Escapement of the Cape rock lobster (*Jasus lalandii*) through the mesh and entrance of commercial traps

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Abstract—Metal-framed traps covered with polyethylene mesh used in the fishery for the South African Cape rock lobster (*Jasus lalandii*) incidentally capture large numbers of undersize (<75 mm CL) specimens. Air-exposure, handling, and release procedures affect captured rock lobsters and reduce the productivity of the stock, which is heavily fished. Optimally, traps should retain legal-size rock lobsters and allow sublegal animals to escape before traps are hauled. Escapement, based on lobster morphometric measurements, through meshes of 62 mm, 75 mm, and 100 mm was investigated theoretically under controlled conditions in an aquarium, and during field trials. SELECT models were used to model escapement, wherever appropriate. Size-selectivity curves based on the logistic model fitted the aquarium and field data better than asymmetrical Richards curves. The lobster length at 50% retention (L_{50}) on the escapement curve for 100-mm mesh in the aquarium (75.5 mm CL) approximated the minimum legal size (75 mm CL); however estimates of L_{50} increased to 77.4 mm in field trials where trap-entrances were sealed, and to 82.2 mm where trap-entrances were open. Therfore, rock lobsters that cannot escape through the mesh of sealed field traps do so through the trap entrance of open traps. By contrast, the wider selection range and lower L_{25} of field, compared to aquarium, trials (SR=8.2 mm vs. 2.6 mm; L_{25}=73.4 mm vs. 74.1 mm), indicate that small lobsters that should be able to escape from 100-mm mesh traps do not always do so. Escapement from 62-mm mesh traps with open entrance funnels increased by 40–60% over sealed traps. The findings of this study with a known size distribution, are related to those of a recent indirect (comparative) study for the same species, and implications for trap surveys, commercial catch rates, and ghost fishing are discussed.

Manuscript submitted 20 March 2003 to the Scientific Editor.

Manuscript approved for publication 1 July 2003 by the Scientific Editor.

Fish Bull. 103:52–62 (2005).

The traps used in lobster and crab fisheries are a versatile fishing gear that can be modified to target specific species and size ranges through choice of design and bait (Miller, 1990). Selection by traps of only the desired size classes reduces sorting time and may increase the catch rates of legal-size animals (Fogarty and Borden, 1980; Everson et al., 1992; Rosa-Pacheco and Ramirez-Rodriguez, 1996). Capture, sorting and release procedures have furthermore been implicated in accidental and stress-induced mortalities (Brown and Caputi, 1983; 1985; Hunt et al., 1986), as well as in sublethal injuries, such as limb loss (legs or antennae), which may retard somatic growth (Davis, 1981; Brown and Caputi, 1985). Air exposure, even over short periods, can induce behavioral changes such as reduced responsiveness to threatening stimuli (Vermeer, 1987) and lead to higher predation risk among released animals (Brown and Caputi, 1983). Furthermore, displacement from home reefs disrupts feeding behavior and can affect growth increments (Brown and Caputi, 1985). Managers of many crustacean trap fisheries have responded to these problems by introducing escape vents of various sizes and shapes (Krouse, 1989; Miller, 1990; Everson et al., 1992; Arana and Ziller, 1994; Rosa-Pacheco and Ramirez-Rodriguez, 1996; Treble et al., 1998; Schoeman et al., 2002a), because they successfully allow undersize specimens to escape (Arana and Ziller, 1994; Treble et al. 1998).

In fisheries management, size selectivity curves are important for estimates of incidental mortality, recruitment in yield-per-recruit analysis, and age- and length-based population models (Millar and Fryer, 1999). Notably, size selectivity can be used to evaluate the minimum legal size (MLS) and the effects of changing escape vent or mesh size regulations on the future productivity of the resource (Treble et al., 1998).

Most selectivity studies on which mesh- or escape vent size are based are comparative (indirect), implying that the size distribution of the population is unknown and that variants of the same gear type are fished simultaneously (Millar and Fryer, 1999). Results from indirect studies can, however, be influenced by trap soak times, trap saturation effects (Miller, 1990), seasonal size and sex-specific patterns in catchability (Pollock and Beyers, 1979), and by differences in morphometric ratios of subpopulations (Fogarty and Borden, 1980; Maynard et al., 1987). These disadvantages are offset by the convenience with which indirect studies measure selectivity under operational conditions. Far fewer direct studies, in which the size distribution of the fished population is known (Millar and Fryer, 1999), have been published, and those that have been published have included several laboratory studies where the escape of crustaceans from traps was monitored (Krouse and Thomas, 1975; Krouse, 1978; Everson et al., 1992). Direct studies do not recreate true commercial conditions, but rather provide a contact-selectivity curve (or retention curve) that quantifies the difference in length distribution between the catch and the population of fish coming in contact with the gear (Millar and Fryer, 1999). This information is useful as a benchmark against which operational, seasonal, and spatial selectivity patterns can be measured.

Commercial fishing for the South African Cape rock lobster (*Jasus lalandii*) originated in the late nineteenth century and reached its pinnacle in the 1950s, when nearly 11,000 tons were landed annually (Pollock, 1986). However, since then catches have declined markedly, especially during the 1990s, when annual catch restrictions based on the assumption of decreased population strength, reduced the yield to 2000–3000 tons per year (Pollock et al., 2000). In response to these operational changes, several recent modifications have been made to the regulations governing gear used in the fishery (Schoeman et al., 2002b). The changes most pertinent to this study took place in 1984, when mesh size was increased from 62 to 100 mm (stretched) to reduce the relative catch of undersize *J. lalandii* (Schoeman et al., 2002b), and during the early 1990s, when the minimum size limit was reduced from its historic level of 89 mm carapace length (CL) to 75 mm CL (Cockcroft and Payne, 1999; Pollock et al., 2000). Despite these two measures, the proportion of the commercial catch <75 mm CL that has to be released remains around 35–40% (MCM[1]). At present, the biomass of the *J. lalandii* resource that is larger than the minimum legal size is estimated at about 6% of its pristine value, whereas the spawning biomass (of mature female rock lobsters) is estimated to be 21% (Johnston, 1998). Consequently, it is clear that the resource is heavily depleted and that there is little scope for wasted production through unnecessary damage to undersize lobsters (Schoeman et al., 2002a).

Most studies on trap selectivity of *J. lalandii* (Newman and Pollock, 1969; Crous, 1976; Pollock and Beyers, 1979) predate the changes to mesh and minimum legal size described above and did not provide selectivity curves. In the only recent study, Schoeman et al. (2002a) used the SELECT (Share Each LEngth class's Catch Total) method (Millar, 1992, Milllar and Walsh, 1992) to investigate the selectivity properties of various modifications to commercial and research traps in comparison with the standard 100-mm stretched mesh trap design. This study was indirect, in that it simulated commercial fishing and compared catch rates in other traps to those made with a small-mesh (62 mm, stretched) trap, which acted as a control.

Several processes are involved in the selectivity of traps: namely the attraction of rock lobsters by bait; their ability to enter traps through trap openings of various sizes, shapes, and localities within the trap; their behavior in and around traps; their escapement through the trap opening and their escapement through mesh openings or escape vents (Miller, 1990). The present study focuses on escapement of captured *J. lalandii* through the mesh of stretched mesh traps and through trap entrances. The aims are to investigate the relationships between CL and other morphometric measures for male rock lobsters in order to use these relationships to estimate theoretical escapement curves for any given mesh size; to compare these curves to observed escapement rates through selected meshes in the aquarium; and to extend these comparisons to field conditions. The overall aim is to determine the optimum mesh characteristics that maximize efficiency in targeting legal-size male *J. lalandii*.

Material and methods

Mesh size of lobster traps

Mesh size is defined as the measurement from inside of knot to inside of knot when the net is stretched in the direction of the long diagonal of the meshes, i.e., lengthwise of the net. Netting is made of polyethylene. Commercial rock lobster traps (Fig. 1) are covered with 100-mm stretched mesh (or 50-mm bars, also measured from the insides of knots), which are stretched in such a manner over the metal frame that the openings are square.

Morphometric variables measured

Following manual trials that involved fitting lobster carapaces of different sizes through an adjustable square hole, three carapace dimensions were identified as likely to play a role in regulating escapement. These were the following: 1) carapace width (CW), measured laterally, across the widest point of the carapace; 2) carapace depth (CD), measured dorsoventrally, extending from the highest point of the dorsal carapace surface to the lowest point on the ventral surface of the thoracic plate; and 3) carapace base (CB), measured ventrally, between the distal edges of the second segment of the last walking legs, with the legs folded flush against the carapace.

Each of these dimensions was measured (±1 mm) for each of 169 male rock lobsters caught in research traps deployed off the Cape Peninsula between 1999 and 2002. Corresponding data regarding carapace length

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[1] MCM (Marine and Coastal Management). 2002. Unpubl. data. MCM, Martin Hamershclacht St., Cape Town, South Africa.

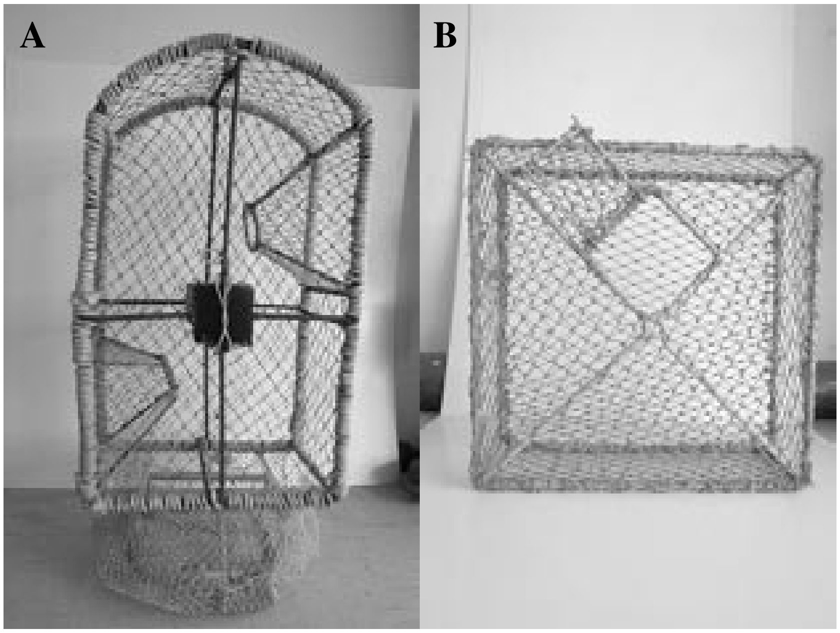

Figure 1

(**A**) Standard metal-framed traps (0.8 m × 0.5 m×1.35 m high) covered with stretched polyethylene mesh used in the commercial fishery for *J. lalandii* and during field experiments (note the 100-mm mesh size covering on the commercial traps, and the 62-mm mesh size on the codend and entrance funnel). (**B**) Metal-framed escapement cages covered with 62-mm (shown), 75-mm, and 100-mm mesh used in the aquarium experiments (frames were 0.6 m × 0.6 m, with a depth of 0.25 m).

(CL), measured mid-dorsally from the posterior edge of the carapace to the anterior tip of the rostral spine, were also collected. This was done because CL is the dimension most frequently mentioned in legislation pertaining to this species (Schoeman et al., 2002b) and has therefore been the focus of most size-based studies (Newman and Pollock, 1969; Pollock and Beyers, 1979; Schoeman et al., 2002a). Relationships between the CL and each of CW, CD, and CB were explored by using simple least-squares regression analyses.

Theoretical calculations of escapement

In order to investigate morphological characteristics that physically limit escapement through meshes of various dimensions as a function of CL, digital photographs were taken of the posterior cross section of 46 male carapaces (tail removed) covering a range of sizes between 40 mm CL and 106 mm CL. Using standard graphics software, we superimposed a square on each image to represent a square of polyethylene mesh, similar to that used in a South African rock lobster trap.

This simulated mesh was orientated so that its base was parallel with the carapace base of the lobster under consideration. It was then proportioned so that each of its sides was equal in length to the corresponding CB. Once this procedure had been completed, the simulated mesh square was rotated and resized so that we could determine the dimensions of the smallest square through which each lobster could pass. This measure was designated the "critical mesh size" for that image.

Critical mesh size was related to CL by using simple linear regression analysis. In this way, the theoretically appropriate mesh aperture required to target all lobster larger than a given size could be predicted from the minimum CL of the target group (for convenience, this CL will be designated the "critical CL").

Aquarium trials

Having addressed the matter of whether or not lobsters theoretically should be able to escape a mesh of given dimensions, the next question to be posed is whether or not they can do so under ideal (laboratory) conditions? For these purposes, three stretched mesh sizes were considered: 1) 62 mm, which coincides with the mesh size used in the commercial fishery prior to 1984 and also with the mesh currently used on traps deployed in the Fishery Independent Monitoring Survey (FIMS) (Schoeman et al., 2002a); 2) 100 mm, which corresponds with the mesh currently used on commercial traps for *J. lalandii*; and 3) 75 mm, which was used to provide information on selectivity for meshes of intermediate aperture dimensions.

Each of these experimental meshes was used to construct an escapement cage by stretching the mesh over a mild-steel frame in order to present square escape apertures of varying dimensions, as determined by the size of the mesh used (Fig. 1). These cages were deployed in an aquarium tank measuring 1.8 m × 1.8 m and having a depth of 1.5 m. Fresh sea water was continuously supplied to this tank by a through-flow system that regulating water temperature between 12° and 16°C, well within the natural temperature range of *J. lalandii* (Heydorn, 1969).

For each mesh size, male rock lobsters of various carapace lengths (373 lobsters measuring 34–91 mm CL for 62-mm mesh; 351 lobsters measuring 34–75 mm CL for 75-mm mesh; and 142 lobsters measuring 70–91 mm CL for 100-mm mesh) were collected live from the sea and transported to the experimental aquarium tank. Care was taken to ensure that approximately equal numbers of lobsters were available for each 2-mm size-class within the respective size ranges, although fewer lobsters tended to be available in size classes towards the ends of the frequency distributions.

Once at the aquarium, lobsters were placed inside the experimental cages in groups of up to 20 and left for 30 minutes. Individuals that did not escape during this period were gently pushed towards the mesh openings, encouraging escapement, where this was possible. Subsequently, the CL frequency distributions were determined both for those lobsters that escaped the mesh as well as those that were retained. Several replicate escapement experiments were conducted for each mesh size, but because the experimental cages were too small to hold large numbers of lobsters, replicate selection curves could not be computed. Instead, all data were pooled for each mesh size for further analyses.

Field trials

The final question to be posed is whether or not lobsters do escape from traps when afforded the opportunity to do so under field conditions? To address this problem, field trials were undertaken off the Western Cape Peninsula during monthly sampling sessions conducted by the research vessel *Sardinops* in July 2000 and from December 2001 to March 2002—a total of five distinct sampling surveys.

Four categories of standard rock lobster traps (Fig. 1) were employed: 1) 62-mm stretched mesh, with entrance funnels open; 2) 62-mm stretched mesh, with entrance funnels blocked by a fine-mesh insert; 3) 100-mm stretched mesh, with entrance funnels open; and 4) 100-mm stretched mesh, with entrance funnels blocked.

Duplicate bottom long-lines consisting of 10 traps each were prepared, of which six were normal commercial traps, and the remaining four were experimental traps, and these 10 traps were spread in haphazard order along the line, excluding the end traps. Into each trap was placed a sample of approximately 40 male rock lobsters, each of which had been measured (CL) and marked by cutting a notch in its uropod. In this way, it was possible to distinguish between lobsters that had been placed in the trap and those that had entered the trap of their own accord.

Experimental traps were deployed without bait, in order to limit their ability to attract lobsters and also to remove one of the prime incentives that captive lobsters might have to remain in a trap, even when it could escape. These trap lines were soaked overnight and on their retrieval, each remaining lobster was remeasured (CL) and inspected to identify specimens that had entered the traps voluntarily. Eight replicates were completed for each of the four categories of traps.

Construction of selectivity curves

The contact-selection curves (*sensu* Millar and Fryer, 1999) for the meshes used in the laboratory and field trials were modeled by using the SELECT method (Millar and Walsh, 1992) as applied to covered codend experiments (Millar and Fryer, 1999). We felt that this approach was warranted because we collected data with respect to lobsters in both a "codend" (those retained in the traps) and a "cover" (those that escaped, but for which data were available by inference).

The logistic and Richards formulations of the general selectivity curve were fitted by using Excel (Microsoft, Redmond, WA) routines (Tokai[2]). These two selectivity functions were chosen because of their relative simplicity, their broad use over a range of different fisheries, and the availability of estimation routines for their parameters (Millar and Fryer, 1999).

The Richards curve has the equation

$$r(l) = \left(\frac{\exp(a + bl)}{1 + \exp(a + bl)} \right)^{\frac{1}{\delta}},$$

where $r(l)$ is the probability that an individual of length l attempting to pass through a mesh of given size will be retained by it (Millar and Fryer, 1999); and a, b, and δ are constants. The logistic curve is the special case of this formulation, where $\delta=1$.

According to these models, the lobster length at 50% retention (L_{50}) and the selection range ($SR=L_{75}-L_{25}$) are defined as follows:

$$L_{50} = \frac{\ln\left(\frac{0.5^{\delta}}{1 - 0.5^{\delta}} \right) - a}{b},$$

simplifying to $L_{50} = -\frac{a}{b}$ when $\delta = 1$, and

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[2] Tokai, T. 2002. Personal commun. Department of Marine Science and Technology, Tokyo University of Fisheries, Konan Minatoku, Tokyo 108, Japan.

$$SR = \frac{\ln\left(\frac{0.75^{\delta}}{1-0.75^{\delta}}\right) - \ln\left(\frac{0.25^{\delta}}{1-0.25^{\delta}}\right)}{b},$$

$$\text{simplifying to } SR = \frac{2\ln(3)}{b}, \text{ when } \delta = 1.$$

All calculations were made on the basis of 2-mm-CL size classes covering the entire size range for each frequency distribution. The 2-mm-CL size classes were used to ensure consistency across models, and also to balance data resolution against the number of size classes expected to have either zero catch or zero escapement (Millar and Fryer, 1999). Wherever necessary, hypothesis tests were conducted in accordance with the recommendations of Millar and Walsh (1992) and Millar and Fryer (1999).

Results

Morphometric relationships

Least-squares regression analysis indicated highly significant linear relationships between CL and each of the other morphometric variables measured (Fig. 2). In each case, at least 97% of the variability in the predictor variable was explained by CL, indicating a high degree of correlation among predictors. Nevertheless, for any given CL, CB was consistently the largest variable measured, whereas CD was the smallest. Furthermore, CB increased more rapidly in response to increasing CL than either CW or CD (ANCOVA: F=115.165; df=2, 167; P<0.001). We therefore concluded that CB would likely be the morphometric variable that limits escapement through stretched square meshes.

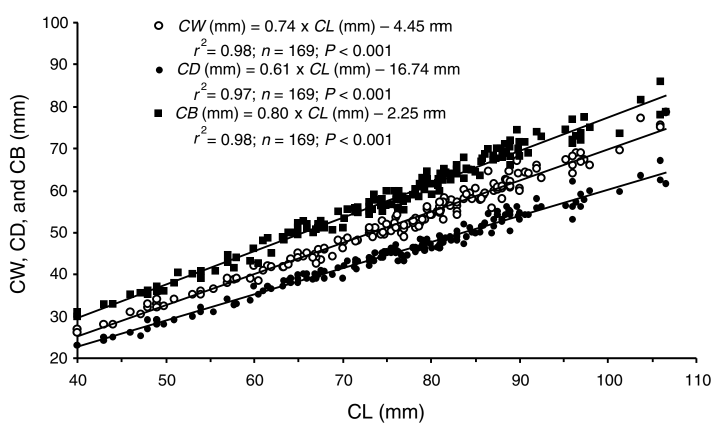

Figure 2

Individual linear relationships between carapace length (CL) and each of carapace width (CW), carapace depth (CD), and carapace base (CB) for *J. lalandii*.

Theoretical calculation of escapement

The mesh size that appeared (on the basis of visual inspection) to limit escapement was expressed as a function of CL with a simple, linear, least-squares regression model (Fig. 3). This relationship was highly significant and explained 99% of the variability in critical mesh size.

Using inverse prediction methods (Zar, 1999), we calculated the critical CL (mean ±95% confidence interval) from the regression model illustrated in Figure 3 for any mesh size. For 62-mm mesh, the critical CL is estimated at 43.8 (±4.12) mm; for the 75-mm mesh the estimate is 52.3 (±4.15) mm; whereas for the 100-mm mesh it is 68.7 (±4.12) mm. Given the implicit assumption that lobsters smaller than the critical CL can escape, but that larger lobsters are retained, the mean critical CL can be used as an estimate of L_{50}.

Aquarium trials

No lobsters larger than 48 mm CL escaped the 62-mm mesh traps in the aquarium and none smaller than 44 mm CL were retained. This finding resulted in an extremely steep selection curve with a narrow *SR* (Fig. 4; Table 1). For the 75-mm mesh, no lobsters larger than 61 mm CL escaped and no lobsters smaller than 54 mm CL were retained. This finding resulted in a slightly more gentle selection curve, but with a reasonably tight *SR* (Fig. 4, Table 1). Similarly, for the 100-mm mesh, no lobsters larger than 79 mm CL escaped and no lobsters smaller than 74 mm CL were retained. This finding resulted in a selection curve that closely resembled that for the 75-mm mesh, except that the curve shifted a few size categories to the right (Fig. 4; Table 1).

For all meshes, the symmetrical logistic model was selected in preference to the asymmetrical Richards model (Table 1), and in all cases the selected model fitted the data reasonably well (Fig. 4). It should, however, be noted that all hypothesis tests were conducted by using the deviance residuals and their degrees of freedom for all size classes sampled. This was necessary because the very tight selection curves (especially for the 62-mm mesh) resulted in relatively small numbers of size classes in which retention probability was neither zero nor one.

The above results indicate that L_{50}-estimates for each mesh size are substantially larger than the corresponding estimates of critical CL from the theoretical escapement model. In fact, assuming that the asymptotic standard errors provided in Table 1 could be converted to 95% confidence intervals by a multiplication factor of two, only the confidence intervals for these statistics from the 62 mm mesh would overlap. By contrast, confidence intervals for the critical CL are well below those for the L_{50} for both the 75 mm mesh and the 100-mm mesh. This impression is confirmed by inspecting the probabilities of

Table 1

Statistics from SELECT analysis for the aquarium escapement trials. Values in parentheses are asymptotic standard errors *sensu* Millar (1993). These standard errors are provided only for the best model fits for each of the various categories of data. Note that all hypothesis tests were conducted by using deviance residuals for the full model and their degrees of freedom (see text for explanation).

	62-mm mesh		75-mm mesh		100-mm mesh	
	Logistic	Richards	Logistic	Richards	Logistic	Richards
a	–76.479 (23.159)	–351.538	–58.217 (10.079)	–400.075	–64.101 (11.655)	–41.224
b (/mm)	1.649 (0.500)	7.463	0.991 (0.173)	6.589	0.849 (0.155)	0.615
δ		6.567		13.173		0.010
L_{50} (mm)	46.389 (0.309)	46.493	58.717 (0.302)	59.333	75.459 (0.376)	75.144
SR (mm)	1.333 (0.404)	0.989	2.216 (0.386)	2.200	2.587 (0.471)	2.567
Selection factor	0.75		0.78		0.76	
H_0: data have binomial distribution (i.e., data are not overdispersed)						
Deviance	0.802	0.209	1.984	1.092	8.675	6.435
df	27	26	19	18	12	11
P-value	1	1	0.999	0.728	0.730	0.843
H_0: δ =1						
Deviance	0.593		0.892		2.240	
df	1		1		1	
P-value	0.441		0.345		0.134	

retention, $r(l)$, by each mesh size of a lobster at its corresponding mean critical CL. For the 62-mm mesh this probability is 0.014 (0.926 at the upper 95% confidence limit for the critical CL); for the 75-mm mesh it is 0.002 (0.096 at the upper 95% confidence limit for the critical CL); and for the 100-mm mesh it is 0.003 (0.099 at the upper 95% confidence limit for the critical CL).

Field trials

Escapement from traps with 62-mm mesh was highly variable both for the traps with entrance funnels left open, as well as for those with entrance funnels that were sealed, but was surprisingly high for the latter (Fig. 5). Furthermore, it is clear that the relationship between proportion of lobsters retained and CL was not logistic, as it was for the larger mesh sizes (Figs. 5 and 6). Instead, simple, least squares regression analysis indicated linear relationships between these variables both for traps with open entrance funnels as well as for those with entrance funnels closed (Fig. 5). There was no difference between the slopes (t=1.138; df=10; P=0.282; common slope=0.795/mm), although their intercepts did differ significantly (t=14.079; df = 11; P<<0.001).

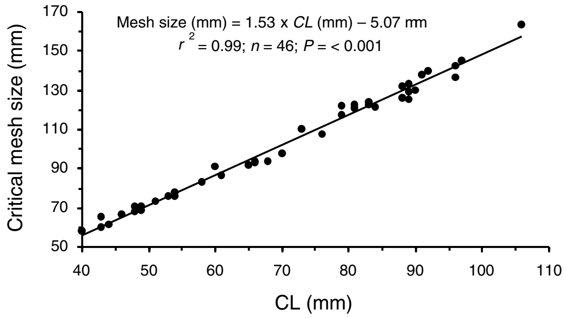

Figure 3

The relationship between carapace length of *J. lalandii* and mesh size below which escape should theoretically not be possible.

No lobsters smaller than 62 mm CL were retained in the 100-mm mesh traps with open entrances, and no upper size limit was reached beyond which escapement was completely eliminated. By contrast, when the entrance funnels to the traps were sealed, no lobsters smaller than 64 mm CL were retained and no lobsters

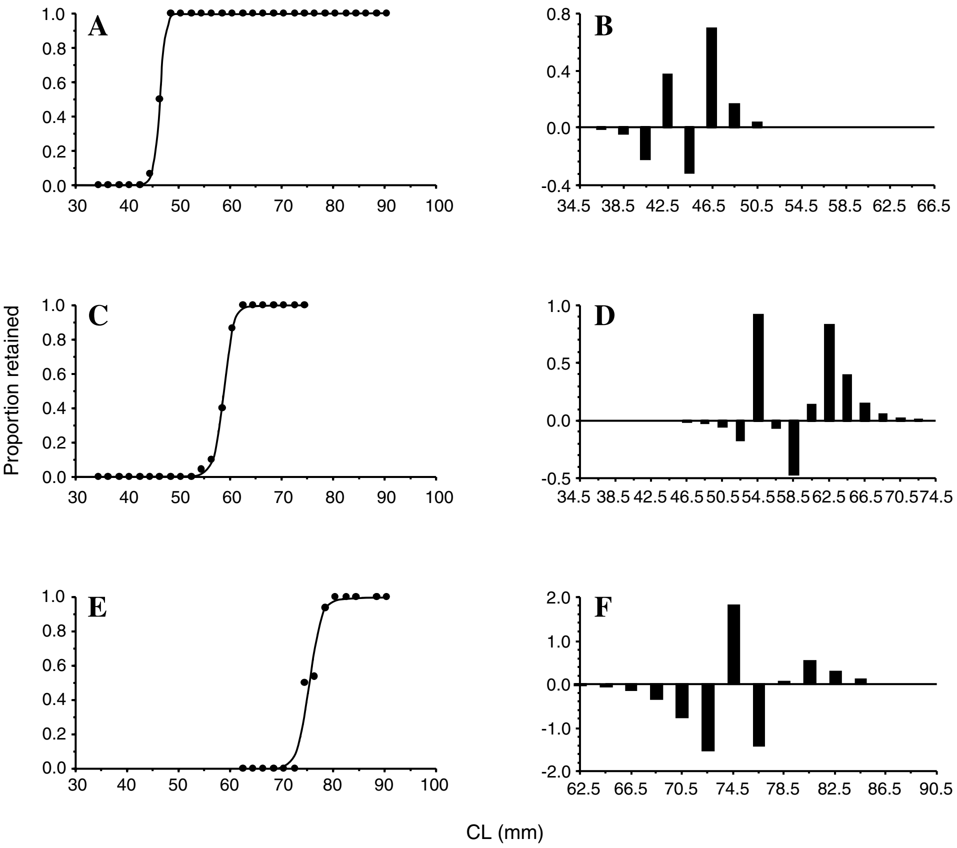

Figure 4

Fitted selectivity curves from the selected models (identified in Table 1) and their deviance residuals for a range of stretched square meshes under aquarium conditions. **A** and **B** are for 62-mm mesh, **C** and **D** are for 75-mm mesh and **E** and **F** are for 100-mm mesh.

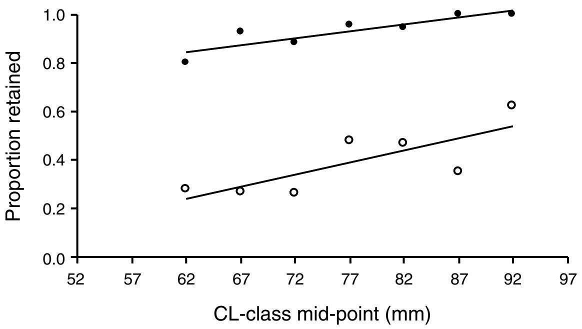

Figure 5

Relationship between proportion of rock lobsters retained by 62-mm mesh trap and carapace length (aggregated into 5-mm size classes). Filled circles represent data from traps with entrance funnels sealed (*Proportion retained*=0.58/mm × *CL* (mm)+48.35; r^2=0.79; *n*=7; *P*=0.008), whereas open circles represent data from traps with entrance funnels open (*Proportion retained*=1.01/mm × *CL* (mm)–38.94; r^2=0.62; *n*=7; *P*=0.036).

larger than 84 mm CL escaped. This resulted in contact selectivity curves for which estimates of both L_{50} and *SR* decreased when captive lobsters were denied the opportunity to escape through the entrance funnels (Fig. 6; Table 2). This finding indicates that considerable numbers of lobsters of all sizes can escape commercial traps by the entrance funnels.

Irrespective of whether the entrance funnels of the traps was sealed, the symmetrical logistic model was selected in preference to the asymmetrical Richards model (Table 2), and the selected model fitted the data reasonably well (Fig. 6; Table 2), although not as well as the models fitted to the aquarium data (Fig. 4; Table 1).

In comparison with the selectivity curves from the aquarium trials with 100-mm mesh, the corresponding curves from field trials indicated that greater numbers of larger lobsters are retained in practice than under laboratory conditions (Figs. 4 and 6). This finding indicates that some lobsters are retained in commercial traps, even though they can escape, which goes some way to explaining the more "scattered" fit of the logistic model compared to the field data.

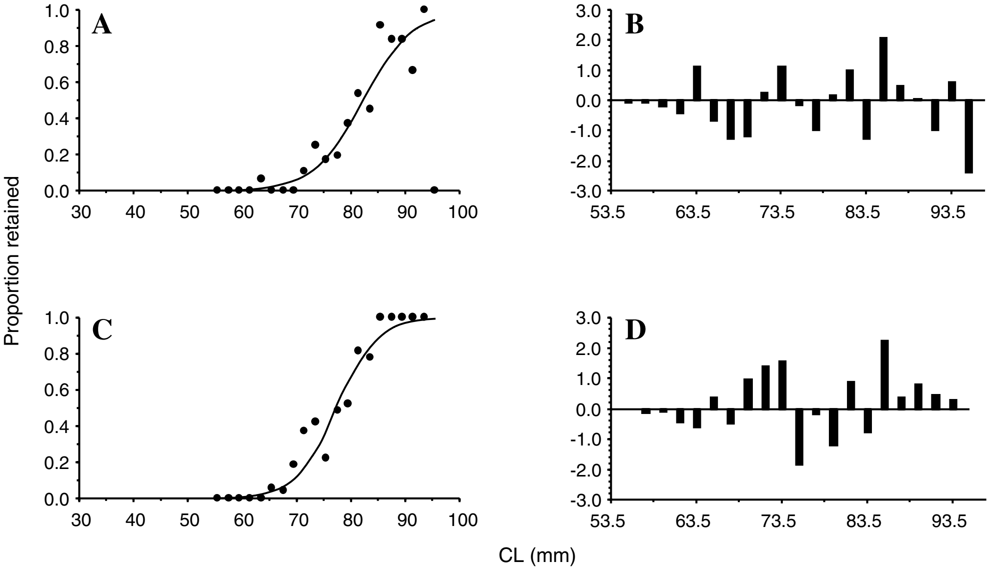

Figure 6

Fitted selectivity curves from the selected models (identified in Table 2) and their deviance residuals for escapement of *J. lalandii* from commercial rock lobster traps covered with 100-mm stretched square meshes under field conditions. **A** and **B** are for traps with open entrance funnels; **C** and **D** are for traps with sealed entrance funnels.

Discussion

This study focuses on escapement of Cape rock lobster (*J. lalandii*) through mesh openings, and on escapement through the trap entrance of commercial traps. Three questions were initially posed, namely: through what mesh size, in theory, can a lobster of given CL escape; are lobsters physically able to escape through this theoretical mesh size, or are there other factors such as orientation and mobility of lobster appendages that prevent escapement; and what proportion of sublegal and legal size lobsters escape through the mesh and trap entrance of commercial traps? In brief, the results showed a weak leak between theoretical values and the ability of the lobsters to escape.

Carapace base (CB) was isolated as the dimension most likely to limit escapement through stretched square meshes. This dimension superceded carapace width and depth, which have been more widely assumed to be the limiting factors to escapement of lobsters (Treble et al., 1998), mainly because our measurement included the width of the last pair of walking legs, folded flush against the carapace. Experimenting with lobster carapaces and an adjustable square hole showed that the joints of these appendages protrude ventrolaterally from the carapace, and the orientation and limited mobility of these appendages would prevent the lobster from escaping. Nevertheless, our theoretical escapement model included all three measurements in the underlying computer simulations to determine the appropriate mesh aperture required to target all lobsters larger than a given size.

The theoretical escapement model produced surprisingly small values of "critical CL" for all three mesh sizes in comparison with the corresponding selectivity curves from the aquarium experiment. This result implies that many rock lobsters that should theoretically not have been able to escape, did so in the aquarium trials. We therefore concluded that the theoretical model was weak and that the mechanics of escapement appear to be more complex than can be shown by simple measurements of the carapace dimensions and may rely also on the orientation of lobsters during escapement (Stasko, 1975).

Selectivity curves developed from aquarium data indicated that an 85-mm-CL lobster should not have been able to escape a 100-mm mesh trap. However, field data indicated that escapement from 100-mm mesh traps with sealed trap openings exceeded 10%. Thus, rock lobsters that should not have been able to escape, according to aquarium experiments, did escape under field conditions. This result was expected, because the mesh of traps used in the commercial fishery (and field experiments) is often unevenly stretched across the metal trap-frame, and therefore some openings lose their square dimensions. This unevenness in the stretch of the mesh was clearly illustrated by a random sample of 40 knot-to-knot aperture measurements from four 100-mm mesh commercial traps, which had diagonal dimensions significantly larger than the 70.71 mm predicted by Pythagoras's theorem (t=4.470; df =39; P<<0.001). In addition, repairs to torn meshes often leave openings that are somewhat larger than 100 mm and that are not square (Groeneveld, personal. observ.). The wider *SR* of the selectivity curve for field data compared to the tight *SR* of the aquarium curves supports this "unevenly stretched mesh" hypothesis.

Paradoxically, a 70-mm-CL lobster, which has a 1% chance of being retained by a 100 mm mesh in the laboratory has an 11% probability of being retained by a trap with the same mesh in the field (even when its entrances are sealed). Thus, some rock lobsters that should, and could have escaped through the 100 mm mesh of the field traps did not. Schoeman et al. (2002a) suggested that small rock lobsters that can escape do not always do so because they use the trap as a refuge against predators. Alternatively, overnight soak times (as used in the field trials) may be too short for all the small rock lobsters to escape. The probability of escape is much reduced during hauling because captive specimens are then pressed into a tight mass within the fine-mesh (62-mm) codend of the trap.

Table 2

Statistics from SELECT analysis for the field escapement trials. Values in parentheses are asymptotic standard errors *sensu* Millar (1993). These standard errors are provided only for the best model fits for each of the various categories of data. Note that all hypothesis tests were conducted by using deviance residuals for the full model and their degrees of freedom (see text for explanation).

	100-mm mesh		100-mm mesh	
	Trap-entrance open		Trap-entrance sealed	
	Logistic	Richards	Logistic	Richards
a	–17.856 (2.460)	–14.299	–20.801 (2.437)	–51.967
b (/mm)	0.217 (0.031)	0.181	0.2686 (0.031)	0.626
δ		0.641		4.238
L_{50} (mm)	82.274 (0.379)	82.222	77.444 (0.379)	78.458
SR (mm)	10.124 (0.498)	10.809	8.181 (0.498)	7.997
Selection factor	0.82		0.77	
H_0: data have binomial distribution (i.e., data are not overdispersed)				
Deviance	21.593	21.257	18.698	15.807
df	19	18	17	16
P-value	0.305	0.267	0.346	0.467
H_0: $\delta = 1$				
Deviance	0.336		2.891	
df	1		1	
P-value	0.562		0.090	

No escapement from sealed 62-mm mesh traps was expected during field trials, based on the aquarium L_{50} of 46.4 (±0.3) mm and the size range of lobsters used in the field (60 mm–95 mm CL). Nevertheless, small losses (0–18%, depending on lobster size; see Fig. 5) did occur. Only two explanations are possible, namely: 1) that lobsters still managed to escaped through the mesh of the sealed 62-mm traps, despite precautions taken to ensure that the meshes of these traps were undamaged and that trap openings were properly sealed; and 2) that some individuals sustained injuries during exposure and handling, and subsequently were cannibalized by the healthy rock lobsters in the traps. This second conclusion is supported by the presence of shell fragments observed in traps after their retrieval. Because these regressions had the same positive slopes, it seems likely that smaller rock lobsters would be more susceptible to injury and cannibalism than larger animals, and their susceptibility holds irrespective of whether the trap entrance is sealed or not.

Escapement from 62-mm mesh traps with open entrance funnels increased by 40–60% compared to escapement from traps with sealed traps (Fig. 5). This finding has significant implications for the FIMS, which relies on catches made by 62-mm mesh traps and is conducted annually as a measure of the relative abundance of the *J. lalandii* resource. During a survey, it is assumed that all the Cape rock lobsters that are captured are retained and that trap-selection is uniform across all the size classes of these lobsters (Johnston, 1998). It appears that neither of these two assumptions can be met: significant escapement does occur through the trap entrance and there is a greater retention of larger specimens than smaller specimens .

When the trap entrance was left open in the 100-mm mesh field trials, L_{50} increased to 82.3 mm (from 77.4 mm in sealed traps), thus indicating that captive Cape rock lobsters can and do use the trap entrance of commercial traps to escape. The open traps also have a wider *SR* of 10.1 mm (compared to 8.2 mm in sealed traps), and therefore animals with a CL of >87 mm (L_{75}=87.3 mm), which are very unlikely to be able to get through the mesh apertures, will still be able to use the trap entrance to exit. The presence of this escape vent implies that there is little danger of ghost-fishing when using this trap type and that Cape rock lobsters of all sizes should be able to vacate the trap once the bait has been consumed. From a commercial viewpoint, however, the problem of leaving traps in the water for too long is that legal-size specimens, which cannot fit through the mesh, will escape through the entrance, thus decreasing catch rates considerably.

The aquarium result (L_{50}=75.1 mm) is considered the most accurate direct measurement of the selectivity of 100-mm square mesh for *J. lalandii*, because care was taken to ensure that the mesh was stretched evenly with square openings across the metal trap-frame and because we made sure that all lobsters that could escape, did, resulting in a tight *SR* of 2.6 mm. This L_{50} is remarkably close to the present MLS of 75 mm CL for the commercial fishery, especially considering that 100-mm mesh was first used when the MLS was 89 mm CL, and that the commercial mesh size remained at 100 mm despite the 14 mm CL reduction in MLS during the early 1990s (Schoeman et al., 2002b). The L_{50} obtained from the field trials with sealed trap openings (77.4 mm) was also close to the present MLS.

In a recent indirect study (i.e., where the size composition of a population was unknown) Schoeman et al. (2002a) found L_{50} to be 79.2 mm (SR=11.1 mm) under commercial operational conditions. The increase in L_{50} (above the 75.1 mm and 77.4 mm found in the direct aquarium and field studies, respectively) is the result of the trap entrances of commercial traps remaining open, so that rock lobsters that are too large to fit through the mesh can still escape through the entrance. In the present direct study, this factor increased the L_{50} from 77.5 mm (sealed entrance) to 82.2 mm (open entrance) for 100-mm mesh. Thus, one conclusion of the indirect study, namely that the South African fishery for *J. lalandii* is unusual in that standard commercial traps are covered with mesh having an aperture considerably wider (L_{50}=79.2 mm CL) than that required to retain Cape rock lobsters of the current MLS (Schoeman et al., 2002a), must now be seen in a different light. The selectivity of the 100-mm stretched mesh itself now appears not to be wider than that which is currently required (based on the direct results). Rather, the indirectly determined L_{50} appears to have been inflated by the numbers of larger lobsters that were able to escape through the trap entrance.

Direct studies of the escapement of crustaceans from pots (Krouse and Thomas, 1975; Krouse, 1978; Everson et al., 1992) have often been criticized because these studies themselves may affect the behavior of the animals and do not include the dynamics of the processes of entry and escapement (Xu and Millar, 1993; Treble et al., 1998). We recognize these weaknesses, but felt that direct studies remain useful because they can be used to set a theoretical benchmark against which the results of indirect studies can be tested, especially if the trap selectivity of the latter depends on area and season. Various insights were gained from the present study, particularly because it closely followed an indirect study of trap selectivity for *J. lalandii* (Schoeman et al., 2002a). In conclusion, this study of escapement of *J. lalandii* through square meshes showed 1) that 100-mm mesh size is, theoretically, near optimal for the fishery; 2) that many Cape rock lobsters that are able to escape through the mesh do not do so; 3) that the rock lobsters that are shown theoretically to be unable to escape through the mesh of commercial traps, often can do so; and 4) that specimens too large to escape through the mesh can escape through the trap entrance.

Acknowledgments

This study would not have been possible without the funding and infrastructure provided by Marine and Coastal Management (Department of Environmental Affairs and Tourism, South Africa). In particular, we would like to thank our colleagues, Steven McCue, Neil van den Heever, and Danie van Zyl for technical support. We are also grateful to the skipper and crew of the research vessel *Sardinops*, which was used to conduct the field trials. J.P.K. received financial assistance from the Fridtjof Nansen and NORAD, and would like to thank his supervisors, Anders Ferno and Geir Blom, at the University of Bergen in Norway, for their assistance with an earlier draft of this manuscript. D.S.S. thanks the University of Port Elizabeth for support in terms of finance and infrastructure. Finally, the constructive comments of three anonymous referees are acknowledged; these aided substantially in clarifying certain parts of the original manuscript.

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