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Rapid population recovery of *Ocypode ceratophthalmus* (Pallas, 1772) (Crustacea: Brachyura: Ocypodidae) after an oil spill in Singapore

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Abstract. An oil spill occurred in the Straits of Singapore (one of the world's busiest shipping lanes) on 25 May 2010. Pre- and post-oil spill population parameters (i.e., abundances, densities, burrow diameters, location of burrows with respect to shore height and size-distribution gradient) of the ghost crab *Ocypode ceratophthalmus* on two adjacent beaches at East Coast Park, Singapore, were compared to study the extent of impact and subsequent recovery rate. The ghost crab population, which was decimated after the oil spill, rebounded within three months to densities close to those that were observed prior to the oil spill. The lower boundary of the recolonised population in September 2010 and January 2011 shifted upshore by about 0.4 m from that documented in September 2006. The zone that was recolonised was between 2.6 m and 2.8 m above Chart Datum in January 2011, directly above the upper limit of the region contacted by the spilled oil, indicating that the crabs avoided settling in sediments that contained oil residues. No distinct size distribution gradient on the shore was observed in the pre- and post-spill populations. This study confirms that the abundance and distribution of *O. ceratophthalmus* provide reliable, sensitive and effective indications of the conditions of beach habitats.

Key words. Biological indicator, ghost crabs, tropical oil spill, population ecology, sandy shores

INTRODUCTION

Escalating world population growth, coastal development, recreational seashore activities, pollution, rising sea levels, and increasing storms from global climate change have degraded sandy shores around the world (Defeo et al., 2009). Sandy beaches have ecological and socio-economic importance as they provide unique ecosystem services and increase economic prosperity for residents and tourists (Davenport & Davenport, 2006). Some of these ecological services include: (1) storing and transporting sediment by waves; (2) dissipating waves and buffering coasts against storms and tsunamis; (3) breaking down pollutants and organic materials in the marine ecosystem; (4) recycling nutrients; (5) filtering large volumes of seawater, and (6) maintaining biodiversity by providing nursery areas for larvae and juvenile fish, breeding grounds for turtles and shorebirds and a unique habitat for many organisms adapted to the beach environment (Carter, 1988; Defeo et al., 2009). Hence, it is essential that suitable approaches be used to manage the ecological health and recreational use of beaches.

Certain species ("bioindicators") can be used to evaluate the health of the environment and provide early signs of environmental deterioration (Dale & Beyeler, 2001). An effective bioindicator shows a measureable and predictable early response to an environmental stress and is resilient enough to survive a wide range and intensity of stresses. Ideally, it should also be a well-studied organism that has a broad geographical distribution and is common where the ecological status of its habitat is of interest or importance. In addition, the methods used to quantify the response should be simple and cost-effective (Noss, 1990; Dale & Beyeler, 2001; Carignan & Villard, 2002).

Only a few common molluscs (clams) and crustaceans (amphipods, mole crabs and ghost crabs) are suitable bioindicators of human disturbance of beaches (see Wenner, 1988; Veloso et al., 2008; Yong & Lim, 2009; La Valle et al., 2011). *Ocypode* spp. or ghost crabs meet many criteria of a suitable ecological indicator (see Lucrezi & Schlacher, 2014). They are conspicuous and common on tropical and sub-tropical beaches globally. In addition, the response of these crabs to human activities can be determined easily by counting the number of active burrows on the shore (Barros, 2001). Yong & Lim (2009) used burrow densities of *Ocypode ceratophthalmus* to indicate the extent of disturbance from human traffic and boating activities (i.e., the presence of boats and dinghies) on the shores of Singapore. Lower densities of *O. ceratophthalmus* burrows were observed at sites with high human traffic and boating activity. In general, the responses of *Ocypode* crabs to anthropogenic disturbances are predictable. Similar trends have been documented in other species of ghost crabs that were subjected to other types of human pressures. For example, lower burrow densities of *O. cordimanus* and *O. ceratophthalmus* in Australia (see Lucrezi & Schlacher, 2014) as well as *O. quadrata* in the United

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States (see Hobbs et al., 2008) were reported for beaches with heavy trampling, beach armouring and high traffic from off-road vehicles. While few sandy-shore organisms are suitable bioindicators of general human disturbances, even fewer are suitable bioindicators of oil pollution.

Oil pollution has strong and lasting negative effects on coastal organisms (Brown & McLachlan, 2002). Effects of oil spilled from the Exxon Valdez tanker on the organisms in the Alaskan coastal ecosystem were still evident more than a decade later (Peterson et al., 2003). There are many studies of the effects of petroleum hydrocarbons on benthic marine invertebrates, but none on the ecological effects of spilled oil on the macrofauna of sandy beaches in the Asia-Pacific region (see de la Huz et al., 2005; Junoy et al., 2005; Lucrezi & Schlacher, 2014). This is a concern because oil spills are very likely in tropical waterways where about 90% of the global production of oil occurs (Nansingh & Jurawan, 1999). Ocypodid crabs are the most conspicuous members of the macrofauna in coastal habitats in tropical and subtropical regions and are, therefore, one of the most susceptible groups of crustaceans to oil spills when the oil enters the intertidal zones of sandy shores. Except for a mention that the percentage of crabs contaminated by oil differed among the ghost crabs *O. ryderi*, *O. ceratophthalmus* and *O. madagascariensis* in South Africa (see Jackson et al., 1991), there is only one quantitative study of the effects of oil pollution on ghost crabs. Significantly higher mortality rates were observed in reproductively active *O. quadrata* individuals than those that were not reproductively active at low concentrations of oil contaminants (Jackson et al., 1981).

Singapore is one of the world's busiest ports and, has the largest oil refinery in Asia (where half the world's supply of crude oil is processed). The Straits of Singapore is at the crossroad of many shipping lanes in the Asia-Pacific region linking West Asia to Europe. High traffic of ships, and in particular oil tankers, increases the risk of oil pollution in the waters around Singapore. In fact, 39 spills of 34 tonnes or more of oil pollutants have occurred since 1960, making the Straits of Malacca and Singapore Straits hot spots of oil pollution (Etkin, 1997). On May 25 2010, an oil tanker, MT Bunga Kelana and a bulk carrier, MV Wally, collided in the Straits of Singapore and spilt about 2500 tonnes of crude oil into the sea off the east coast of Singapore. The oil slick reached the coastal areas on the east of Singapore a day later and covered 7.2 km of the beach at East Coast Park (Gunasingham & Liew, 2010). Physical and chemical methods were used to remove and contain the spread of the oil on the water surface and shore. The clean-up operation took 10 days to complete with the aid of containment booms, skimmers, imbiber absorbents and 30 tonnes of dispersants (Elias, 2010). No ghost crab burrows were observed for a few months after the clean-up until September 2010 when many burrows excavated by juvenile *O. ceratophthalmus* were observed on the beaches of the east coast of Singapore.

The existence of pre-spill data on the ghost crab abundance, population densities, age-structure and distribution on the shore at East Coast Park (Yong & Lim, 2009) provided a rare opportunity to examine the ecological effects of a major oil spill on *Ocypode ceratophthalmus* (one of the top predators on the beach). The objectives of this study were to compare the following parameters of the pre- and post-spill *O. ceratophthalmus* populations: (1) abundance and density; (2) size-frequency distribution; (3) population distribution with respect to shore height, and (4) size-distribution gradient on the shore.

MATERIAL AND METHODS

Study site. The study was conducted at the sandy beaches of East Coast Park, Singapore (latitude 1°18'29"S and longitude 103°56'27"E). This stretch of public coastline has high human traffic the whole year round and recreational activities such as camping, windsurfing, sailing and fishing, occur frequently at the beach. In 2006, Yong & Lim (2009) studied the East Coast Park ghost crab population at seven sites with different levels of human disturbance. As the oil spill completely decimated the ghost crab population at all seven sites in 2010, no spatial control (i.e., one that did not receive oil) was available for study (as described by Green, 1979). Hence, we can compare the seven sites before and after the oil spill but not areas that were and were not oiled after the spill. Crabs were absent from all the sites for the first three months after the oil-spill (June to August 2010), and recolonised all of the sites from September 2010 onwards. The two most accessible sites, C and D, from Yong & Lim (2009) were monitored for this study. In 2006, both beaches had shorelines of about 120-m length and were categorised as 'high disturbance' sites. Fishing boats also were moored on the shores of site C adding to the disturbance from high human traffic. When this study was conducted in 2010, all the fishing boats had been cleared from site C and beach camping was the dominant activity instead. In addition, heavy construction work (e.g., piling installation) began in November 2010 at site D and reduced the original 120-m shoreline by half.

Sampling. Post-spill data were collected from June 2010 to January 2011. Juvenile ghost crabs were observed at sites C and D in September 2010, three months after the oil spill. Burrow recording was conducted only on days with appropriate tides (for accessibility to the study site), good weather, and on days that were not public holidays (to avoid high human disturbance). Hence, no data were available for October, November and part of December 2010 due to these constraints. The pre-spill data for a three-month period (June to August 2006) for sites C and D, from the study by Yong & Lim (2009), were used for comparisons. Fieldwork was conducted during low tide on non-rainy mornings at dawn from about 0700 hours until 1000 hours. Early sampling ensured a better estimation of burrows as ghost crabs plug up their burrows as the temperature increases during the day. Fieldwork at site C for pre- and post-spill periods was conducted on 15 and 12 days respectively. At site D, we had 10 days of pre-spill data and nine days of post-spill data.

Burrow density for each sampling session was determined by calculating the number of burrows per 100 m^2. The diameter of each burrow was measured to the nearest 0.1 cm with a ruler. Size of the crab occupants was determined by establishing the relationship between crab size and the diameter of the burrow that they excavate. To minimise disturbance of the crab populations at the study sites, the relationship was determined with a population of *O. ceratophthalmus* at a neighbouring bay with similar sediment characteristics (see Yong & Lim, 2009). The burrow diameters of 22 randomly-selected open burrows of freshly-emerged *O. ceratophthalmus* were measured before the respective crab occupants were captured for morphometric measurements. None of the crab occupants were observed to exchange burrows before the measurements. Carapace widths of the crabs were measured to the nearest 0.01 mm with a pair of digital Vernier calipers (Mitutoyo). These sampling methods allow long term non-invasive monitoring of the crab population at the study sites over a long duration of time. The distance of each burrow from the Mean High Water Spring (MHWS) tide-level (2.7 m above Chart Datum) was measured on six days: 2 August 2006 (Pre 1a), 4 August 2006 (Pre 1b), 11 September 2010 (Post 1a), 12 September 2010 (Post 1b) and 8 January 2011 (Post 2a), 9 January 2011 (Post 2b). Each burrow location with respect to shore height was calculated by simple geometry using the gradient of the shore (10° inclination). Scatterplots of the location of burrows with respect to shore height and corresponding carapace widths were plotted to determine the distribution of the ghost crab population on elevation gradient as well as size-distribution gradient of crabs on the beach before and after the oil spill. A 0.2 m zone (in vertical height above Chart Datum) with the highest abundance of burrows was identified. The percentage of burrows that occur within this 0.2 m zone was then calculated.

Data analyses. Two-sample t-tests were used to test for the difference in the abundance of burrows before and after the oil spill for sites C and D, after testing for equality of variance (site C: Levene's test statistic = 0.21, $p = 0.650$), (site D: Levene's test statistic = 1.89, $p = 0.187$). The densities of burrows between the pre- and post-spill periods for the sites C and D data were tested for homogeneity of variance (Levene's test statistic = 3.56, $p = 0.022$). After ln-transformation, the densities showed homoscedasticity (Levene's test statistic = 1.31, $p = 0.284$) and a Two-way Analysis of Variance (ANOVA) was used to compare the pre- and post-spill densities at the two study sites. Size of crab occupants of all the burrows sampled were calculated from the regression of the burrow diameter (BD) and carapace width (CW) of *O. ceratophthalmus*: BD = 0.17CW - 0.37 (Fig. 1). The r^2 of 0.96 indicates that the burrow diameter was closely related to the size of the crab and suggests that the estimated CW from the regression equation is an accurate representation of the crab sizes in the populations.

Population size distributions of the crabs on six sampling days at three periods: pre-spill (2, 4 August 2006), three months post-spill (11, 12 September 2010) and seven months post- spill (8, 9 January 2011) were determined. The Kolmogorov-Smirnov test was first used to compare the size distributions between the two replicate sampling days

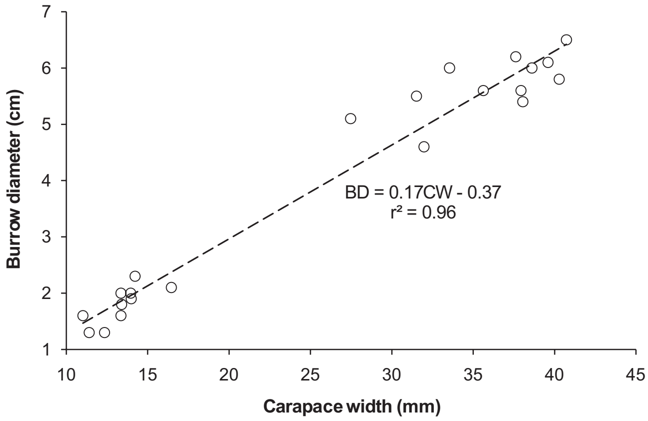

Fig. 1. Scatterplot and fitted regression line for Burrow diameter against Carapace width for *Ocypode ceratophthalmus* from East Coast Beach, Singapore ($r^2 = 0.96$).

within each period of the study. In the absence of significant difference between the two sampling days' size distributions, further comparisons of the distributions between the sampling periods: pre-spill vs three months post-spill and three months post-spill vs seven months post-spill using the data from the day with the larger population size were carried out with the Kolmogorov-Smirnov test. A t-test was used to test for the difference in carapace width of the pre-spill population on 2 August 2006 and the post-spill population on 8 January 2011 after testing for equality of variance (F-test statistic = 0.81, $p = 0.144$).

RESULTS

Abundance and density. Before the oil spill, the mean abundance of crabs at site C was generally higher than that at site D (Fig. 2a). Post-spill data showed the absence of crabs from June to August 2010 (Fig. 2b). When the crabs recolonised the sites three months after the oil spill, site C generally had a slightly larger number of crabs than site D (Fig. 2b) except for September 2010. In December 2010, there were few crabs at both sites (Fig. 2b). By January 2011, the abundance for both sites had increased to pre-spill levels. The mean abundance of burrows for the pre- and post-spill periods at site C were similar ($t = 1.72$, df = 25, $p = 0.098$; 84.7 ± 8.0 burrows ≈ 66.1 ± 6.8 burrows; mean ± S.E., respectively) (Fig. 2c). There was also no significant difference in the mean abundance of burrows for the pre- and post-spill periods at site D ($t = 0.26$, df = 17, $p = 0.801$; 61.9 ± 5.6 burrows ≈ 65.1 ± 12.0 burrows; mean ± S.E., respectively) (Fig. 2c).

In general, a similar trend to the abundance data was observed for mean densities of the pre- and post-spill populations (Fig. 3a, b). It should be noted that for site D, although it might appear that the crab abundance had decreased, the density of crabs was not affected as the area of the study site was halved. Results of the Two-way ANOVA showed that the interaction term, 'Site × Period', for mean density was significant ($F_{1,42} = 12.35$, $p < 0.05$), hence, no further analyses were carried out. The interaction between the two factors is clearly seen in Fig. 3c: prior to the oil spill, site D had lower densities than site C (5.2 ± 0.5 < 7.1 ± 0.7

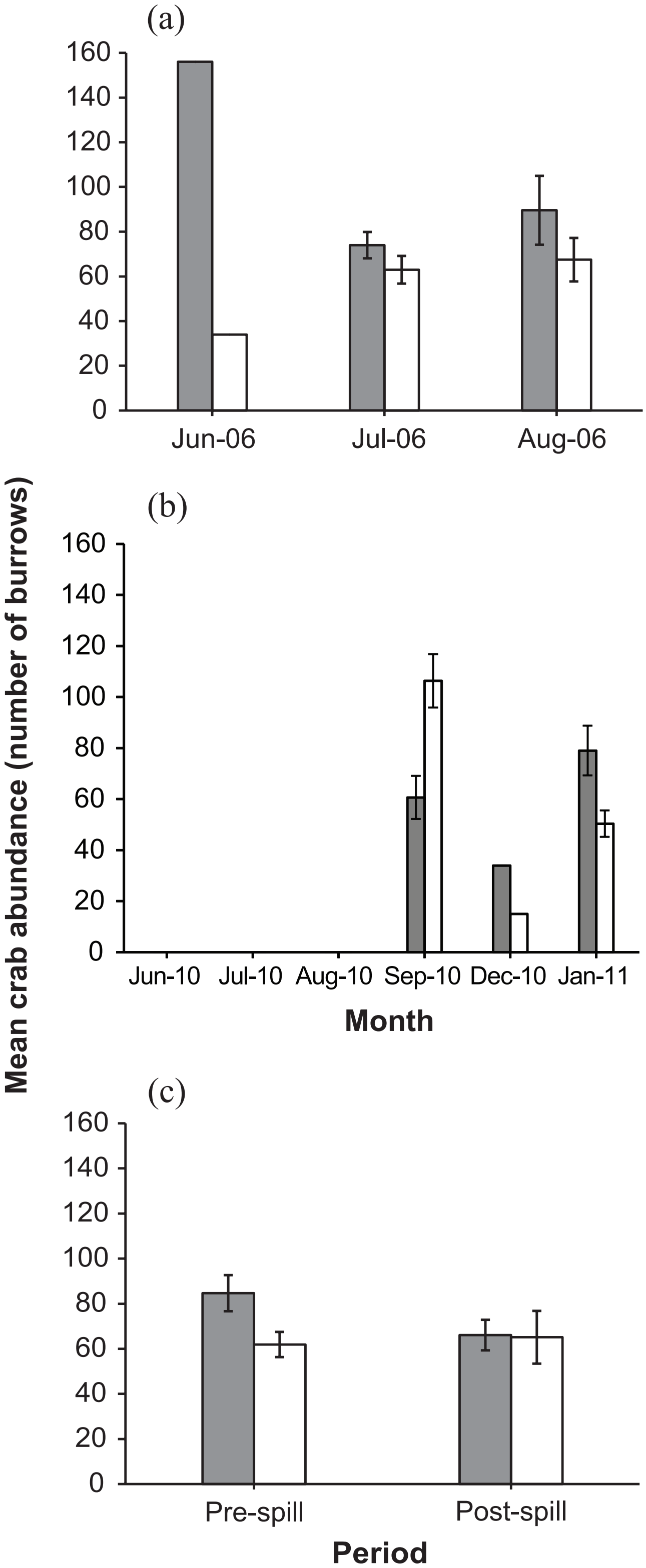

Fig. 2. Mean abundance ± S.E. of *Ocypode ceratophthalmus* burrows at East Coast Park: (a) Pre-spill period (June–August 2006); (b) Post-spill period (September, December 2010 and January 2011); (c) Pre- and Post-spill periods (combined data for three months). ■, site C; □, site D.

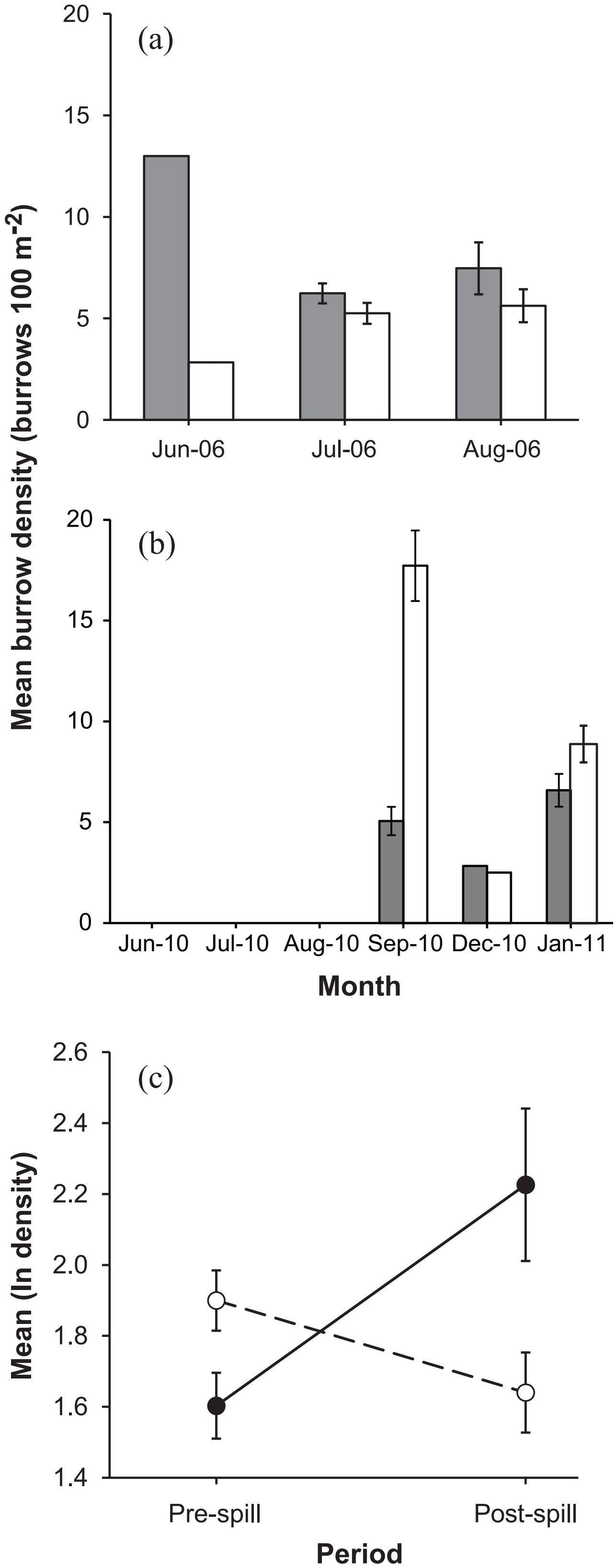

Fig. 3. Mean density ± S.E. of *Ocypode ceratophthalmus* burrows at East Coast Park: (a) Pre-spill period (June–August 2006); (b) Post-spill period (June 2010–January 2011); (c) Interaction plot of fitted mean ln density ± S.E. across Site and Period. ■, ○-----○, site C; □, ●——● site D.

burrows per 100 m^2); however, this trend was reversed after the oil spill (10.9 ± 2.0 > 5.5 ± 0.6 burrows per 100 m^2).

Population size and size-frequency distribution. The mean population sizes on the two sampling days at the two sites for each period were: N = 206 ± 5 crabs (August 2006), N = 164 ± 13 crabs (September 2010) and N = 145 ± 18 crabs (January 2011); mean ± S.E. Results of the Kolmogorov-Smirnov test indicated that the crab size distributions on the two replicate sampling days within each period were not significantly different (Table 1). There was significant difference in the size distribution between the pre-spill and post-spill population in September 2010: Pre 1a vs Post 1b (Kolmogorov-Smirnov test, D = 0.197, n_1 = 210, n_2 = 177, p = 0.001) and between the post-spill populations in September 2010 and January 2011: Post 1b vs Post 2a (Kolmogorov-Smirnov test, D = 0.497, n_1 = 177, n_2 = 160, p = 0.000) (Table 1). The mean carapace width of the pre-spill population on 2 August 2006 was significantly greater than that of the post-spill population on 8 January 2011 (t = 7.74, df = 368, p = 0.000; 24.30 ± 0.58 mm cf. 17.13 ± 0.74 mm; mean ± S.E., respectively). In the pre-spill population, the modal size class of CW was between 20 to 24 mm (Fig. 4a) whereas the modal size class of CW of the post-spill population in September 2010 (Fig. 4b) was 16 to 20 mm. Large numbers of small crabs (mode at size class of CW of 8 to 12 mm) colonised the shore (Fig. 4c) in January 2011. Crabs ranging from CW of 10 mm to 45 mm were distributed across the entire zone of burrow occurrence (Fig. 5a, b). In January 2011, even small crabs with CW between 5 mm and 10 mm were present (Fig. 5c).

Before the oil spill on 2 August 2006, a 0.2 m wide stretch of the beach ranging from 2.1 m to 2.3 m above Chart Datum was identified as the zone of tidal heights with the highest abundance of burrows (Fig. 5a). Around 64% of the *Ocypode ceratophthalmus* burrows occurred in this 0.2 m band with few burrows excavated beyond the 2.5 m level (Fig. 5a). Three months after the oil-spill on 12 September 2010, 64% of the burrows were still found within the 0.2 m band of tidal heights with the highest abundance of burrows (Fig. 5b). However, the 0.2 m band had shifted upshore and ranged between 2.5 m and 2.7 m above Chart Datum (Fig. 5b). Seven months post-oil spill on 8 January 2011, 68% of the burrows were distributed within the 0.2 m band which ranged between 2.6 m to 2.8 m above Chart Datum, past the MHWS tide-level (Fig. 5c).

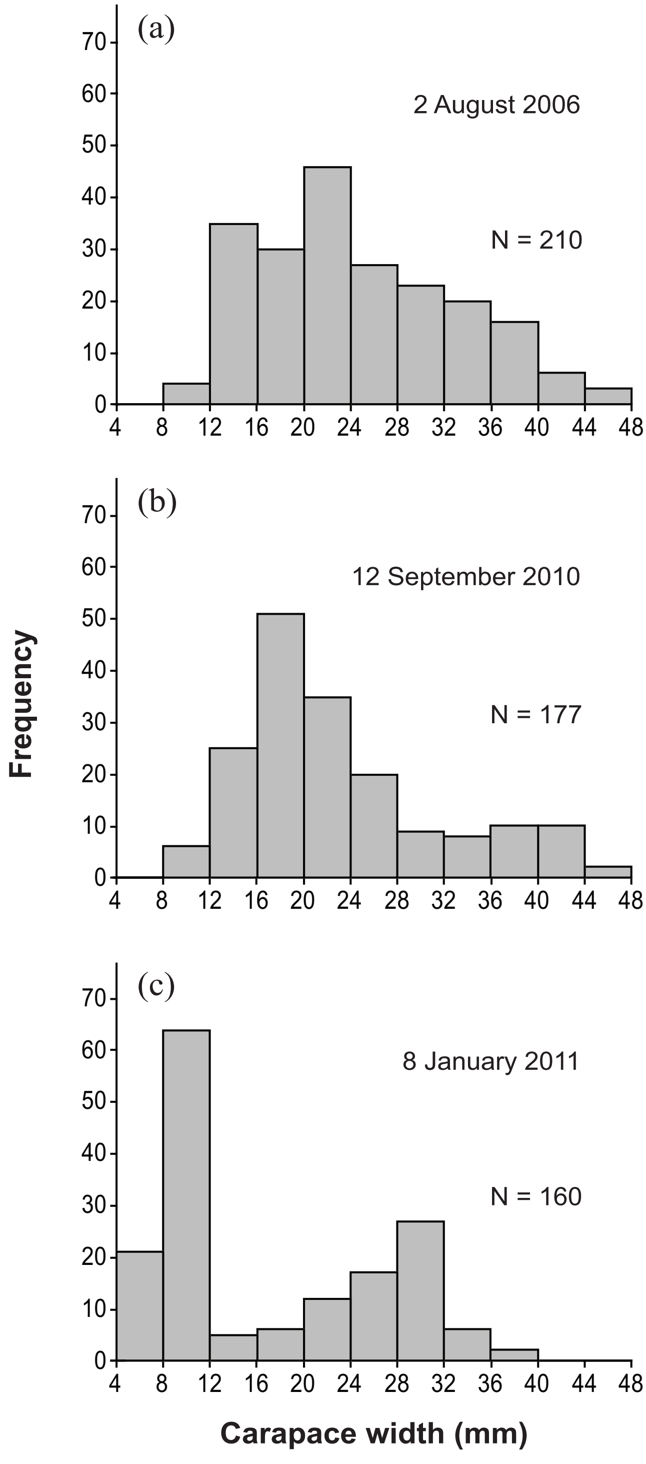

Fig. 4. Size distributions of the *Ocypode ceratophthalmus* populations at East Coast Park, Singapore on three sampling days: (a) Pre-spill period: August 2, 2006; (b) Post-spill period (three months after oil spill): September 12, 2010; (c) Post-spill period (seven months after oil spill): January 8, 2011.

DISCUSSION

Abundance and density. Prior to the oil spill in 2010, although both study sites were classified by Yong & Lim (2009) as shores that had high human disturbance, it can be seen that ghost crab abundance at site C was generally higher than that at site D. This could be due to the occasional presence of discarded fish from the fishing boats at site C, which may have supported higher crab abundance despite the considerable physical disturbance from beached fishing boats. This trend was not observed when the crabs recolonised the beaches three months after the oil spill (i.e., in September 2010); instead, there were fewer crabs at site C than at site D. Increased human traffic due to camping activities as well as the absence of extra food source (i.e., discarded fish from fishing boats) could perhaps explain the temporal difference. The abundance of crabs decreased substantially in December 2010 at both sites. This can be partly attributed to the seasonal year-end monsoon rains as well as the disturbance caused by the construction at the sides of the bay, which began in

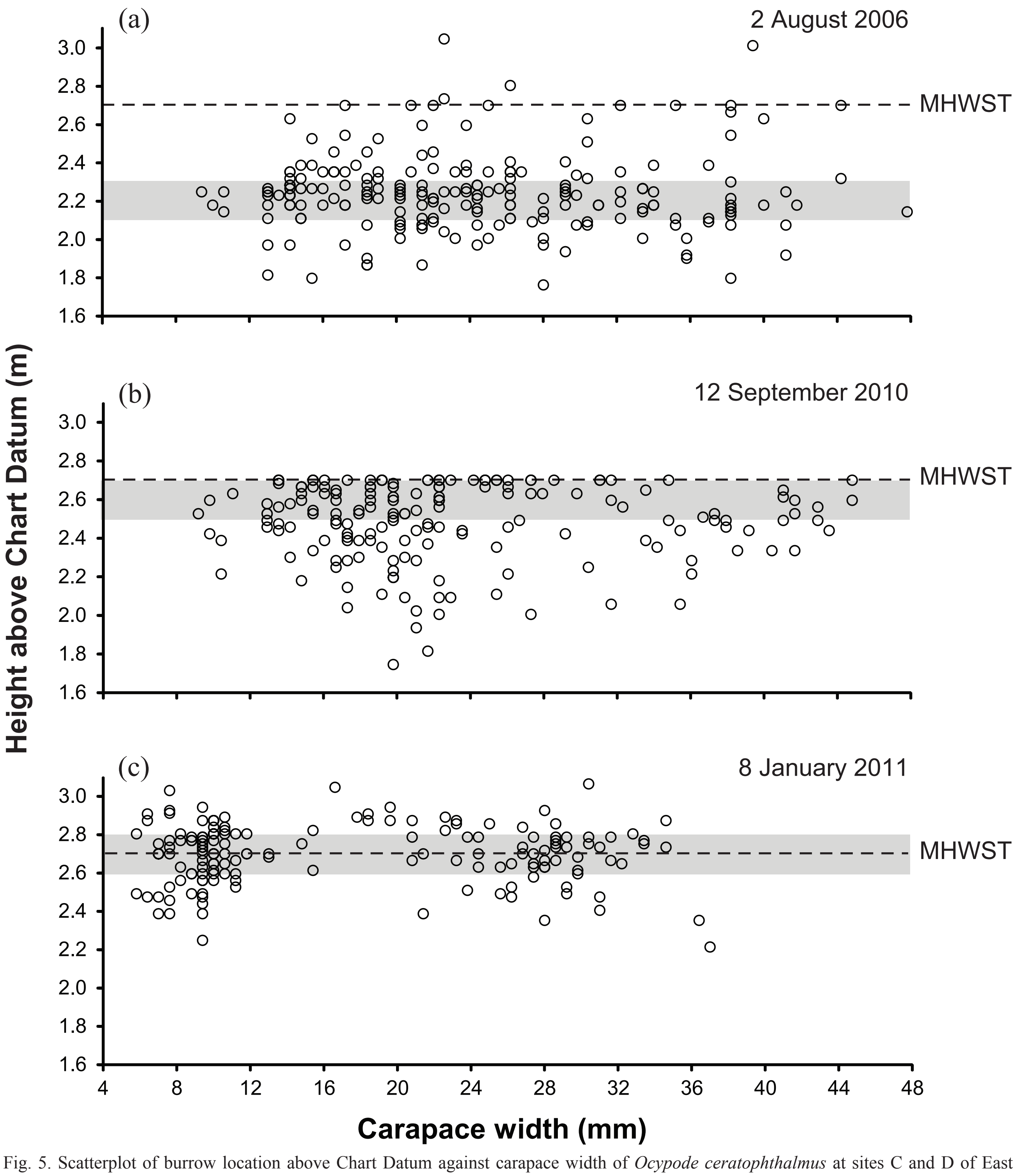

Fig. 5. Scatterplot of burrow location above Chart Datum against carapace width of *Ocypode ceratophthalmus* at sites C and D of East Coast Park, Singapore on three common sampling days: (a) Pre-spill period: August 2, 2006; (b) Post-spill period (three months after oil spill): September 12, 2010; (c) Post-spill period (seven months after oil spill): January 8, 2011. ----- MHWST, Mean High Water Spring tide-level; ○, location of burrows; ■, zone of 0.2 m in vertical height above Chart Datum where ≈ 64% of the burrows were clustered.

Table 1. Results of the Kolmogorov-Smirnov test comparing the *Ocypode ceratophthalmus* size distributions between pre-spill and post-spill sampling dates at sites C and D. n.s., not significant; sig, significant.

Sampling date	Mean carapace width ± S.E. (mm)	N	D	p	
Pre-spill					
2/8/2006 (Pre 1a)	24.30 ± 0.50	210			
4/8/2006 (Pre 1b)	25.00 ± 0.54	201			
Pre 1a vs Pre 1b			0.091	0.345	n.s.
Post-spill					
(after three months)					
11/9/2010 (Post 1a)	23.84 ± 0.80	151			
12/9/2010 (Post 1b)	22.26 ± 0.63	177			
Post 1a vs Post 1b			0.080	0.662	n.s.
(after seven months)					
8/1/2011 (Post 2a)	17.14 ± 0.74	160			
9/1/2011 (Post 2b)	18.58 ± 0.86	129			
Post 2a vs Post 2b			0.113	0.307	n.s.
Pre 1a vs Post 1b		210, 177	0.197	0.001	sig.
Post 1b vs Post 2a		177, 160	0.497	0.000	sig.

November. The mean abundance for the combined 3-month periods of pre- and post-spill periods was quite similar. The higher density observed at site D during the recovery period could be due to the decrease in human traffic at the construction site. Furthermore, since ghost crabs are most active at night, they would have already burrowed into the sand before the disturbance caused by the construction began during the daylight hours.

Population size and size-frequency distribution. Population sizes did not fluctuate appreciably for the six chosen sampling days; small variations in the population size on the different days of sampling are expected due to the different weather conditions that affected the emergence rate of the crabs (see Lim & Wong, 2010). At our sites, fewer ghost crab burrows were observed when there is high cloud cover and when the temperature was elevated. There were a few occasions when the rates of emergence were greatly reduced after heavy rain during the night just before the sampling session – the data for these sampling dates were excluded from this study. In addition, freshly-plugged burrows were sometimes observed when the temperature increased in the late morning.

The shift in the mean carapace width of the pre-spill population from 24.30 ± 0.58 mm in 2006 to 17.14 ± 0.74 mm in January 2011 indicates that the recolonised population had a smaller population size structure than the pre-spill population. This suggests that the pre-spill population had a lower recruitment rate or a higher growth rate as compared to the post-spill population. Predation of the juvenile crabs by adult crabs and the competition for limited resources may prevent settled megalopae from reaching crab stage, thus, resulting in low recruitment in the pre-spill population. The large number of burrows of small crabs observed seven months after the oil spill (i.e., January 2011), indicated that a fresh bout of recruitment must have occurred. The low number of crabs between 20 to 40 mm CW further indicates that there probably was a high crab mortality rate in September 2010, thereby creating the opportunity for a second wave of recruitment, since the post-spill population was probably not at its carrying capacity.

Members from a few local environmental interest groups reported the presence of many dead or moribund ghost crabs, other types of crabs and fish on the beach during the clean-up operation for the oil spill. Experiments have shown that reproductively active *Ocypode quadrata* were more susceptible to low concentrations of oil contaminants than non-reproductively active crabs (Jackson et al., 1981). This could be the reason for the high mortality rate observed in the mature crab population during the spill.

Population distribution with respect to shore height and size distribution on shore. There was no distinct segregation of the small and large-sized crabs: crabs 10 mm to 45 mm in CW were found in the entire zone with burrows before and after the oil spill (Fig. 5a, b). When there was a second bout of recruitment seven months after the oil-spill, small crabs with CW between 5 mm and 10 mm were also distributed throughout the entire range of the burrow zone (Fig. 5c). There were no crabs larger than 40 mm in CW in January 2011, perhaps due to higher mortality experienced in the reproductively-active crabs (see Jackson et al., 1981) as well as the higher probability of encountering oil residues in the deeper burrows excavated by the larger crabs. The absence of a size-gradient pattern of *Ocypode ceratophthalmus* distribution in our study, contrasted with that reported for *O. quadrata* whereby larger crabs were usually found higher up on the shore in Texas, USA and Brazil (see Hill & Hunter, 1973; Turra et al., 2005). In addition, juvenile *O. gaudichaudii* occurred at upper shore and the mature crabs at lower shore in Panama (observations by AYPY). Juvenile

O. quadrata, according to Fisher & Tevesz (1979), being more prone to desiccation, were restricted to the lower shore levels because they were unable to excavate deep burrows to reach the water table if they inhabited the upper regions. This suggests that *O. ceratophthalmus* could be more tolerant to desiccation than *O. quadrata*. *Ocypode quadrata* has been shown to use suction to draw water from the sand across setal tufts located at the bases of the second and third walking legs, into the branchial chambers (see Wolcott, 1984). At our study sites, juvenile *O. ceratophthalmus* were unusually active above ground during January 2011.

The *O. ceratophthalmus* population at these East Coast Park sites showed a remarkably rapid recovery rate after being totally wiped out by the oil spill. It should be noted that large quantities of the surface sand that was soaked with oil were removed during the immediate clean-up operation although there could still be a substantial amount of oil pollutants in the deeper layers of sand. Hence oil seepage into the upper layers of the substratum was reduced and relatively clean sand would have been available for megalopae to recolonise. However, as the new population matured, higher mortality probably occurred in the larger, reproductively-active crabs (see Jackson et al., 1981) as they excavated deeper burrows and became affected by the oil residues that accumulated at greater substratum depth. Growth rate of the crabs could also be affected by the oil residues. A seven-year study on the fiddler crab, *Uca pugnax*, by Krebs & Burns (1977) showed that high sediment oil content reduced population density and recruitment rate, increased mortality rate and the retention of toxic petroleum hydrocarbon skewed sex-ratios and caused behavioural disorders in the crabs. Forty years later, Culbertson et al. (2007) reported that some biological effects on *U. pugnax* persisted: crabs collected from Wild Harbour, United States (with oiled-sediments) excavated shallower burrows, showed slower escape responses and feeding rates compared to those from a non-polluted marsh.

Oil residues appeared to have a greater impact on the crabs of the lower shore since the ghost crabs burrowed primarily further upshore after the oil spill. Similarly, the abundance and diversity of macrobenthos on the lower shores of the sandy beaches of Moreton Island, Australia were reduced by the oil residues when compared with that at the mid- and upper shores (Lucrezi & Schlacher, 2014). In contrast, species diversity on the upper shores of the sandy beaches in Galicia of north-western Spain were more affected by the oil pollutants from the 'Prestige' oil spill (de la Huz et al., 2005; Junoy et al., 2005). The differences could be due to the toxicity of the different types of oil contaminants present and the environmental conditions at the various geographical locations (Lucrezi & Schlacher, 2014).

During the oil spill in Singapore, the highest tides (and thus the upper limit of the oil pollution) reached 2.4 to 2.5 m above Chart Datum, and this corresponded with a shift in the majority of burrow excavation to levels above 2.4 m. Interestingly, the ghost crab population shifted its distribution correspondingly with most of the burrows excavated at the level above 2.4 m. This suggests that the crabs preferred to inhabit the uncontaminated sediment found above this shore height. These results provide the first quantitative evidence, to substantiate the anecdotal statement, that ghost crabs moved further up the beach slope to avoid the oiled foreshore in the aftermath of the Ixtoc 1 oil spill in Texas in 1979 (see Jernigan & Reidenauer, 1986). The upshore shift of the 0.2 m zone (Fig. 5c) to above the MHWST level was most interesting, as it showed that *O. ceratophthalmus* is a sensitive yet resilient bioindicator species, that is able to detect changes in the level of pollutants and respond to the changes within a relatively short time (within seven months). Further work could be carried out to determine if this 0.2 m zone of ghost crab occurrence would shift back to the original tidal levels of 2.1 m to 2.3 m when the depths of the shore are no longer contaminated with oil residues.

Common macrofauna on sandy shores include molluscs, crustaceans and polychaetes (McLachlan, 2001). In general, suspension feeders (mostly bivalves) are considered to be less sensitive to oil pollution than deposit feeders (Junoy et al., 2005). Amphipods are sensitive to oil pollutants and disappear rapidly after oil spills (Gómez Gesteira & Dauvin, 2000). In contrast, polychaetes such as those in the Capitellidae and the Cirratulidae families are pollutant-tolerant and proliferate quickly, to become the dominant group for one to three years after oil spills (Sanders et al. 1980; Gómez Gesteira & Dauvin, 2000). Several studies have explored the use of various alternatives of the polychaete/amphipod ratio to identify the ratio, that best reflects the impact of oil spill on the benthic community studied (Gómez Gesteira & Dauvin, 2000; Dauvin & Ruellet, 2007). Although the use of amphipods and polychaetes as bioindicators is promising, there are limitations. Amphipods are sensitive bioindicators but they recover slowly after an oil spill. It took 15 years for the *Ampelisca* amphipods to attain the density at which they occurred before the oil spill (Gómez Gesteira & Dauvin, 2000). This could be due to their low colonisation rate (caused by weak dispersion capability and low fecundity). There are also constraints in the use of polychaetes. The sampling of these benthic worms involves invasive sediment collection. Furthermore, identification and enumeration of polychaetes are tedious and require long hours of microscope work.

To date, there is no commonly established bioindicator for the pollution impact on sandy shores. From the results of this study, it can be seen that although the population of *O. ceratophthalmus* was completely decimated after the oil spill, recolonisation occurred rapidly within a period of only three months. The remarkable trophic plasticity of ghost crabs (Lucrezi & Schlacher, 2014) could have insulated them from the exposure to substrate pollutants as compared to other intertidal macrofauna that are deposit feeders, e.g., fiddler crabs, amphipods (see Krebs & Burns, 1977; Gómez Gesteira & Dauvin, 2000). Moreover, ghost crabs are potentially successful recolonisers since they are able to absorb oxygen directly from the air without the need to circulate large volume of potentially polluted water over their gills. As *O. ceratophthalmus* is a widely-distributed conspicuous tropical species inhabiting sandy shore habitats, the estimation of its abundance by burrow enumeration is relatively easy and non-invasive—hence, this species of ghost crab has the potential to serve as a simple and effective macro-bioindicator for oil pollution.

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