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Assessment of stone crab (Lithodidae) density on the South Georgia slope using baited video cameras

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During January 2000 a baited video camera system was deployed fifteen times at depths of 719–1518 m around the Subantarctic island of South Georgia. Four species of lithodid (Anomura: Lithodidae) crab (*Paralomis formosa, P. spinosissima*, *Lithodes* sp., and *Neolithodes diomedeae*) were attracted to the baits of which *Paralomis formosa* was the most abundant. Using arrival rate at baits, predictions of odour plume size, and observations of walking speed the abundance of the stone crab, *Paralomis formosa*, was estimated. Numbers of crabs increased rapidly following bait emplacement, with total numbers observed in the 4.9 m^2 field of view exceeding 50 within 200 minutes on three occasions. Current speed was used to predict the area of the odour plume, and by integrating the area to account for scavenger speed the effective area of the odour plume was obtained. The density of crabs, estimated from the increase in crab numbers per unit area of odour plume, averaged 8313 individuals km^{-2} (range 1100–25 600). Density was not significantly correlated with depth, temperature, or current speed and variability was attributed to substrate form.

Keywords: *Paralomis formosa*, *spinosissima*, scavenging.

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Introduction

Stone crabs (lithodids) are cold-water species, found in shallow water at high latitudes, but limited to deep-water in temperate and tropical areas. Lithodids are scavengers, which are commercially exploited by pot-fisheries and world-wide catches amounted to approximately 47 000 metric tonnes in 1998 (FAO, 1999). The principal fishery is for king crabs off Alaska, which targets red king crab, *Paralithodes camtschaticus*, but also takes blue king crab, *Paralithodes platypus*, and golden king crab, *Lithodes aequispinus* (Zheng and Kruse, 2000). Red king crab attain the highest value and landings peaked at 83 000 tonnes in 1980, but have since declined markedly as a consequence of poor recruitment (Zheng and Kruse, 2000), high harvest rates and increased natural mortality (Collie and Kruse, 1998). In the South Atlantic, fisheries have developed in the Beagle Channel and off Tierra del Fuego for South American king crab, *Lithodes antarcticus* syn. *Lithodes santolla* (Vinuesa *et al*., 1995; Wyngaard and Iorio, 1995), and false southern king crab, *Paralomis granulosa*, which has also been targeted around the Falklands (Hoggarth, 1993).

From the early 1990s there has been interest in exploiting stone crabs in South Georgia waters, and following a workshop on crabs held by the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) in 1993 precautionary catch limits have been set for some species. The crab fishery is currently an exploratory fishery regulated by CCAMLR and subject to an exploratory fishing plan, with a catch limit of 1600 tonnes per annum and minimum size limits of 102-mm carapace length for *Paralomis formosa*, and

90 mm for *P. spinosissima*. Although some information is available on the biological characteristics of these crabs and their fisheries (López-Abellán and Balguerías, 1994; Otto and Macintosh, 1996), absolute estimates of crab biomass have proven difficult to derive (Watters, 1997). Moreover, most information is currently limited to the shallower species, *P. spinosissima*, which has been the target of the current exploratory fishery (Otto and Macintosh, 1996; Watters, 1997).

A potential fishery species needs to be marketable, abundant and relatively easy to capture. One of the first tasks in investigating the potential of a new fishery is to determine the size and location of the resource. The assessment of crustacean populations is notoriously difficult (Haefner, 1985) and in the deep water around South Georgia the bottom topography precludes a trawl survey and depletion methods such as the DeLury method require an active fishery. An alternate approach to estimating the abundance of scavengers is to monitor their rates of arrival at a bait placed on the sea floor and, using assumptions about the size and shape of odour plumes and estimates of walking speed (Sainte-Marie and Hargrave, 1987), density can be estimated. These methods have been applied to amphipods (Sainte-Marie and Hargrave, 1987) and hagfish (Martini *et al.*, 1997), whilst a simpler method using first arrival time at bait has been used to estimate abundance of scavenging deep-sea fish (Priede and Merrett, 1996).

During a 1997 photographic study, directed at estimating densities of the toothfish *Dissostichus eleginoides* around South Georgia, large numbers of lithodid crabs were attracted to bait at depths greater than 700 m (Yau *et al.*, 2001). The present paper describes the results of a subsequent study aimed at estimating densities of crabs at depths of 719–1518 m around South Georgia using baited video cameras.

Methods

Experimental procedure

As part of the biannual South Georgia groundfish survey in January 2000, two AUDOS (Aberdeen University Deep Ocean Submersibles) rigs were deployed from the Falklands registered fishing vessel "Argos Galicia".

The AUDOS are autonomous lander vehicles designed to photograph and track scavenging fish and invertebrates on the seafloor (Priede and Bagley, 2000). Two AUDOS lander vehicles were operated around South Georgia in January 2000. AUDOS-I consisted of an aluminium frame onto which was mounted a programmable digital video camera (JVC Colour Video Camera, TK-C1380 in housing with controller), current meter (Sensortec), twin acoustic releases (Mors AR and RT), a battery and two 50 watt deep-sea lights (Deep-Sea Power & Light, Inc.). AUDOS-II was a simplified version lacking the current meter and equipped with a single acoustic release (Mors RT). Buoyancy was provided by glass spheres (Benthos, Inc., each giving 24 kg positive buoyancy) attached to a 100 m mooring line.

The AUDOS rigs descended by free-fall with 100 kg of ballast, which held the rigs in position on the seafloor. The ballast, with a graduated cross and baits attached, remained on the seafloor and was connected to the AUDOS vehicle by a 2-m length of wire. The cross therefore rested 30–50 cm above the seafloor on top of the ballast, and the positive buoyancy of the mooring line held the AUDOS 2 m above the cross. Each deployment was baited with four squid, *Illex argentinus*, hung from the cross, with sardines inserted in the mantle cavity and attached to the ballast (total 800 g).

Each experiment lasted 6 h and the AUDOS video cameras recorded a total of one hour of video. The camera was programmed to record 45 consecutive seconds in each 2.5 min for the first two hours; 45 s in each 5 min for the next two hours and 45 s every 15 min during hours 5 and 6. The camera recorded onto digital videotape and, after recovery, a copy was made on to SVHS. The camera viewed an area of sea-floor of approximately 4.9 m^2. The current meter was programmed to record depth, temperature, current direction, and current speed at one-minute intervals throughout the deployment.

On completion of the experiment the AUDOS were released from the ballast by an acoustic signal from a Mors deck unit (TT301) via a transponder, lowered into the water. When the ballast was released the vehicles surfaced at a rate of approximately 0.8 m s^{-1} under their own buoyancy. On the surface a marker buoy, attached to the end of the mooring, and incorporating a VHF radio beacon (Novatech) and large pink flag, aided in location and recovery.

The AUDOS-I was deployed nine times and the AUDOS-II on six occasions (Table 1 and Figure 1). Typically the two rigs were deployed in close proximity, but at slightly different depths, so that the current meter data could be used to analyse data from both experiments.

Analysis of data

Video sequences were analysed on a high-resolution colour monitor. Crabs were identified, where possible, using relevant texts (e.g. Macpherson, 1988) and reference collections of crabs taken from shallow-water trawl surveys. Crab numbers were counted in each sequence, although when numbers were in excess of 30 the count was approximate. Carapace width (CW) was measured on crabs from each experiment, using the graduated cross as a scale. Carapace length is the

Table 1. Date, time location and depth of AUDOS Deployments during the South Georgia survey on *Argos Galicia* in January 2000.

Deployment	AUDOS	Date	GMT	Location	Latitude	Longitude	Depth (m)
1	I	17 Jan 00	00:02	Shag Rocks	53°16.9′S	42°22.1′W	719
2	I	17 Jan 00	23:12	Shag Rocks	53°26.2′S	41°35.6′W	1085
3	I	21 Jan 00	23:38	South Georgia	53°35.5′S	36°20.9′W	1035
4	I	22 Jan 00	21:51	South Georgia	54°05.5′S	35°20.9′W	1114
5	II	22 Jan 00	22:02	South Georgia	54°05.0′S	35°20.1′W	1294
6	I	23 Jan 00	23:38	South Georgia	54°37.3′S	34°47.6′W	780
7	II	23 Jan 00	23:59	South Georgia	54°36.8′S	34°42.8′W	1005
8	I	24 Jan 00	22:45	South Georgia	54°38.1′S	34°37.6′W	1250
9	II	24 Jan 00	23:10	South Georgia	54°38.1′S	34°32.6′W	1518
10	I	26 Jan 00	08:23	South Georgia	54°50.7′S	38°31.5′W	1120
11	II	26 Jan 00	08:32	South Georgia	54°50.9′S	38°31.5′W	1335
12	I	27 Jan 00	15:21	South Georgia	54°23.7′S	39°28.7′W	946
13	II	27 Jan 00	15:39	South Georgia	54°23.9′S	39°23.6′W	1202
14	I	29 Jan 00	14:31	Shag Rocks	53°36.1′S	40°44.9′W	1283
15	II	29 Jan 00	14:47	Shag Rocks	53°36.2′S	40°45.7′W	1140

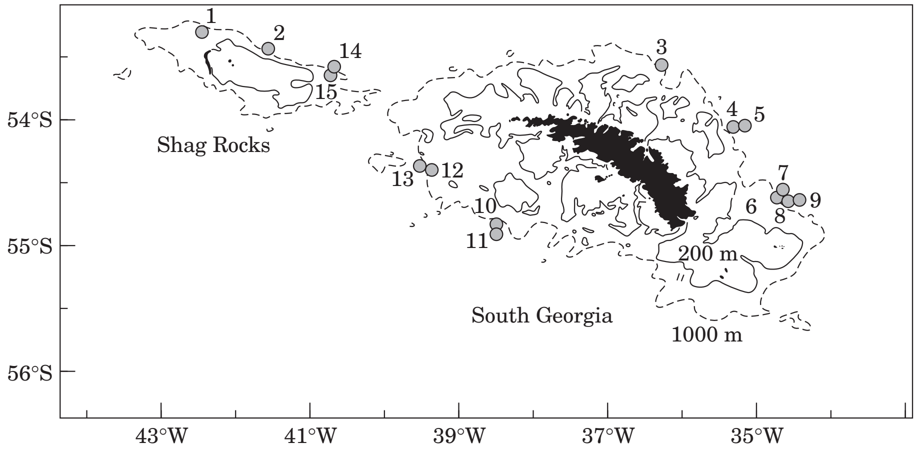

Figure 1. Map of the South Georgia area showing locations of AUDOS deployments in January 2000.

standard measurement of size in king crabs, but could not be easily measured on the video sequences. Walking speeds of crabs were measured during suitable sequences.

Scavenger abundance was estimated from their arrival rate at the bait. It is assumed that as the odour from the bait dispersed on the bottom current an odour plume develops and all the crabs within the area of this plume will move upstream towards the bait source. Current velocity was used to predict the area of the odour plume over time (Engas and Lokkeborg, 1994; Sainte-Marie and Hargrave, 1987) and the area of odour influence was compared to the numbers of scavengers attracted. The area of the odour plume was assumed to be an ellipse ($A = \pi LW/4$) (Stanley *et al.*, 1985). The length of the odour plume (L) was calculated from the current velocity and the time elapsed since bait deployment. The maximum width of the plume (W) was calculated from the equations of Sainte-Marie and Hargrave (1987) and Stanley *et al.* (1985):

$$W = 2aL^{b}((b+d)/b)^{0.5}e^{0.5} \tag{1}$$

with:

$$a = B_y/V_c \tag{2}$$

where V_c is the current velocity; L is the plume length; W is the plume width; B_y is the diffusivity constant (estimated at 10^{-3} m s^{-1} in deep waters (Sainte-Marie and Hargrave, 1987)). The constants b and d are assumed to equal 1 (Sainte-Marie and Hargrave, 1987).

These equations estimated the area of the odour plume, however scavengers arriving at bait at time t were attracted from shorter distances since they must swim or walk upstream to the bait after contacting the plume. The relationship between current speed (Vc) and scavenger speed (Vs) was used to determine the maximum distance (Ls) from which the scavengers could have reached the bait at time t:

$$\mathrm{Ls} = \frac{\mathrm{Vs}}{\mathrm{Vs} + \mathrm{Vc}} \times \mathrm{L} \tag{3}$$

The area of the odour plume (an ellipse) was then integrated from L = 0 to L = Ls to calculate the area from which the scavengers were attracted. An ellipse is described by the equation:

$$y = \frac{W}{L}\sqrt{L^2 - x^2} \tag{4}$$

Where x is the independent variable (x-axis) and y the dependent variable (y-axis). Integration of Equation (4) gives the area of the ellipse and the effective area (A_E) of the odour plume was calculated by integrating from L_0 to L_S.

$$A_E = \left\{ \frac{W}{L} S \left[\sqrt{\left(\frac{L}{2}\right)^2 - S^2} \right] + \left(\frac{L}{2}\right)^2 \sin^{-1}\frac{2S}{L} \right\} - \left\{ \frac{W}{L} \left[\left(\frac{L}{2}\right)^2 \sin^{-1}\frac{-L}{L} \right] \right\} \tag{5}$$

where S = Ls − 0.5L.

The number of crabs at the bait was plotted against effective area of the odour plume, which increased gradually over time. A regression line was fitted to the data indicating the rate of increase of scavenger numbers with increase in effective area of the odour plume over time. The slope of this line gives a direct estimate of local density of the crab population (crab numbers m^{-2}) in the vicinity of the lander vehicles. The shape of the odour plume will change if the direction of the current changes, and this will affect the arrival rate of crabs. Therefore the density estimates were usually based on the initial arrival rate of crabs providing the current remained stable (usually the first 60–100 min). This time also coincided with most intense period of video footage. Statistical analyses were carried out using MINITAB.

Results

AUDOS-I carried a current meter, which measured horizontal current speed and direction and recorded temperature (Table 2). Current speeds were typically low, with an average speed of approximately 60 mm s^{-1}. Bottom temperature varied from 1.4 to 2.2°C. Details of the bottom substrate type and numbers of crabs attracted to bait at each deployment are given in Table 2.

Species composition

The most abundant species attracted to the bait was the stone crab, *Paralomis formosa*, which could usually be distinguished from *P. spinosissima* and other lithodids by the relative absence of spines on the carapace surface. *P. formosa* was seen in all deployments, with numbers in excess of 15 in all but one deployment and in excess of 100 in Deployment 12. *Neolithodes diomedeae* was seen at eight of the deployments, but the maximum number present at one time was two. A further species of crab, *Lithodes* sp. was seen, but was difficult to distinguish from *P. spinosissima* in the video sequences. Other scavenging fish and invertebrates were identified in the videos and full details of the fauna identified during the 2000 video survey and the 1997 photographic survey are given in Yau *et al.* (in press).

In most deployments the numbers of crabs at the bait increased rapidly, presumably as the area of odour plume increased, before reaching a plateau. Figure 2 shows the temperature, current speed, current direction, and numbers of crabs in Deployment 12. Only in the deployments where the seafloor was stony did the crab numbers not increase rapidly (e.g. Deployment 11). The *Paralomis* crabs were relatively uniform in size (CW 60–120 mm; mean 75 mm).

Paralomis formosa walking speed was determined from 101 video sequences (Figure 3). The mean speed was 32 mm s^{-1} (range 10–68 mm s^{-1}) and was positively correlated with carapace width (Spearman rank correlation r = 0.546; p = 0.001).

Assessment of crab abundance

Using the current speed and the mean walking speed of crabs, the effective area of the odour plume was calculated for each minute following touchdown in each deployment. Theoretically, if the crabs are evenly distributed numbers should increase linearly with the increase in the effective area of the odour plume. Numbers of crabs and effective area of the odour plume were plotted for each deployment (see Figure 4) and in most cases the slopes of the lines had an initial linear shape. In Deployments 8 and 11 there was a time lag before the crabs responded, but once the crabs' response was detected it correlated with the increase in odour plume. In Deployment 11 this appeared to be due to low current speed and current direction changing during the initial period, but could not be accounted for in Deployment 8. As a consequence of this, the abundance estimate is based on the time period 98–178 min in Deployment 8 and 90–123 min in Deployment 11. In all other deployments the start time was when the bait arrived on the seafloor.

Density was estimated from the mean increase in crab numbers per unit of effective area for each

Table 2. Seafloor temperature, substrate type, mean current speed (during assessment period), maximum numbers, arrival rate, and abundance estimate for the stone crab *Paralomis formosa* for each deployment of the AUDOS at South Georgia in January 2000. PTT=post touch down of the AUDOS.

Deployment	Bottom temp. (°C)	Substrate type	Mean current (mm s^{-1})	*Paralomis formosa* max	Arrival rate (crabs m^{-2} odour plume)	Time period for estimate (min PTT)	Abundance estimate (crabs km^{-2})	Correlation between crab numbers and odour plume area (r^2)
1	2.2	Sand/mud, small stones	70	40	0.002	0–140	2000	0.880
2	1.8	Sand/mud, small stones	16	23	0.0101	0–108	10 100	0.958
3	1.6	Sand/mud	53	74	0.0168	0–68	16 800	0.956
4	1.6	Sand/mud, small stones	55	19	0.0038	0–60	3800	0.835
5		Sand/mud	54	27	0.0091	0–53	9100	0.866
6	1.9	Sand/mud, small stones	68	39	0.0092	0–58	9200	0.799
7		Sand/mud, small stones	67	22	0.0073	0–80	7300	0.937
8	1.4	Sand/mud, small stones	78	12	0.0011	98–178	1100	0.838
9		Sand/mud (steep slope)	72	18	0.0027	0–123	2700	0.826
10	1.6	Sand/mud, small stones	42	21	0.0036	0–85	3600	0.847
11		Rocks, patches of sand	42	4	0.0021	90–123	2100	0.892
12	1.7	Sand/mud	40	108	0.0256	0–60	25 600	0.897
13		Sand/mud	42	50	0.017	0–38	17 000	0.750
14	1.7	Sand/mud, small stones	48	21	0.0036	0–110	3600	0.967
15		Sand/mud, small stones	40	24	0.0107	0–40	10 700	0.959

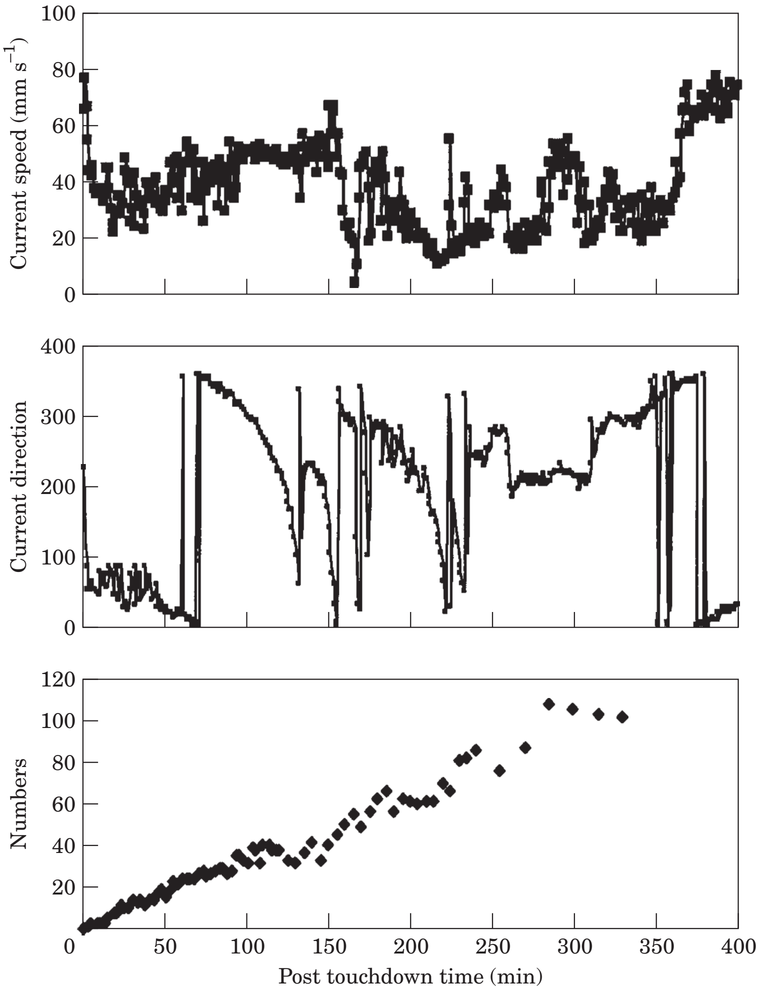

Figure 2. AUDOS Deployment 12: current speed and direction, and numbers of crabs (*Paralomis formosa*).

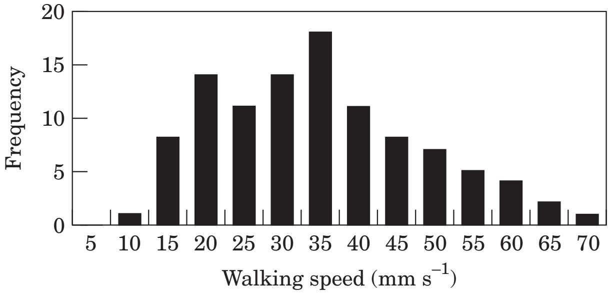

Figure 3. Frequency distribution of walking speeds of the lithodid crab *Paralomis formosa* from video sequences.

deployment (Table 2). Estimates of crab density varied from 1100 to 25 600 individuals km^{-2} (mean density 8313 individuals km^{-2}; s.d. 6992). Correlations were investigated between maximum crab numbers, density, temperature, depth and current velocity. Only the correlation between estimated density and maximum numbers was significant ($r=0.884$; $p<0.001$).

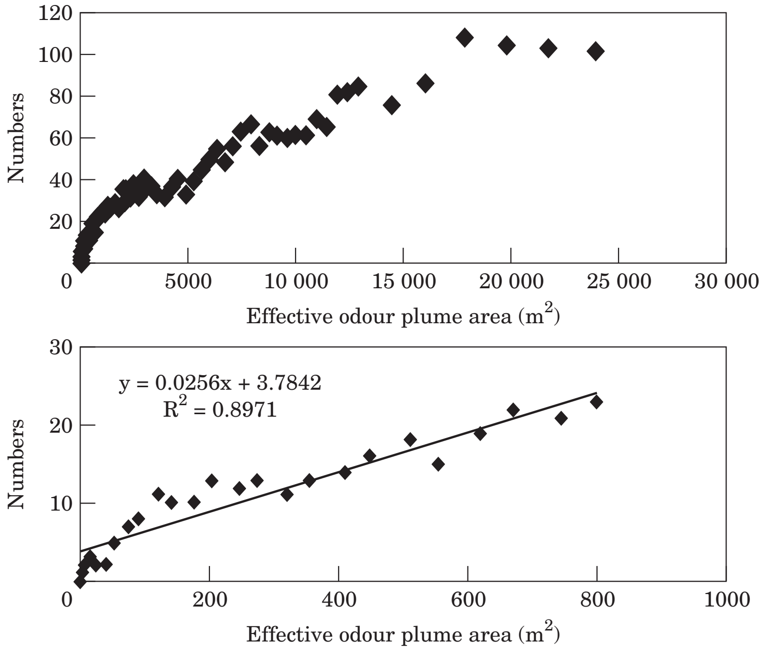

Figure 4. AUDOS Deployment 12: effective area of the odour plume plotted against crab (*Paralomis formosa*) numbers in the whole experiment (above) and for the time period that density estimates of crabs were made (below). The slope of the relationship is equivalent to the number of crabs m^{-2}.

Discussion

The results indicate that stone crabs are abundant at depths of 700–1500 m on the South Georgia slope, and although specific identification was not possible for all individuals, the dominant species was clearly *Paralomis formosa*. *P. spinosissima* was present in some of the shallower stations, but the low resolution of the video sequences made it difficult to distinguish *P. spinosissima* from *P. formosa,* particularly among smaller individuals. In a similar survey in 1997 that used a higher resolution 35 mm camera, *P. spinosissima* was only found at depths<1000 m (Yau *et al.*, in press). *Neolithodes diomedeae* were seen in small numbers at eight deployments, whilst crabs of the genus *Lithodes* were present but were usually difficult to distinguish from the other species.

Numerical density of *Paralomis* was estimated by predicting the size of the effective odour plume, in a method similar to that applied by Sainte-Marie and Hargrave (1987) to amphipods and Martini *et al.* (1997) to hagfish. The method relies on accurate measurements of current speed and knowledge of scavenger speed, but also makes assumptions about the size and shape of the odour plume and the distribution, sensory thresholds and behaviour of the crabs (see Lokkeborg, 1994; McQuinn *et al.*, 1988; Sainte-Marie and Hargrave, 1987).

Following bait emplacement, the odour plume will undergo an initial growth phase as the bait is dispersed, succeeded by a shrinking phase as the release of attractants from the odour declines (Engas and Lokkeborg, 1994), and clearly any abundance estimates must be made during the growth phase. The use of the current meter allows for the accurate measurement of the length of the odour plume, however the calculation of the plume width, and hence area, relied on the estimation of other parameters, such as lateral diffusion. In addition, changes in current direction will alter the shape and area of the odour plume (Engas and Lokkeborg, 1994). However the errors generated by these parameters have been minimised in the present study by generally utilising the first 60–100 min following bait emplacement to estimate abundance. Bottom topography may also influence the odour plume, if the bait lands on a steep slope the plume could be carried off the seafloor and hence reduce the number of crabs attracted. The video sequences gave an indication of the slope in the precise location of the bait, but nothing can be known from outside the field of view. In at least one deployment, the bait landed on a steep slope.

The model assumes that the crabs are evenly distributed on the sea-floor, which is supported by the correlations between crab numbers and effective area during the initial phase, however a completely even or random distribution is unlikely particularly as other crab species are known to aggregate (e.g. Miller, 1975). An immediate locomotor response by the crabs, once the odour plume has been contacted, is also assumed, which is unlikely. Crab walking speeds were measured from the video footage, however it is unlikely that crabs walk directly or without stopping to the bait. Furthermore the estimate assumes that all crabs arriving remain within the field of view of the camera, which is probably not the case. Overestimation of crab response and approach speed and early departure of crabs will lead to an underestimate of numbers, though the latter source of error has been minimised by utilising a short time period after bait emplacement. Crabs that arrived at the bait early may macerate the bait and therefore increase odour leaching, thus attracting more crabs (Cyr and Sainte-Marie, 1995; Lapointe and Sainte-Marie, 1992).

The chemosensory threshold of lithodid crabs has been investigated in the laboratory (Zhou and Shirley, 1997a), but values obtained are difficult to apply to a field study. Crustaceans rely almost exclusively on chemoreception for finding food (Zimmerfaust, 1987) and can detect odour from a food source at very low concentrations (Ache, 1982), but the response threshold of the crabs may be considerably higher than the detection threshold (Engas and Lokkeborg, 1994; Pearson and Olla, 1977; Zimmerfaust and Case, 1983). It will depend on starvation level, reproductive state and molt stage of the crab (Zimmerfaust, 1989) and environmental variables such as temperature and current speed. Again, using the initial part of the experiment when the odour will be at its strongest should illicit the greatest response of the crabs, nevertheless, this may cause an underestimate of the crab abundance.

This method of abundance estimation differs from that applied to scavenging fish using the AUDOS camera system (Priede and Merrett, 1996; Yau *et al.*, 2001). In the case of fish only the time of arrival of the first fish is used and it is assumed that the fish are mobile and encounter the odour plume at radius L from the bait source. The density of fish approximates to one fish per area described by a hexagon of radius L. For deep sea benthic fishes this method correlates well with independent trawl swept area estimates of abundance. The present method provides a much more precise method of determining abundance, utilising the arrival rate of up to 100 animals instead of just one individual per bait deployment, however its application to mobile scavenging fish is complicated by their foraging behaviour. Many scavenging fish actively seek odour plumes rather than wait for the plume to reach them and, their staying time at the bait is often short, making it difficult to determine total numbers attracted. Maximum numbers seen at bait are a consequence of arrival rate and staying time and in the present study correlated well with abundance estimates. However in many cases simple scavenger numbers cannot be used as an abundance index and Priede and Merrett (1998) demonstrated a negative correlation in some situations. The odour plume algorithms for estimation of population density are influenced by both current and scavenger speed. Yau *et al.* (2000) analysed these effects and showed that greatest errors occur with slower moving animals. It is therefore important to directly measure travelling speeds, which can be achieved by telemetry in fish or from video sequences for smaller scavengers such as crabs.

The estimates of stone crab abundance are effectively point measures and difficult to extrapolate to the whole South Georgia slope, particularly as there was considerable variability in the arrival rates, maximum numbers and abundance estimates of *P. formosa*. Repeat deployments were not undertaken due to the constraints of other sampling programmes, but would be an important aspect of further research. However it should be noted that the two deployments with the highest abundance estimates (12 and 13) were located just 2 nmi apart, albeit at different depths. Crab maximum numbers and abundance estimates were not correlated with depth or temperature and the form of the substrate was probably more important in determining crab abundance as is the case with *P. camtschaticus* (Zhou and Shirley, 1998). Although the abundance estimates derived here are difficult to relate to the total biomass they provide a useful index of abundance, which can be compared between years. In order to determine the total number and biomass of crabs at South Georgia it will be necessary to map the substrate and undertake a more detailed study, ideally supported by an alternative measure of abundance.

The abundance estimates for *P. formosa* derived here are higher than those obtained by Zhou and Shirley (1997b, 1998) for *P. camtschaticus* in an Alaskan fjord, where the mean density was 5100 crabs km^{-2}, with a maximum of 8600 crabs km^{-2}. The relatively small size of *P. formosa* may make them unattractive as a commercial resource, as was the case with *P. granulosa* in the Falklands, but this may be countered by the high level of abundance. Using a mean carapace width of 75 mm and the following equation relating carapace width (CW) to body weight (BW) ($BW = 0.0001\ CW^{3.3032}$; $r^2 = 0.898$; $n = 306$: M. Purves, Imperial College, London, unpublished data) gives an estimated crab biomass of 1298 kg km^{-2}. If the *Paralomis* crabs are to be commercially exploited at South Georgia detailed studies of the biology will need to be undertaken, probably in parallel with an exploratory fishery. Little is known about the biology of *P. formosa* or the other lithodid crabs seen in the study. *Paralomis formosa* and *P. spinosissima* have also been seen at baited cameras in deep-water around the Falkland Islands, but not in such high abundance as at South Georgia (Collins *et al.*, 1999). Initially management may rely on biological information from currently exploited lithodids such as *P. granulosa* in the Southwest Atlantic (Hoggarth, 1993; Lovrich and Vinuesa, 1993, 1995, 1999) and *P. platypus*, *Paralithodes camtschaticus* and *L. aequispinus* from Alaska (e.g. Stevens, 1990; Zheng and Kruse, 2000; Zheng *et al.*, 1997) which are better known.

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