

## THE BIOLOGY, ECOLOGY AND DEVELOPMENT OF FISHERY MANAGEMENT ADVICE FOR THE ANOMURAN CRABS AT SOUTH GEORGIA (CCAMLR SUBAREA 48.3)

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### Abstract

This review summarises the available information on the biology and ecology of the lithodids at South Georgia and provides an overview of the development of a management regime for them. Finally it aims to highlight areas in which further research should be directed in order to provide information on which to base the most appropriate assessment and management methods in light of continuing interest in the regional crab fishery. Considerable gaps in our knowledge of the biology, ecology and demography of the lithodid species at South Georgia remain. Uncertainty surrounds estimates of biomass, growth rates and long-term survivorship of discards of the targeted species. In addition, there is doubt surrounding the identification of the less frequently caught species. The ecosystem interactions and function of all lithodids in the region remain poorly understood with great uncertainty surrounding their trophic ecology and life histories. Recent analyses suggest that the current precautionary catch limit may not be sustainable in the long term if it were reached consistently. Further research to address many of the areas outlined above should be undertaken if there is continued interest in the fishery. However, low market value and interest coupled with the very high level of discarding are likely to render the fishery commercially unviable.

### Introduction

Members of the anomuran crustacean family Lithodidae (commonly known as stone crabs or king crabs) are distributed globally in the deep sea, with a few genera occurring inter-tidally at high latitudes in the northern hemisphere (Thatje et al., 2005; Hall and Thatje, 2009). Lithodids occupy predominantly cold water habitats and temperature is thought to be a constraining factor in their distribution. Lower and upper thermal limits of approximately 0.5°C and 15°C respectively govern their distribution (Thatje and Arntz, 2003; Hall and Thatje, 2011). Lithodids support important fisheries

in higher-latitude regions of both the northern and southern hemisphere. Valuable fisheries, including the red king crab (*Paralithodes camtschaticus*) and golden king crab fisheries of the northern Pacific and the ‘centolla’ (*Lithodes santolla*) fisheries of southern South America, have developed in recent decades (Otto and MacIntosh, 1996). However, overfishing of lithodid resources has been widespread leading to a major decline in catches in many regions (Lovrich, 1997; Zaklan, 2002).

Lithodids occur in both the Antarctic and sub-Antarctic regions but in the former their distribution is restricted to areas of warmer water

Table 1: History of directed crab fishing in CCAMLR Subarea 48.3.

Date	Vessel	Species retained	Total catch (tonnes)
July/August 1992	<i>Pro Surveyor</i> (USA)	<i>Paralomis</i> sp.	299
September 1995–January 1996	<i>American Champion</i> (USA)	<i>P. spinosissima</i>	497
August 1999 (14 days)	<i>Argos Helena</i> (GBR)	<i>P. spinosissima</i> and <i>P. formosa</i>	2.2
March/June 2002 (42 days)	<i>Kinpo Maru No. 58</i> (JPN)	<i>P. spinosissima</i> and <i>P. formosa</i>	111.7
2006/07 (3 days)	<i>Argos Georgia</i> (GBR)	<i>P. spinosissima</i> and <i>P. formosa</i>	0.3
August–October 2010	<i>Tamango</i> (RUS)	<i>P. spinosissima</i> and <i>P. formosa</i>	62

(above 0.5°C) where they occur at low densities (Hall and Thatje, 2011). They are absent from some of the coldest regions such as the Weddell Sea but recent studies have suggested that there may have been recent movement of crabs into higher-latitude areas following warmer water incursions (Smith et al., 2011). In contrast, lithodids are widespread and found at high densities in sub-Antarctic regions, including South Georgia, where they have been the subject of repeated, but largely unsuccessful, exploratory fisheries since the early 1990s (Watters, 1997; Purves et al., 2003).

The majority of data relating to lithodid crab biology and ecology at South Georgia has been obtained from a limited number of directed fishery surveys conducted in the region since 1992 (Table 1). Additional information is available from Spanish (López Abellán and Balguerías, 1994) and UK demersal trawl surveys, baited camera deployments (i.e. Collins et al., 2002; Yau et al., 2002) and a limited number of scientific research cruises that have been carried out on the South Georgia shelf (Lovrich et al., 2005). Lithodid crabs also constitute a considerable part of the by-catch associated with pot fishing for Patagonian toothfish (*Dissostichus eleginoides*) at South Georgia (Agnew et al., 2001). Laboratory studies on adult growth, reproduction and larval development have been conducted by the British Antarctic Survey on material collected from the exploratory fishery and demersal trawl surveys.

This review summarises the available information relating to the biology and ecology of the lithodids at South Georgia and provides an overview of the development of a management regime for them. Finally, it aims to highlight areas in

which further research should be directed in order to provide information on which to base the most appropriate assessment and management methods in light of continuing interest in the regional crab fishery.

## Biological and ecological information

### Species composition

Five species of lithodid representing three genera have been reported from the Shag Rocks and South Georgia region (Purves et al., 2003). Three species of the genus *Paralomis*, *P. spinosissima* (Birstein and Vinogradov, 1972), *P. formosa* (Henderson, 1888) and *P. anamerae* (Macpherson, 1988) occur along with *Neolithodes diomedea* (Benedict, 1894) and *L. murrayi* (Henderson, 1888). The presence at South Georgia of *P. formosa* and *P. spinosissima* (which have formed the majority of catches of the exploratory fishing in the region to date) and *N. diomedea* has been known for many decades (Macpherson, 1988). However, *P. anamerae* and *L. murrayi* were first described at South Georgia by Purves et al. (2003) following the analysis of catches from the exploratory pot fishery for crabs conducted in the region in 2000/01. A limited number of specimens of these species were identified morphologically and compared with material held in the Natural History Museum, London. However, no additional taxonomic studies or detailed genetic analyses of South Georgia lithodids have been conducted to date, and therefore some doubt about the identity of the more recently identified species remains. Further research is required in order to resolve the ambiguities that remain concerning the identity of species of lithodid in the region.

## Distribution

### Bathymetric distribution

Information on the depth distribution of the lithodids at South Georgia has largely been derived from exploratory fishery data. Data obtained from demersal trawl surveys and baited camera deployments is used here to provide additional information from depths largely unsampled by the exploratory fisheries.

Despite some overlap in the depth distribution of the three *Paralomis* species, clear depth preferences are observed. *Paralomis spinosissima* inhabits the shallowest depths and is generally found in water depths less than 800 m. Peak abundances have been observed at depths of < 400 m (where it is the dominant crab species) with catch rates declining thereafter (Watters, 1997; Purves et al., 2003). *Paralomis formosa* is found at depths greater than 300 m and abundance is observed to increase with depth, reaching a peak between 800 and 1 400 m. *Paralomis anemerae* has an intermediate depth distribution (Purves et al., 2003) and has been found at depths of 600–1 200 m, although the depth for peak abundance is not known due to limited sampling.

*Neolithodes diomedae* is one of the deepest occurring lithodids and has been caught at depths exceeding 2 500 m. At South Georgia it is frequently recorded deeper than 1 000 m in the fishery but individuals have been caught in low numbers by both demersal trawl surveys and pots at depths of 420–430 m. Limited data are available on the bathymetric distribution of *L. murrayi* at South Georgia where a total of 16 individuals have been caught at depths between 450 m and 605 m representing the greatest depths at which this circum-polar species has been recorded.

Depth segregation by sex has been observed for both *P. spinosissima* and *P. formosa*, although patterns differ between the species. In the shallower living species *P. spinosissima*, the ratio of males/females in exploratory fishery catches increases. Of the catch, 76% was male at the maximum depths the species was observed. Conversely, for *P. formosa* the percentage of males in catches decreased from 70% at the shallower extent of their depth distribution to < 50% at depths > 1 000 m.

## Spatial distribution

Information on the spatial distribution of lithodids at South Georgia and Shag Rocks is limited. The fine-scale analysis of crab density from the exploratory pot fishery is restricted to an analysis of *P. spinosissima* catch rates (Watters, 1997) which were found at their highest densities to the northwest of South Georgia. Results from Purves et al. (2003) suggest that there was little regional difference in the probability of encountering crabs at South Georgia, albeit over large-scale areas (Shag Rocks, East SG and North SG). However, additional analysis of data obtained from Spanish (López Abellán and Balguerías, 1994) and UK demersal trawl surveys (Figure 1) indicate a greater degree of spatial structuring in the distribution of *P. formosa* and *P. spinosissima*. *Paralomis spinosissima* is found across all of the deeper shelf and shelf break regions but is found at its highest densities on the northwest shelf and slope of South Georgia (Figure 1a). Coastal and shallow shelf areas have very low densities of *P. spinosissima* but they are also found in low numbers in the deep gullies that radiate outward from the island. Limited trawl survey data suggests that *P. formosa* density is highest in the slope region to the north of the island (Figure 1b). Insufficient information is available to assess the fine-scale distribution of the other lithodid species. An assessment of crab density using baited video cameras (Collins et al., 2002) indicates that distribution and abundance may be related to variability in substrate type. Densities of *P. formosa* were lowest over areas of hard substrate (rock and sand patches) and higher on areas of mud and small stones. Temperature and current speed was not thought to influence the distribution of crabs, although data remains sparse.

## General biology

In common with most lithodids, the carapaces of the species found at South Georgia are pear-shaped (pyriform) and are heavily calcified, bearing a variable number of either spines (*P. spinosissima*, *N. diomedae*) or small granules (*P. formosa*, *P. anemerae*). All species have a well-defined rostrum and possess heavily pigmented eyes. The first pair of pereopods bear well-developed claws with the right cheliped (crusher claw) more robust than the left (cutter). There are three further pairs of walking legs with the fifth pair folded under the carapace and not obvious externally. In all

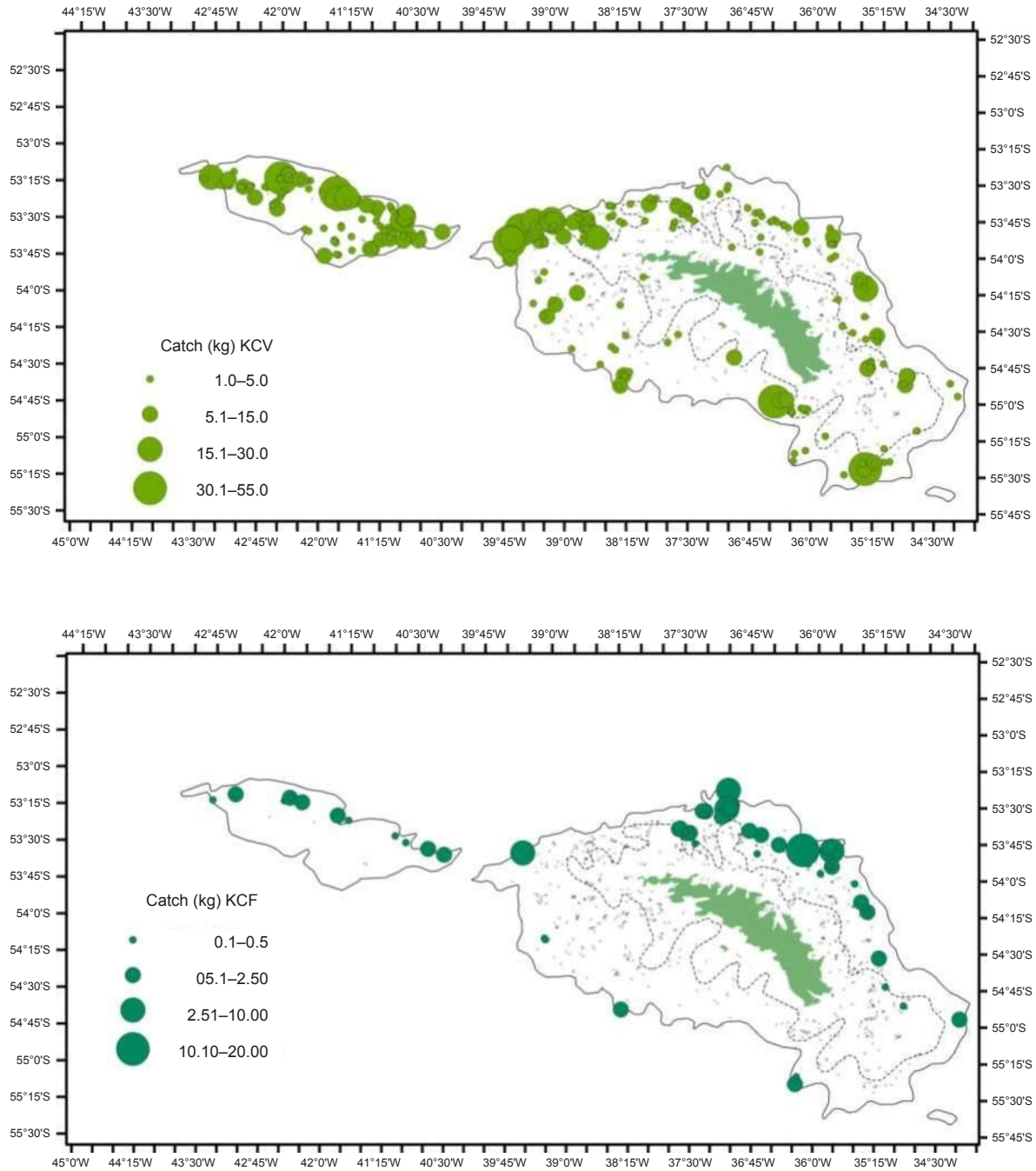


Figure 1: Catch (kg/half-hour tow) of *Paralomis spinosissima* (top) *P. formosa* (bottom) in UK trawl survey data (1990–2010).

species the sexes are easily separated by examination of the abdomen. Female abdominal plates are more developed on the right-hand side resulting in strong asymmetry of the abdomen. Pleopods are also absent in males.

Size

The largest of the South Georgia lithodids, *N. diomedae*, is known to reach sizes in excess

of 130 mm (carapace length, CL) with weights in excess of 1 000 g (Morley et al., 2006). However, examination of images from the autonomous camera system suggests that this species may grow much larger with CL approaching 150 mm. Total width (including legs) may exceed 500 mm. CLs in excess of 107 mm with weights of 1 180 g have been recorded for *P. spinosissima* (Table 2), whilst the smaller *P. formosa* attains a carapace length of 103 mm and a weight of 700 g. *Paralomis*

*anemerae*, whilst poorly studied, has been observed to reach a maximum size of 73 mm (CL) at South Georgia. No information on the size of *L. murrayi* is available for the South Georgia shelf. In common with other lithodids, males have been observed to attain a greater maximum size than females in all of the species examined to date (Purves et al., 2003). The standard measurement of crab size is CL (Otto and MacIntosh, 1996), however, carapace width, CW (an easier to take but less reliable measure) has often been reported in the literature. Parameters describing the relationship between CL and CW are available for some species (Table 3) as well as length–weight relationships (Table 4).

### Growth

In common with all crustaceans, estimating age and growth rate of the lithodids is problematic. The lack of persistent hard body parts as a result of continual ecdysis means there are no structures present, analogous to otoliths in fish or statoliths in cephalopods, that record age or growth. In addition, it is very hard to resolve age–length cohorts within length–frequency data (i.e. Purves et al., 2003), which appear to be unimodal. Consequently, information on growth rates or moult frequency for South Georgia lithodids is sparse. Intra-season tagging studies at South Georgia (Watters, 1997) were used to estimate standing stock biomass via mark-recapture analysis but were not suitable for assessing growth as ‘time at liberty’ was so short. Limited laboratory studies on captive adult *P. spinosissima* indicate a long inter-moult duration in excess of 850 days (Reid et al., 2006) but growth increments-at-moult were not provided in this study. The intermoult period is longer than has been observed in other species of lithodids from lower latitudes (Calcagno et al., 2005), including the closely related *P. granulosa*. Further evidence of a long intermoult period in *P. spinosissima* was provided by Otto and MacIntosh (1996) who observed considerable biological fouling on the carapace of sexually mature crabs. Intermoult duration (and therefore growth) is known to be inversely related to temperature, which suggests that lithodids at South Georgia have slower growth rates than those found at lower latitudes such as *P. granulosa*. This species reaches a similar maximum size to *P. spinosissima* after 12 years (Lovrich and Vinuesa, 1999) and enters the fishery at an approximate age of 15 years (Lovrich, 1997).

### Reproduction and life cycle

In contrast to the most abundant and commercially important lithodid species found on the Patagonian shelf (*P. granulosa*, Hoggarth, 1993, and *L. sentolla*, Lovrich and Vinuesa, 1993; Thatje et al., 2003) very little is known about the life history of lithodids at South Georgia. Laboratory studies on reproduction have been limited to *P. spinosissima* whilst fishery-derived information for *P. formosa* and *P. anemerae* has been temporally and spatially restricted. However, it is thought there is a high degree of similarity in life histories between species and much can be inferred from the more extensive research carried out on species to the north of the Polar Front. Life history traits for South Georgia lithodids are summarised in Table 2.

Moult in sexually mature lithodids is believed to tie in with their reproductive cycle. In the majority of species this process is seasonal (Lovrich and Vinuesa, 1999). Mating occurs between a male with a hard shell and a female with a very recently moulted soft shell. Eggs are immediately fertilised externally as there is no means of sperm storage. Moult (and therefore mating) in *P. spinosissima* has been observed year-round but may be skewed towards the summer months (Reid et al., 2006), although it is suggested that in deep living species reproduction may become aseasonal and not linked to seasonal productivity change or temperature. Further evidence to support this is the year-round presence of gravid females bearing eggs at different developmental stages (Otto and MacIntosh, 1996). Moult and mating frequency is currently undetermined (see above) but it is likely that mature adults reproduce less than once every two years.

A comparative study of aspects of reproduction in the lithodids at South Georgia (Morley et al., 2006) showed that eggs are large and yolky but vary in size between all the species examined with the largest eggs found in the deeper living species, *N. diomedae*. Fecundity is closely related to body size within a species, with a near-linear increase in fecundity observed with increasing carapace length. Relative fecundity was lowest in *N. diomedae* (largest eggs) and highest in the shallower living *P. spinosissima* (smaller eggs). Large eggs have the potential to store high energy reserves which facilitates endotrophic larval development. All species of South Georgia lithodids are thought to show extended lecithotrophic development, although this has only been confirmed in *P. spinosissima*.

Table 2: Summary of life history traits for lithodid crabs in CCAMLR Subarea 48.3. CL – carapace length; CW – carapace width.

Trait	<i>Paralomis formosa</i>	<i>P. spinosissima</i>	<i>Neolithodes diomedea</i>	<i>P. anamerae</i>	<i>Lithodes murrayi</i>
Depth distribution (m)	400–1 600	135–800	420–2 500	600–1 200	450–605
Size range CL (mm)	40–103	63–126	72–137	56–73	
Size range CW (mm)	56–110	52–132	70–150		
Size range of adult crabs (g)	66–700	80–1 400	214–1 043	64–125	
Size-at-maturity (mm) – males (CL/CW)	64/68	67.3/73.4			
Size-at-maturity (mm) – females (CL/CW)	55.1/57.1	61.2/67.7			
Absolute fecundity	1 500–4 500	900–12 000	2 800–8 800		
Relative fecundity ((eggs g <sup>-1</sup> body weight) (mean ± SD))	16.6 ± 4.64	17.7 ± 5.25	13.5 ± 5.6		

Table 3: Regression parameters for the relationship between carapace width (CW) and carapace length (CL) where CW = CLa + b (from Purves et al., 2003).

Species	a	b	R – sq	n
<i>Paralomis spinosissima</i>	6.457	0.994	0.977	367
<i>P. formosa</i>	1.976	1.032	0.969	351
<i>P. anamerae</i>	5.70	0.917	0.979	28

Table 4: Regression parameters for *Paralomis spinosissima* for the relationship between log weight and log length (from Otto and MacIntosh, 1996).

Crab type	Log weight to log length			
	a	b	R – sq	n
Normal ♂	-8.66	3.36	97.9	435
Parasitised ♂	-7.14	2.97	97	159
Normal ♀	-5.98	2.71	96.7	255
Parasitised ♀	-6.84	2.9	98.2	105

Egg development time in *P. spinosissima* has been estimated between 14 and 18 months (Watts et al., 2005) which is similar to the egg development duration seen in *P. granulosa*. Hatching mode in *P. spinosissima* is typical of other southern hemisphere lithodids with low numbers of larvae released over an extended and continuous period that may last for over two to three months.

Larval and early juvenile development of *P. spinosissima* has been described in detail from laboratory rearing observations (Watts et al., 2005). There is an abbreviated larval development with two zoeal stages followed by a benthic megalopa stage, which closely matches the developmental patterns seen in the congener *P. granulosa*. The larval cycle is thought to be completely endotrophic and can be completed successfully in the absence of food. The two zoeal stages appear to be morphologically adapted to a pelagic lifestyle and may exhibit demersal drifting behaviour through this developmental period prior to settlement. Lithodid zoeal stages have not been recorded in plankton trawls at South Georgia and uncertainty surrounds development times of larvae in vivo. No data on larval development for the other South Georgia lithodids is currently available.

Very small *P. spinosissima* (~ 20 mm CL) have occasionally been caught in demersal survey trawls on the South Georgia shelf (Belchier pers. obs.) but it is not clear which habitats are favoured by lithodid juveniles. In the coastal regions of the Patagonian shelf, small juvenile specimens of *P. granulosa* and *L. santolla* have been found among holdfasts of giant kelp *Macrocystis pyrifera* (Cárdenas et al., 2007). It is not known whether juvenile lithodids inhabit these environments at South Georgia, although sampling of the kelp zone has been very limited.

#### Size at sexual maturity

Since fishery operations began in 1992 there has been considerable effort directed towards establishing size at sexual maturity for the crab species at South Georgia in order to set appropriate minimum landing. Male size at sexual maturity has been determined from the allometric relationship between CL and dominant (right) chela size (either length or height). The intersect of regression lines fitted to log-transformed CL and chela size data represents the length at which males become mature

(Somerton and Otto, 1986; Watters and Hobday, 1998; Purves et al., 2003). Current estimates of size at sexual maturity are provided in Table 2.

#### Trophic ecology

In common with all lithodids, the South Georgia species are scavengers that are known to be attracted to a wide variety of different baits, including fish and squid. Beyond this, little is known about the natural diets of these species as directed dietary studies have not been carried out. Detailed diet analysis of *P. granulosa* in the Beagle Channel, Tierra del Fuego (Comoglio and Amin, 1999) showed the species to have a diverse diet, preying on a representative selection of the local benthic species, including molluscs, crustaceans, echinoderms and polychaetes.

Lithodids are known to form a component of the diet of large adult Patagonian toothfish (*D. eleginoides*) at South Georgia (Pilling et al., 2001) but are not thought to play a major part in the diet of other predatory species.

#### Parasitism

A very high prevalence of the rhizocephalan barnacle parasite *Briarosaccus callosus* has been recorded on *P. spinosissima*. Infection of South Georgia crabs was first described by Boschma (1962) and it is thought to be the same parasite as that which infects *P. granulosa* on the Patagonian shelf. The main effect of the parasite is to castrate the host crab, meaning they are no longer part of the spawning stock. They are also known to affect growth (Hoggarth, 1990; Otto and MacIntosh, 1992; Watters, 1998) causing changed morphometry, and can potentially increase mortality (Basson, 1994). Infection rates have been observed to vary spatially and between sexes (Watters, 1998). These factors clearly are of relevance to stock management and need to be considered in assessing potential harvest regimes. Infection rates of 15% have been reported for *P. spinosissima* at South Georgia (Otto and MacIntosh, 1992), although recent data obtained from pot fishing at South Georgia indicated a far lower level of infection (2.5%, Peatman pers. comm.). Levels of *B. callosus* infection in *P. formosa* were an order of magnitude lower (0.3%) than in *P. spinosissima*. Female *P. spinosissima* were observed to have higher rates of *B. callosus* infection than males (4.6% and 1.7% respectively).

Yau et al. (2000) described a close association between *P. formosa* and a liparid fish (*Careproctus* sp.) at South Georgia. Examination of images obtained from the AUDOS autonomous camera system showed the adult and juvenile fish ‘hitching a ride’ on the carapaces of crabs at depths of 625–1 487 m. It has since been established that fish lay their eggs within the gill chambers of crabs, and fish larvae are likely to be retained within the gill cavity after hatching and may cause damage to the gills. The level of infestation of *P. formosa* by *Careproctus* sp. is unknown.

## Development of management advice

Historic attempts at generating stock assessments and relevant research

### Initial assessment of *P. spinosissima* in 1992

In 1992 the king crab fishery targeting *P. spinosissima* and, to a lesser extent, *P. formosa* began operation at South Georgia (CCAMLR Subarea 48.3) (Basson and Hoggarth, 1994). In response, the CCAMLR Working Group on Fish Stock Assessment (WG-FSA) set about estimating the standing stock of commercially sized male *P. spinosissima* in Subarea 48.3 by multiplying the average catch of commercially sized crabs by area fished (17 tonnes per n mile<sup>2</sup>). This was then raised by the total fishable area in Subarea 48.3 between 200 and 1 000 m depth (SC-CAMLR, 1992). The area fished by the vessel was estimated assuming an effective fishing radius of half the distance between pots and a catchability of 1 for commercially sized male crabs. This resulted in an initial estimate of 155 000 tonnes of commercially sized male *P. spinosissima* (i.e. CW > 102 mm) in Subarea 48.3. However, WG-FSA recognised that habitat for *P. spinosissima* may only be a portion of the 200 to 1 000 m depth stratum and consequently reduced the estimate by 50% and 70%. This resulted in a calculated standing stock estimate of 48 000–78 000 tonnes of commercially sized male *P. spinosissima* in Subarea 48.3.

### Production models

Watters (1993a) presented production models that were fitted to CPUE data from the FV *Pro Surveyor*’s 1991/92 fishing operations using various assumptions of recruitment. Estimates of appropriate short-term catch limits were made for the area

fished in the 1991/92 season. The report noted that it would be necessary to determine whether growth or movement was predominantly responsible for recruitment in the area fished in the 1991/92 season before the catch limits could be extrapolated to the South Georgia fishery as a whole. The importance of determining the main driver of recruitment was one of the main objectives of the Experimental Harvest Regime (EHR) implemented in the 1993/94 season (see section below).

### Assessment of *P. spinosissima* based on mark-recapture data (1996)

The FV *American Champion* undertook a tagging program of *P. spinosissima* in the 1995/96 season as part of Phase 2 of the EHR; 6 000 tagged crabs were released with 2 000 releases in each of the three depletion squares. Four tagged crabs were recaptured with an average time-at-liberty of one to five weeks. Watters (1997) applied an unbiased estimator of population size to the mark-recapture data and estimated 95% confidence intervals for the density of legal-sized male *P. spinosissima* (i.e. CW > 102 mm) to range from 16 000 to 264 000 crabs per n mile<sup>2</sup> depending on the assumed movement speed of the crabs. This equates to approximately 20 to 140 tonnes per n mile<sup>2</sup> assuming an average weight of 1.1 kg for a legal-sized male, as used by Otto and MacIntosh (1992). The report noted that the uncertainty surrounding the estimates of density was largely due to the small number of recaptures. Additionally, the report noted that a variety of the assumptions implicit to the approach used were likely to be violated and the density estimates were likely to be overestimates. The author noted that the lowest 95% confidence interval of density was similar to the estimate of Otto and MacIntosh (1992). Watters (1997) also fitted GAMs to CPUE data of the FV *American Champion* from Phase 1 of the EHR in the 1994/95 season and concluded that the spatial differences in depth-specific CPUE suggested that local abundance estimates of standing stock should not be extrapolated to the whole of Subarea 48.3 without consideration of these spatial differences.

### Density estimates of *P. formosa* using baited video camera

Collins et al. (2002) estimated the density of *P. formosa* between 700 and 1 500 m depth using



a baited video camera system. The bait's odour plume size was estimated and *P. formosa* crab density was estimated from the observed increase in crab density per unit area of odour plume. The report estimated the total *P. formosa* density at approximately 4.5 tonnes per n mile<sup>2</sup>. Collins et al. (2002) noted that the estimates of total stock density presented are localised estimates and extrapolation to the whole of South Georgia would be difficult, but repeated studies could provide an index of abundance for comparison between years. It is important to note that it is difficult to compare the density estimates of *P. formosa* from Collins et al. (2002) with those for *P. spinosissima* in sections 'Initial assessment of *P. spinosissima* in 1992' and 'Production models' as the latter estimates are for legal-sized male *P. spinosissima*, whereas the former is for all *P. formosa*.

#### Evolution of management controls in place

Options for long-term management of the crab fishery in Subarea 48.3 were first examined in detail at CCAMLR's Workshop on the Management of the Antarctic Crab Fishery (WS-CRAB, SC-CAMLR, 1993b). The Workshop concluded that indirect and direct management controls that had been extensively applied to other crab fisheries, commonly size, sex and season restrictions (indirect) and catch or effort restrictions (direct), would be appropriate for the management of the Antarctic crab fishery. The Workshop also noted that the combination of direct and indirect controls should protect the stock from reproductive failure in the short term, even if catches are unsustainable in the long term. The fishery is managed under a single species approach due to the likely insignificant ecosystem role and importance of the species (Basson and Hogarth, 1994).

#### Catch limits

In 1992 estimates of conservative catch levels for the stock of *P. spinosissima* were attempted, recognising that insufficient data were available to produce reliable estimates of sustainable yields. Otto and MacIntosh (1992) noted that catch rates and depth distributions of commercially sized *P. spinosissima* in Subarea 48.3 were similar to those of the Aleutian Island golden king crab (*L. aequispinum*) fishery. In light of this the annual production estimates (catch per unit fishing area)

of Aleutian Islands golden king crabs was applied to the fishable area between 200 and 1 000 m in Area 48, resulting in an estimate of total annual production of 6 000 tonnes of commercially sized male crabs across Area 48, with 2 100 tonnes in Subarea 48.3. This represents less than 5% of the lowest estimate of exploitable (i.e. commercially sized male) standing stock derived by WG-FSA in 1992. The catch limit of the fishery was set at 1 600 tonnes for the 1992/93 season, but the catch limit would only be in force if more than three vessels fished (SC-CAMLR, 1992). In the 1993/94 season the catch limit was set at 1 600 tonnes irrespective of the number of notified vessels for the fishery (SC-CAMLR, 1993a).

The catch limit of 1 600 tonnes in force since the 1992/93 season has not been updated, predominantly due to the lack of sufficient data to provide an assessment of the *P. spinosissima* stock and the generally low commercial interest in the fishery due to concerns regarding economic viability (e.g. SC-CAMLR, 2010, paragraph 5.178).

#### Size limits

In the 1991/92 season data from an initial 22-day trip of the US vessel FV *Pro Surveyor* in Subarea 48.3 were used to estimate size at sexual maturity for *P. spinosissima* (Otto and MacIntosh, 1992). WG-FSA estimated size at 50% sexual maturity (SM50) for male *P. spinosissima* to be 75 and 66 mm at South Georgia and Shag Rocks respectively. WG-FSA also estimated that size limits of 94 and 84 mm, at South Georgia and Shag Rocks respectively, would be appropriate to ensure males have the opportunity to contribute to at least one breeding season on average assuming carapace length percentage growth increments of North Pacific lithodids. WG-FSA also commented that male *P. formosa* are likely to mature at a smaller size than *P. spinosissima*, although it was not possible to estimate the SM50 for the species.

WG-FSA recommended that minimum carapace width limits for *P. spinosissima* be set at a minimum of 115% of SM50 in order to maximise yield per recruit, noting that the larger minimum carapace width limits chosen for the FV *Pro Surveyor*, 102 and 95 mm for South Georgia and Shag Rocks respectively, were set to ensure product quality. WG-FSA recommended that minimum carapace width limits for *P. formosa* be set at 82 or 90 mm,

noting that the majority of male *P. formosa* caught during the initial 22-day trip had smaller carapace widths than 90 mm.

Minimum carapace width limits for *P. spinosissima* and *P. formosa* were set at 102 and 90 mm respectively for the 1992/93 season (Conservation Measure (CM) 60/XI), on the basis of the analysis presented in Otto and MacIntosh (1992) and the subsequent recommendations of WG-FSA and the Scientific Committee (SC-CAMLR, 1992).

WG-FSA requested in 1995 that data be collected to estimate the size at sexual maturity of *P. formosa* (SC-CAMLR, 1995). Watters (1996) concluded that there was not adequate biological reasoning to revise the size limit in force based on analysis of data from the 1995/96 season, and the Scientific Committee advised that the size limit remain at 90 mm (SC-CAMLR, 1996).

The minimum carapace width limit for *P. spinosissima* was revised to 94 mm for the 2001/02 season (SC-CAMLR, 2002), based on the original analysis presented in Otto and MacIntosh (1992). This was done to reflect the biological rationale of the size limit, i.e. allowing males at least one opportunity to contribute to a breeding season before capture, whereas the 102 mm size limit was set due to the processing requirements of the time.

#### Retention of males only in catch

The requirement to release all female crabs caught in Area 48 was initially included in the permit for exploratory research fishing issued by the US National Marine Fisheries Service to the FV *Pro Surveyor* for exploratory fishing activities in Area 48 in the 1991/1992 season. This requirement was then included in CM 60/XI for the 1992/93 season and has subsequently remained, e.g. CM 52-01 (2010) for the 2010/11 season.

#### Experimental Harvest Regime (EHR)

Watters (1993b) outlined a proposal for an experimental management strategy for the crab fishery in Subarea 48.3 designed to provide data on: the large-scale spatial distribution patterns of *P. spinosissima* in Subarea 48.3; the impact of the fishery on these patterns; the presence and location of aggregations; the recovery of areas after intense depletion episodes; and the drivers behind monthly

shifts in size frequency. The proposed strategy was comprised of three phases, summarised by SC-CAMLR (1993a) as:

*Phase 1 – survey of the crab distribution around South Georgia at the start of the first fishing season by fishing in designated blocks. After completion, normal fishing operations would continue until the TAC for that season was attained or the vessels voluntarily left the fishery.*

*Phase 2 – series of depletion experiments conducted in local areas to start at the beginning of the second fishing season. After Phase 2 normal fishing operations would be conducted.*

*Phase 3 – fishing effort would be redirected to the local areas depleted during Phase 2. This would occur towards the end of the second fishing season. It would commence just prior to cessation of the fishery resulting from the TAC being attained or by each vessel wishing to voluntarily leave the fishery.'*

SC-CAMLR (1993a) noted that the proposed strategy offered the best approach to obtain data for a meaningful assessment of the crab stock dynamics and the fishery. An EHR was constructed on the basis of the proposed strategy in Watters (1993b) and incorporated into the management of the fishery in CM 75/XII. CM 75/XII was in place from 1993/94 to 1995/96, with a slight modification for the 1995/96 season to allow the location of the small squares to be determined by the vessel captain (see SC-CAMLR, 1995, paragraph 4.106).

Data collected by the FV *American Champion* during the 1995/96 season indicated that depletion estimators were not appropriate to estimate local abundances of *P. spinosissima* (e.g. Watters, 1997). As a consequence, Phase 2 of the EHR was redrafted for the 1996/97 and 1997/98 seasons to remove the requirement for depletion experiments (CM 90/XV) and the Scientific Committee and WG-FSA would advise the Commission on what should be required under Phase 2 if any vessel initiated Phase 1 in these seasons (SC-CAMLR, 1996, paragraph 4.129). Possible alternatives suggested for Phase 2 included repeating Phase 1 or conducting a mark-recapture program (SC-CAMLR, 1996, paragraph 4.183). For the 1999/2000 season it was recognised that Phase 2 could be removed from the EHR as there was no need at the time

to require vessels to conduct activities under Phase 2 (SC-CAMLR, 1999). Since the 1999/2000 season the EHR has remained in place essentially unchanged, currently Annex B of CM 52-01 (CCAMLR, 2010).

#### Recent harvest regime

The management controls currently in place, and detailed in CM 52-01 (2010), can be summarised as:

- a maximum of one vessel per Member
- a total catch of 1 600 tonnes
- only male *P. spinosissima* and *P. formosa* with carapace widths exceeding 94 and 90 mm (respectively) may be retained
- any vessel participating in the fishery must have completed the requirements of the EHR before commencing normal fishing operations.

#### Analysis of the impact of harvest regime on target stocks

The retained proportion of catch in the fishery has historically been low (SC-CAMLR, 2010), with estimates of 9% and 14% by number for *P. spinosissima* and *P. formosa* respectively (SC-CAMLR, 1999). The retention rate of *P. spinosissima* was higher in the 2009/10 season at 36% by number. The low retention rates in the fishery are mainly due to the high numbers of females and undersized males in catches. These individuals are commonly released alive, although a small proportion are released injured or discarded dead due to damage from the gear, other crabs, handling, etc. However, legal-sized males can also be released alive or discarded dead due to low commercial value, mainly due to missing or small claws or legs.

Purves et al. (2003) conducted re-immersion experiments on crab by-catch caught in the experimental pot fishery targeting toothfish (*D. eleginoides*) in response to concern of the high numbers of crabs released in the fishery and potential high associated mortality rates (e.g. SC-CAMLR, 1999). Species and the type of handling of the crabs were important factors for estimates of mortality rates for released individuals, hereafter termed 'release mortality'. Release mortality rates were estimated

to be 12–13% and 16–23% for *P. spinosissima* and *P. formosa* respectively for vessels where sorting occurred on a horizontal conveyor belt, and 51–62% and 42–50% for *P. spinosissima* and *P. formosa* respectively if crabs were passed down a vertical chute before sorting. It is important to note that the release mortality estimates only factor in immediate mortality and do not include longer-term mortality, for example increased mortality during moulting, so the estimates presented could be under-estimates. Retained catch proportions and release mortality rates summarised here suggest that up to six individuals could die for every one individual retained, depending on species composition of catches, the handling of the crabs etc., so reported catches could be substantially lower than total removals for the stock.

Furthermore, analysis presented in Peatman (2007) suggests that the current precautionary catch limit of 1 600 tonnes may not be sustainable in the long term if the catch limit were to be reached consistently. The analysis in Peatman (2007) was based on output from a size-based population model with high levels of (unquantified) uncertainty in the model's estimates. Nevertheless, applying estimates of release mortality to recorded catches to estimate total removals from the stock would ensure that total removals are less likely to exceed the precautionary catch limit of 1 600 tonnes.

Destruction of parasitised crabs is a commonly suggested method to reduce parasite prevalence rates in host crab populations (e.g. Basson, 1994) and the process of checking for parasite infection should not increase handling mortality in discarded crabs (Watters, 1997). However, it is unlikely that it would be feasible to check all crabs for parasite infection during commercial fishing operations due to the large numbers of small crabs observed in catches.

#### Potential commercial viability of the fishery

The low numbers of legal-sized crabs in catches has led to concerns about the economic viability of the fishery (e.g. most recently SC-CAMLR, 2010, paragraph 5.178). A reduction in the retainable size limit for males could increase the retainable proportion of catches in the fishery, and, if coupled with a suitable reduction in catch limit for the fishery, could result in an equivalent impact on the stock due to the reduction in discard mortality. It has

also been suggested that permitting the retention of females would have little impact on the recruitment potential of the stock, particularly if harvest refuges are in place (Watters, 1997). However, female and undersized males have low commercial value due to the small size of their legs and claws (e.g. Otto and MacIntosh, 1992) and consequently it is unlikely that reducing the legal size limit or permitting the retaining of females will result in an increase in the retained proportion of catches and a subsequent increase in economic viability of the fishery. This is supported by the fact that some smaller legal-sized males are currently released due to low commercial value. Thus it is unlikely that females and/or currently undersized males would be processed and retained if it were allowed.

## Conclusions

This review has highlighted considerable gaps in our knowledge of the biology, ecology and demography of the lithodid species at South Georgia. Uncertainty surrounds estimates of biomass, growth rates and long-term survivorship of discards and individuals of the targeted species released alive. In addition, there is doubt surrounding the identification of the less-frequently caught species. The ecosystem interactions and function of all lithodids in the region is poorly understood, with great uncertainty surrounding their trophic ecology and life histories. Recent analyses suggest that the current precautionary catch limit may not be sustainable in the long term if it were reached consistently. Further research to address many of the areas outlined above should be undertaken if there is continued interest in the fishery. However, it should be noted that 2009/10 notwithstanding, there has been very little commercial interest in the fishery in recent seasons. Low market value for crabs coupled with the very low catch rates of legal-sized males is likely to render the fishery commercially unviable in the future.

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## References

- Agnew, D.J., T.M. Daw, G.M. Pilling and M.G. Purves. 2001. Fishing for toothfish using pots: Results of trials undertaken around South Georgia, March–May 2000. *CCAMLR Science*, 8: 93–105.
- Basson, M. 1994. A preliminary investigation of the possible effects of rhizocephalan parasitism on the management of the crab fishery around South Georgia. *CCAMLR Science*, 1: 175–192.
- Basson, M. and D.D. Hoggarth. 1994. Management and assessment options for the crab fishery around South Georgia. *CCAMLR Science*, 1: 193–202.
- Benedict, J.E. 1894. Descriptions of new genera and species of crabs of the family Lithodidae, with notes on the young of *Lithodes camtschaticus* and *Lithodes brevipes*. *Proceedings of the United States National Museum*, 17: 479–488.
- Birstein, Y.A. and L.G. Vinogradov. 1972. Crustacea (Decapoda, Anomura, Lithodidae) of the Atlantic sector of the Antarctic, South America and South Africa. *Zoologicheskii Zhurnal*, 51 (13): 351–363.
- Boschma, H. 1962. *Rhizocephala*. *Discovery Rep.*, 33: 55–94.
- Calcagno, J.A., G.A. Lovrich, S. Thatje, U. Nettelmann and K. Anger. 2005. First year growth in the lithodids *Lithodes santolla* and *Paralomis granulosa* reared at different temperatures. *J. Sea Res.*, 54 (3): 221–230.
- Cárdenas, C.A., J.I. Cañete., S. Oyarzún and A. Mansilla. 2007. Podding of juvenile king crabs *Lithodes santolla* (Molina, 1782) (Crustacea) in association with holdfasts of *Macrocystis pyrifera* (Linnaeus) C. Agardh, 1980. *Invest. Mar., Valparaíso*, 35 (1): 105–110.
- CCAMLR. 2010. *Schedule of Conservation Measures in Force, 2010/11*. CCAMLR, Hobart, Australia: 224 pp.
- Collins, M.A., C. Yau, F. Guilfoyle, P. Bagley, I. Everson, I.G. Priede and D. Agnew. 2002. Assessment of stone crab (Lithodidae) density

- on the South Georgia slope using baited video cameras. *ICES J. Mar. Sci.*, 59 (2): 370–379.
- Comoglio, L.I. and O.A. Amin. 1999. Feeding habits of the false southern king crab *Paralomis granulosa* (Lithodidae) in the Beagle Channel, Tierra del Fuego, Argentina. *Sci. Mar.*, 63 (Suppl. 1): 361–366
- Hall, S. and S. Thatje. 2011. Temperature-driven biogeography of the deep-sea family Lithodidae (Crustacea: Decapoda: Anomura) in the Southern Ocean. *Polar Biol.*, 34 (3): 363–370. doi: 10.1007/s00300-010-0890-0.
- Hall, S. and S. Thatje. 2009. Global bottlenecks in the distribution of marine Crustacea: temperature constraints in the family Lithodidae. *J. Biogeogr.*, 36 (11): 2125–2135.
- Henderson, J.R. 1888. The voyage of H.M.S. Challenger. Report on the Anomura collected by H.M.S. Challenger during the Years 1873–76. *Report on the scientific results of the Voyage of H.M.S. Challenger during the years 1873–76. Zoology*, 27: 1–221.
- Hoggarth, D.D. 1990. The effects of parasitism by the rhizocephalan, *Briarosaccus callosus* Boschma on the lithodid crab, *Paralomis granulosa* (Jacquinot) in the Falkland Islands. *Crustaceana*, 59 (2): 156–170.
- Hoggarth, D. 1993. The life history of the lithodid crab, *Paralomis granulosa*, in the Falkland Islands. *ICES J. Mar. Sci.*, 50 (4): 405–424.
- López Abellán, L.J. and E. Balguerías. 1994. On the presence of *Paralomis spinosissima* and *Paralomis formosa* in catches taken during the Spanish survey Antartida 8611. *CCAMLR Science*, 1: 165–173.
- Lovrich, G.A. 1997. La pesquería mixta de las centollas *Lithodes santolla* y *Paralomis granulosa* (Anomura: Lithodidae) en Tierra del Fuego, Argentina. *Inv. Mar.*, Valparaíso (Chile), 25: 41–57.
- Lovrich, G.A. and J.H. Vinuesa. 1993. Reproductive biology of the false southern king crab (*Paralomis granulosa*, Lithodidae) in the Beagle Channel, Argentina. *Fish. Bull.*, 91 (4): 664–675.
- Lovrich, G.A. and J.H. Vinuesa. 1999. Reproductive potential of the lithodids *Lithodes santolla* and *Paralomis granulosa* (Anomura, Decapoda) in the Beagle Channel, Argentina. *Sci. Mar.*, 63 (Suppl. 1): 355–360.
- Lovrich, G.A., M.C. Romero, F. Tapella, and S. Thatje. 2005. Distribution, reproductive and energetic conditions of decapods crustaceans along the Scotia Arc (Southern Ocean). *Sci. Mar.*, 69 (Suppl. 2): 183–193.
- Macpherson, E. 1988. Revision of the family Lithodidae Samouelle, 1819 (Crustacea, Decapoda, Anomura) in the Atlantic Ocean. *Monogr. Zool. Mar.*, 2: 9–153.
- Morley, S.A., M. Belchier, J. Dickson and T. Mulvey. 2006. Reproductive strategies of sub-Antarctic lithodid crabs vary with habitat depth. *Polar Biol.*, 29 (7): 581–584.
- Otto, R.S. and R.A. MacIntosh. 1992. A preliminary report on research conducted during experimental crab fishing in the Antarctic during 1992 (CCAMLR Area 48). Document *WG-FSA-92/29*. CCAMLR, Hobart, Australia: 26 pp.
- Otto, R.S. and R.A. MacIntosh. 1996. Observations on the biology of the lithodid crab *Paralomis spinosissima* from the Southern Ocean near South Georgia. In: *High Latitude crabs: Biology, Management and Economics*. Alaska Sea Grant College Progr. Rep. No. 96-02. University of Alaska, Fairbanks: 627–647.
- Peatman, T. 2007. *Analysis of harvest regimes for the king crab fishery around South Georgia*. MSc thesis. Imperial College, London.
- Pilling, G.M., M.G. Purves, T.M. Daw, D.A. Agnew and J.C. Xavier. 2001. The stomach contents of Patagonian toothfish around South Georgia (South Atlantic). *J. Fish. Biol.*, 59 (5): 1370–1384.
- Purves, M.G., D.J. Agnew, G. Moreno, T. Daw, C. Yau and G. Pilling. 2003. Distribution, demography, and discard mortality of crabs caught as by-catch in an experimental pot fishery for toothfish (*Dissostichus eleginoides*) in the South Atlantic. *Fish. Bull.*, 101 (4): 874–888.

- Reid, W.D.K., J. Watts, S. Clarke, M. Belchier and S. Thatje. 2006. Egg development, hatching rhythm and moult patterns in *Paralomis spinosissima* (Decapoda: Anomura: Paguroidea: Lithodidae) from South Georgia waters (Southern Ocean). *Polar Biol.*, 30 (9): 1213–1218.
- SC-CAMLR. 1992. Report of the Working Group on Fish Stock Assessment. In: *Report of the Eleventh Meeting of the Scientific Committee (SC-CAMLR-XI)*, Annex 5. CCAMLR, Hobart, Australia: 183–345.
- SC-CAMLR. 1993a. *Report of the Twelfth Meeting of the Scientific Committee (SC-CAMLR-XII)*. CCAMLR, Hobart, Australia: 431 pp.
- SC-CAMLR. 1993b. Report of the Workshop on the Management of the Antarctic Crab Fishery. In: *Report of the Twelfth Meeting of the Scientific Committee (SC-CAMLR-XII)*, Annex 5, Appendix E. CCAMLR, Hobart, Australia: 265–297.
- SC-CAMLR. 1995. Report of the Working Group on Fish Stock Assessment. In: *Report of the Fourteenth Meeting of the Scientific Committee (SC-CAMLR-XIV)*, Annex 5. CCAMLR, Hobart, Australia: 255–454.
- SC-CAMLR. 1996. *Report of the Fifteenth Meeting of the Scientific Committee (SC-CAMLR-XV)*. CCAMLR, Hobart, Australia: 456 pp.
- SC-CAMLR. 1999. Report of the Working Group on Fish Stock Assessment. In: *Report of the Eighteenth Meeting of the Scientific Committee (SC-CAMLR-XVIII)*, Annex 5. CCAMLR, Hobart, Australia: 227–445.
- SC-CAMLR. 2002. *Report of the Twenty-first Meeting of the Scientific Committee (SC-CAMLR-XXIX)*. CCAMLR, Hobart, Australia: 524 pp.
- SC-CAMLR. 2010. *Report of the Twenty-ninth Meeting of the Scientific Committee (SC-CAMLR-XXIX)*. CCAMLR, Hobart, Australia: 420 pp.
- Smith, C.R., L.J. Grange, D.L. Honig, L. Naudts, B. Huber, L. Guidi and E. Domack. 2011. A large population of king crabs in Palmer Deep on the west Antarctic Peninsula shelf and potential invasive impacts. *Proc. Roy. Soc. B: Biol. Sci.* doi:10.1098/rspb.1496
- Somerton, D.A. and R.S. Otto. 1986. Distribution and reproductive biology of the golden king crab, *Lithodes aequispina*, in the eastern Bering Sea. *Fish. Bull.*, 84 (3): 571–584.
- Thatje, S. and W.E. Arntz. 2003. Antarctic reptant decapods: more than a myth? *Polar Biol.*, 27 (4): 195–201.
- Thatje, S., J.A. Calcagno, G.A. Lovrich, F.J. Sartoris and K. Anger. 2003. Extended hatching periods in the subantarctic lithodid crabs *Lithodes santolla* and *Paralomis granulosa* (Crustacea : Decapoda : Lithodidae). *Helgol. Mar. Res.*, 57 (2): 110–113.
- Thatje, S., K. Anger, J.A. Calcagno, G.A. Lovrich, H.O. Portner and W.E. Arntz. 2005. Challenging the cold: crabs reconquer the Antarctic. *Ecology*, 86 (3): 619–625.
- Watters, G. 1993a. Using production models to assess the stock of *Paralomis spinosissima* around South Georgia Island. Document *WG-FSA-93/23*. CCAMLR, Hobart, Australia.
- Watters, G. 1993b. Proposal for an experimental crab fishery in Subarea 48.3. Document *WG-FSA-93/22*. CCAMLR, Hobart, Australia.
- Watters, G. 1996. Estimation of size at maturity and calculation of an appropriate size limit for male *P. formosa*. Document *WG-FSA-96/35*. CCAMLR, Hobart, Australia.
- Watters, G. 1997. Preliminary analysis of data collected during the experimental phases of the 1994/95 and 1995/96 Antarctic crab fishing seasons. *CCAMLR Science*, 4: 141–159.
- Watters, G. 1998. Prevalence of parasitized and hyperparasitized crabs near South Georgia. *Mar. Ecol. Progr. Ser.*, 170: 215–229.
- Watters, G. and A.J. Hobday. 1998. A new method for estimating the morphometric size at maturity of crabs. *Can. J. Fish. Aquat. Sci.*, 55 (3): 704–714.

- Watts, J., S. Thatje, S. Clarke and M. Belchier. 2005. A description of larval and early juvenile development in *Paralomis spinosissima* (Decapoda: Anomura: Paguroidea: Lithodidae) from South Georgia waters (Southern Ocean). *Polar Biol.*, 29 (12): 1028–1038.
- Yau, C., M.A. Collins, P.M. Bagley, I. Everson and I.G. Priede. 2002. Scavenging by megabenthos and demersal fish on the South Georgia slope. *Ant. Sci.*, 14 (1): 16–24.
- Yau, C., M.A. Collins and I. Everson. 2000. Commensalism between a liparid fish (*Careproctus* sp.) and stone crabs (Lithodidae) photographed in situ using a baited camera. *J. Mar. Biol. Assoc. UK*, 80 (2): 379–380.
- Zaklan, S.D. 2002. Review of the family Lithodidae (Crustacea: Anomura: Paguroidea): Distribution, biology, and fisheries. In: Paul, A.J., E.G. Dawe, R. Elnor, G.S. Jamieson, G.H. Kruse, R.S. Otto, B. Sainte-Marie, T.C. Shirley and D. Woodby (Eds). *Crabs in Cold Water Regions: Biology, Management, and Economics*. University of Alaska Sea Grant College Program AK-SG-02-01, Fairbanks, AK, USA: 751–845.

