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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 thoroughabout 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

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