fossorial decapod crustaceans.

activity (e.g. relocation), crabs having been killed during surface activity, or burrows that have more than one opening. The frequency of burrow sharing may vary according to cycles in reproductive behaviour (e.g. males guarding receptive females, sexually mature females occasionally digging burrows which intercept male burrows or sharing burrows with males during the breeding season; Linsenmair, 1967,

Fellows, 1973, Hughes, 1973) or with predation risk (e.g. individuals escaping to nearest burrow regardless of whether it is occupied; Warren, 1990 and references therein). In settings where tides and waves do not cover burrow openings frequently, empty burrows may also result from imprecise homing behaviours of crabs after undertaking sojourns on the surface. Individuals that do not return to the original burrow either
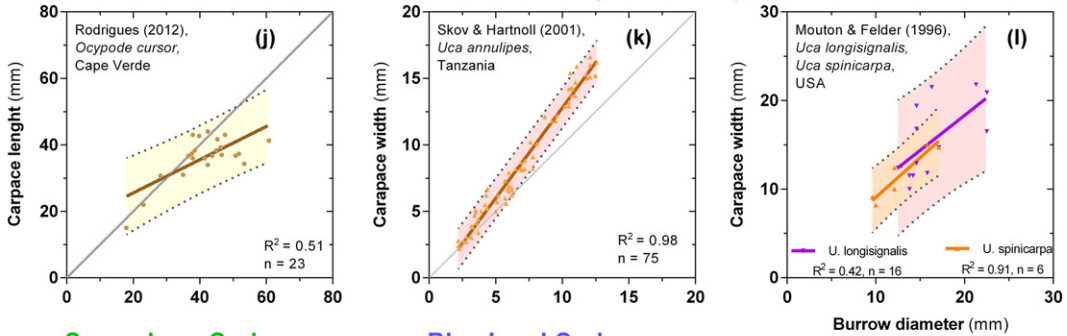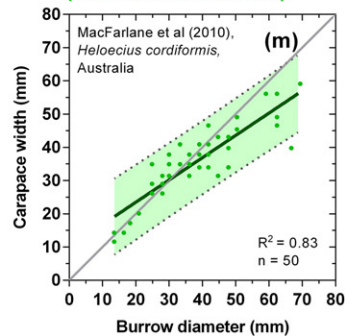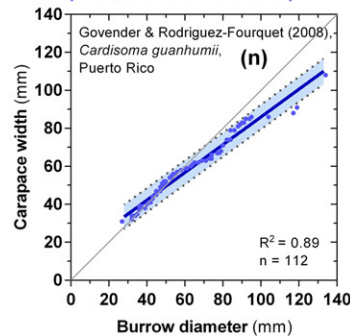
Fig. 2. Relationship between burrow size (opening diameter) and body size (carapace width or length) in marine, fossorial brachyuran crabs.

Table 2

Summary statistics of studies analysed in this paper that examined the relationship between burrow counts and density in marine, fossorial, decapod crustaceans.

Higher taxon	Species	Country (Lat., Long.)	n	R^2	Slope	(95% CI Slope)	Median density	Prediction interval (95%) at median density	Prediction error at median	Source
Infraorder Brachyura										
Superfamily Grapsoidea										
*Fam.*Sesarmidae										
	Chiromantes dehaani	China (31.67, 121.65)	66	0.17	0.61	(0.28–0.94)	8.00	−2.82–18.82	134%	Xiong et al. (2010)
Fam. Varunidae										
	Helograpsus haswellianus	Australia (−27.58, 153.25)	16	0.97	1.01	(0.91–1.11)	16.25	12.23–20.27	24%	Breitfuss (2003)
Fam. Dotillidae										
	Ilyoplax deschampsi	China (31.67, 121.65)	19	0.22	0.37	(0.02–0.73)	183.00	37.03–328.97	80%	Xiong et al. (2010)
Superfamily Ocypodoidea										
Fam. Dotillidae										
	Dotilla fenestrata	Mozambique (−26.06, 32.90)	37	0.66	1.01	(0.76–1.26)	200.00	−11.23–411.23	105%	Flores et al. (2005)
Fam. Heloeciidae										
	Heloecius cordiformis	Australia (−33.57, 151.3)	39	0.94	0.83	(0.76–0.90)	18.00	12.17–23.84	32%	MacFarlane (2010)
	Heloecius cordiformis	Australia (−34.03, 151.15)	21	0.70	0.93	(0.64–1.24)	62.50	37.10–87.90	41%	Warren (1990)
Fam. Ocypodidae										
	Uca annulipes	Mozambique (−26.03, 32.92)	176	0.37	0.56	(0.45–0.66)	34.00	8.42–59.58	75%	Macia et al. (2001)
	Ocypode quadrata	Brazil (−24.52, −47.17)	9	0.83	0.39	(0.23–0.55)	22.00	−0.36–44.36	102%	Pombo and Turra (2013)
	Ocypode quadrata	Brazil (−9.67, −35.74)	4	0.93	0.25	(0.05–0.44)	0.03	0.005–0.061	86%	Silva and Calado (2013)
Superfamily Portunoidea										
Fam. Portunidae										
	Scylla serrata	Tanzania (−8.01, 39.76)	3	0.90	0.11	(−0.36–0.58)	0.03	−0.47–0.53	1538%	Barnes et al. (2002)
Infraorder Axiidea										
Fam. Callianassidae										
	Trypaea australiensis & Biffarius arenosus	Australia (−38.22, 145.30)	104	0.58	0.37	(0.31–0.43)	380.00	66.50–693.50	82%	Butler and Bird (2007)
	Trypaea australiensis	Australia (−27.40, 153.44)	169	0.66	0.09	(0.07–0.10)	4.00	−4.60–12.60	211%	McPhee and Skilleter (2002)

Table 3
Summary statistics of studies analysed in this paper that examined the relationship between burrow opening diameter and body size in marine, fossorial, brachyuran crabs.

Higher taxon	Species	Country (Lat., Long.)	Habitat	n	R^2	Slope	(95% CI slope)	Median observed body size in mm	Prediction interval (95%) at median body size	Prediction error at median	Source
Supefamily Ocypodoidea											
Family Ocypodidae											
	Ocypode ceratophthalma	China (22.25, 114.25)	Sandy beach	31	0.80	0.56	(0.46–0.67)	15.62	10.00–21.24	36%	Chan et al. (2006)
	Ocypode ceratophthalma	Thailand (8.89, 99.91)	Sandy beach	63	0.64	0.47	(0.38–0.56)	13.07	5.88–20.25	55%	Lim et al. (2011)
	Ocypode ceratophthalma	Thailand (7.81, 98.4)	Sandy beach	15	0.81	0.55	(0.40–0.71)	16.69	5.82–27.56	65%	Yong et al. (2011)
	Ocypode ceratophthalma	Singapore (1.29, 103.91)	Sandy beach	22	0.96	0.57	(0.52–0.62)	29.69	24.79–34.59	16%	Lim and Yong (2015)
	Ocypode quadrata	USA (34.69, −76.69)	Sandy beach	15	0.98	1.03	(0.95–1.11)	38.13	34.54–41.72	9%	Wolcott (1978)
	Ocypode quadrata	Brazil (−30.27, −50.24)	Sandy beach	147	0.95	0.93	(0.89–0.96)	20.36	16.3–24.43	20%	Alberto and Fontoura (1999)
	Ocypode quadrata	Mexico (18.65, −95.1)	Sandy beach	86	0.57	0.76	(0.62–0.91)	18.41	10.28–26.54	44%	Valero-Pacheco et al. (2007)
	Ocypode cursor	Cyprus (35.33, 33.49)	Sandy beach	21	0.92	0.77	(0.67–0.88)	33.25	25.94–40.57	22%	Strachan et al. (1999)
	Ocypode cursor	Turkey (36.77, 35.79)	Sandy beach	24	0.95	0.91	(0.81–0.99)	11.12	7.24–15.01	35%	Türeli et al. (2009)
	Ocypode cursor	Cape Verde (16.13, −22.67)	Sandy beach	23	0.51	0.50	(0.28–0.73)	36.93	26.68–47.18	28%	Rodrigues (2012)
	Uca annulipes	Tanzania (−6.15, 39.2)	Mangroves	65	0.97	1.36	(1.31–1.42)	7.89	6.39–9.38	19%	Skov and Hartnoll (2001)
	Uca longisignalis	USA (29.61, −92.67)	Salt marsh	14	0.43	0.79	(0.21–1.36)	13.80	6.35–21.25	54%	Mouton and Felder (1996)
	Uca spinicarpa	USA (29.61, −92.67)	Salt marsh	6	0.88	0.89	(0.44–1.35)	11.20	7.85–14.55	30%	Mouton and Felder (1996)
Fam.Heloeciidae											
	Heloecius cordiformis	Australia (−33.65, 151.16)	Mangrove/mudflat	39	0.77	0.67	(0.55–0.79)	34.74	23.68–45.79	32%	MacFarlane (2010)
Superfamily Grapsoidea											
Family Gecarcinidae											
	Cardisoma guanhumi	Puerto Rico (18.26, −65.63)	na	63	0.97	0.73	(0.70–0.76)	57.94	51.63–64.25	11%	Govender and Rodríguez-Fourquet (2008)

need to construct a new burrow or opportunistically inhabit an established one, resulting in some burrows becoming vacant (Lucrezi and Schlacher, 2014).

We found that in many studies burrow counts yielded density estimates that had prediction intervals double or half the size of the predicted density values. It will largely be a matter of judgement by investigators whether the magnitude of this prediction uncertainty is 'acceptable' for the purpose of their study (e.g. desired effect size and precision of this effect) and hence the method is deemed to be 'reliable' or 'robust'. Authors appear to differ considerably in their judgement on this matter. Many papers that measure ghost crab burrow counts assume that these counts provide accurate estimates of density. Whether this holds true cannot be determined at present, simply because there are too few published data on the relationship between burrow and organism counts in ghost crabs.

We show that body size can in most cases be predicted with greater accuracy from burrow sizes than can density from burrow counts. The relationship between burrow and organism size is, however, not constant among congenerics or among conspecifics sampled at different sites. The implication of this variability is that validations of indirect methods using burrows (i.e. tests on how dimensions of burrows match with dimensions of individuals inhabiting burrows) need to be done specifically for local conditions (i.e. be study specific, or in extreme cases, even weather-specific or dependant on seasons). Given the variability we found in this review, it will rarely be valid to apply scaling functions derived from data at other sites or for other species.

There are also a number of situations where burrow counts will be impractical. Burrow openings can be masked by strong winds, tidal currents, swash events (especially during storms), and trampling (Schlacher et al., 2013a, 2013b). After such events, counts may, however, be more accurate when crabs re-emerge and hence every entrance is likely to be more indicative of an 'active' burrow. Ghost crabs near the poleward edge of their distributional range retreat to deeper burrows to avoid low surface temperatures during winter. Such 'hibernating' crabs plug their burrow entrances which become indistinct after a few days, making it impossible to index these populations by surveying burrows entrances during the colder months of the year (Schoeman et al., 2015). Using burrow counts as abundance and size proxies also requires field workers to distinguish consistently between the entrances of inhabited and abandoned burrows and to disregard holes in the sediment that are not of biological origin. Furthermore, burrow entrances should, ideally, be distinct between species. On some temperate sandy beaches these conditions can be challenging to meet: few ghost crab burrows can be interspersed among large numbers of burrows dug by amphipods and isopods and numerous smaller (diameter ca. 3–6 mm) holes are created in the sand by infiltrating swash displacing air from the underlying sand matrix (Schlacher and Schoeman pers. obs.); such situations require highly experienced field operators to make burrow proxies useful.

Modern ethical practices that seek to minimize harm to individuals and their habitat are increasingly important considerations, favouring the adoption of non-intrusive and environmentally benign techniques in ecology (Vivian and Schlacher, 2015, Williams et al., 2015). In this context, we reason that burrow proxies will remain an important tool in many situations (but see alternatives below), chiefly because they have a much lower environmental footprint than collections of animals, especially fossorial species that tunnel deep into the seafloor or beaches (Lucrezi et al., 2009a, 2009b, 2010, Lucrezi and Schlacher, 2010, Schlacher and Lucrezi, 2010a, 2010b, 2010c) (Table 4).

Whenever extraction of animals from the sediment is judged impractical or ethically unacceptable, alternative methods of sampling fossorial species are required. Using burrow counts and entrance measurements is widespread and common (Schlacher et al., 2014, Stelling-Wood et al., 2016), but not without shortcomings (Table 5). Alternatives to burrow proxies exist currently mainly in the form of:

Table 4
Factors influencing choice of method (e.g. physical collections of animals, visual censuses, or proxies) to estimate the abundance or body size of fossorial, decapod crustaceans.

Criterion	Notes, considerations
Biological and environmental attributes	
Feasibility and ease of observing and/or catching individuals directly	Abundance, size, colouration (camouflage), time spent on surface, sensitivity to observer presence, etc.;
The nature of the substratum and/or vegetation	Highly compact sediment with rooted large plants (e.g. mangroves) or dense smaller plants (e.g. seagrass) is difficult to excavate and the practice is environmentally destructive.
Ethical	
Environmental ethics and animal welfare	Disturbing, handling, collecting and/or sacrificing of individuals need solid ethical and moral justification which may not always be obtainable if alternative, non-intrusive methods are available;
Presence of sensitive species, habitats, or other environmental features of conservation or other significance	Disturbance of conservation-listed species and their habitats should be minimal or be avoided altogether;
Social	
Disturbance of people; public safety, etc.	Particularly important on recreational beaches where sampling sites are frequented by many users;
Cultural	
Sites of cultural and spiritual significance and connections	Critically important to avoid disturbance to protected and sacred places;
Post-collection analysis	
Animals required for tissue samples or other analyses requiring specimens	Likely to apply for environmental impact studies examining chemical pollution, physiological parameters, taxonomic studies, and genetic investigations;
Occupational health and safety	
Adequate risk management for employees undertaking field work	Particularly relevant in situations where physical collections of specimens require substantial physical exertion, are undertaken in harsh conditions (e.g. heat, cold, rain, biting and stinging animals) or over prolonged periods;
Logistics & costs	
Broad range of variables, mostly relating to size and quality of workforce, availability of research funds and accessibility of sites.	Number, motivation, fatigue of field workers; depth of water; depth of burrows; time taken to extract animals from sediment; availability of equipment; etc.

Table 5
Principal advantages and shortcomings of the three main methods used to estimate abundance and/or body size in burrowing, marine decapods.

Pros	Cons
Burrow proxies	
— Generally small environmental footprint;	— Occupancy rate varies with depth of burrows (higher for deeper burrows);
— Easy, quick, cheap, requiring little specialised equipment in intertidal areas;	— Not always possible to distinguish between co-existing species in the same habitat;
— Thought to approximate the total population, rather than the proportion active at a given time and thus available for visual census;	— Largely unknown whether environmental conditions (e.g. looser sediment collapsing burrows, presence of buried shell hash or stones) or human interference (e.g. trampling) influence rates of burrow abandonment during constructions or the longevity of burrows;
— Limited disturbance to environment, cultural sites and other beach users;	— Compromised by weather, currents, tides, human interference that can obliterate burrows or mask signs of occupancy (e.g. tracks, excavated sediment near entrance, food scraps);
— No killing of animals and (presumably) low stress experienced by fossorial individuals;	— Environmental conditions across the shore may influence entrance longevity (e.g. likely to persist longer in vegetated dunes, higher on shore above tide and swash reach);
	— Field ecologists must be able to distinguish between burrows and 'burrow-like' holes, and also between burrows that are active and those that are not.
	— Burrow entrances may be obscured by vegetation; this is relevant for estimating abundance in coastal dunes, seagrass meadows or similar habitats;
	— Conventionally, burrow counts are made for 'active' burrows judged to have been recently constructed, maintained or occupied by an individual on the basis of surface marks associated with these activities (e.g. tracks, presence of excavated sand, remains of food items etc.). However, burrows without any obvious signs of recent activity may in fact be occupied (Pombo and Turra, 2013).
Visual census	
— Can be done from a distance if required (consideration for sites that are difficult to access);	— Disturbance by observers (or other events) causes animals to retreat inside burrows;
— Longer duration recordings are feasible and cheap, using consumer cameras in water-resistant housings (e.g. GoPro cameras);	— Technically challenging for nocturnal animals;
— Provides data on numbers of active individuals – important in the context of predator-prey or other species interactions studies;	— Limited to part of population that is active (e.g. fails to account for individuals not leaving burrow such as ovigerous females);
— Generally can distinguish among species;	— Small and/or cryptically coloured individuals are difficult to detect; this can be compounded in habitats with high relief and/or vegetation;
— Behaviour data can complement counts;	— Constrained by weather, currents, tides, waves;
— Obtain a record (when using image-based sampling) of all species and data that can be revisited at a later date for QC or for other projects; data can be archived, which is important in impact assessments for legal reasons.	— Can generate large amount of video footage or photos, that requires large time investment to analyse in the lab;
Physical collections	
— Specimens available for laboratory analyses (e.g. toxicant levels, physiological condition, reproductive state, genetics, biomarkers, etc.);	— Stress, injury, mortality to animals;
	— Habitat damage;
— Direct abundance and body size estimates may be more accurate if individuals can be consistently and efficiently extracted from the sediment;	— Interference with cultural values or social uses;
	— Burrow excavation difficult in areas of high root density in vegetated habitats;
— Separate abundance and body-size values available;	— Technically challenging in deeper waters;

Table 5 (*continued*)

Pros	Cons
— Ability for specimens to be re-counted or re-analysed at a later date; — Can yield data at species level resolution;	— Repeat observations biased if habitat altered during collections and/or removal of individuals and associated mortality; — For impact assessments it can be difficult to attribute disturbance to the 'impact' being monitored and not the monitoring itself if severe and repeated disturbance to animal populations and their habitats. — Possibility of injury to field workers where repeated manual excavations of large volumes of sediment are required.

(1) visual surveys (using binoculars, cameras, drones); (2) trapping; and (3) tagging (mark-recapture, tracking).

It is standard practice to visually count crabs in mangrove forests (Skov and Hartnoll, 2001). Visual daytime counts, using binoculars, are theoretically feasible for ghost crabs on beaches that have little or no human activity, but impracticable on others were ghost crabs become mainly nocturnal in the presence of humans (Lucrezi and Schlacher, 2014). Surface-active ghost crabs can, however, be counted at night using red lights to lower observer disturbance (Peterson et al., 2013). For crabs in mangrove forests, there is published evidence that visual counts tend to yield lower abundance values, with the magnitude of under-estimation ranging between 27 and 40% depending on species and site (Macia et al., 2001, Skov and Hartnoll, 2001).

Camera traps are now routinely employed on ocean beaches to sample vertebrates (Huijbers et al., 2013, Brown et al., 2015, Huijbers et al., 2015a, 2015b, Schlacher et al., 2015). Current camera models do capture images of larger crabs during colder weather (Schlacher pers. obs), but commercially available movement sensors are presently not sensitive enough to routinely detect the majority of crabs; this is likely to change as technologies improve. We also suggest that drones can be used to undertake image-based sampling of burrow entrances and surface-active crabs.

Future surveys can also take advantage of temperature differences between burrows and the sediment surface or between crabs and the surrounding sediments, using thermal imaging equipment. Crabs active on the surface can also be caught by investigators chasing them down with alacrity and determination (e.g. Schlacher et al., 2007, Schlacher and Lucrezi, 2010a), but this is rarely going to be quantitative or comparable between studies and sites as 'ghost hunters' change or age. There is also the possibility of "capping off" (tramping or sweeping them closed) burrows and revisiting them after nightfall to count the number of holes reopened.

Trapping (e.g. pitfalls) is a standard method to survey crabs in mangrove forests (Smith Iii et al., 1991), but generally yields fewer individuals of ghost crabs on beaches and in coastal dunes (Schlacher et al., 2011). The efficiency of traps may be improved with "fall-away" platforms around the perimeter that encourage crabs to explore beyond the rim of the bucket until their weight overwhelms the pivot point, and they are dumped into the trap.

Mark–release–recapture is a long-established and widely used technique to estimate population abundance in diverse groups of vertebrates and invertebrates (Hagler and Jackson, 2001). It offers fruitful opportunities for low-invasive sampling of crabs and other larger crustaceans, provided that catch issues (cf. trapping limitations above) can be overcome. When combined with cutting-edge tracking devices (e.g. miniaturized GPS tags) and bio-loggers, the breadth of data derived from such approaches will provide far greater insight into crustacean biology and ecology than can be gleaned from indirect burrow counts.

All animals that are active in the environment will alter the 'soundscape', albeit often in subtle ways. This property is now widely employed in ecological studies (McIver et al., 2014, Staaterman et al., 2014, Towsey et al., 2014) and hence modern acoustic techniques can be fruitfully extended to studies targeting fossorial crustaceans

above and below water. It may also be possible to develop chemical sensors that detect crabs based on specific gaseous signatures.

5. Recommendations

As a minimum set, we suggest that all investigators using burrow proxies for fossorial species undertake five fundamental steps:

1. Explicitly report the criteria used in selecting a specific method.
2. Validate the use of burrow proxies in the field by deriving models that can predict population densities and body size of individuals with known error. Investigators should then report model parameters and prediction uncertainty.
3. Undertake field validation of indirect methods at multiple time points, but at least before and after the work is undertaken, to test for temporal change.
4. Test whether scaling relationships between burrow counts and entrance size and the predicted densities and body sizes of individuals change significantly with: a) habitat conditions (e.g. sediment grain size, organic content, moisture, elevation, compactness, depth, wave exposure); b) seasons or other periodic events (e.g. monsoons, ENSO); c) the intensity, type and frequency of human activities; or d) geographic location (e.g. latitudinal differences).
5. Develop and adopt new technologies (e.g. drones, thermal, chemical or acoustic sensors).

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